Methods of Dendrochronology

Applications in the Environmental Sciences

Edited by

E. R. Cook

Tree-Ring Laboratory, Lamont-Doherty Geological Observatory,
Columbia University, New York, U.S.A.

and

L. A. Kairiukstis

IIASA, Laxenburg, Austria and
Lithuanian Academy of Sciences, U.S.S.R.

Springer-Science+Business Media, B.V.

Library of Congress Cataloging in Publication Data

Methods of dendrochronology : applications in the environmental
science / E. Cook and L. Kairiukstis, editors.
p. cm.
Includes bibliographical references.

1. Dendrochronology. 2. Ecology. I. Cook, E. (Edward)
II. Kairikūkštis, Leonardas.
QK477.2.A6M48 1989
582.16'0372--dc20 89-48124

ISBN 978-90-481-4060-2 ISBN 978-94-015-7879-0 (eBook)
DOI 10.1007/978-94-015-7879-0

Reprinted 1992

Printed on acid-free paper

CHAPTER 2

Primary Data

Chapter Leader: J.R. Pilcher
Chapter Contributors: F.H. Schweingruber, L. Kairiukstis, S. Shiyatov, M. Worbes, V.G. Kolishchuk, E.A. Vaganov, R. Jagels, and F.W. Telewski

2.1. Sample Selection

F.H. Schweingruber, L. Kairiukstis, and S. Shiyatov

2.1.1. Introduction

The search and selection of suitable regions, sites, species, and trees are fundamentally important in dendrochronological studies. Practically every dendrochronological study states the locality from which the material is taken and the number of tree rings contained in the samples and the chronologies. However, only in dendroecological papers are the principles of site and specimen selection described (e.g., Mueller-Stoll, 1951; Jazewitsch, 1961; Fritts, 1965; Shiyatov, 1973, 1986; Bitvinskas, 1974; Lovelius, 1979). LaMarche *et al.* (1982) point out the potentials and limits of dendrochronological studies in historical and ecological fields. These depend primarily on the aims and the tasks of the investigator, and their accuracy determines the quality of the tree-ring chronologies obtained. This section focuses on the importance of the sampling strategies for various applications of dendrochronology.

2.1.2. Selection of a study area

The most appropriate regions for dendroclimatological investigations are those where trees grow at their climatic distribution limit and where climatic factors greatly affect tree-ring variability (e.g., northern, southern, upper, and lower distribution limits of forest communities and tree species). However, in many cases

E. R. Cook and L. A. Kairiukstis (eds.), Methods of Dendrochronology, 23–96.

reliable climatic information may be obtained from growth variations of trees growing under more favorable conditions.

Regions with optimal tree-growth conditions are also well suited for reconstructing such non-climatic factors as competition between species and individuals, forest fires, pest attack, etc. Therefore, at an early stage of study, an investigator should become acquainted with schemes of botanical and geographical subdivision of large territories and with detailed zonation of the study area. The principles of geobotanical zonation are different in various countries, which presents difficulties for a comparative evaluation of general conditions of forest vegetation growth at widely separated regions. Geobotanical characteristics of the large regions, for example, the Soviet Union, may be taken from monographs like *Vegetation Cover of the USSR: Explanations to the Geobotanical Map, Scale 1:4,000,000 1956* and *Vegetation of the European Part of the USSR, 1980.* Most areas of the globe now have some similar broad-scale vegetation descriptions (e.g., Rowe, 1972, for Canada; or Loucks, 1962, for the Maritime Provinces).

2.1.3. Selection of sites

Within the limits of certain regions one may choose sites with the maximum tree growth response to changes in the factors of interest. For example, to study precipitation reconstruction, tree samples should be taken from the driest sites where moisture would most probably be the limiting factor. To reconstruct thermal conditions, the most appropriate sites would be those where trees do not have a limited water supply. Selection of proper sites permits a climatic signal to be revealed in the rings of trees growing in regions optimal for forest development.

This is a principle that at first glance seems to run contrary to statistical considerations requiring random sampling. However, tree and site selection is an extension of the principle of limiting factors, the concept of ecological amplitude and replication. Differences in site lead to differences in the most important limiting factors. Thus, it is important to choose the specific site and to replicate within this site, so that all the sampled trees will have the same or similar signals (LaMarche *et al.*, 1982).

