Secciones extraidas del libro: Tree Rings, Basic and Applications of Dendrochronology
Fritz Hans Schweingruber, Kluber Academic Publishers. 1993

Tree-ring research and geomorphology

Dendrochronology can provide important information about the changes which have taken place on the surface of the earth. Whenever an event has an effect on trees or forests this is reflected in the structure of the shoot and the tree ring. As trees put on an annual growth increment, those changes can be dated. In many cases it is possible to determine both the intensity and the duration — be it days or thousands of years — of such occurrences.

Reaction mechanisms in trees

The tree provides a good example of an organism which has adapted well to its environment. Since this environment has been subject to considerable change in the course of evolution, the tree itself has developed into a flexible organism: its living tissues are capable of adapting to or reacting against changed conditions.

A number of parts of the tree are capable of such adaptation:

The shoots

Adventitious shoots are formed where it is necessary to change the direction and rate of growth. The shoot-system may also form roots.

The roots

Can react in the same way as the shoots and are capable of taking over the functions of the shoots.

Those tissues which are capable of division

In particular the cambium: these tissues can accelerate or retard the production of new cells; the offspring are able to form other types of cells, such as those comprising callous tissue or resin ducts.

Living cells

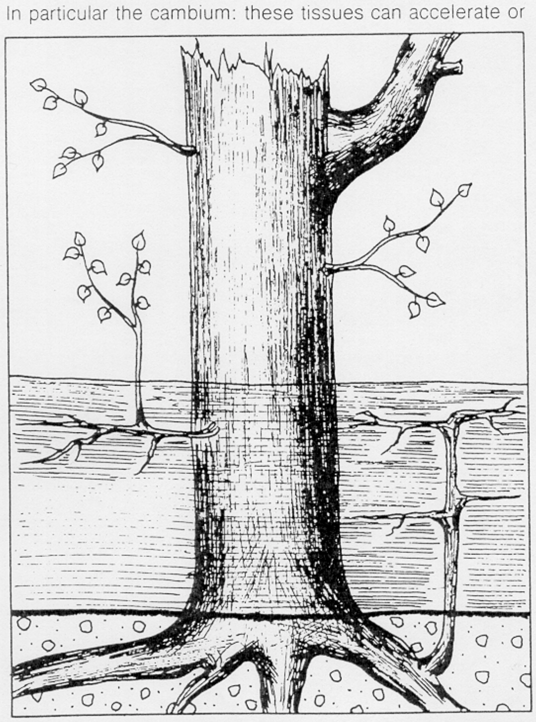
These can react to changes in the environment through slower or faster cell wall growth and through the formation of special substances, such as those which comprise heartwood and compression wood.

Dead cells

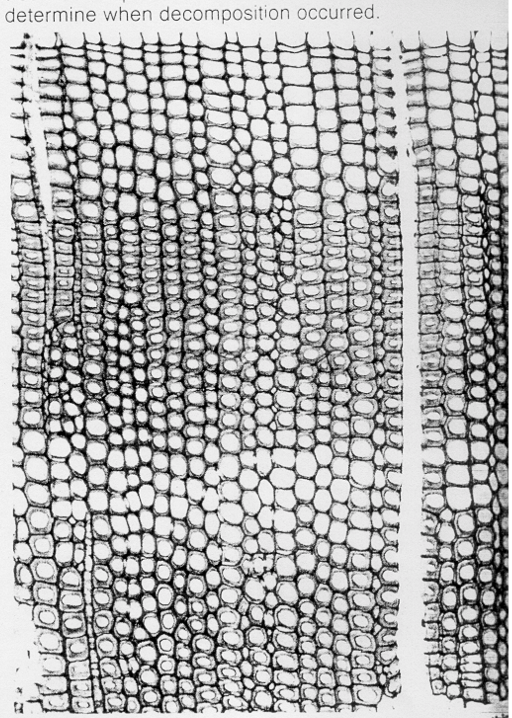
Are the source of information about how and why an organism has died. Depending on the amount of stress to which a tree is exposed, either individual cells, or the whole organ concerned or even the tree itself will die. Each of these reactions can be isolated and dated.

The way in which wood has decomposed

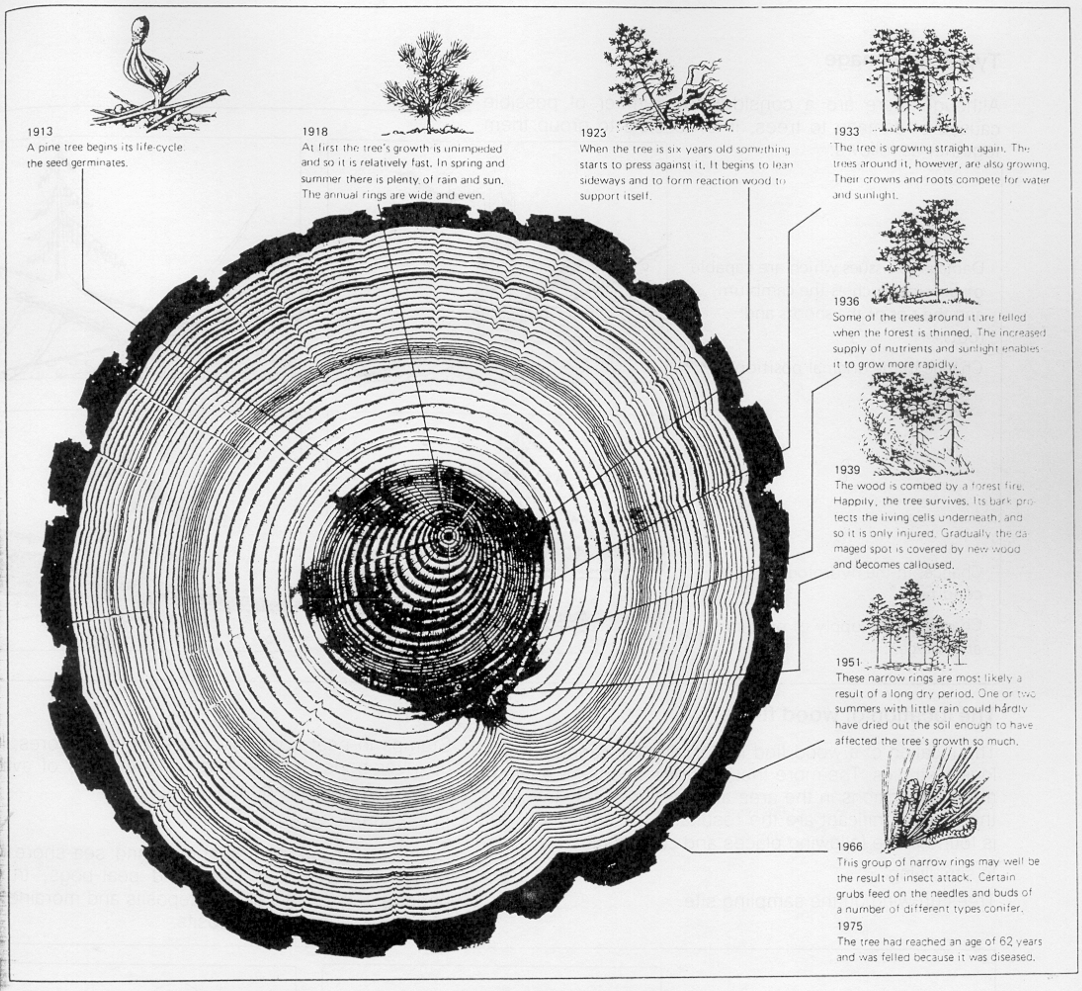
Indicates something about the conditions to which the tree was exposed after it died. It is often possible to determine when decomposition occurred.



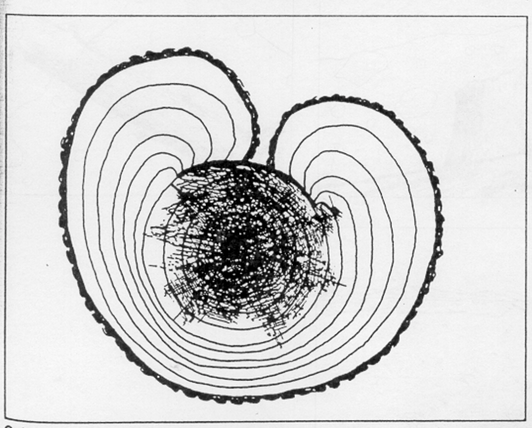
Adventitious roots and shoots formed by the cambium of the root and shoot systems.



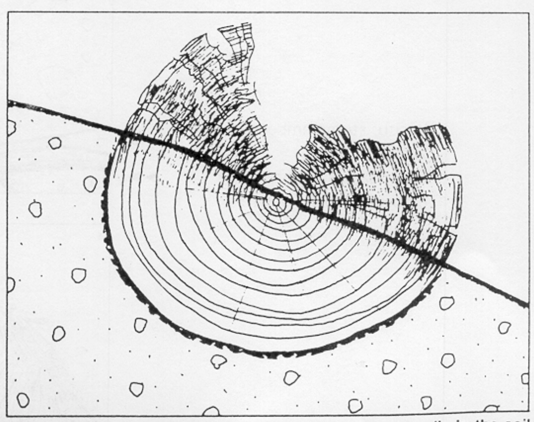
The formation of large and small cells showing the different thi ness of cell walls.



The reaction of an individual tree to different environmental factors (Wald and Umwelt).



Callousing over a part of the trunk that was damaged and had begun to rot. The year in which the tree was damaged and the infection occurred can be determined.



A trunk which is half buried. As the part which is actually in the soil has been well preserved, the year in which the tree was felled can be determined.

Types of damage

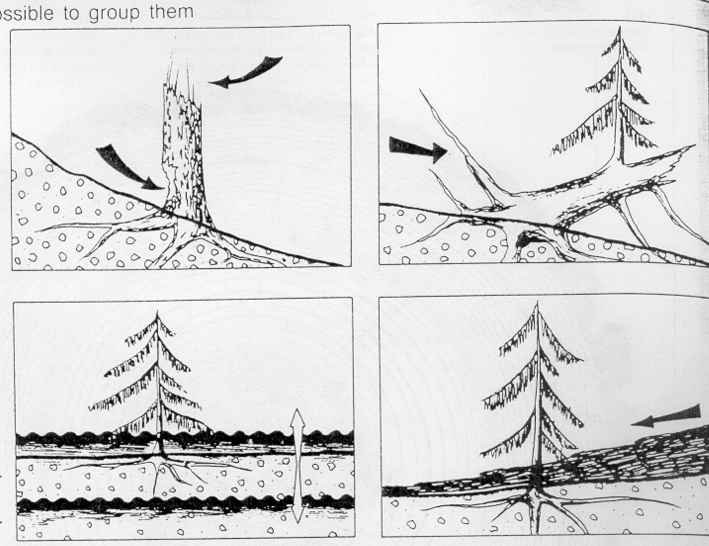
Although there are a considerable number of possible causes of damage to trees, it is possible to group them together as follows:

Damage to tissues which are capable of division, such as the cambium, and the tips of the shoots and roots. ▶

Change in the original position. ▶▶

Changes in the hydrological conditions. ▶

Change in the supply of nutrients and oxygen. ▶▶



The location of wood finds

The location of a wood find is decisive for dendrochronological studies. The more that is known about the environmental conditions in the area and the time scale involved, the more significant are the results of the analysis. Wood is found in the following places and conditions:

In situ, living

Trees growing on the sampling site.

Dead

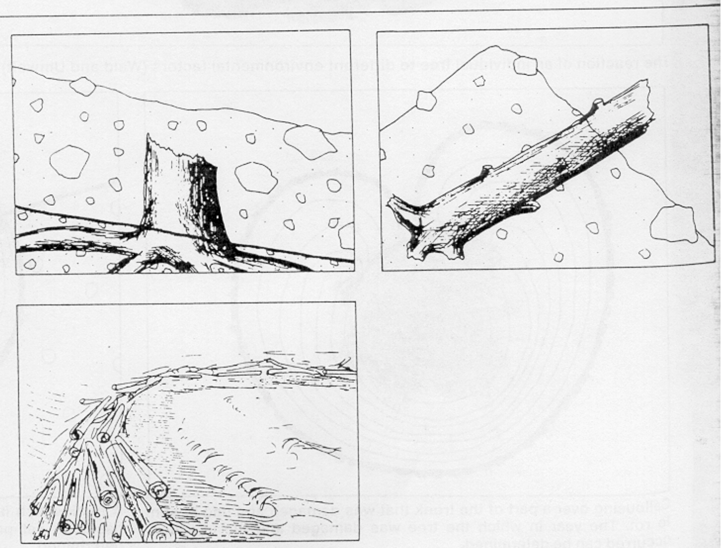
Stumps in peat-bogs and lakes, on sea-shores, in silted up river beds, on the edge of the paths of avalanches and under volcanic deposits.

In secondary locations

Driftwood on lakes, sea-shores and sea-shore terraces. Sunken driftwood in lakes and peat-bogs; trunks embedded in gravel in alluvial deposits and moraines; pieces of wood in avalanche deposits.

