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Heikki Hänninen

Boreal and Temperate Trees in a Changing Climate

Modelling the Ecophysiology of
Seasonality



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Modelling the Ecophysiology of Seasonality

 Springer

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Biometeorology

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*To
the memory of my mother (1920–2008)
and
the memory of Lisa Lena (1957–2013)*

Preface

Boreal and temperate trees grow under climatic conditions in which the ambient air temperature displays pronounced seasonal variation. Unlike herbs and grasses, trees overwinter without a sheltering snow cover, so that they are exposed to all the harsh climatic conditions. That is why their climatic adaptation is based on their annual cycle of development, whereby the frost-hardy dormant phase and the susceptible growth phase are synchronised with the seasonality of the climate. There is a long and rich research tradition focusing on this key adaptive strategy of boreal and temperate trees, not only because trees are major elements of forest ecosystems but also because many of these tree species are economically important for forestry or horticulture. More recently, the projected climate change has dramatically increased scholarly interest in the annual cycle of trees.

The last few decades have seen increasing use of dynamic simulation models in studies of the annual cycle of boreal and temperate trees. In this book I review these studies and introduce some new ideas. Having worked on the subject for more than 30 years, I have no doubt developed a personal approach to the work, and I do not try to hide that in this volume, either. I mainly concentrate on my own research and other work closely related to it. This should not be taken as any disparagement of the studies not reviewed in the same detail or not reviewed at all. Rather, this choice was made in order to keep the presentation concise and uniform throughout the book, as a detailed discussion of all relevant literature would have required a much larger and much more diverse treatise. This is true especially because during the last 10 years or so, I have been very glad to see a dramatic increase in the number of studies published in the field. In some cases I make critical notes on approaches where I see problems in the methods applied. It is my sincere wish that my presentation should facilitate scientific discussion, also in cases where my choices differ from those of some colleagues.

In line with my long-term research strategy, I put the main emphasis on the combining of modelling and empirical studies. Thus, the book is directed not only to modellers but also to experimental tree ecophysiologicalists, and the bridging of the gap between these two research traditions is a major theme. Consequently, the

number of formulae presented is relatively low, and besides modelling studies, I also discuss related empirical research. Because of the vast number of empirical publications about the annual cycle of boreal and temperate trees, a comprehensive review of them is inevitably outside the scope of the book. When discussing the effects of climate change, I mainly concentrate on the overwintering of trees. This choice is a deliberate one, caused not only by the orientation of my own expertise but also by the need to emphasise the ecological importance of the often neglected overwintering period of the trees.

Depending on the background of the reader, the chapters of the book may be readable independently from each other. Even so, the book is planned to form an integrated unity, so that optimally the chapters should be read in sequence. The principles of dynamic modelling are presented in Chap. 2 for those readers who may not be previously familiar with this research tool. Throughout the text, special emphasis is devoted to thorough explanations of the concepts and modelling principles presented. Specialist readers familiar with the topic may find the text even too elementary and lengthy at times, but I have made that choice deliberately, for I wish to serve a wide audience, including advanced graduate and postgraduate students.

Basically, this treatise belongs to the discipline of whole-tree ecophysiology. It seems to me that time is becoming ripe for a synthesis of the whole-tree modelling approach and the physiological and molecular approach, the two of which have largely been pursued in isolation from each other so far. However, rather than trying to make such a synthesis, my aim is to explicate the whole-tree modelling approach for the benefit of forthcoming efforts towards a synthesis. I also briefly discuss the upscaling of ecophysiological information from the whole-tree level to the stand and the ecosystem level. I hope this facilitates the introduction of biologically realistic ecophysiological models of the annual cycle of boreal and temperate trees into the larger-scale ecological models currently applied in climate change research.

I take a historical approach, so that rather than just describing the state of the art at the time of writing, I also discuss the evolution of the art over time into its present form of different concepts, theories, and models. I hope this approach helps the reader to get a deep understanding of the subject, including the perception that in several cases the present theories and models are hardly the final ones. Furthermore, the conceptualisation of many of the models discussed has changed over time; by explaining the changes I hope to help the reader to compare old publications with recent ones. Last but not least, by taking the historical approach, I want to acknowledge the work of many early researchers who are often forgotten. The foundation for projecting the effects of climate change on boreal and temperate trees was laid by these early researchers long before climate change became an issue. Today this heritage is needed more than ever before.

It goes without saying that the 30 years of work summarised here would not have been possible without collaboration with supervisors, colleagues, students, and technicians. Tapani Repo was my nearest colleague in the 1980s and 1990s, when the foundation for this book was laid in our research group at the University of

Joensuu (currently the University of Eastern Finland). My doctoral supervisors Paavo Pelkonen and Veikko Koski conveyed the Finnish research tradition pertaining to the annual cycle of boreal trees to me. Ilkka Leinonen completed his PhD in our group and had a major impact on our research. At the very beginning of my research career, Pertti ‘Pepe’ Hari familiarised me with the principles of dynamic modelling in tree ecophysiology and with the relevance of the philosophy of science for the practical researcher. I have been glad to continue cooperation with these friends over the years.

The review paper I published in 2007 with Koen Kramer is the backbone of this book in several ways. Two other, more recent joint papers, published with Karen Tanino and Olavi Junttila, were a great help in finalising the manuscript. It is not possible here to mention all my other collaborators over the years, and even the most important ones make quite a long list: Risto Häkkinen, Seppo Kellomäki, Pasi Kolari, Kari Laine, Tarja Lehto, Sune Linder, Tapio Linkosalo, Jaana Luoranen, Annikki Mäkelä, Eero Nikinmaa, Jouni Partanen, Risto Rikala, Outi Savolainen, Heikki Smolander, Marja-Liisa Sutinen, Kari Taulavuori, and Gang Zhang.

After moving to Helsinki in 1997, I have broadened my scope to cover other plant life forms in addition to forest trees. This would not have been possible without my colleagues and students in Helsinki, who have expertise in dwarf shrubs, herbs, and grasses: Timo Saarinen, Robin Lundell, Helena Åström, Sirpa Rasmus, and Friederike Gehrmann. It has been a great pleasure for me to see that the approach developed for trees works in our PECC (Plant Ecophysiology and Climate Change) group for other plant life forms as well. Some of our studies addressing the other plant life forms are mentioned in passing.