In many areas promising sites for dendrochronological studies are found in mountainous regions, where contrasts may be found in a small territory and where diverse catastrophic factors (such as snow avalanches, mud flows, rock avalanches, glacier advance) greatly influence tree growth. However, dendroclimatic relationships are often difficult to establish here owing to a lack of long climate records and the great variety of microclimatic, mesoclimatic, and macroclimatic conditions. In all areas, site selection for ecological and climatic studies may be influenced by the location of climatic-recording stations. Environmental gradients are examined by selecting specific sites along the environmental gradient (Fritts *et al.*, 1969; Norton, 1983a) and by building strong site chronologies so that any differences reflecting the gradient may be statistically tested. Two general principles should be considered when selecting sites:

Site homogeneity largely determines the quality of the chronology. A site chronology should only be constructed from trees from the same class of site. In the most opportune cases it is possible to find sufficient trees within a small area. Often, however, it is necessary to group together trees from different places but with the same site conditions to obtain a chronology. The units of collection are best identified by means of phytosociological relevés or at least floristic descriptions. These surveys also permit an understanding of the relationship of ecological conditions on sites far from each other, which is not possible on the basis of topographical or geological descriptions alone.

Stand development affects cambial activity. Wherever possible, only trees of the same social status (e.g., dominant, codominant) should be grouped into a site chronology. The variability owing to competition is thus reduced, although it cannot be completely eliminated, particularly in intensively managed forests where a number of silvicultural operations are conducted within a relatively short time. If, however, the study concerns stand development, then trees of each social status should be examined.

2.1.4. Selection of species

In some areas of the world, dendrochronology is not possible because appropriate trees are not available. Trees in these areas may show an absence of annual rings, insufficient variability from ring to ring for cross-dating to be established, missing rings, or interannual growth bands. In many areas there are no trees of sufficient age for useful dendrochronology. Many trees growing in the tropics do not produce distinct annual layers, or, if they do, there is no visible pattern common among trees that can be used for cross-dating (Eckstein *et al.*, 1981).

Appendix A lists the species for which tree-ring chronologies have been published or for which it appears dendrochronology has been possible. Many are represented by chronologies that are held in the International Tree-Ring Data Bank. The majority of chronologies from the USSR is from species of *Pinus*, *Picea*, and *Larix*. In western North America *Pinus* also supplies many of the chronologies together with *Pseudotsuga*, *Libocedrus*, and *Juniperus*.

The longest-lived species of dendrochronological interest are *Pinus aristata* and *P. longaevea* (up to 4,000 years) (Ferguson, 1969) growing in western North America and *Juniperus turkestanica* (up to 2,000 years) growing in Middle Asia (Mukhamedshin, 1968). The most sensitive tree-ring chronologies in the Eastern Hemisphere have been obtained from *Larix* species. This can be attributed to their ecological and biological peculiarities: light-loving, yearly defoliation, and efficient use of environmental resources in biomass accumulation (Shiyatov, 1967, 1986).

Of the angiospermous species, the most widely used are of *Quercus*, particularly in Europe and eastern North America. The second longest chronology in the world, after the bristlecone pine (*Pinus aristata*), is from English oak (*Quercus robur*) (Pilcher *et al.*, 1984). Oak has been widely used for archaeological dating, dendroclimatology, radiocarbon calibration, and dendroecology

(Eckstein, 1972; Brown *et al.*, 1986; Becker, 1986; Kostin, 1963; Bitvinskas and Kairaitis, 1975; Leuschner and Delorme, 1984). In the Southern Hemisphere, *Nothofagus* has proved a valuable broadleaf genus (Ogden, 1982; Norton, 1983b,c).

In conclusion any tree or shrub species that meets the following requirements can be used for a dendrochronological study:

- It produces distinguishable rings for most years.
- It possesses ring features that can be cross-dated dendrochronologically
- It attains sufficient age to provide the time control required for a particular investigation.