In situ: stump embedded in sediment. ▶

Secondary position: trunk embedded in sediment. ▶▶



Secondary position: driftwood.

Geomorphological processes which are reflected in the growth of a tree

There are a considerable number of environmental changes which may affect the growth of a tree. The change may help or hinder growth in some way, or even cause the death of the tree. The following geomorphological processes and occurrences can be traced in trees which have been exposed to them (Shroder, 1987; Timell, 1986):

Volcanic activity:
ash rain, fires, lava flows, the damming up of lakes, heavy rainfall, climatic changes

Snow movement:
avalanches, snow creep, snow break

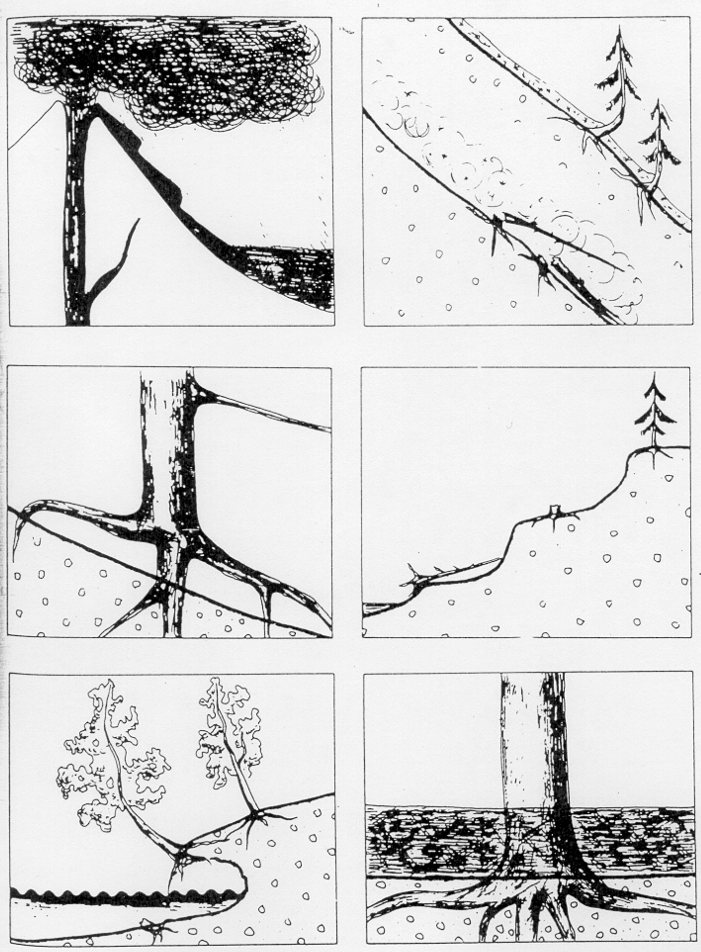
Ice movement:
the advance of glacier tongues into wooded areas, ice pressure on the shores of wooded river valleys

Earth movement:
the rise and fall of land masses, landslides, slope creep, rock falls, mudflows, erosion of the earth at root level

Hydrological changes:
waves, currents, tidal amplitude, ice movements, changes in the water-level

Aeolian processes:
loess deposition, sand dune shift

Human activity:
the clearing of wooded areas may result not only in direct damage to trees, but may also cause changes in the run-off of rivers.



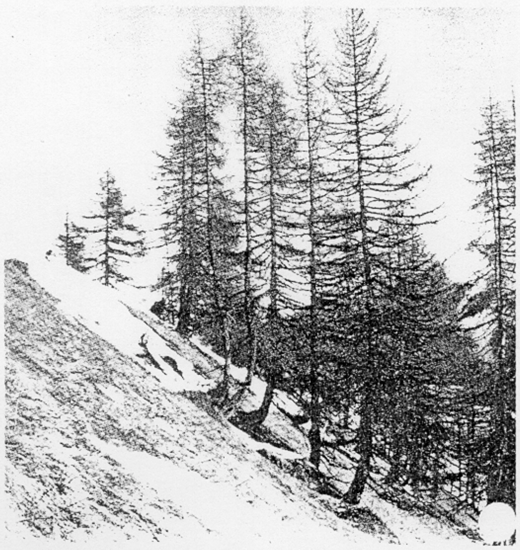
◄◄ Volcanic activity: lava, ash rain.
◄ Snow: snow-creep, avalanches.

◄◄ Erosion: washing away of the surface soil.
◄ Rise and fall of land masses, trunks on sea-shore terraces.

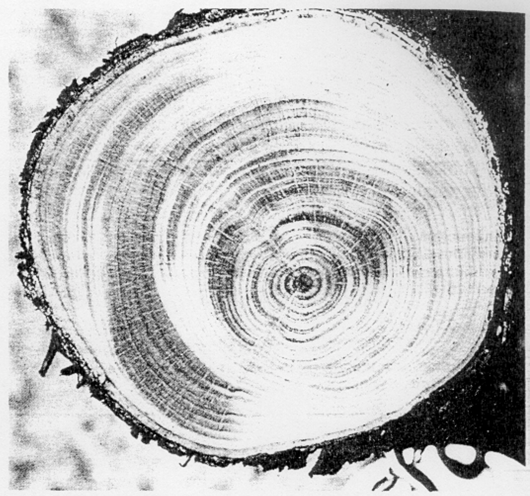
◄◄ Erosion: undermining of river banks.
◄ Accumulation: covering of existing surfaces.

Earth and slope movements take place all over the world, whether they be as landslides, slope creep or as rise and fall of subsoil. In densely populated areas records usually exist about such occurrences. In unpopulated areas, however, only trees can provide information about the extent and frequency of such events. Surprisingly enough, only very few scientists have used the tree as a source of information, whether it be merely through determining the age of trees or observing the changing growth rates in annual ring sequences. In 1971 Alestalo tried to compile data about the intensity of cryogenic earth movement by observing the eccentricity of inclined trees growing on slopes bordering moors and lakes. But the most important work was carried out by Shroder (1978 and 1980) who studied the slow creep of a wooded, volcanic debris slope in Utah, U.S.A., in great detail. He took about 1000 core samples and took cross-sections from the trunks of 220 trees and recorded all the variations in tree ring sequences which could possibly be attributed to slope movement.

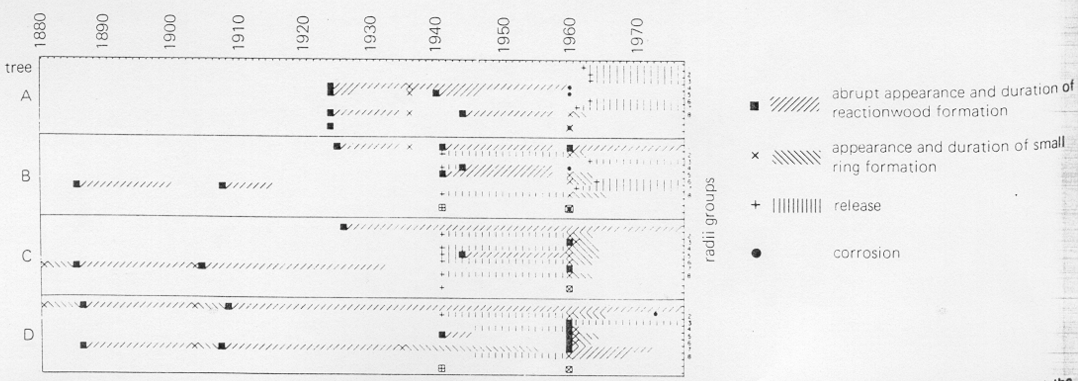
Variations along several radii were determined, dated and presented in graphical form for every tree observed and because the position of each was noted, every dated occurrence could be charted. For instance, one single rockfall, which could be dated by scars on trees, began a period of slope movement which lasted from 1905 till 1910.



Trees with bent trunks growing on an unstable, creeping slope (Lenz, 1967).



Cross-section through the base of the trunk of a pine tree growing on an unstable slope above the forest limit in the Alps.

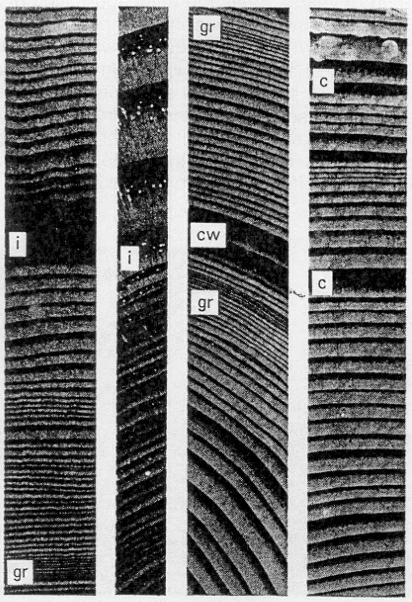


Information chart of four trees with several different radii. In the years 1922, 1938 and 1958 in particular, earth movement changed the position of trees and influenced their rate of growth over a long period. Shroder 1978.

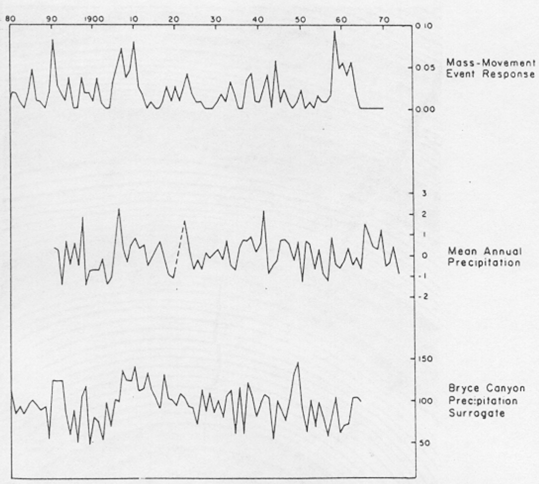
Shroder, 1978; Alestalo, 1971; Timell, 1986; Higashi et al., 1971

If the number of growth reactions are plotted on a graph in a so-called event — response curve, a relationship to climatic events such as extreme precipitation, both long and short term, can be established. The curve takes into account the number of events based on the number of trees studied.

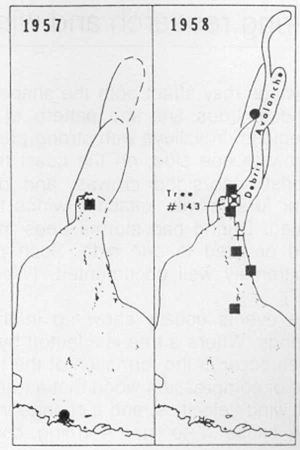
$$\text{Event-index curve (I)} = \frac{\text{Total number of events}}{\text{Number of trees studied}} \times 100$$



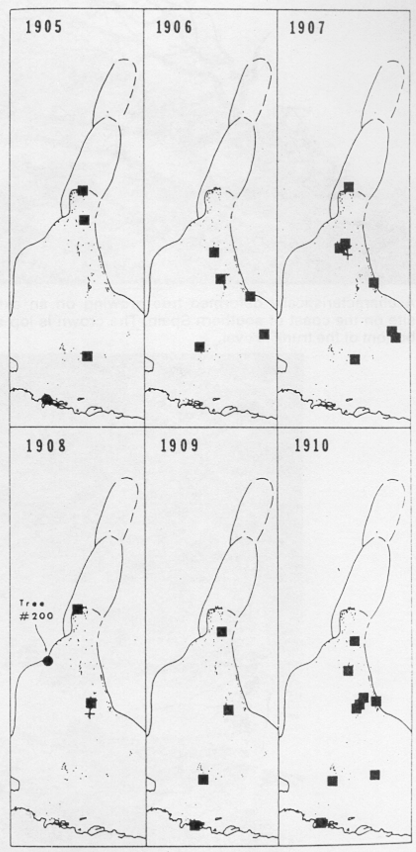
Characteristic in tree-ringsequences growing on instable slopes. cw/c: compression wood, gr: growth suppression, i: injury.



Tree-ring curve of trees growing on a debris slope in Utah. Frequent earth movements and variations in annual rings in 1905 seem to bear a relationship to the extremely high annual precipitation (Shroder, 1978).



In 1958 only one part of the debris slope moved. This is borne out by the concentrated number of events in annual ring sequences (Shroder, 1978).



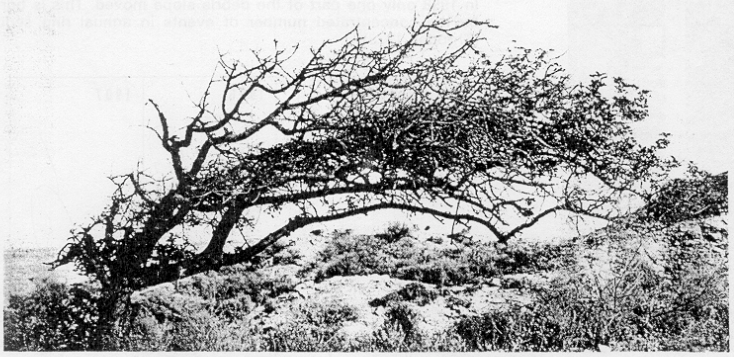
In 1905 a rockfall triggered off slope movement which continued for six years. During extremely wet periods tree-ring events are distributed quite regularly over the whole area (Shroder, 1978).