Margaret Deignan of Springer invited me to write this book, and she has given me indispensable help throughout the preparation of the manuscript. I am especially grateful for her patience over the long years it took me to complete the book. Valuable technical help was also provided by Timo Bazuin, Takeesha Moerland-Torpey, and Chitra Sundarajan.

The entire manuscript was thoroughly commented on by Olavi Junttila. His comments were especially useful because in addition to providing constructive criticism, he also encouraged me to focus on my cup of tea – the modelling approach – rather than trying to broaden the scope to cover related topics, about which my colleagues have much more to say. I also received comments on the entire manuscript from Tapani Repo, and large parts of it were commented on by Risto Häkkinen, Pepe Hari, Øystein Johnsen, Pasi Kolari, Veikko Koski, Tapio Linkosalo, Robin Lundell, Marja-Liisa Sutinen, Karen Tanino, and Kari Taulavuori. More restricted but nevertheless useful comments were provided by Helena Åström, Koen Kramer, Xavier Morin, and Timo Saarinen. In addition, I received useful hints for literature references from Heikki Henttonen, Øystein Johnsen, Pasi Kolari, Robin Lundell, Jaana Luoranen, Timo Saarinen, Sirpa Rasmus, Karen Tanino, and Jan Weckström.

Ilkka Juuso, Robin Lundell, and Timo Saarinen provided technical help in drawing the figures. The following persons provided me with photographs: Juho

Aalto, Eeva Pudas, Risto Rikala, Timo Saarinen, Annika Saarto, and Sirkka Sutinen. Tapani Repo and Jaana Luoranen provided me with data for redrawing published figures.

My access to the long-term set of data collected by the Finnish Meteorological Institute and digitalised by the Finnish Forest Research Institute (currently Natural Resources Institute Finland) was made possible through cooperation with Pepe Hari, Risto Häkkinen, Heikki Tuomenvirta, and Tapio Linkosalo. Kimmo Ruosteenoja provided me unpublished climatic scenarios for Finland.

The language of the manuscript was carefully revised by Pekka Hirvonen, professor (emer.) of English. He spent a countless number of hours editing the text. During the multi-year process, he also taught me a lot about the nuances of English.

The writing of this book was economically supported by the Kone Foundation, the Academy of Finland (project 122194), and the Finnish Cultural Foundation.

I am grateful to all, including many not mentioned above, who have helped me in various ways over the years. To many of the collaborators named, I am also grateful for their friendship. ‘I have been privileged to carry out my studies in a research community where only the joy of life and laughter have overridden scientific enthusiasm’. These words, quoted from the preface to my doctoral thesis, are as true today as they were 25 years ago.

Helsinki, Finland
November 2015

Heikki Hänninen

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Chapter 1

Climatic Adaptation of Boreal and Temperate Tree Species

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Abstract Boreal and temperate trees grow under climatic conditions in which the ambient air temperature displays pronounced seasonal variation. Unlike herbs and grasses, trees overwinter without a sheltering snow cover, so that they are exposed to all the harsh climatic conditions. That is why their climatic adaptation is based on their annual cycle of development, whereby the frost-hardy dormant phase and the susceptible growth phase are synchronised with the seasonality of the climate. The main aspects of this adaptive strategy of trees are briefly discussed, emphasising both the geographical and the year-to-year variation of the seasonal air temperature conditions. Many boreal and temperate tree species have large ranges of geographical distribution, so that their different provenances have adapted to the particular local climate prevailing at their native growing site. The extent of the geographical variation in air temperature crucial for this adaptation is highlighted by examining the climatic records of four locations within the European distribution range of *Pinus sylvestris*. The extent of the year-to-year variation is similarly highlighted by examining a 92-year climatic record from Jyväskylä, central Finland. In the coolest summer, the temperature sum in Jyväskylä was similar to the average temperature sum 600 km north of Jyväskylä; and in the warmest summer it was similar to the average temperature sum 600 km south of Jyväskylä. This limited analysis suffices to reveal the extent of the climatic year-to-year variation that trees need to acclimate to at their native growing site.

Keywords Annual cycle • Boreal trees • Climatic adaptation • Climatic variation • Ecophysiological modelling • Seasonality • Temperate trees

1.1 Thermal Conditions in the Boreal and the Temperate Zone

1.1.1 *Seasonal and Geographical Variation*

At the highest latitudes of the globe, the climate is too cold to support tree growth, so that a biome of treeless tundra is formed there (Breckle 2002). Although the climate of the forested regions at somewhat lower latitudes is warmer, these regions are also characterized by winter seasons with air temperatures dropping below zero for prolonged periods. The seasonal occurrence of frost sets special requirements on the climatic adaptation of tree species growing in these conditions (Sarvas 1972, 1974; Larcher 2003; Crawford 2008).¹

The forested regions from the high to the intermediate latitudes of the northern hemisphere are broadly classified into two biomes. South of the arctic tundra, there is a large circumpolar biome of boreal coniferous forest (Breckle 2002). The climate in the boreal zone is typically classified as cool, though temperate and cold climates are also represented (Larcher 2003). Besides the dominating coniferous tree species, most of which are evergreen, broadleaved species are also common in the boreal zone. In the forested regions located further south, broadleaved deciduous tree species become dominant. These regions belong to the biome of temperate broadleaved forest (Breckle 2002).

There is a distinct seasonal pattern of incoming solar radiation in the boreal and the temperate zone, and this seasonality of radiation produces a similar seasonal pattern of air temperature. The summer season, with plenty of incoming solar radiation and relatively high air temperatures, alternates with the winter season, with both the amount of incoming radiation and the air temperatures relatively low (Bonan 2008). Though the seasonal patterns of air temperature in the boreal and the temperate zone are thus generally similar, there are also great geographical differences between the thermal conditions of these zones.