2.1.5. Selection of stands

The selection of stands is dependent on the purpose of the scientific investigation. When climate is to be reconstructed it is desirable to minimize the effect of competition in dendrochronological series by taking samples from open forests or scattered trees. Where possible it is better to sample in old growth rather than secondary forest. Therefore, a detailed description of the community with special attention to origin and development stage of the stand is preferred. Undisturbed stands that fulfill requirements of age, year-to-year ring-width variability, and cross-dating are sometimes difficult to find, so some disturbances made by man in stand structure may be unavoidable. However, it is important that the sampled forest communities have not been similarly damaged by fires, wind, or other catastrophic factors to extract reliable climatic information from tree rings. Having said this, in some areas such as the Mediterranean and Western Europe there are no trees that can truly be considered free from the influence of man or fire or both. In such cases, special care must be made to remove as best as possible these non-climatic effects. Chapter 3 discusses some methods of removing such non-climatic noise.

A quite different stand selection strategy may be used for dendroecological studies. Here, stands are selected that are likely to be influenced by specific factors, be they natural or man-made. Examples are forest fires, insect defoliations, and pollution.

2.1.6. Selection of trees

There are two ways to select sample trees. First, they may be randomly chosen from small (up to 0.5–1.0 ha) sample plots that are usually set up for forestry purposes. Though maximum homogeneity of the conditions in each plot is maintained, it is not always possible to find a sufficient number of old trees suitable for dendroclimatic studies. This procedure is more frequently used for studies of non-climatic factors where randomness in the statistical sampling design may be crucial to the success of the study.

The principles of tree selection for dating and reconstructing non-climatic factors are quite different from those used for selecting trees in dendroclimatic studies. For example, timing of a snow avalanche is primarily based on the dating of mechanically damaged, dead, or leaning trees. Each tree should be described in detail and numbered in some cases so that it will be possible to extend the chronology by future sampling. Brubaker and Greene (1979) and Swetnam *et al.* (1985) chose replicated samples from host and non-host species to evaluate differences in growth associated with the effects of periodic insect attacks on trees. For an investigation of pollution impacts on the forest, different principles of tree selection must also be used.

In the second main sampling strategy, trees are selected from the same site type but from a considerably greater area, the size depending on the homogeneity of the region and the aims of the study. The sampling site should be climatically and geobotanically homogeneous. In this case, it is possible to select a sufficient number of old trees to obtain a chronology of maximum duration. This method is mainly used for dendroclimatic studies. To obtain a mean tree-ring chronology, 20–30 trees are usually used. In regions and sites where tree growth depends very much on one or another limiting factor, a reliable chronology may be constructed using five to seven trees.

For densitometric studies, two cores from at least 12 trees are usually sufficient. For ring-width analysis, a sample of two cores from each of 20 trees is recommended. Studies on individual features such as frequency of wounding or abrupt growth changes require samples from more than 20 trees. If circuit uniformity of the ring widths within a tree is very high compared with the differences in annual growth among trees, then single core samples of more trees are preferable. In extreme growth conditions, for example, at the upper distribution limit of scattered trees with flaglike crowns and eccentric annual rings, measurement and dating of rings are possible only on a single radius (from the lee side of the trunk) where annual ring widths are widest. Dead or fallen trees may be sampled from the upper or middle parts of the trunk as the peripheral rings are very narrow at the base of the trunk.

Dominant trees provide the most reliable climatic information and reflect growth dynamics of the whole stand with more precision (Dmitrieva, 1959; Komin, 1970a). Trees with a relatively sparse crown, massive and irregularly tapering trunk, few but heavy branches, and a general unsymmetric appearance are usually the oldest with the strongest year-to-year ring-width variability, which is associated with a strong climatic response (Fritts, 1976). As peripheral rings in the oldest dying trees are usually very narrow, with slight variation in width, trees of different ages should be used to get sensitive and homogeneous chronologies. Using uneven-aged tree specimens may assist cross-dating of the oldest trees (Shiyatov, 1986).

2.1.7. Sampling a single tree

Growth varies within an individual tree. This variability is greatest at the base of the stem and smallest in the crown section. To obtain the longest possible ring sequences with a minimum of individual variability, samples are taken at breast height. Where stem disks are available, it is possible to exclude all the irregularities (compression wood, tension wood, abrupt or localized changes in ring width, and wound tissue). However, samples are usually obtained with an increment borer. With two cores per tree, a large part of the individual variability can be eliminated through averaging.