Tree-ring research and wind

Strong winds may affect both the shape and appearance of individual trees and the pattern of vegetation over whole regions. In valleys with strong prevailing winds the trees grow to one side, on the coast the trees develop characteristic lop-sided crowns, and on the edges of woods or forests with katabatic winds the trees tend to be stunted. During bad storms trees may be damaged, uprooted or tilted to one side. Such phenomena have been extremely well documented. (Wendel, Hewson *et al.*, 1977).

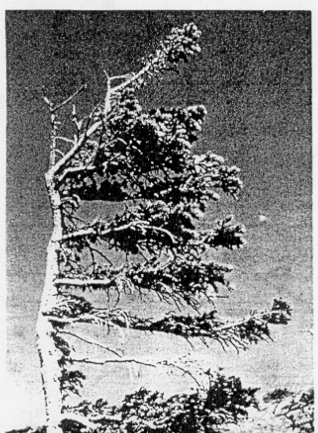
These events usually show up in the trunk and the annual rings. Where a tree is affected by prevailing winds anomalies occur in the formation of the trunk; the amount and type of compression wood that a tree develops reflect differing wind velocities, and a change in the angle of the tree will cause it to start forming compression wood zones, a process which will continue over a long period of time.

This sort of biological signal assumes particular importance in times when the possibility of harnessing wind power is being considered, because it is rare for meteorologists to record wind speeds in the same place over a period of years. Today the main application of annual ring research in this area lies in attempting to trace the relationship between the effect of wind on trees and its climatological aspects. As is shown in more detail below, the wind may have a direct effect on a tree or it may affect its growth in some indirect way, through the movement of slopes or snow for example, or through changes in light conditions or in the length of the vegetation period or through the effect of salt-spray in coastal areas.

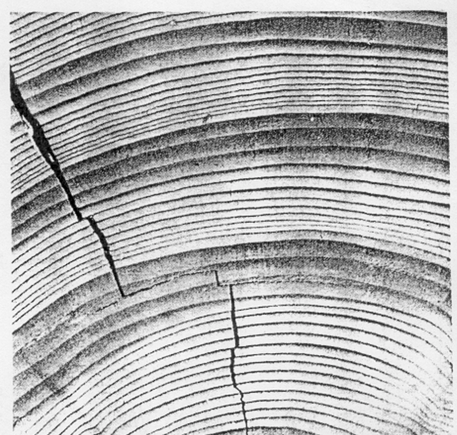


A characteristically deformed tree growing on an extremely windy site on the coast of southern Spain. The crown is lop-sided, and the bottom of the trunk is oval.

Poplars in a river valley, growing at an angle.



***Picea engelmannii* on the upper timberline in Colorado. The crown has been deformed by the wind.**



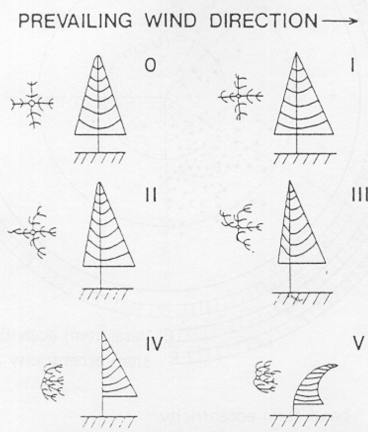
Wind-stressed trees commonly exhibit sudden changes in the tree ring width, or the formation of compression wood.

Wendel-Hewson et al., 1977; Wade and Hewson, 1980; Timell, 1986

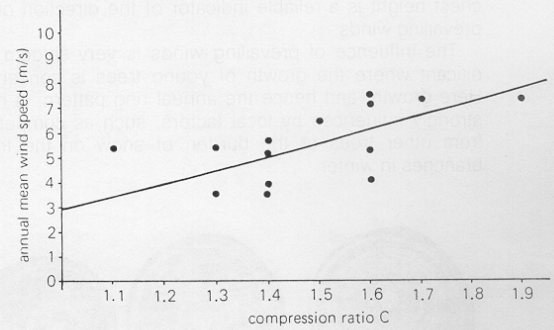
The relationship to wind velocity

There is a direct relationship between the annual wind velocity on the one hand and the reaction and shape of the tree on the other. Changes in the wind speed can be seen in the variation, from year to year, in the proportion of compression wood: such changes can be expressed in terms of the compression ratio.

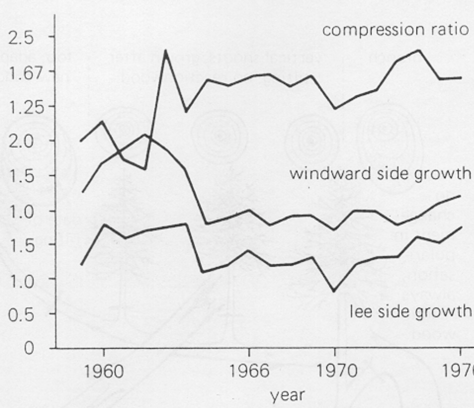
This area has received relatively little attention from dendrochronologists: neither the reaction of particular species to wind-related phenomena nor the response of the tree to an increase in wind speed have been thoroughly investigated.



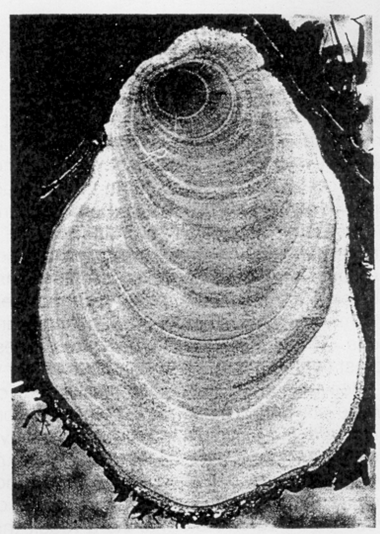
The classification of crown shapes in conifers. Trees with regular crowns have not been affected by wind (0). With increasing wind speed the crowns become correspondingly lopsided, the extremes being flag (IV) and dwarf forms. This classification is generally referred to as the Griggs—Putnam index (Wade *et al.*, 1979).



By plotting the crown shapes of a number of different trees against annual mean wind speed it is possible to illustrate the close relationship between meteorological factors and biological reactions (Wade *et al.*, 1979).



Anomalous growth in trees affected by wind can be expressed as an annual compression ratio. This is obtained by dividing the tree ring widths for the leeward side by those for the windward side. The annual wind stress can thus be clearly seen (Wade *et al.*, 1977).



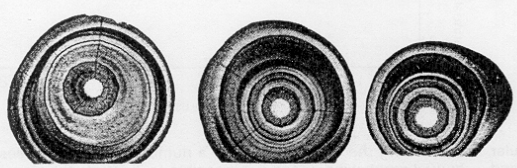
A section through a trunk showing strong asymmetry, taken from a tree in an exposed stand of dwarf trees. Conifers form larger and thicker-walled cambial cells on the leeward than they do on the windward side. The cambium on the windward side of the trunk may die off completely, with the result that the tree grows only on one side.

The effect of wind direction on the tree

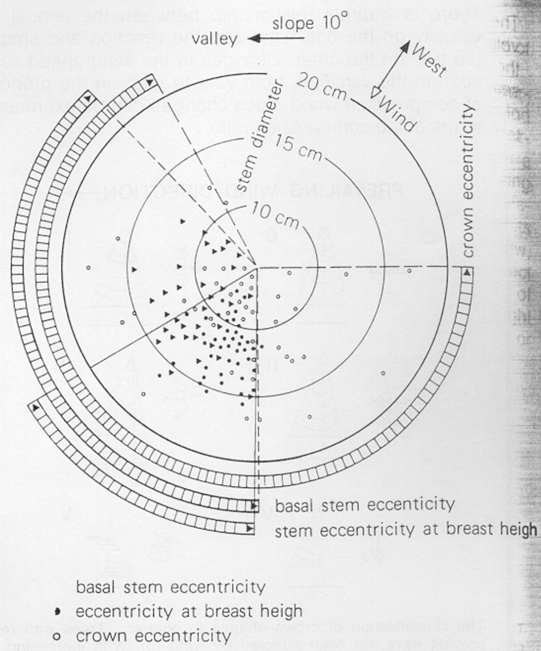
In very exposed areas the direction of the prevailing winds can be clearly seen in the shape that the crowns of the trees take on. There are a number of crown shapes which are characteristically caused by particular types of wind: the flag-shape crown, with branches on only one side, or those of the knee-high dwarf trees. Not all species react in the same way to the same influences, however.

All stunted or dwarf trees have eccentrically-formed trunks. A study of a closed 90-year-old Lodgepole pine stand (*Pinus contorta*) revealed that trunk eccentricity at chest height is a reliable indicator of the direction of the prevailing winds.

The influence of prevailing winds is very seldom significant where the growth of young trees is concerned. Here growth, and hence the annual ring pattern, is more strongly influenced by local factors, such as competition from other trees or the burden of snow on the tree's branches in winter.



Picea abies **trunks: growth is eccentric and compression wood is formed all round the trunks and on one side of them as a result of the trees being subjected to strong winds when they were young.**

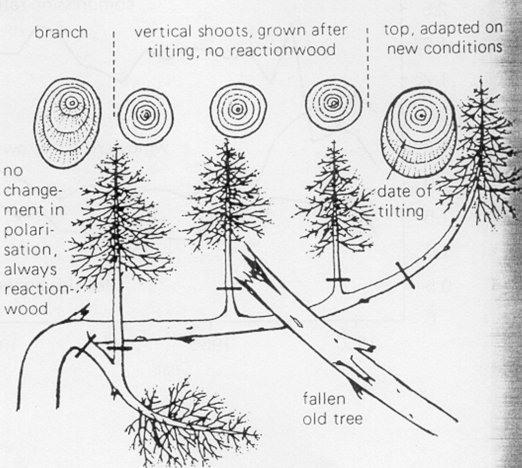


Abnormalities in crowns schape, stem eccentricity at chest-height and in ground level in a 90 year old Lodgepole pine stand (*Pinus contorta*) in the very exposed Front Range area, Colorado. The results from the stem eccentricity at chest-height are the most reliable.

The effect of extreme wind conditions on the tree

Heavy storms or other extreme conditions may upset the equilibrium of an individual tree for a short time. Here the tree reacts by forming reaction wood over a period of one or two years. Trees which have been pushed sideways or bent over in some way in a storm react to the new conditions in various ways: there is a change in direction of growth in the crown, branches produce vertical shoots and tension (deciduous) compression wood (coniferous) are formed in the trunk. In woods or forests which are not subject to forestry management the frequency with which storms occur can be ascertained by dating these reactions. The rate of decomposition of trees lying on the forest floor can be determined in the same way.

Heavy storms often affect ecological conditions in a whole stand of trees. Where the crown or the roots are damaged the tree reacts by forming very narrow rings. Trees which have been tilted sideways put on a spurt of very rapid growth and form pressure wood. Space and consequently better light conditions are created for the trees which survive storms. As a result their growth rate increases sharply. Quite often the age structure and the distribution of species in a stand also undergo a change. This sort of effect on woodlands has received relatively little attention from dendrochronologists.



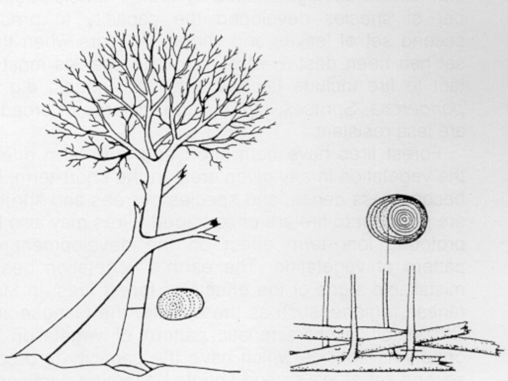
A damaged fir showing cross-sections through individual shoots. When sections are taken through the main shoots it is possible to determine when the tree started to grow lop-sidedly by looking at the formation of the compression wood. From the age of the upright shoots the length of time that the tree needed to regenerate can be determined.