A large part of this geographical variation can be attributed to two main gradients. Firstly, the climate generally gets cooler when one moves from south to north. Thus the mean annual temperature in temperate forests is usually in the range of +5 to +15 °C, depending on the location, whereas in the boreal forests further north the mean annual temperature is typically only a few degrees above zero and, in the coldest part of the zone, even below zero (Whittaker 1975). Secondly, maritime regions are characterized by mild winters and cool summers, whereas continental regions further away from the sea are characterized by cold winters and warm summers (Bonan 2008). Thus the annual range of air

¹ Throughout the present volume, the concept of adaptation is used for the genetic adjustment of the tree populations to their native environments, the adjustment being caused by natural selection working over evolutionary time scales. Correspondingly, the concept of acclimation is used for the physiological adjustment of individual trees to the environmental conditions prevailing at their growing site during their life cycle.

temperatures is wider in continental than in maritime regions. In Yakutsk, Siberia, for instance, the annual range of mean monthly temperatures is about 70 °C, with the wintertime minimum and the summertime maximum of approximately -50 °C and $+20$ °C, respectively (Archibold 1995).

Many boreal and temperate tree species have large ranges of geographical distribution, so that their different provenances have adapted to the particular local climate prevailing at their native growing site (Langlet 1971; Rehfeldt et al. 1999; Aitken and Hannerz 2001; Savolainen et al. 2007). This important aspect of the climatic adaptation of boreal and temperate tree species is discussed in detail in Chap. 6. An idea of the extent of the geographical climate variation can be formed from an analysis of short-term temperature records gathered at four locations in Europe, representing a restricted part of the geographical distribution range of *Pinus sylvestris* (Fig. 1.1). Among these four locations, the mean annual temperature is the highest in Eskdalemuir, Scotland ($+7.1$ °C), and the lowest in Murmansk, northwestern Russia (-0.2 °C). Out of the remaining two locations, Jyväskylä, central Finland, has a mean annual temperature of $+2.7$ °C and Voronez, southern Russia, the second highest at $+6.0$ °C.

In studies addressing the seasonality and climatic adaptation of boreal and temperate tree species, it is necessary to also examine the seasonal pattern of air temperatures, not just the average level indicated by the mean annual temperature. Among the four locations examined here, for instance, there is only a relatively small difference in the mean annual temperature between Eskdalemuir and Voronez (Fig. 1.1a), but the seasonal pattern of mean monthly temperatures is drastically different at these two locations (Fig. 1.1b). In the maritime climate of Eskdalemuir, the mean monthly temperature remains slightly above zero even in winter, to rise to approximately $+13$ °C in summer. Thus the annual range of the mean monthly temperature in Eskdalemuir is only slightly over 10 °C (Fig. 1.1b). At the other end of the spectrum is Voronez. Due to its relatively southern location, the mean monthly temperature does not drop much below -10 °C in winter, whereas in summer it approaches $+20$ °C. Thus the annual range of the mean monthly temperature is about 30 °C (Fig. 1.1b). Accordingly, the air temperature's rate of rising in spring and dropping in autumn is higher in Voronez than in Eskdalemuir.

The other two locations, Jyväskylä and Murmansk, represent intermediate positions in this seasonal comparison. It is noteworthy that despite the northern location and generally cold climate of Murmansk (Fig. 1.1a), its mean temperature in July is almost as high as that of the otherwise much warmer and more southern Eskdalemuir (Fig. 1.1b). Furthermore, with the exception of Eskdalemuir, the mid-winter temperatures are almost equal in the four locations. This would not be the case if a location from the most continental part of the geographical range of *Pinus sylvestris* in Siberia had been included in the comparison (Archibold 1995).

There are also drastic differences among the four locations in the annual accumulation of temperature sum (Fig. 1.1c).² In the warm and continental climate

²This essential concept is defined in Sect. 2.3, and its ecophysiological interpretation is discussed in Sect. 3.2.1.2.

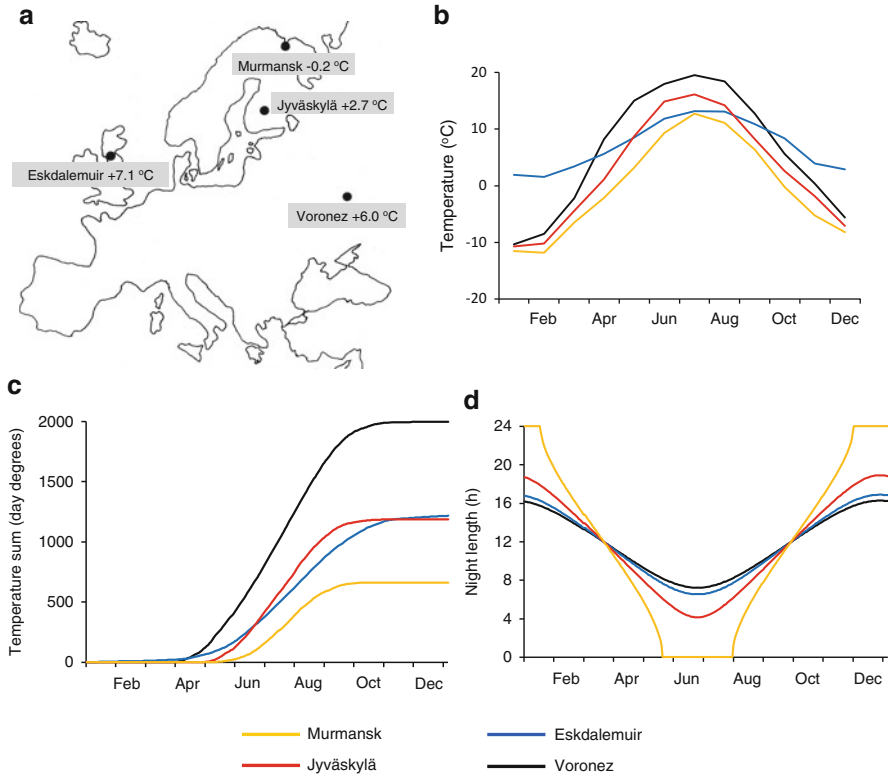


Fig. 1.1 Seasonal and geographical variation of the thermal and night length conditions in the European distribution range of *Pinus sylvestris*. **(a)** The locations of the four meteorological stations, with their respective mean annual air temperatures (Modified from Hänninen and Hari 1996, and published with the permission of the Finnish Forest Research Institute, currently the Natural Resources Institute Finland, and the Finnish Society of Forest Science). **(b)** The seasonal patterns of the mean monthly air temperatures at the four locations. **(c)** Average seasonal patterns of temperature sum accumulation at the four locations. The temperature sum is expressed in day degree units calculated with a threshold temperature of +5 °C (Sect. 2.3). **(d)** The seasonal patterns of night length, i.e., the length of the period during the diurnal cycle when the sun is below the horizon, at the four locations. The temperature indices have been calculated on the basis of standard air temperature records collected by the national meteorological institutes at the four locations during the 15 years of 1966–1980

of Voronez, the temperature sum starts to accumulate in early April, and by the end of the growing season, an average of almost 2000 day degree units has accumulated. In the colder climate of Murmansk, the accumulation starts about 1 month later, and the average total accumulation at the end of the growing season is about one third of the total accumulation in Voronez (Fig. 1.1c).