For our own studies we apply the following criteria for sampling:

- Avoid sampling in the vicinity of a wound.
- Avoid sampling in the vicinity of reaction wood.
- Avoid buttresses and the upslope and downslope sides of trees growing on sloping ground (to avoid reaction wood). The absolute compass direction does not appear to be of any great importance.

However, not all irregularities are predictable. Consequently, it is best to sample a few more trees than necessary so that anomalous cores may be discarded. In studies on slope or snow movements or on the influence of wind, attention must be paid to the side of the trunk with compression wood in conifers or tension wood in broadleaves. In this case, the anomalies being avoided using the above criteria are of interest. Individual variability in the final chronology decreases with an increasing number of samples. For this reason several trees are cored on each site. In densitometric studies, variability owing to technical processing can be greatly reduced by taking cores as nearly perpendicular to the fiber orientation as possible. This requires the use of a support for the increment borer (Schweingruber, 1983). The more carefully and appropriately the sites and trees are selected, the fewer the trees that have to be sampled and thus the less the work involved.

It should be borne in mind that coring injures the tree. Even with careful work, a bore hole is left. The hole becomes sealed and grown over within a few years. In the case of conifers, treatment is seldom necessary. Broadleaves, however, react physiologically, the result being radial disk-shaped discolorations around the bore hole. Furthermore, fungal infection often follows. As a minimum preventative measure, the holes should be plugged with wax to prevent the entry of spores. Opinions on the effectiveness of this and further treatments vary, but the dendrochronologist should follow the wishes of the tree owner if in doubt.

2.1.8. Search for ancient wood

To extend tree-ring chronologies beyond the limits of old living trees, historical, archaeological, or subfossil timbers must be sought. Such wood can be found in old buildings, in works of art, and in the ground as natural and cultural remains. It is most frequently discovered in human settlements and burial places, in river, lake, and marine deposits, and in peat bogs and permafrost soils.

Based on wood from Holocene deposits, continuous tree-ring chronologies covering all or part of the last eight millennia have been constructed (Ferguson, 1970; LaMarche and Harlan, 1973; Pilcher *et al.*, 1984; Becker, 1986; Leuschner and Delorme, 1984). Ancient wood is preserved when its weathering is hindered, for example, in dry air or in waterlogged or frozen ground. In some regions with a continental climate at the upper tree line, trunk and root remains are preserved on the surface for more than 1,000 years (Ferguson, 1968; Shiyatov, 1986), and in one instance for some 45 million years (Basinger, 1984). The layered annual structure of charred wood is also well preserved.

The bulk of subfossil wood is available from alluvial deposits, and a search for it is easier as rivers wash away their banks. One should bear in mind that exact estimation of growth conditions of the past is not always possible if the wood was used for buildings or works of cultural and everyday use. Even buried wood may have traveled some distance before preservation.

2.1.9. Site recording

The importance of good site recording cannot be too strongly stressed. The data generated by a particular project may be of value to other projects not envisaged by the sampler, but only if the site information recorded is adequate. Appendix B gives examples of two site-recording sheets to suggest a desirable and a minimum standard (the minimum being based on the entry requirements for the International Tree-Ring Data Bank). In addition to factual information about the site, the record sheet should include a brief description of the site, e.g., "old pine stand with earlier pasturage, with dense undergrowth, on deep brown soil, on gentle south facing slope. Stand possibly planted." The site notes should also include the aims of the study or reason for sampling, e.g., "part of a climatological sampling network" or "study of Mayfly epidemics."

2.1.10. Preliminary assessment of samples

Every study begins with a search phase. At this stage, the optimum information should be obtained with the least effort. To that end those features of the core that are easy to identify visually are examined. These are:

- Mean ring width.
- Sensitivity (frequency of visually recognizable signatures or pointer years).
- Frequency and date of abrupt changes in ring width.
- Rot, wounds, compression wood.

The final decisions on the selection of sites are made in the course of this work.