Holtmeier, 1971

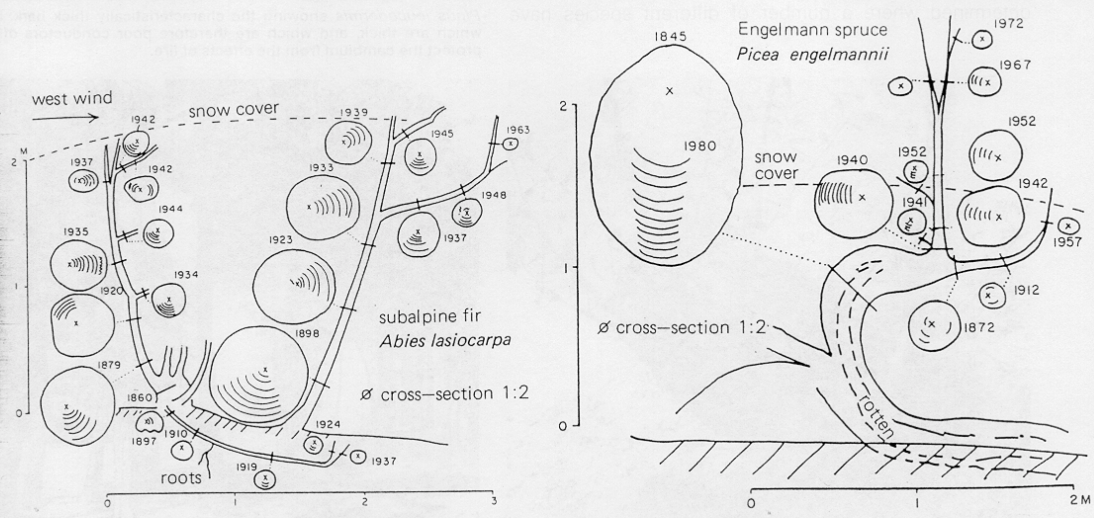
The effect of wind on environmental conditions

The extent to which wind influences the tree's habitat can be seen especially clearly in subalpine areas with stands of dwarf or stunted trees (Holtmeier, 1981). Here the growth of the tree is affected both by changes in wind speed and direction and by different amounts of snow. Shoots which are protected by a layer of snow will survive the winter but will nonetheless have a shorter vegetation period, depending on the time at which the buds appear. Shoots which are above the snow cover can benefit from warm winter days but are at the same time exposed to the various dangers associated with frost, such as frost-drought. Here the needles continue to transpire, and because the necessary replacement cannot be drawn from the frozen soil, there is a danger of their drying out.

Even relatively minor changes in the tree's growing conditions, such as the loss of a branch which had previously afforded protection, slight changes in the topography resulting from avalanches, landslides or road building, or minor climatic changes, will affect the growth of the tree. Most of these types of changes can be seen in the age structure, the growth rate and the proportion of reaction wood in different parts of the trunk. The examples given below illustrate how sensitively trees react to changes. Every single change has a direct effect on the tree, either changing the growth pattern of the tree or causing the shoots or even the trees themselves to die off. These stunted trees enjoy an extremely precarious equilibrium. Unlike trees in wooded areas in temperate zones, they have no sort of buffer to protect them from extreme climatic conditions. The fact that individual stands are able to survive over hundreds and even thousands of years is attributable solely to their capacity for vegetative regeneration through the formation of roots by the branches.



During storms older trees quite often fall onto younger ones, pushing them sideways or causing them to fall to the ground. It is possible to say when such storms occur by examining the formation of reaction wood in trees which have been affected in this way or in the branches which start to grow vertically after such damage has ocurred.



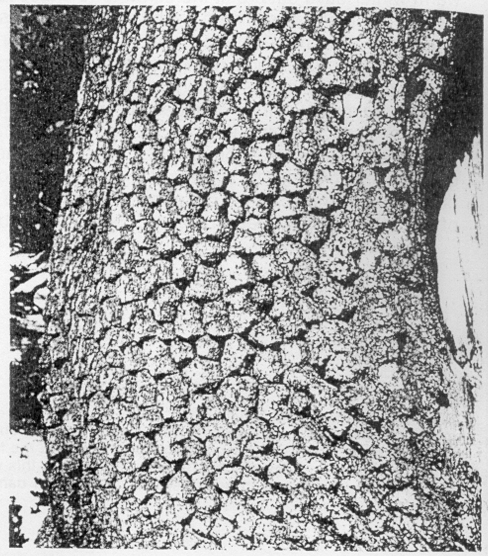
Age structure in stunted trees on exposed timberline sites with heavy snowfall. The subalpine fir (*Abies lasiocarpa*); and Engelmann spruce (*Picea engelmannii*). The growth pattern is reflected in the age of the individual shoots. Damage caused by frost-drought, avalanches or rockfalls results in abrupt changes in the annual ring width, while that caused by strong prevailing winds results in the formation of compression wood. The study of such phenomena enables a picture to be built up of local micro-climatic conditions. (Kienast and Schweingruber, 1986.)

Since time immemorial forest fires have constituted an important natural aspect of the ecosystem in many parts of the world (White, 1972). It has sometimes happened that the development of flora and fauna, and even of human cultures, has been largely determined by the occurrence of forest fires. Fires were caused naturally by lightning; later human activity led deliberately or accidentally to fires being started. In the course of time trees which are to some extent resistant to fire became dominant.

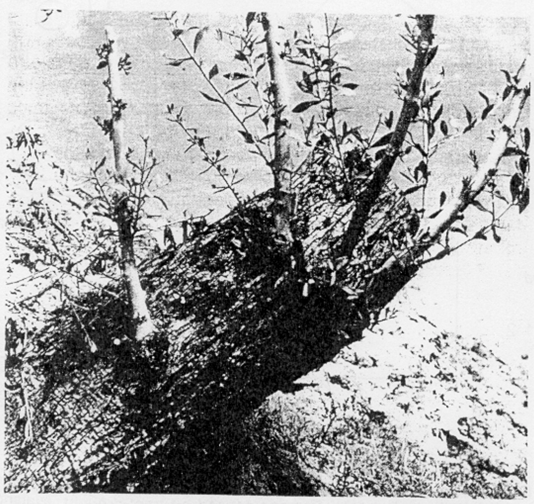
Thick bark and scales on the twigs and buds provide direct protection against the effects of fire. Wood that is rich in resin helps to prevent the biological decomposition that follows damage caused by fire. A considerable number of species developed the capacity to produce a second set of leaves and shoots in years when the first set had been destroyed by fire. The species most resistant to fire include larches and many pines, e.g. *Pinus ponderosa*. Spruces, firs and the majority of broadleaves are less resistant.

Forest fires have both short and long-term effects on the vegetation in any given area. In the short-term, stands become less dense, and species of trees and shrubs that are resistant to fire are encouraged. Fires may also have a profound long-term effect on the development of the pattern of vegetation. The earth's vegetation bears unmistakable signs of the effects of forest fires. In Mediterranean regions, such as the Maccie, the Garigue and the Chapparall, a characteristic pattern of vegetation developed with species which have the capacity to produce a second set of leaves and shoots becoming dominant. The frequent occurrences of forest fires has to a certain extent determined where a number of different species have become dominant: *Araucaria araucana* over large areas of South America and certain pine species in the west of North America.

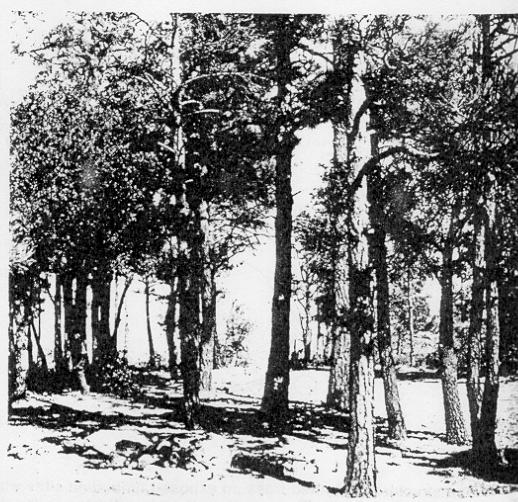
The effect of forest fires and their history has been documented (White, 1972; Alexander 1979; Stokes *et al.*, 1980).



Pinus leucodermis **showing the characteristically thick bark. Barks which are thick, and which are therefore poor conductors of heat, protect the cambium from the effects of fire.**



An olive tree which has been damaged by fire and has as a result produced shoots. It is primarily broadleaves which have the capacity for vegetative regeneration.



A sparse *Pinus ponderosa* stand in the dry zone of the south-west of the U.S.A. It is very often the young trees which are destroyed in forest fires.

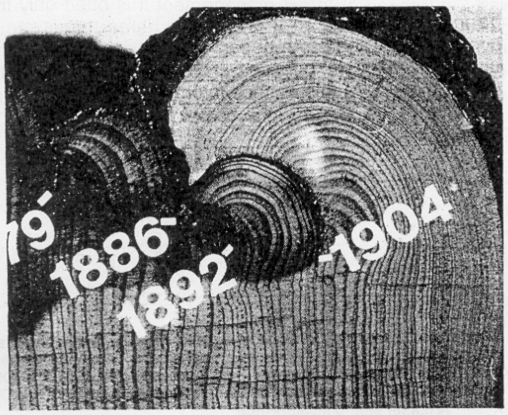
Stokes et al., 1980; Alexander, 1979

The effect of fire on the tree-ring pattern

Fire affects the tree-ring pattern in a number of different ways. According to the degree and extent of the damage to the crown — the assimilating organ — the cambium reacts in a particular way:

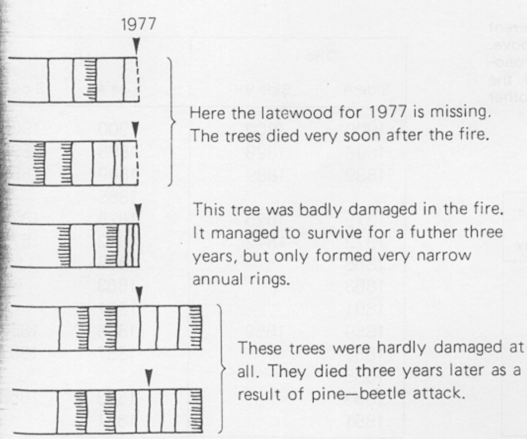
- the action of heat on the trunk causes callus tissue to be formed locally or false rings to develop;
- in conifers tangential traumatic resin canals may be formed;
- the most obvious effects of damage by fire are the scars it leaves.

Only those species with cells containing substances with a fungicidal effect such as pines (resin) and larches and Tsuga species (heartwood substances) remain free of the fungoid infection and subsequent damage that may result from fire.

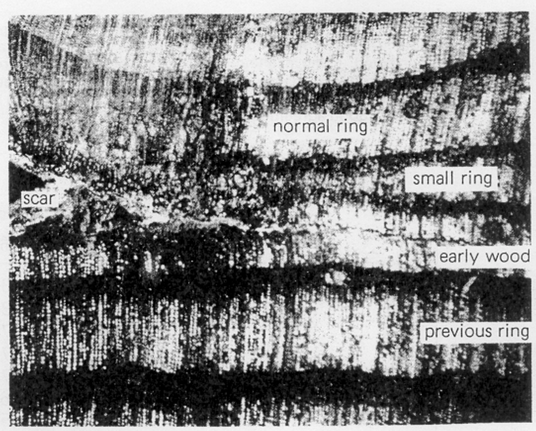


Section through the trunk of a *Pinus ponderosa*, showing three fire scars. Since 1904 the Forest Service has been successful in containing the number and extent of forest fires in the U.S.A. (Dietrich and Swetnam, 1982).

A *Pinus ponderosa* which has sustained a lot of damage by fire. This characteristic scarring is commonly referred to as a 'catface'.



Diagrams illustrating different cambial reactions to fire. This fire occurred in the summer of 1977 in an area of Ponderosa pine in Boulder, Colorado.



Photograph (taken with a macro-lens) of a cambium which has been badly damaged by fire. The fire interrupted the formation of the earlywood, which means that it must have occurred in June or thereabouts (Swetnam, unpublished).

Dietrich et al., 1983.

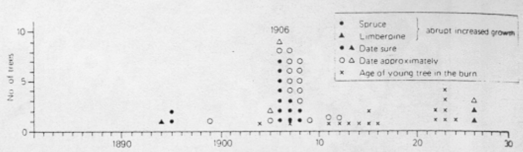
Dating forest fires

Using information obtained from pollen analysis it is possible to build up a picture of the relative frequency with which forest fires have occurred in particular centuries in the Holocene era.

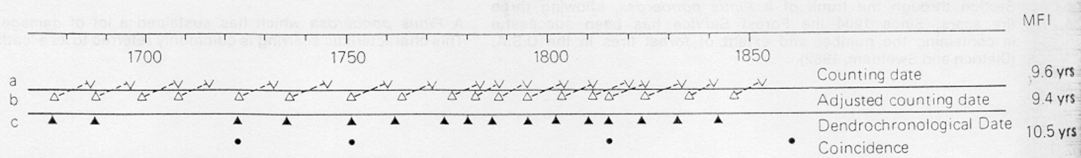
In those areas where there are relatively few fires, e.g. the temperate and boreal zones, the geographical extent of fires can still be determined after hundreds of years. The growth release which occurs in those trees which are on the edge of an area affected by a fire enables the date of the last fire in that area to be ascertained. A fire which broke out in 1905 in the Front Range near Boulder, Colorado, for example, was provisionally dated from growth release in Engelmann spruce. This dating was then confirmed by determining the age of the vigorous young growth which had occurred in these trees. All the firs (*Abies lasciocarpa*) now growing on the area affected by the fire germinated after 1905.