The remaining two locations, Jyväskylä and Eskdalemuir, display an almost identical average total accumulation of temperature sum, about 1200 day degree

units in both. Otherwise, too, the seasonal pattern is quite similar in these two locations, except that in the maritime climate of Eskdalemuir, the accumulation of temperature sum starts earlier and stops later than in the more continental climate of Jyväskylä. In fact, there are many years in Eskdalemuir with the temperature sum accumulation going on even in mid-winter. The difference between Eskdalemuir and Jyväskylä in the wintertime accumulation of temperature sum, though relatively minor in the overall climatological comparison (Fig. 1.1c), has a drastic effect on the climatic adaptation of the tree species. The ecophysiological importance of these climatic geographical differences is discussed in Sect. 6.3.4.

1.1.2 Year-to-Year Variation

The climate of the boreal and temperate zones is characterized by large year-to-year variation (Bonan 2008). In Jyväskylä, central Finland (Fig. 1.1a), the year-to-year range of the daily mean temperature over 92 years was about 35 °C in winter and about 20 °C in summer (Fig. 1.2a). Similarly, there is also large year-to-year variation in the temperature sum accumulated during the growing season (Koski and Sievänen 1985). In Jyväskylä, the average total accumulation of temperature sum over 92 years was about 1150 day degree units, with the minimum and maximum accumulations at about 750 and 1500 units, respectively (Fig. 1.2b). Because of the large year-to-year variation in the accumulation of temperature sum, there is also great year-to-year variation in the dates when a given value of temperature sum is reached. For instance, the temperature sum of 600 day degrees was attained on July 6 at the earliest and on August 17 at the latest, so that the range of the date of attaining this temperature sum in Jyväskylä was 42 days (Fig. 1.2b).

The magnitude of the year-to-year variation in the accumulation of temperature sum is further emphasized by a comparison of the minimum and maximum accumulation of temperature sum in Jyväskylä with the geographical variation in the average accumulation of temperature sum. The minimum Jyväskylä accumulation of 750 day degree units corresponds to the average accumulation in Kittilä, located in Finnish Lapland about 600 km north of Jyväskylä. Similarly, the maximum accumulation of 1500 day degree units corresponds to the average accumulation in southern Estonia, about 600 km south of Jyväskylä (Viherä-Aarnio et al. 2005). In all, then, considering the most extreme years, the year-to-year variation of air temperature sum accumulation in Jyväskylä corresponds to a geographical distance of about 1200 km in the north-south direction as regards the average accumulation of temperature sum.

The dates of both the last frosts in the spring and the first frosts in the autumn are essential for the climatic adaptation of boreal and temperate tree species. In Jyväskylä, the date of the last frost of -5 °C or below varied from March 27 to May 13, i.e., by 47 days, over 92 years, and the date of the first autumn frost from September 25 to December 1, i.e., by 67 days (Fig. 1.2c). Furthermore, there was practically no correlation between the date of the last frost and the first frost in the

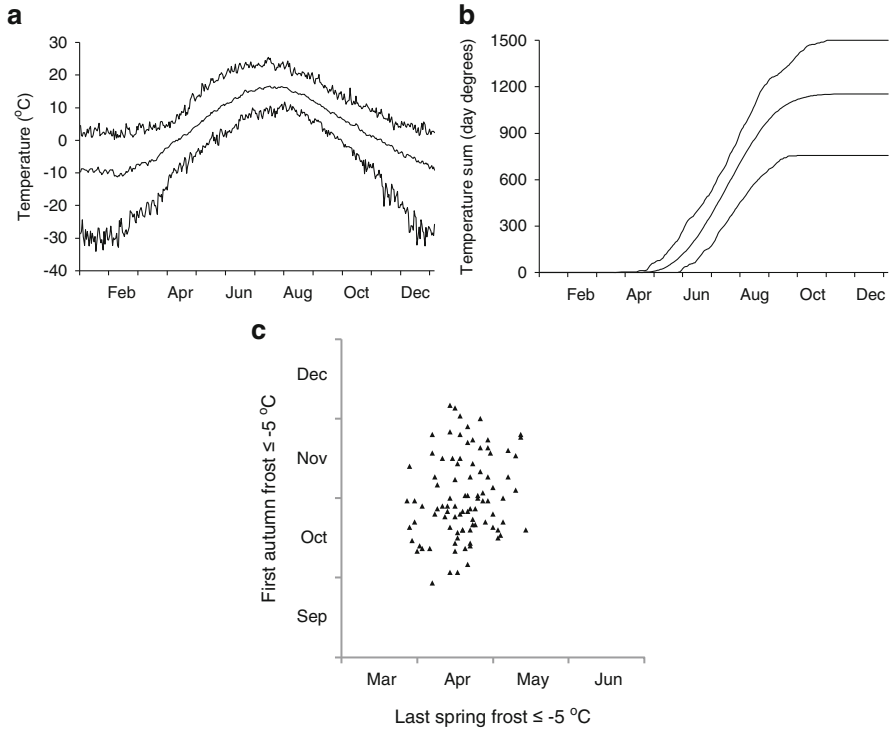


Fig. 1.2 Year-to-year variation of air temperature in Jyväskylä, central Finland ($62^{\circ}14'N$, $25^{\circ}44'E$, 115 m asl; Fig. 1.1a). (a) The daily mean air temperature, with its year-to-year minimum (*lower curve*), mean (*middle curve*), and maximum (*upper curve*). (b) The corresponding three statistics for the accumulation of temperature sum during the growing season. A threshold temperature of $+5^{\circ}C$ was used in the calculations (Sect. 2.3). (c) The timing of the occurrence of the last spring frost with the daily minimum air temperature $T_{\min} \leq -5^{\circ}C$ (*horizontal axis*) and the corresponding first autumn frost (*vertical axis*); each symbol corresponds to one year. The results are based on standard air temperature records collected by the Finnish Meteorological Institute in Jyväskylä over the period of 1883–1980. On account of missing observations, the years 1911–1916 were excluded, so that the coverage of the data is 92 years

same year, so that a spring with a late termination of the frost season, for instance, was equally likely to be followed by an early or late onset of the autumn frost season (Fig. 1.2c).