During sample collection, the basic assumptions of the research problem may be tested by visual inspection of each core. Aberrant cores may be discarded when it is possible to detect what feature of the tree or the site caused the abnormality. However, care should be taken not to bias unintentionally the collection in a way that will invalidate later analyses. This phase of selection is often ignored once the samples reach the laboratory, with the outcome that good results may be obscured and the amount of work increased. Many statistical misfits can be recognized as such in the field. Samples collected previously may be unsuitable for certain studies if they were collected with different aims in mind. Samples from rigid networks may also be unsuitable, as the sites may not be homogeneous and may fail to meet the criteria for a valid ecological study.

2.1.11. Examples of sampling strategies

Dendrochronology can be applied to a wide spectrum of fields, and the range of sampling strategies is correspondingly broad. The basic principles are illustrated by the following three examples.

Example 1: Dendroclimatology Using Continental Networks

Fritts (1965), Kutzbach and Guetter (1980), and LaMarche *et al.* (1982) have shown how ring-width chronologies from ecologically different sites in the western USA and the Southern Hemisphere can be analyzed statistically to obtain reconstructions of the climate for given areas and years.

Selection of sites and trees. By selecting trees growing at their altitudinal, elevational, and latitudinal range limits, it is possible to maximize particular ecological factors in the tree rings. Trees growing near the northern or upper timberlines contain most information on temperature, while those growing near the lower-elevation, arid timberline provide more information on precipitation (see *Figure 2.1*).

The density of sites within a network can be increased within a study area by including local extreme sites. In deciduous forests, for instance, sites in hollows affected by cold air drainage may be climatically more sensitive than those in the surrounding normal sites; at the upper timberline in arid areas only those trees growing on north-facing slopes with deep soils contain worthwhile information on temperature. In every case, phytosociological findings indicate the special features and suitability of a site. Through strict application of this ecological principle of selection, it is possible to eliminate diffuse ecological effects, particularly those that are not limiting every year, and to emphasize those that are most commonly limiting each year.

Methods. Where applicable, densitometry is one of the most suitable methods for the reconstruction of summer temperatures in the Northern Hemisphere. Determination of maximum density allows year-by-year reconstruction for large areas. Additional information from ring widths may also be included in some cases. For the reconstruction of precipitation, ring width is often used (Fritts, 1976; Fritts *et al.*, 1979; Kienast, 1985). Most hardwoods, Araucariaceae, certain Cupressaceae, and five-needled pines are less suitable for densitometric analysis.

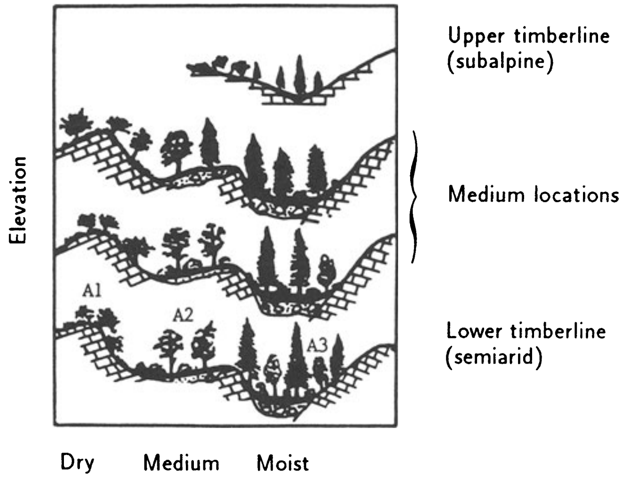

Figure 2.1. By selecting trees growing at their altitudinal and latitudinal range limits, it is possible to maximize particular ecological factors in the tree rings. Trees growing near the northern or upper timberlines contain most information on temperature, while those growing near the lower-elevation, arid timberline provide more information on precipitation.

Example 2: Dendroecology

The aim of dendroecology is the determination of the year-by-year interplay of relationships among climate, site conditions, and tree growth to assess exogenous and endogenous factors that influence the growth of a plant community.

Selection of sites, species, and trees. Definition of the research program is made on the basis of geobotanical, climatological, topographical, and geological characteristics assessed from maps, aerial photographs, and field inspections.