The most accurate picture of forest fire history can be derived by dating the fire scars on the trees. Species which are resistant to fire and to the decomposition that follows fire damage tend to be affected only at the base of the trunk. Where this occurs the cambium immediately begins to protect the injured area with callus tissue, which forms a scar. In order to determine precisely the number of fires that have occurred and when they occurred, it is necessary to examine discs from the trunks of trees, which of course involves felling the trees. It is not possible to say in which years fires broke out merely by examining and counting the rings, since — especially in trees in dry areas — some annual rings may be missing. It is therefore necessary to date the fire scars dendrochronologically, either with the help of skeleton plots, or by identifying a number of climatically-dependent pointer years. (Dietrich *et al.*, 1983).

Since some trees remain undamaged in almost any fire, an accurate picture of the incidence of fires in a given area can really be obtained only by examining both sides of a fire scar, and by looking at a good number of trees. Dates obtained for fires in the recent past should be checked against fire records kept by forestry agencies or against other contemporary documents wherever possible. The geographical spread of a fire can, where necessary, be ascertained using aerial photographs. For the purposes of forest management it is often only the average incidence of fire in a given area that is required. In such cases it is therefore generally sufficient to divide the number of years in question by the number of known fires. In the U.S.A. this method is only used for the period before 1880, i.e. for the time before there was active fire prevention.



The numbers of trees at the edge of an area affected by fire showing sudden growth release. The figures relate to a timberline site in Niwot Ridge, Boulder, Colorado. The fire occurred in 1905 and the instances of growth release concentrate on the period 1906 to 1908. (Kienast and Schweingruber, 1986.)



A comparison between dates obtained by fire-scars using different methods: (a) dates obtained by counting the tree rings; (b) as above, but corrected, using existing scar chronologies; (c) dendrochronologically produced dates using cross-dating. Only three of the sixteen dates agree in all cases. The mean fire intervals, on the other hand, show good agreement (Madany *et al.*, 1982).

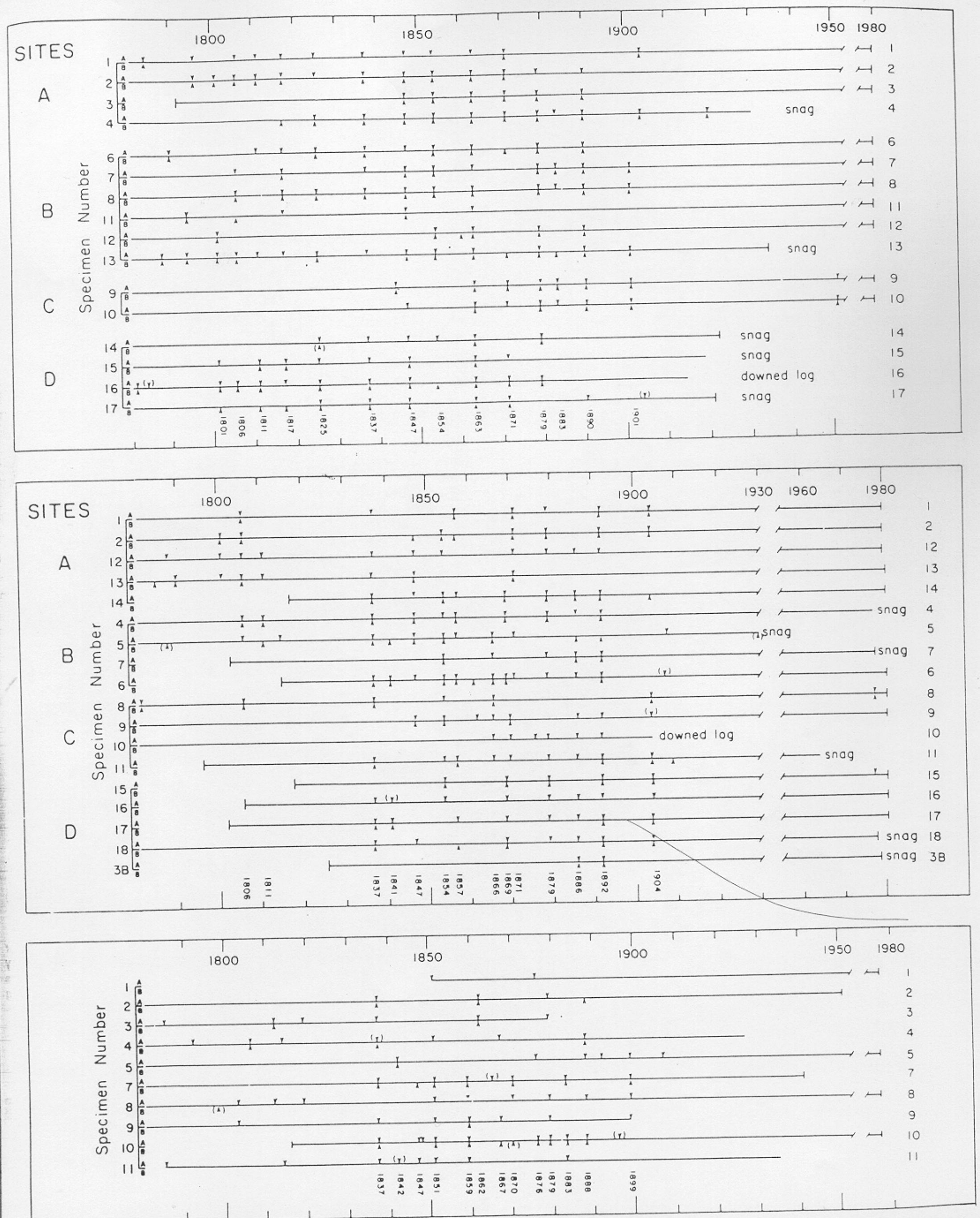
Sample tree number 13	16	17	18	Composite fire scar chronology
1871				1871
	1842			1842
1785	1785	1785	1785	1785
1757	1757		1757	1757
1752				1752
		1632		1632
		1595		1595

A comparison between the fire scars for a number of different trees from a narrowly-defined site. It is possible to determine the exact number of fires that have occurred in a particular area only by examining a large number of trees (Arno and Sneck, 1983).

Disc 1 Side A	Disc 1 Side B	Disc 2 Side A	Disc 2 Side B
1900	1900	1900	1900
1898	1898	1898	1898
1889	1889	1889	1889
		1885	
1875	1875	1875	1875
1872	1872	1872	1872
1865		1865	
1863		1863	
1861		1861	
1859	1859	1859	1859
1857		1857	1857
1855			
1853		1853	1853
1851		1851	

A comparison between the dates obtained for fire scars by dating the left and right-hand sides of catfaces. The exact number of fires that have occurred can be ascertained only by dating whole catfaces dendrochronologically (Dietrich and Swetnam, 1983).

Arno and Sneck, 1977; Madany et al., 1982; Dietrich and Swetnam, 1982; Swetnam and Dietrich, 1983

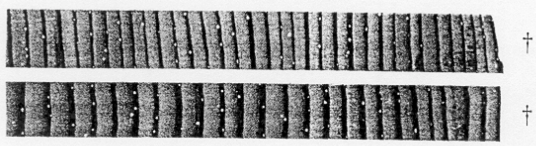


Dendrochronological dating of fire scars on Pinus ponderosa from three separate sites in the Gila Wilderness in southwestern New Mexico. In that many of the fires ranged over wide areas it is likely that this dating will yield information about precipitation in summer. The fire scar free period before 1837 corresponds to a very wet period. Since 1904 the U.S. Forest Servive has had considerable success in keeping the number and extent of fires under control (Adapted from Swetnam, Dietrich, 1983).

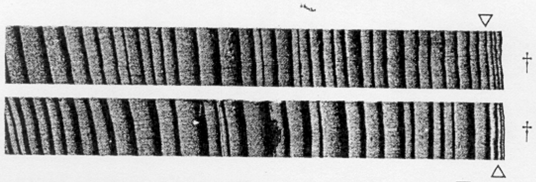
Swetnam and Dietrich, 1983.

Damage to tree-ring patterns

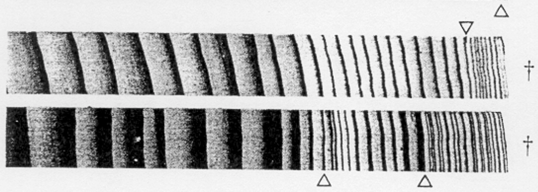
In forestry research the problem of bad infestations by insects was previously regarded primarily from the economic point of view because dying trees, reduced growth, increased risk of disease, delays in producing new shoots, all have an adverse effect on profits (Timell 1986). At the present time, thanks in some measure to annual ring research, it has been realized that 'harmful' insects play a part in the ecological cycle and therefore their activities are of considerable importance. The most valuable aspect of tree-ring research for the entomologist is that it can throw light on those insect behavior patterns which have long term effects. Insects are selected for investigation which profoundly influence the physiology of the tree, especially those which damage the light-assimilating foliage of the crown, thus impairing the process of photosynthesis. The resulting poor rate of growth can be seen clearly in the annual rings.



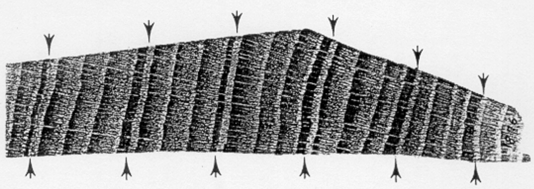
Abrupt halt in growth. There is no gradual slowing down in growth just before the tree dies. Insects which attack the cambium, e.g. bark beetle, can cause the death of a tree from one year to the next. Lodgepole pine, Bend, Oregon, 1984.



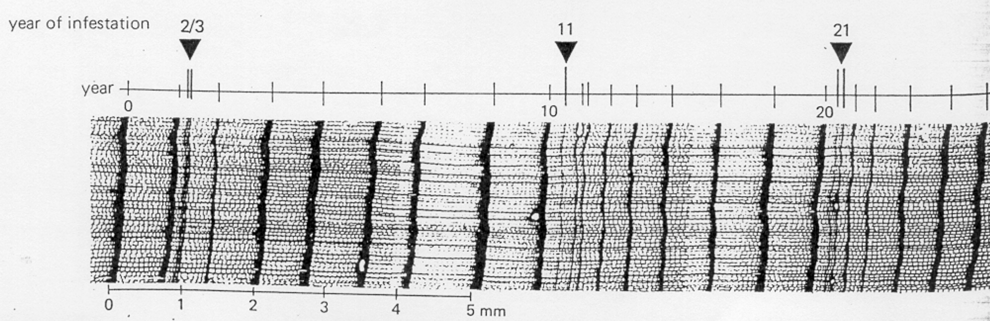
Short-term growth reduction before the tree dies. Spruce budworms caused severe damage to the crown of the tree in two to three consecutive years. The tree died in the course of the third year. Colorado blue spruce (*Picea pungens*), Nederland, Colorado. Douglas fir (*Pseudotsuga menziesii*) Nederland, Colorado, 1983.



Recurring growth reduction over a period o' several years before a tree died. Spruce budworms attacked the tree during the whole of this period. Red spruce (*Picea rubens*), Quebec, Canada. First attack — 9 years before the tree died in 1983. Douglas fir (*Pseudotsuga menziesii*), Colorado Springs. First phase of attack from about 1950 to 1955. Second phase — from about 1963.



Tree-ring series of an oak in Denmark showing periodic damage to tree rings, caused by cockchafers (Christensen, unpublished).



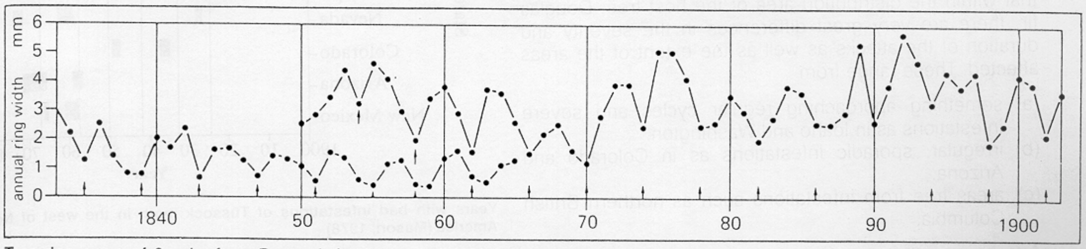
Tree-ring sequence of a larch in the Valais, Switzerland, showing periodically recurring growth disturbances as a result of regular and repeated, severe infestations of grey larch bud moth (Schweingruber, 1979).