Though only a few air temperature indices were reported here, and for one location only (Fig. 1.2), they may be sufficient to give the reader an idea of the magnitude of the year-to-year variation in the thermal conditions of the boreal and the temperate zone. The large year-to-year variation and the low predictability of the air temperature constitute an additional requirement for the climatic adaptation of the boreal and temperate tree species. The trees are exceptionally long-lived perennials, so that it is not sufficient for them to acclimate to the average seasonal climatic pattern, though it involves a large range of variation in itself (Fig. 1.1b).

Rather, the trees need to acclimate to the climatic conditions of all years, including the most exceptional ones (Koski and Sievänen 1985; Fig. 1.2).

1.2 Night Length in the Boreal and the Temperate Zone

Solar radiation provides the energy source for all green plants, including the trees in the boreal and temperate regions (Larcher 2003). It goes without saying, then, that the seasonality of incoming solar radiation is of major importance for the photosynthetic production of boreal and temperate trees. However, as has been known for long, the seasonality of the light-climate also has other important effects on boreal and temperate trees and many other plants as well (Garner and Allard 1923). These effects are mediated by the relative lengths of the dark part ('night') and the light part ('day') in the diurnal cycle, and they are generally referred to as photoperiodic effects (Thomas and Vince-Prue 1977).

The causal factor in the induction of height growth cessation in boreal and temperate trees is often (Nitsch 1957; Howe et al. 1996), but not always (Håbjørg 1972; Junttila and Kaurin 1985, 1990), night length rather than day length. Regarding several other photoperiodic effects in the annual cycle of the trees, we lack experimental studies that do away with the relationship between day length and night length, so that we do not know which one of them is the causal factor. The modelling studies discussed in the present volume usually refer to night length, so that the concept of night length, NL, is constantly used in the present volume as well.

Night length varies seasonally according to a fixed pattern determined by the latitude. The pattern varies geographically so that the difference between maximum night length during the cold season and minimum night length during the warm season is small at low latitudes and increases as one goes north or south towards the poles. The extreme difference occurs at the highest latitudes, with their periods of polar night (NL = 24 h) and of midnight sun (NL = 0 h) (Bonan 2008). The four locations of the geographical distribution range of *Pinus sylvestris* examined here also evince considerable variation in the seasonal pattern of night length (Fig. 1.1d) though the southernmost regions of the distribution range in Turkey and Spain (Sarvas 1964) are not included in this comparison.

1.3 The Annual Cycle as an Adaptive Strategy

Many plant species are able to tolerate short-term episodic frosts even in the active growth phase. That is especially the case with alpine plant species growing above the tree line in tropical regions (Larcher 2003; Crawford 2008). In these conditions, a heavy night frost may occur at any time of the year, so that the frost survival of the plants cannot be based on seasonal synchronisation of plant development with the

climate. The acclimation of these plants involves several biophysical and physiological mechanisms. A crucial one is supercooling, i.e., the lowering of the tissue temperature below the freezing point of the cell sap without forming ice crystals (Sakai and Larcher 1987; Körner 2003). This strategy of frost survival is traditionally referred to as freezing avoidance (Levitt 1980; Larcher 2003).

In boreal and temperate zones, the freezing temperatures occur seasonally rather than episodically (Sakai and Larcher 1987). This implies that overwintering is essential for the frost survival of plants in these zones. Many perennial herbs and grasses overwinter below an insulating and protecting snow cover, and some even in the soil, where not only snow but also the soil itself protects the overwintering plant organs. In Raunkiaer's (1934) classification, the former plants belong to the life form *hemicytophytes* (Gr. hemi = half; cypto = hidden) and the latter to the life form *cryptophytes*. In contrast, trees belong to the class of *phanerophytes* (Raunkiaer 1934), i.e., except for the roots, they overwinter above the snow cover. During long-lasting seasonal exposure to severe frosts, ice crystals are formed in extracellular spaces in the tree tissues, so that the frost survival of trees is largely based on freezing tolerance (Levitt 1980; Larcher 2003). Due to this extracellular freezing, part of the cellular water is lost to the extracellular ice, which leads to dehydration and lowering of the freezing point of the cell sap (Sutinen et al. 2001). The development of freezing tolerance requires dormancy, i.e., cessation of growth (Weiser 1970; Fuchigami et al. 1982; Junttila 2007). Therefore, as discussed in more detail in Sect. 5.3, studies of the development of freezing tolerance in trees often address growth cessation also.³

The seasonally occurring frosts of the boreal and temperate regions, despite their large year-to-year variation (Fig. 1.2c), are still relatively predictable in comparison with the episodic occurrence of frosts in the tropics, and that makes the frost survival strategy based on dormancy possible. Thus, with proper synchronization of the frost hardy dormant phase and the susceptible active growth phase with the seasonality of the air temperature, the trees can grow even at sites where the temperature may drop dozens of degrees below zero in winter (Weiser 1970; Sutinen et al. 1992). In the present volume, the concept of the *annual cycle of development* is used in a broad sense, so that in addition to morphological changes (Sarvas 1972, 1974), it is also used for all biophysical and physiological changes that relate to the seasonal alternation of the dormant and the active phase of the trees (Weiser 1970; Perry 1971; Fuchigami et al. 1982).