For investigations of changes of interaction between factors, such as climate and plant-community reactions in the Soviet Union, the profile method was used (Bitvinskas, 1978b; Lovelius, 1979). In one example of a north–south profile, 41 study areas (2,692 trees) were chosen for sampling in typical parts of Kolapechora, Valdai–Onega, Baltic–Belorussian subprovinces, North European taiga province, Polessje subprovince as well as in the Carpathian subprovince of the Central European province (see *Figure 2.2*). Such studies enabled a distinction to be made between differences in climate and plant community interactions. For example, it is possible to find small vegetation zones within an area that are distinct and may be similar to the plant communities many hundreds of kilometers away. Hence, to assess the biological productivity, typical sites of each region and subprovince should be selected. For the identification of typical sites in terms of geobotanical site characteristics for dendrochronological studies, local geobotanical or forest-site classifications can be used. The selection of typical trees can be made according to the descriptions above.

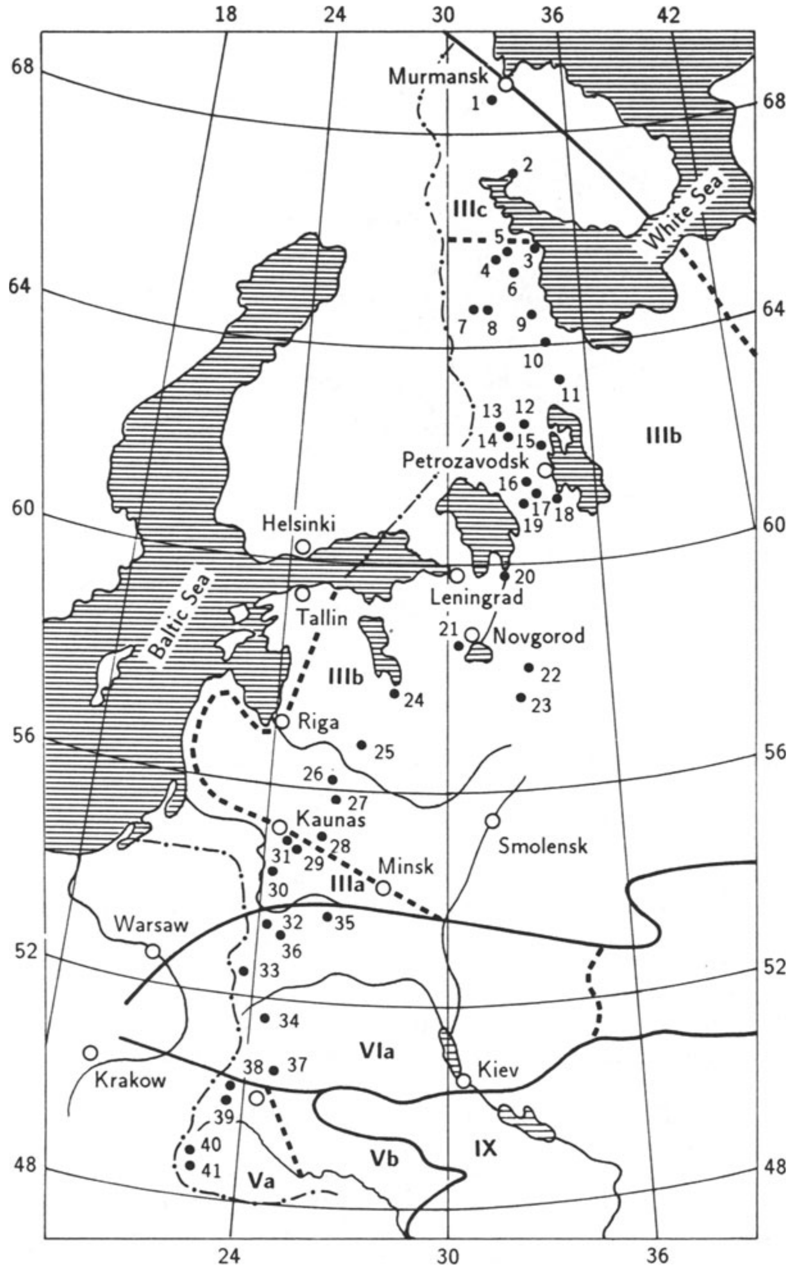

Figure 2.2. A north–south profile in which 41 study areas (2,692 trees) were chosen for sampling in typical parts of Kolapechora, Valdai–Onega, Baltic–Belorussian subprovinces, North European taiga province, Polessje subprovince as well as in the Carpathian subprovince of the Central European province.