Swetnam et al., 1985

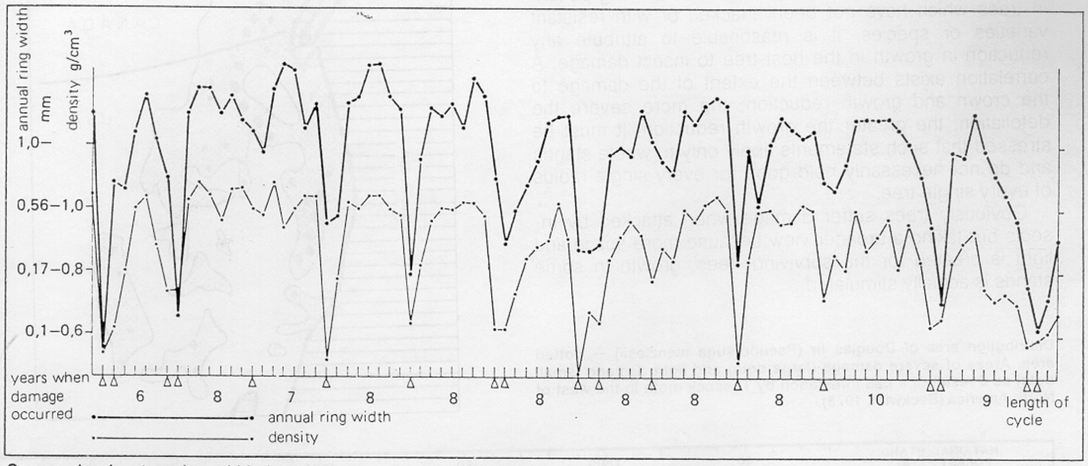
Insect damage recurring at regular intervals

Cockchafers occur in large numbers every 3 to 5 years; the larch bud moth has a cycle of between 6 and 10 years. Many tree trunks from buildings in the Valais show that since the 15th century there have been attacks on approximately 12 occasions each century. Observations of tree-ring series from the 10th century and Roman times confirm this.

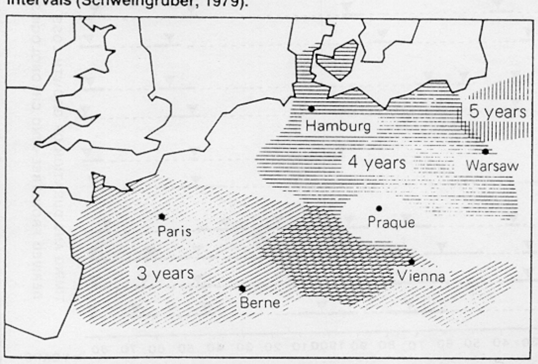
Larch bud moth does not seem to have existed in the Alps in pre-Roman times. There is no evidence of damage attributable to this insect in fossil trunks from pre-Christian times. During the last 2000 years varieties of larch seem to have evolved which are resistant to attack by larch bud moth.



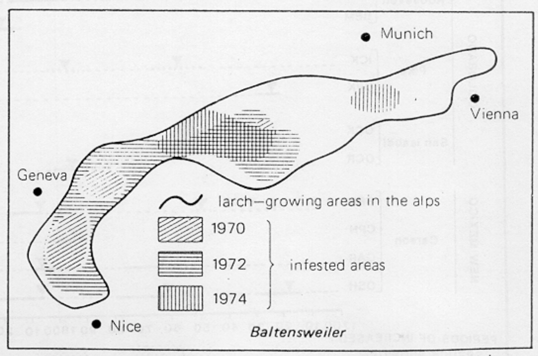
Tree-ring curve of 2 oaks from Denmark for the period 1830—1900, showing recurring damage at regular 4-year intervals (Christensen, unpublished).



Curves showing tree-ring width (top) and maximum density (bottom) of a larch in the Valais, Switzerland. Damage occurs at irregular intervals (Schweingruber, 1979).



Distribution map for cockchafers (*Melolontha melolontha* and *M. hippocastani*) with 3, 4 and 5 year development cycles. By examining tree-ring patterns of trees in these areas, it can be established if environmental conditions on the sites had varied, either as a result of climatic changes or human activity (Simplified, Schwenke 1974—1978).



Map showing the extent of damage caused by larch bud moth in various years. In 1970 it was concentrated in the western Alps, in 1974 in the east. A study of tree rings would show whether this recently discovered shift from west to east actually began hundreds of years ago (Baltensweiler 1971—1975, simplified).

Baltensweiler, 1976; Kulman, 1971; Schweingruber, 1979; Varley, 1978.

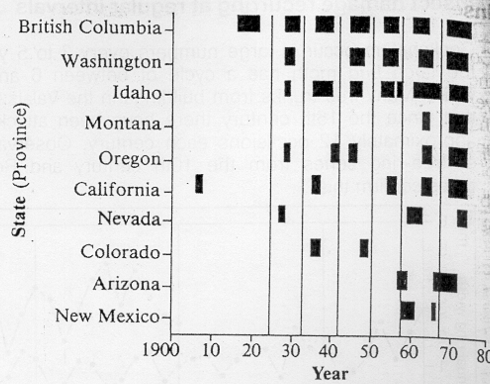
Insect damage which does not recur at regular intervals

Most of the insects which are responsible for defoliating trees do not develop in short, regular cycles — a conclusion based on studies spanning a long period of time and annual ring sequences. It is well known that individual trees and whole stands have suffered from insect damage for centuries. An important addition to our knowledge has been that, even in a bad infestation, not all the trees of one species in a given area are attacked simultaneously. Taking the example of the Tussock moth it can be shown that within the distribution area of the host tree, Douglas fir, there are very great differences in the severity and duration of the attacks as well as the extent of the areas affected. These range from

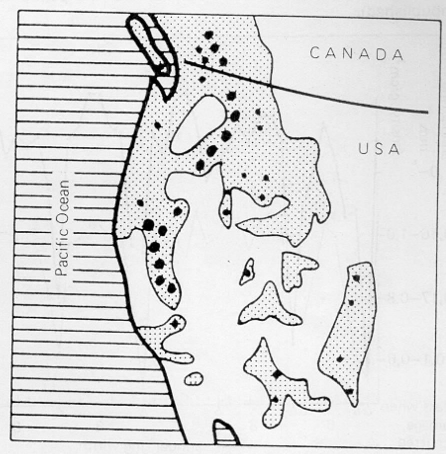
(a) something approaching regular cycles and severe infestations as in Idaho and Washington.
(b) irregular, sporadic infestations as in Colorado and Arizona.
(c) areas free from infestations such as northern British Columbia.

Attacks or outbreaks often show up in the pattern of the tree rings. If a comparison can be made with ring pattern in trees which have not been attacked or with resistant varieties or species, it is reasonable to attribute any reduction in growth in the host tree to insect damage. A correlation exists between the extent of the damage to the crown and growth reduction; the more severe the defoliation, the greater the growth reduction. It must be stressed that such statements apply only to whole stands and do not necessarily hold good for every single radius of every single tree.

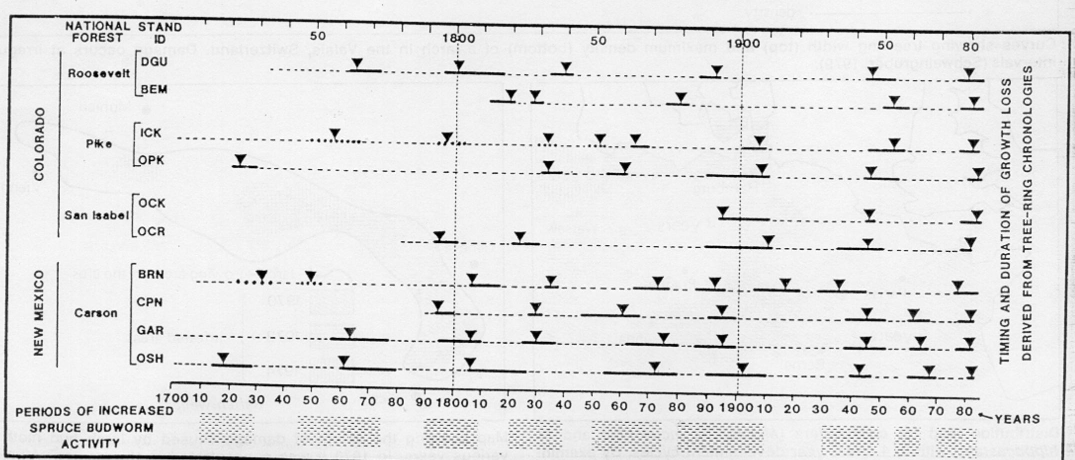
Obviously trees suffer damage when attacked by insects but taking a broader view because more space and light is created for the surviving trees, growth in some stands is actually stimulated.



Years with bad infestations of Tussock moth in the west of North America (Mason, 1978).



Distribution area of Douglas fir (Pseudotsuga menziesii) — dotted area. Areas of severe damage (large dots) and light damage (small dots) as a result of a bad infestation by Tussock moth in the west of North America (Beckwith, 1978).



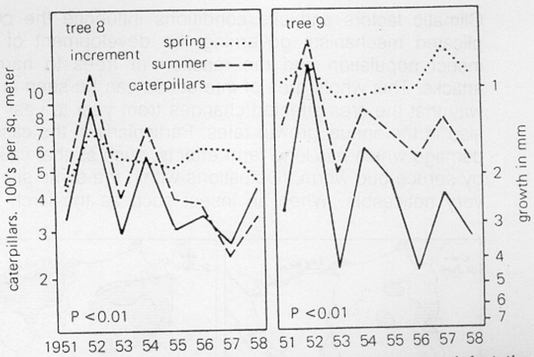
Spruce Budworm growth loss (reduction in radial increment) and duration of growth loss periods, estimated from growth differences of Douglas fir (host species) and Ponderosa pine (not host species) in some National Forests in Colorado and New Mexico. The infestations do not occur in regular intervals (Swetnam, unpublished).

Wickman, 1978, 1980; Beckwith, 1978; Mason, 1978.

The extent of damage

This has been well documented in publications on forestry-related subjects (Kulman, 1971). Damage to the crown takes many shapes and forms. These range from the shedding of just a few leaves, to whole sections of the tree being enmeshed in a web, woven by insects, to the tree being stripped completely bare of leaves. Every reduction in the light-assimilating foliage means a reduction in the amount of tissue formed by photosynthesis. This shows up in the annual rings, except when the loss is made good by drawing on reserves of stored nutrients. Losses in the crown and trunk are highly variable, even in the same tree. If only a few branches are defoliated, then the growth increments are only affected in these branches. Where a whole section of the crown is defoliated, then the annual rings, particularly at the base of the trunk are narrow whereas those in the crown and the root flange are formed normally. Only when the whole of crown is severely damaged, particularly the young leaves which are very important to the physiology of the tree, does radial growth and the production of cell tissue for the whole tree fall to a fraction of what it was previously. If there is only one isolated attack the width of the annual rings is back to normal within 3 to 4 years, the density of the latewood within 1 to 2 years.

The best way of assessing the extent of damage is to study a great many trees on one uniform site.



Relationship between the extent of damage caused by an infestation of cockchafers (number of caterpillars per m²) and the widths of earlywood and latewood in the annual rings. The latewood width correlates closely with the total area of the leaves. (Varley and Gradwell, 1962).

Pseudotsuga menziesii

Tree No.	1981		1982		1983		
	Ew	Lw	Ew	Lw	Ew	Lw	
1	●	●	○	○	•	•	dead
2	●	●	○	○	•	•	dead
3	●	●	•	•	•	•	dead
4	●	●	•	•	•	–	dead
5	●	●	•	•	•	–	dead
6	●	●	•	•	•	–	dead
7	●	•	•	•	•	–	dead
8	●	•	•	•	•	–	dead
9	●	●	•	•	–	–	dead
10	●	●	•	–	–	–	dead

Symbols for ring width
● normal
○ reduced
• heavily reduced
– missing

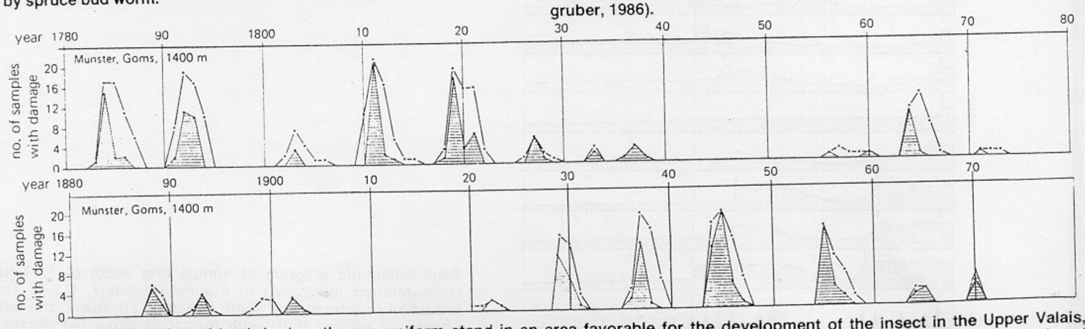
Nederland, moist site

Picea pungens

Tree No.	1978		1979		1980		1981		1982		1983		Needle-lost, %
	Ew	Lw	Ew	Lw	Ew	Lw	Ew	Lw	Ew	Lw	Ew	Lw	
1	●	●	●	●	●	●	●	●	○	○	○	○	50
2	○	○	○	○	○	○	○	○	○	○	○	○	50
3	●	●	●	●	●	●	○	○	•	•	•	•	60
4	●	●	●	●	○	○	○	○	•	•	•	•	60
5	●	●	●	●	●	●	•	•	•	•	•	•	90
6	●	●	●	●	●	●	•	•	•	•	•	•	90
7	●	●	●	●	●	○	○	○	•	•	•	–	60
8	●	●	●	●	●	●	○	•	•	•	•	–	95
9	●	●	●	○	○	○	○	○	•	•	•	–	50
10	●	●	●	○	•	•	•	•	•	•	•	–	50
11	●	●	○	○	•	•	•	•	•	•	•	–	90
12	●	●	●	●	•	•	•	•	•	•	•	–	dead
13	●	●	○	○	○	○	○	○	•	•	•	•	75

Nederland, moist site

Semi-quantitative representation of earlywood and latewood widths in Douglas fir (*Pseudotsuga menziesii*) and Blue Colorado spruce (*Picea pungens*) on a uniform site in Nederland, Colorado, infested by spruce bud worm. Spruces, were first attacked in 1978 but survived several infestations. By 1983 the crowns were certainly thin but the trees were still alive. The Douglas firs were first attacked in 1981, after the third infestation they were either dead or dying (Kienast and Schweingruber, 1986).