The regulation of the annual cycle of development takes place as a result of interaction between genetic and environmental factors, so that each genotype reacts to the environmental cues in its specific way (Sarvas 1972, 1974; Ekberg et al. 1979; Tanino et al. 2010). Understanding this interaction is the key to

³In evolutionary terms, there is a trade-off involved in the life form of phanerophytes, i.e., trees have traded off the benefits of a sheltering snow cover in winter for superiority in the competition for light during the growing season. As freezing stress has a lot in common with drought stress at the cellular level, Larcher (1995) put forward the interesting hypothesis that the frost hardiness of plants has its evolutionary origin in drought hardiness.

understanding the climatic adaptation of boreal and temperate tree species and is therefore also crucial for any attempt to project the effects of climate change on these trees. Accordingly, the interaction between genetic and environmental factors in the regulation of the annual cycle of boreal and temperate trees is the leading theme throughout the present volume.

1.4 Organisation of the Book

Today, mathematical dynamic models are an essential part of studies of the annual cycle of boreal and temperate trees, especially where the effects of the projected climate change on trees are addressed (Cannell 1985; Murray et al. 1989; Hänninen and Kramer 2007; Kramer and Hänninen 2009; Morin et al. 2009; Rammig et al. 2010; Caffarra et al. 2011a, b; Chuine et al. 2013). The models have also been used in studies addressing other woody plants (Pop et al. 2000; Van Wijk et al. 2003; Lundell et al. 2008; Jones et al. 2015) and in studies using remote sensing to investigate the phenology of the entire plant community (Picard et al. 2005; Delbart and Picard 2007).

In this book, modelling studies of the annual cycle are discussed with the emphasis on integrating modelling with empirical research. To grasp the message of the book, the reader needs to understand some underlying principles of the dynamic modelling of the annual cycle. To this end, a tutorial on the principles of dynamic modelling, starting from some general principles of the philosophy of science, is provided in Chap. 2.

In the next three chapters, various aspects of the annual cycle of boreal and temperate trees are discussed. Chap. 3 addresses phenological phenomena, such as the timing of vegetative bud burst and height growth cessation. Due to the multitude of phenomena addressed and the exceptionally emphasized need for conceptual clarification, Chap. 3 is longer than the next two chapters. Chapter 4 is devoted to the seasonality of photosynthesis and Chap. 5 to that of frost hardiness. The leading theme of the whole volume, i.e., the interaction of environmental and genetic factors in the regulation of the annual cycle, is re-examined in Chap. 6, where evolutionary aspects of trees are specifically discussed. Next, the scaling up of the implications from the seasonal phenomena of trees to higher organisational levels is briefly discussed in Chap. 7 on the basis of the whole-tree considerations presented in Chaps. 3, 4, 5, and 6. In Chap. 7, the considerations range all the way from the level of the individual tree to the stand level and even to the global level.

The ultimate aim of this volume is to examine the effects of the projected anthropogenic climate change on boreal and temperate trees. That is the theme of Chap. 8, so that the first seven chapters serve as an *ouverture* of sorts to Chap. 8. Much simpler and more straightforward approaches, such as the ‘niche-based’ or ‘climatic envelope’ modelling, are available for evaluating the effects of climate change on various biota, including boreal and temperate trees (Bakkenes et al. 2002; Thomas et al. 2004; Hijmans and Graham 2006). However, despite the useful first

approximations of the effects of climate change obtained with these approaches, it is the main postulate of the present volume that the projections obtained with these methods need to be augmented with more detailed approaches, where the pertinent biophysical and ecophysiological phenomena are explicitly addressed. It is for this reason that the lengthy *ouverture* is needed. But facilitating the applied research related to climate change is not the only motivation for this chapter and Chaps. 2, 3, 4, 5, 6, and 7. Rather, understanding the climatic adaptation of boreal and temperate tree species is a scientifically fascinating theme for basic research as such. Furthermore, such an understanding already has several important practical applications in the present climate, especially in horticulture and forestry (Campbell 1974; Cannell et al. 1985; Saure 1985; Hänninen et al. 2009; Halaly et al. 2011). Finally, the conclusions for the entire volume are presented in Chap. 9.

References

- Aitken, S. N., & Hannerz, M. (2001). Genecology and gene resource management strategies for conifer cold hardiness. In F. J. Bigras & S. J. Colombo (Eds.), *Conifer cold hardiness* (pp. 23–53). Dordrecht: Kluwer Academic Publishers.
- Archibold, O. W. (1995). *Ecology of world vegetation*. London: Chapman & Hall. 510 p.
- Bakkenes, M., Alkemade, J. R. M., Ihle, F., Leemans, R., & Latour, J. B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, 8, 390–407.
- Bonan, G. (2008). *Ecological climatology. Concepts and applications*. Cambridge: Cambridge University Press. 550 p.
- Breckle, S.-W. (2002). *Walter's vegetation of the Earth. The ecological systems of the geo-biosphere* (4th ed.). Berlin: Springer-Verlag. 527 p.
- Caffarra, A., Donnelly, A., Chuine, I., & Jones, M. B. (2011a). Modelling the timing of *Betula pubescens* budburst. I. Temperature and photoperiod: a conceptual model. *Climate Research*, 46, 147–157.
- Caffarra, A., Donnelly, A., & Chuine, I. (2011b). Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research*, 46, 159–170.
- Campbell, R. K. (1974). Use of phenology for examining provenance transfers in reforestation of Douglas-fir. *Journal of Applied Ecology*, 11, 1069–1080.
- Cannell, M. G. R. (1985). Analysis of risks of frost damage to forest trees in Britain. In P. M. A. Tigerstedt, P. Puttonen, & V. Koski (Eds.), *Crop physiology of forest trees* (pp. 153–166). Helsinki: Helsinki University Press.
- Cannell, M. G. R., Murray, M. B., & Sheppard, L. J. (1985). Frost avoidance by selection for late budburst in *Picea sitchensis*. *Journal of Applied Ecology*, 22, 931–941.
- Chuine, I., de Cortazar-Atauri, I. G., Kramer, K., & Hänninen, H. (2013). Plant development models. In: M. D. Schwartz (Ed.), *Phenology: An integrative environmental science, Second Edition* (pp. 275–293). Dordrecht: Springer.
- Crawford, R. M. M. (2008). *Plants at the margin. Ecological limits and climate change*. Cambridge: Cambridge University Press. 478 p.
- Delbart, N., & Picard, G. (2007). Modeling the date of leaf appearance in low-arctic tundra. *Global Change Biology*, 13, 2551–2562.
- Eikberg, I., Eriksson, G., & Dormling, I. (1979). Photoperiodic reactions in conifer species. *Holarctic Ecology*, 2, 255–263.