Methods. Simple methods should be used at first, e.g., registration of pointer years as well as long-term and abrupt growth changes (see Chapter 5). Measurements of ring width and density can naturally also be used. This involves considerably more work, but may be more appropriate for some species.

Example 3: Pollution Research

Since dendrochronology is practically the only discipline that can provide the long-term historical dimension in pollution research on forested ecosystems, the range of applications is very wide and, in almost every case, politically important. The following problem areas can be investigated:

- Local: damage to trees and forests in the immediate vicinity of an emission source (Thompson, 1981; Fox *et al.*, 1986). Damage to and the state of health of trees in cities (Joos, 1987).
- Regional/national: comparison of the state of health of forests in areas with different population densities or exposure to different anthropogenic hazards (McLaughlin *et al.*, 1987).
- Continental/hemispheric: investigation of tree growth in relation to climatic and environmental changes caused by CO_2, acid rain, nitrogen oxides, and other very large-scale mechanisms (Hughes, 1987b).

Selection of sites and trees. Vinš and Markva (1972), Stravinskiene (1981), Thompson (1981), and Fox *et al.* (1986) obtained replicate samples of trees at increasing distances from a pollution source to study the relative growth effects attributed to proximity of pollution sources. Stands free of pollution were sampled for controls. Selection of trees of different species but with the same social status (16–20 per species and site) on homogeneous sites is desirable. Selection is based primarily on ecological gradients: dry to moist, acidic to basic, low to high elevation, outside and inside inversion layers, close to or far from suspected emission sources. Loss of radial increment owing to pollution as expressed in dendrochronological indices seems to be enough for increment calculations in forestry. In such studies, it may be necessary to compare a large number of trees and sites. Several hundred trees may not be sufficient, depending on the strength of the suspected pollution signal being investigated.

As the spatial scale progresses from the local effects of high pollution to chronic effects of regional background levels of pollution, the required number of sites and sampled trees may increase enormously. This is because of the lower level of impact that chronic, low-level pollution may have on trees. However, additional sampling design problems occur because regional studies may cross through vegetation, climate, and soil gradients that could confound the subsequent analyses. McLaughlin *et al.* (1987) provide an example of this kind of study.

With regard to continental and hemispheric studies, no sampling design has been satisfactorily formulated. However, the first attempts at hemispheric-scale investigations are in progress using existing tree-ring data collected for other purposes (Hughes, 1987b).

Method. When very large sample numbers are required, the use of the simplest methods may be necessary. The classic skeleton plot or the shortened version using pointer years may be used to record the onset, duration, and intensity of abrupt growth changes (see Chapter 5). At a higher level of analysis the influence of climate on ring width of trees in polluted areas may be factored out using the ring width from trees in unpolluted areas as controls (*Figure 2.3*; Thompson, 1981) or can be calculated by and removed from the tree-ring widths (Cook *et al.*, 1987; Cook, 1987a,b).