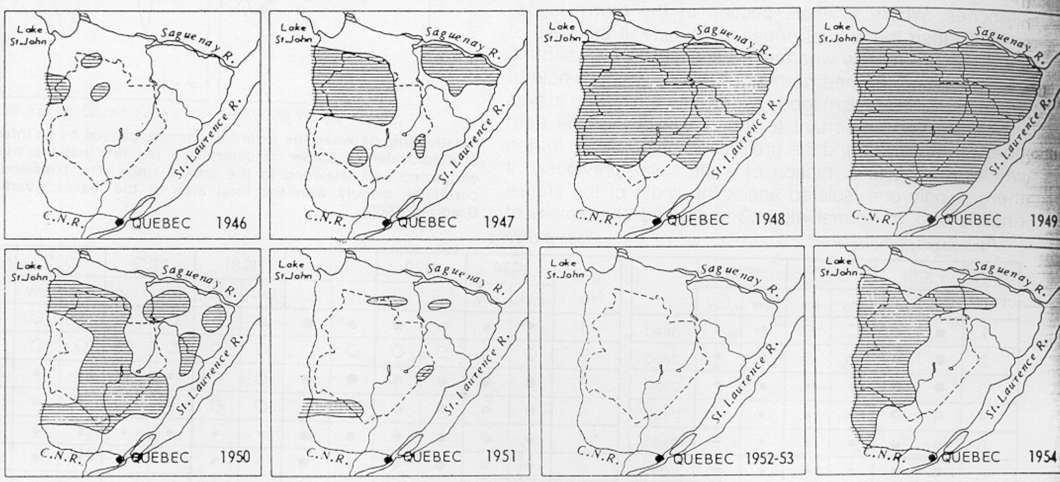


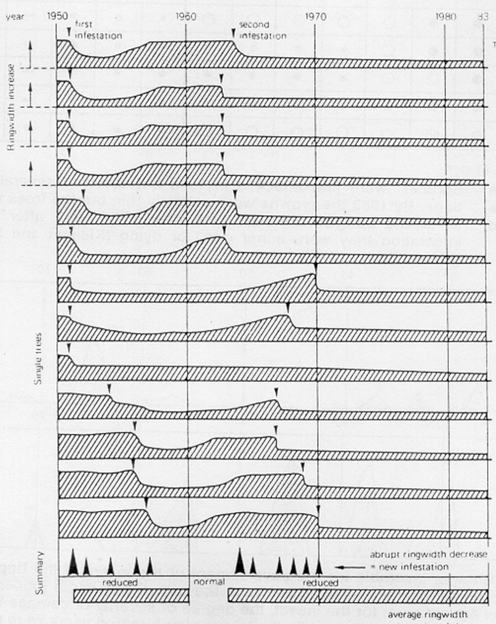
Extent of an infestation of larch bud moth on a uniform stand in an area favorable for the development of the insect in the Upper Valais, Switzerland. The degree of damage is measured according to the number of trees affected per year, the annual ring width (upper line) and the maximum density (lower line). Even in an area where conditions are optimum for the insect, the degree of severity of damage varies in a period of time. The periods 1780 to 1820 and 1920 to 1960 stand out as being very bad, while the intervening hundred years were practically free from damage (Schweingruber, 1979).

Schweingruber, 1979; Kulman, 1971; Varley and Gradwell, 1962.

Relationship between a site and the climate

Climatic factors and site conditions influence the complicated mechanism governing the development of the insect population and the reaction of trees to harmful attacks. This whole area of interaction can be seen in the way that the area affected changes from year to year and also in the annual growth rates. Particularly in the case of damage which has long term effects, such as that caused by spruce bud worm, fluctuations within the same site are very noticeable. When an insect such as the larch bud moth, which recurs in regular cycles, is studied it can be seen that within a large area some climatic regions are affected more often than others. Presumably unfavourable climates, e.g. cool ones or those with long dry summer periods, inhibit the growth of this particular insect. Annual ring analysis investigations, taking both time and geographical area into account, can throw light on this complicated relationship.

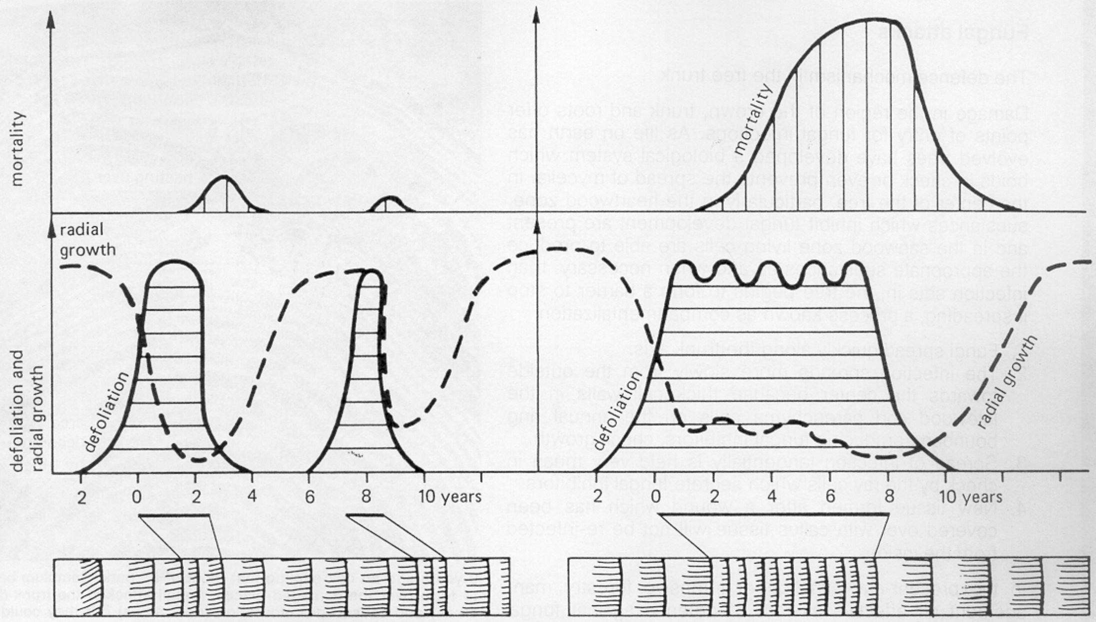




Regions with average and heavy defoliation in firs (*Abies balsamea*) as a result of attack by spruce bud worm (*Choristoneura fumiferana*) in the Laurentide Park region, Quebec, Canada, between 1946 and 1954. The severity of the attack and the shape and size of the area affected changed from year to year (Blais, 1964).

Semi-schematic diagram of annual ring width of 13 Douglas firs (*Pseudotsuga menziesii*) in Colorado Springs, U.S.A. The abrupt reduction in annual ring width indicates an attack, the subsequent phases of narrow ring width formation show the duration of the infestation. The trees were felled in different years. The years 1960 to 1962 are noticeable for being practically free from damage. A second wave of damage occurred in 1963.

Relationship between defoliation, radial growth and mortality rate



Effect of short-lived attacks e.g. by larch bud moth (*Zeiraphera diniana*) recurring at regular intervals. Larches may be attacked twice in the early summer. As new needles are formed each time, wood growth comes practically to a halt and no reserves are laid down in such a year. In alpine regions two attacks in one year mean there is a 5 to 10% chance of a tree dying. When only one attack occurs, the risk is reduced to around 1%. Radial growth returns to normal after 3 to 4 years; the density of the latewood is back to normal levels after 2 to 3 years.

Effect of a longer-lasting attack, e.g. by spruce budworm (*Choristoneura fumifera*). After the first defoliation, severe but not complete, radial growth rate drops dramatically. If the trees continue to lose needles in the succeeding years, growth rate is reduced appreciably. If the density of the crown becomes so low that it is no longer able to supply nutrients for the formation of new needles and earlywood cells, the tree dies as soon as all the reserves laid down in the parenchyma cells have been used up. The longer the duration of the attack, the greater the mortality rate; it can reach 90%. What usually happens is that the attacks are just severe enough to keep the tree on the border-line between living and dying for years. (Adapted from MacLean 1981.)

Conclusions

The following ideas originate primarily from Wickmann, 1979. Trees and tree-damaging insects have existed in every geological period. Insect infestations have affected woodland in epidemic proportions for millions of years. It is known that larches in the Swiss alps are infested by larch bud moths every 7 or 8 years. The areas where damage occurs are clearly defined for each type of insect. Growth reduction occurs in trees over the entire infested area, but actual cases of mortality are limited to a few individual trees in a stand and to a few places within an affected area. Looked at from the economic point of view what has been described must be regarded as a loss (growth reduction, dead trees, under-stocked stands), but from the biological point of view the death of some trees can be regarded as an opening up of the forests which, once the insect population has departed, will lead to an increase in the number of germinating seedlings and a much faster growth rate in the surviving trees. Particularly in the rather unstable situation which exists near avalanche gullies is this an ecological advantage, for insect plagues mean a return to the situation which existed in an earlier stage of forest development when stands were very well stocked and they performed a valuable protective role.

If today's areas of damage are larger than before, and this hypothesis has still to be proved, it could be as a result of the age structure and species composition of the forests, in other words, infestations are a reaction to the 'man-made' forest. Fighting the attacks with chemical or biological measures is wrong and can be justified only in terms of short-sighted, economic interests. The aim of forestry planners should be to create a forest which corresponds as closely as possible to natural conditions.

Taking a broader view, insect activities can be regarded as regulating rather than destroying. A new topic for discussion arises. Is there a connection between the relatively large areas of insect infestations and changes in the environment? When we find out where and for how long large areas of insect infestation have occurred, it will be possible to get an idea as to whether such a connection could exist.

Wickman, 1979; MacLean, 1981.

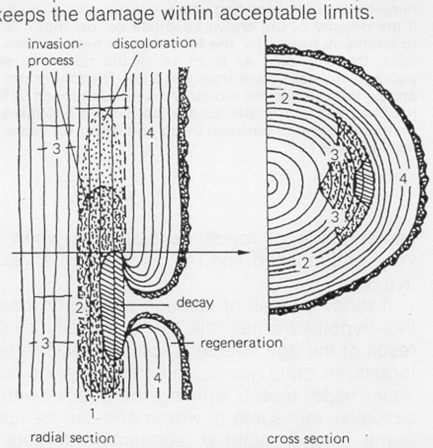
Fungal attacks

The defence mechanism in the tree trunk

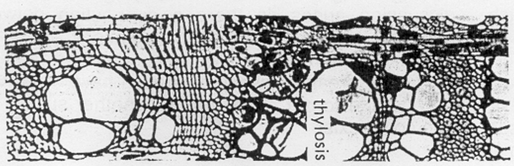
Damage in the region of the crown, trunk and roots offer points of entry for fungal infections. As life on earth has evolved trees have developed a biological system which holds in check or even prevents the spread of mycelia. In the center of the tree, particularly in the heartwood zone, substances which inhibit fungal development are present and in the sapwood zone living cells are able to produce the appropriate substances as and when necessary. If an infection sets in, the tree begins to form a barrier to stop it spreading, a process known as compartmentalization.