- Fuchigami, L. H., Weiser, C. J., Kobayashi, K., Timmis, R., & Gusta, L. V. (1982). A degree growth stage ($^{\circ}\text{GS}$) model and cold acclimation in temperate woody plants. In P. H. Li & A. Sakai (Eds.), *Plant cold hardiness and freezing stress. Mechanisms and crop implications* (Vol. 2, pp. 93–116). New York: Academic Press.
- Garner, W. W., & Allard, H. A. (1923). Further studies in photoperiodism, the response of the plant to relative length of day and night. *Journal of Agricultural Research*, 23, 871–920.
- Håbjørg, A. (1972). Effects of light quality, light intensity and night temperature on growth and development of three latitudinal populations of *Betula pubescens* Ehrh. *Scientific Reports of the Agricultural University of Norway*, 51(26), 1–17.
- Halaly, T., Zion, B., Arbel, A., Regev, R., Barak, M., & Or, E. (2011). Short exposure to sublethal heat shock facilitates dormancy release in grapevines. *American Journal of Enology and Viticulture*, 62, 106–112.
- Hänninen, H., & Hari, P. (1996). The implications of geographical variation in climate for differentiation of bud dormancy ecotypes in Scots pine. In P. Hari, J. Ross, M. Mecke (Eds.), *Production process of Scots pine; Geographical variation and models. Acta Forestalia Fennica*, 254, 11–21.
- Hänninen, H., & Kramer, K. (2007). A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fennica*, 41, 167–205.
- Hänninen, H., Luoranen, J., Rikala, R., & Smolander, H. (2009). Late termination of freezer storage increases the risk of autumn frost damage to Norway spruce seedlings. *Silva Fennica*, 43, 817–830.
- Hijmans, R. J., & Graham, C. H. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12, 2272–2281.
- Howe, G. T., Gardner, G., Hackett, W. P., & Furnier, G. R. (1996). Phytochrome control of short-day-induced bud set in black cottonwood. *Physiologia Plantarum*, 97, 95–103.
- Jones, H. G., Gordon, S. L., & Brennan, R. M. (2015). Chilling requirement of Ribes cultivars. *Frontiers in Plant Science*, 5, Article 767. doi:10.3389/fpls.2014.00767.
- Junttila, O. (2007). Regulation of annual shoot growth cycle in northern tree species. In E. Taulavuori & K. Taulavuori (Eds.), *Physiology of northern plants under changing environment* (pp. 177–210). Kerala: Research Signpost.
- Junttila, O., & Kaurin, Å. (1985). Climatic control of apical growth cessation in latitudinal ecotypes of *Salix pentandra* L. In Å. Kaurin, O. Junttila, & J. Nilsen (Eds.), *Plant production in the north* (pp. 83–91). Tromsø: Norwegian University Press.
- Junttila, O., & Kaurin, Å. (1990). Environmental control of cold acclimation in *Salix pentandra*. *Scandinavian Journal of Forest Research*, 5, 195–204.
- Körner, C. (2003). *Alpine plant life. Functional plant ecology of high mountain ecosystems* (2nd ed.). Berlin: Springer-Verlag. 344 p.
- Koski, V., & Sievänen, R. (1985). Timing of growth cessation in relation to the variations in the growing season. In P. M. A. Tigerstedt, P. Puttonen, & V. Koski (Eds.), *Crop physiology of forest trees* (pp. 167–193). Helsinki: Helsinki University Press.
- Kramer, K., & Hänninen, H. (2009). The annual cycle of development of trees and process-based modelling of growth to scale up from the tree to the stand. In: A. Noormets (Ed.), *Phenology of ecosystem processes* (pp 201–227). Dordrecht: Springer.
- Langlet, O. (1971). Two hundred years genealogy. *Taxon*, 20, 653–721.
- Larcher, W. (1995). *Physiological plant ecology. Ecophysiology and stress physiology of functional groups* (3rd ed.). Berlin: Springer. 506 p.
- Larcher, W. (2003). *Physiological plant ecology. Ecophysiology and stress physiology of functional groups* (4th ed.). Berlin: Springer-Verlag. 513 p.
- Levitt, J. (1980). *Responses of plants to environmental stresses* (Chilling, freezing, and high temperature stresses 2nd ed., Vol. I). New York: Academic Press. 497 p.
- Lundell, R., Saarinen, T., Åström, H., & Hänninen, H. (2008). The boreal dwarf shrub *Vaccinium vitis-idaea* retains its capacity for photosynthesis through the winter. *Botany*, 86, 491–500.