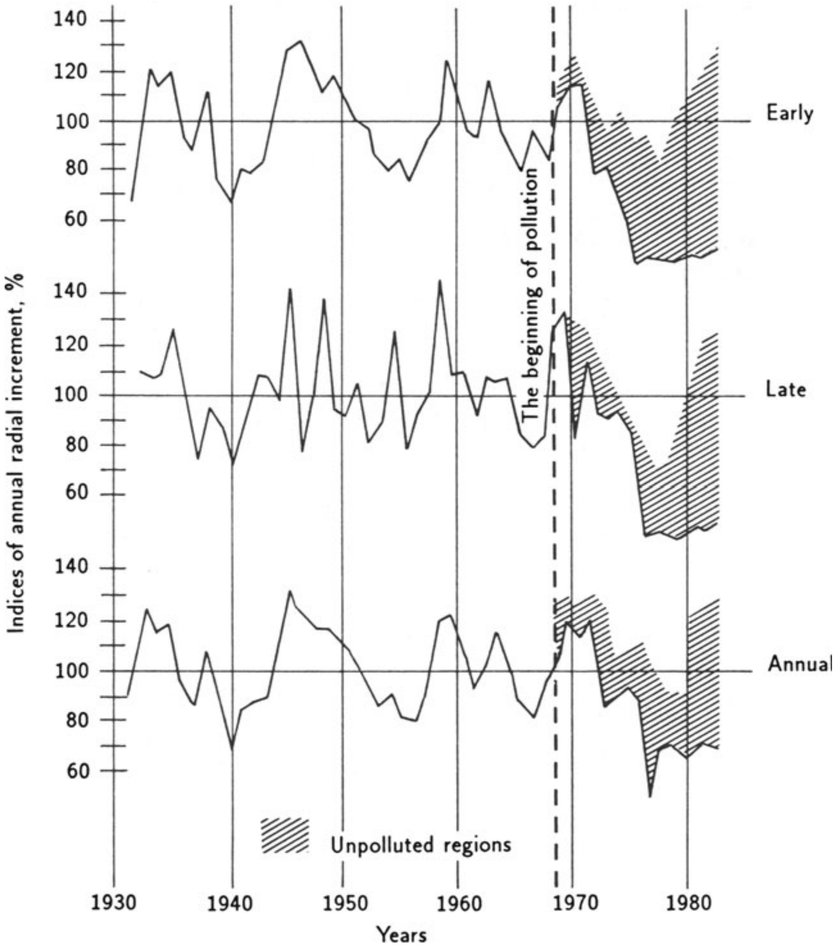

Figure 2.3. Variation of early, late, and annual ring width of *Pinus sylvestris* growing in a considerably polluted region. The hatched area is the loss of radial increment when compared with tree-ring widths from comparatively unpolluted regions.

It is difficult to understand pollution-induced growth changes because knowledge about translocation and fixation of elements in different parts of the tree is incomplete. It is known that pollution reduces cambial activity, increases K+ ion permeability, and increases the potassium residue in annual rings (Kairiukstis *et al.*, 1987b). It is not clear, however, how much time it will take before pollution causes abrupt growth changes. Regional and continental damage attributed to air pollution is more difficult to assess. The selection of sites can be the same as that of dendrochronological studies. A simple but powerful tool was introduced by Schweingruber *et al.* (1983). Severe growth reductions were recorded directly on the core or timber slice from thousands of trees from central Switzerland and the results mapped. All non-climatically caused tree-ring variations (aging, woodland management, etc.) were statistically eliminated as much as possible. All tree-ring series of a site that cross-date were then averaged, and the climatic impact was reconstructed according to the methods described in Chapter 4. The pollutant damage may then be assessed. In the case where the tree-growth baseline manifests distinct regularities (rhythmical, cyclical, etc.), dendrochronological prediction of increment damages can also be made (Kairiukstis *et al.*, 1987b,c).

2.1.12. Conclusion

The basis of every good dendrochronological study is the selection of samples according to biological–ecological criteria. The first important step in the somewhat lengthy process of dendrochronological analysis therefore takes place in the forest itself. Neither the most accurate measurements nor the most sophisticated statistical treatment can compensate for errors made here. The selection of trees, sites, and methods should primarily be made according to the aims of the study. One case may involve the use of complicated methods for the analysis of a single tree, while another may require simple observations of 5,000 trees. Dendrochronology today offers many methods, and it is important to decide which is the most appropriate for the task at hand.

2.2. Site and Sample Selection in Tropical Forests
M. Worbes

2.2.1. Introduction

Annual growth rings have been shown to occur in many tree species throughout the entire tropical zone (*Figure 2.4*; Coster, 1927, 1928; Mariaux, 1981; Worbes, 1986). Nevertheless, the idea still persists that tree growth under the "uniform tropical climate" is continuous. The growth rings frequently observed in tropical wood are often attributed to endogenous rhythms. Review articles tend to emphasize the difficulties of research on growth periodicity in tropical tree species rather than the successes achieved. Such research has generally been