- Morin, X., Lechowicz, M. J., Augspurger, C., O'Keefe, J., Viner, D., & Chuine, I. (2009). Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology*, *15*, 961–975.
- Murray, M. B., Cannell, M. G. R., & Smith, R. I. (1989). Date of budburst of fifteen tree species in Britain following climatic warming. *Journal of Applied Ecology*, *26*, 693–700.
- Nitsch, J. P. (1957). Photoperiodism in woody plants. *Proceedings of the American Society for Horticultural Science*, *70*, 526–544.
- Perry, T. O. (1971). Dormancy of trees in winter. *Science*, *171*, 29–36.
- Picard, G., Quegan, S., Delbart, N., Lomas, M. R., Le Toan, T., & Woodward, F. I. (2005). Bud-burst modelling in Siberia and its impact on quantifying the carbon budget. *Global Change Biology*, *11*, 2164–2176.
- Pop, E. W., Oberbauer, S. F., & Starr, G. (2000). Predicting vegetative bud break in two arctic deciduous shrub species, *Salix pulchra* and *Betula nana*. *Oecologia*, *124*, 176–184.
- Rammig, A., Jönsson, A. M., Hickler, T., Smith, B., Bähring, L., & Sykes, M. T. (2010). Impacts of changing frost regimes on Swedish forests: Incorporating cold hardiness in a regional ecosystem model. *Ecological Modelling*, *221*, 303–313.
- Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography*. Oxford: Clarendon Press. 632 p.
- Rehfeldt, G. E., Ying, C. C., Spittlehouse, D. L., & Hamilton, D. A., Jr. (1999). Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs*, *69*, 375–407.
- Sakai, A., & Larcher, W. (1987). *Frost survival of plants. Responses and adaptation to freezing stress*. Berlin: Springer-Verlag. 321 pp.
- Sarvas, R. (1964). *Havupuu*. Porvoo: Werner Söderström Osakeyhtiö. 531 p.
- Sarvas, R. (1972). Investigations on the annual cycle of development of forest trees. Active period. *Communicationes Instituti Forestalis Fenniae*, *76*(3), 1–110.
- Sarvas, R. (1974). Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Communicationes Instituti Forestalis Fenniae*, *84*(1), 1–101.
- Saure, M. C. (1985). Dormancy release in deciduous fruit trees. *Horticultural Reviews*, *7*, 239–300.
- Savolainen, O., Pyhäjärvi, T., & Knürr, T. (2007). Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 595–619.
- Sutinen, M.-L., Palta, J. P., & Reich, P. B. (1992). Seasonal differences in freezing stress resistance of needles of *Pinus nigra* and *Pinus resinosa*: Evaluation of the electrolyte leakage method. *Tree Physiology*, *11*, 241–254.
- Sutinen, M.-L., Arora, R., Wisniewski, M., Ashworth, E., Strimbeck, R., & Palta, J. (2001). Mechanisms of frost survival and freeze-damage in nature. In F. J. Bigras & S. J. Colombo (Eds.), *Conifer cold hardiness* (pp. 89–120). Dordrecht: Kluwer Academic Publishers.
- Tanino, K. K., Kalcsits, L., Silim, S., Kendall, E., & Gray, G. R. (2010). Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: A working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant Molecular Biology*, *73*, 49–65.
- Thomas, B., & Vince-Prue, D. (1977). *Photoperiodism in plants* (2nd ed.). San Diego: Academic Press. 428 p.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*, 145–148.
- Van Wijk, M. T., Williams, M., Laundre, J. A., & Shaver, G. R. (2003). Interannual variability of plant phenology in tussock tundra: Modelling interactions of plant productivity, plant phenology, snowmelt and soil thaw. *Global Change Biology*, *9*, 743–758.

- Viherä-Aarnio, A., Häkkinen, R., Partanen, J., Luomajoki, A., & Koski, V. (2005). Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. *Tree Physiology*, *25*, 101–108.
- Weiser, C. J. (1970). Cold resistance and injury in woody plants. *Science*, *169*, 1269–1278.
- Whittaker, R. H. (1975). *Communities and ecosystems* (2nd ed.). New York: Macmillan Publishing Co. 385 p.

Chapter 2

Dynamic Modelling of the Annual Cycle

Contents

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Abstract A hypothetico-deductive framework for dynamic ecophysiological modelling of the annual cycle of boreal and temperate trees is described and discussed. In the framework used, the modelling is closely associated with experimental and observational empirical studies, so that inductive ('empirical') and deductive ('theoretical') phases alternate in the research. Computer simulations are deductive, and their results therefore contain nothing but implications of the assumptions of the model used in the simulations. Empirical data are used either for inductive formulation of the models or for testing the models after deducing their predictions by means of simulations. In dynamic modelling, the time courses of seasonal ecophysiological processes are simulated by first calculating the momentary rate of development on the basis of the input data of environmental factors, such as air temperature and night length. After that, the time course of the state of development is obtained by mathematical integration of the rate of development with respect to time. A unifying notation is described for the rate and state variables of different aspects of the annual cycle. Diverse model categories, based on major differences in the ecophysiological phenomena addressed, are described and compared. Finally, the realism, accuracy, and generality of the models are discussed. A novel concept of coverage is introduced for use in the assessment of the realism of the models. Biological levels of organisation, vertical reduction, and emergent properties are briefly discussed in relation to the realism of the models. The framework described and discussed in this chapter forms the basis for the subsequent chapters, in which different aspects of the annual cycle in boreal and temperate trees are addressed.

Keywords Annual cycle • Boreal trees • Computer simulations • Day degrees • Dynamic models • Ecophysiological modelling • Modelling framework • Model realism • Seasonality • Temperate trees

2.1 A Hypothetico-Deductive Modelling Framework

In the philosophy of science, research is generally divided into two main categories, which are referred to as inductive and deductive research. In broad terms, induction refers to empirical research: whenever consistent results are obtained in empirical data, they are generalised into a rule, model, or theory (Niiniluoto 1983). Historically, the development of any scientific discipline is typically inductive at the early stages, when the research has not yet produced many generalised concepts and theories. In tree ecophysiology, inductive research is exemplified by determining the environmental responses of ecophysiological phenomena, such as photosynthesis or frost hardening/dehardening, on the basis of experiments carried out in controlled conditions (Hänninen and Lundell 2007).

At a later stage in the history of the scientific discipline, when generalised concepts and theories have accumulated, the research often adopts a deductive (or ‘theoretical’) approach and starts applying the hypothetico-deductive method (HDM; Haila 1982; Niiniluoto 1983). Now the starting point is a generalised theory, which is to be tested against data from a particular study specifically designed for the purpose. First, predictions to be tested by means of various experimental designs are derived (deduced) from the theory. The research takes an “if x then y ” approach: if the theory or model x is true, then a given experiment will yield the results y . With such logical inference (or calculations), maximally efficient experimental designs are planned (Hänninen 1990a, b). Second, the experiment is carried out and its results are compared with the predictions of the theory to be tested. In this way, the theory is either falsified or corroborated, i.e., supported, by the experimental data (Niiniluoto 1983). Deductive inference is also applied whenever a simulation model is run on a computer (Hänninen and Lundell 2007). In this case, the computer calculates the implications that the generalised model used in the simulations produces for the particular case specified by the input data (Fig. 2.1).

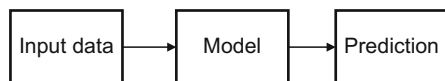


Fig. 2.1 The deductive principle of using mathematical models for research calculations. The formulae of the model, together with the input data, determine the prediction of the model. In this way the prediction of the model is a logical necessity implied by the model for the particular set of input data used, so that the prediction contains nothing new as such. Even so, the calculations are needed in practical research, since it is generally not possible to see the implications directly from the structure of the model and the input data