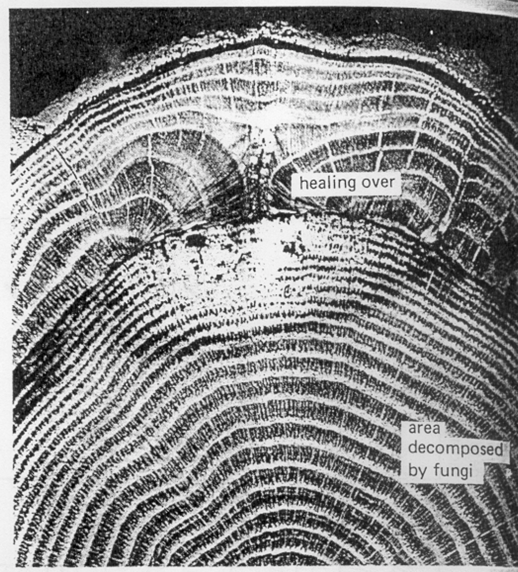
1. Fungi spread quickly along the trunk axis.
2. The infection spreads more slowly from the outside towards the center because thick cell walls in the latewood and parenchyma cells on the annual ring boundary, producing fungal inhibitors, check growth.
3. Spread of infection tangentially is held very much in check by the ray cells which secrete fungal inhibitors.
4. New tissue formed after a wound which has been covered over with callus tissue will not be re-infected from the inside.

In the present-day situation of intensive forestry management an effective system of defence against fungal disease becomes very important. Mechanical damage, caused by heavy machinery or grazing animals, creates vulnerable places but the natural defence system of the tree keeps the damage within acceptable limits.

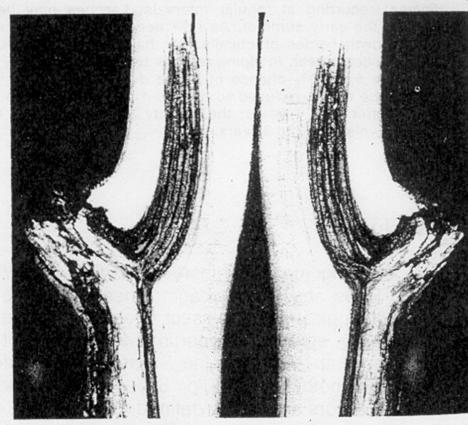


The branch of a bush was broken off. Fungal decomposition of the branch and the tissue below the wound set in. The wound then began to heal over. Fungal filaments spread along the longitudinal axis in the centre of the trunk but came to a halt at the annual ring boundary (Shigo, 1983).





9 years ago an oak sapling lost most of its bark. Cambium began to form over the damaged places. Fungii attacked the trunk (light areas) and caused discolouration (dark areas) but they could not infect the new tissue (Shigo, 1983).

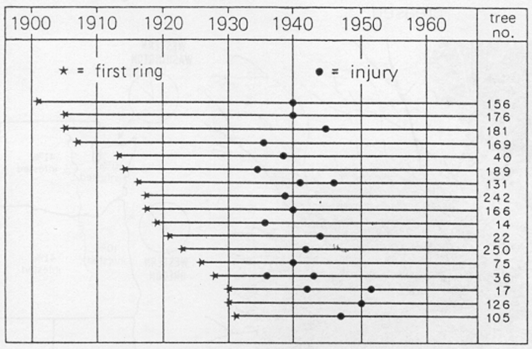


The biological defence system in the trunk (Shigo, 1977).

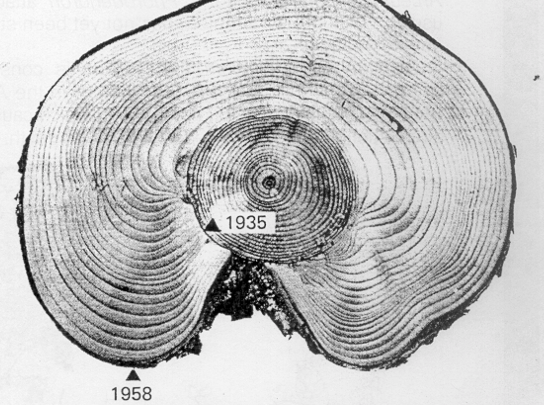
Tangential barriers in an American elm after being infected by Dutch elm disease. First of all a broad band of parenchyma cells was laid down. The vessels then formed were soon blocked by tyloses and filled with dark-coloured substances (Shigo *et al.*, 1980).

Damage due to peeling

In a meadow in the Swiss alps Bazzigher (1973) discovered extensive peeling damage caused by goats which led to a bad fungal infection in the open wounds. 74% of all spruces were damaged. By studying the callus tissue, the time when the damage occurred could be fixed as being between 1935 and 1945. Of the 441 trees examined 43% showed signs of fungal attack in the wounds, 10% had areas of discoloration and only 17% were healthy.



The relationship between various spruces and the time when peeling damage occurred. Callous tissue shows that the damage occurred mainly between 1935 and 1945 (Bazzigher, 1973).

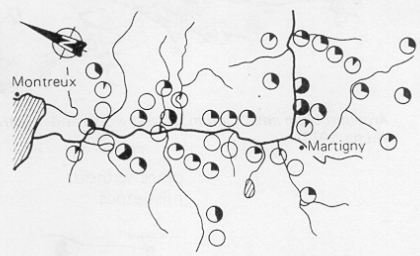


Cross-section through a spruce suffering from peeling damage. Wood formed before 1935 has been decomposed by fungii. Wood formed at a later date has been attacked by a second fungal infection. Along the annual ring boundary signs of the activity of the natural defence system can be seen, either in the stages of decomposition (dark areas) or in stages of penetration (discoloured zones) (Bazzigher, 1973).

Condition of spruce forests

Niederer and Nippel (1984) working in the Rhone Valley, Switzerland, examined the condition of trees in mountain areas. About a quarter of all apparently healthy spruces were found to be rotten in the center when core samples were taken at chest height. The stability of these trees is maintained only by the tangential fungal defence system, formed annually, parallel to the tree rings. This supports the healthy tubular-shaped woody section.

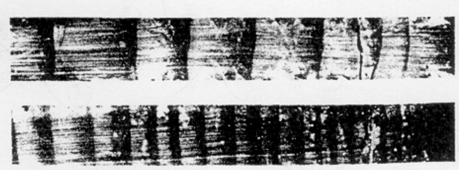
The specific, fungus inhibiting qualities of the outermost, water-conducting rings is the only explanation for the fact that the mountain forests continue to function as protective entities despite being badly diseased.



Proportion of spruces with rotten cores in the lower Rhone valley, Switzerland 16 trees were bored at chest height on each site (Niederer and Nippel, 1984).

Growth-inhibiting effect of *Armillaria Mellea* (Honey Fungus)

On the basis of one investigation it emerged that fungi can inhibit the growth of spruces. (Hrib *et al.*, 1983). The honey fungus causes growth reductions, particularly in artificial stands. Losses are incurred as a result of growth reduction and the death of trees.



Healthy spruces have broad annual rings; those attacked by the honey fungus have narrow ones (Hřib, 1983).

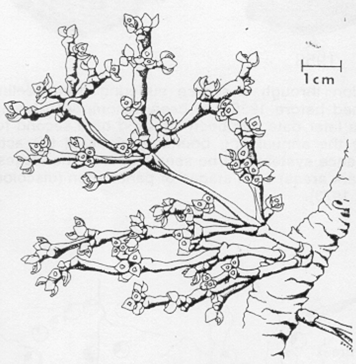
Mistletoe

Forestry research workers, particularly in North America, have investigated the problem of the growth of the parasite mistletoe. Many different varieties of the species *Arceuthobium, Viscum* and *Phorodendron* attack trees, usually conifers. The problem has not yet been studied by dendrochronologists.

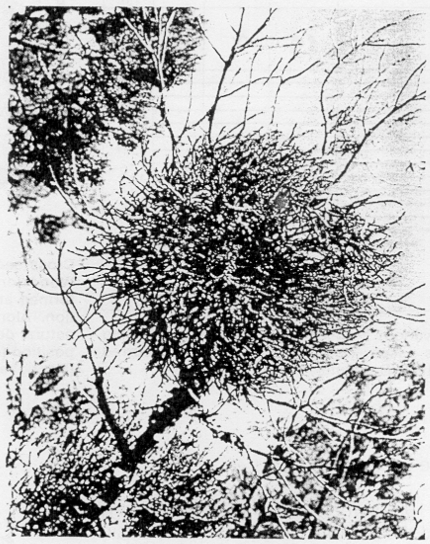
Damage to trees from this source is considerable. Every year 3.2 million board feet are lost in the American west as a result of attacks of mistletoe, which cause either a reduction in growth in the host tree or its death.

Growth damage

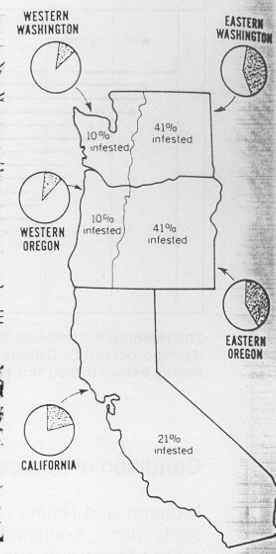
Once a seedling has attached itself to a branch the vitality of the tree is reduced. Suckers penetrate the vascular system of the host tree, tapping water, nutrients and assimilated substances. At the point where the mistletoe penetrates the tree the cambium reacts by producing callus tissue and an above average number of cells. The formation of new cells, which is normally distributed throughout the tree, becomes concentrated at this point of infection, which means the vigor in this area is increased.



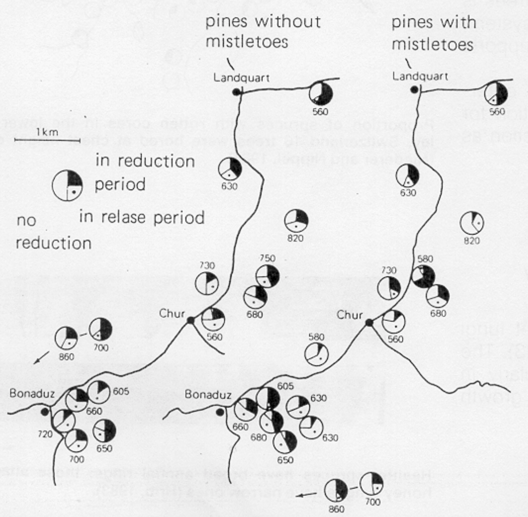
Arceuthobium americanum (Hawksworth and Wiens, 1972).

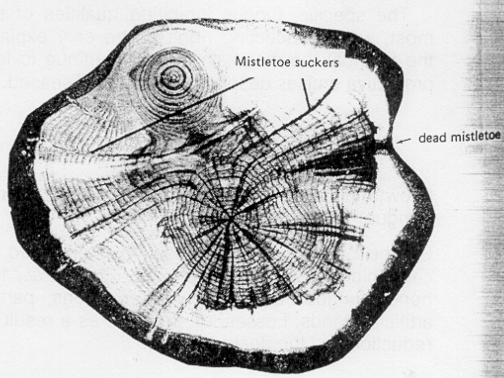


Arceuthobium sp. on oak.



Percent of comercial forest area infested with dwarf mistletoe in California (Bolsinger, 1978).





Suckers of *Viscum album* on *Abies alba.*

Radial growth of pines (Pinus sylvestris) with and without Viscum attak in forests near Chur, Switzerland. On each site 16 trees have been cored. The black part of the circle shows the percentage of trees reduced in growth. Growth is in this case not negatively influenced by mistletoes (Schweingruber *et al.*, 1986).

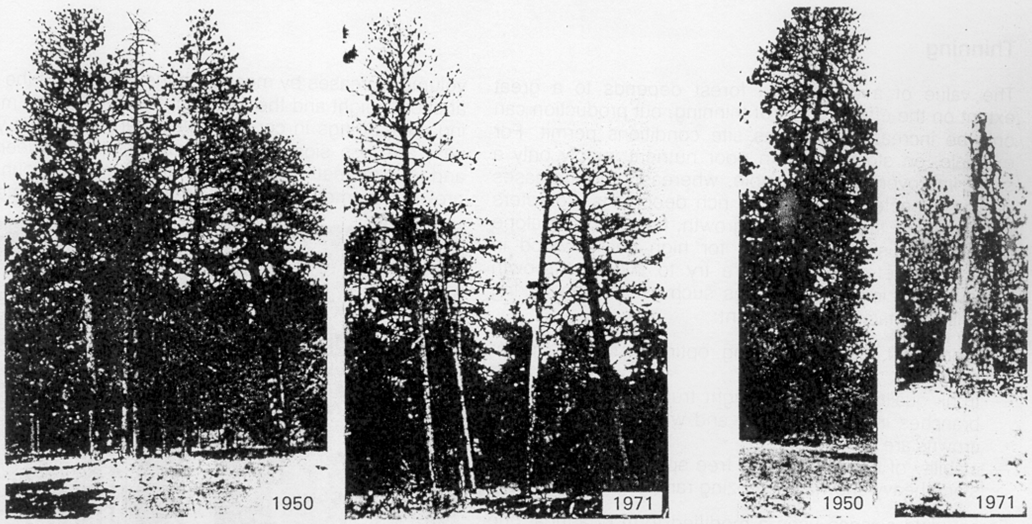
Hawksworth et al., 1972; Bolsinger, 1978; Scharpf et al. (edit.), 1978.

Damage

The condition of a tree or a whole stand can be changed, both in the short and long-term by a mistletoe attack.

The extent of damage ranges from the loss of a few twigs to the destruction of whole forests. Generally weaker trees rather than stronger are attacked.

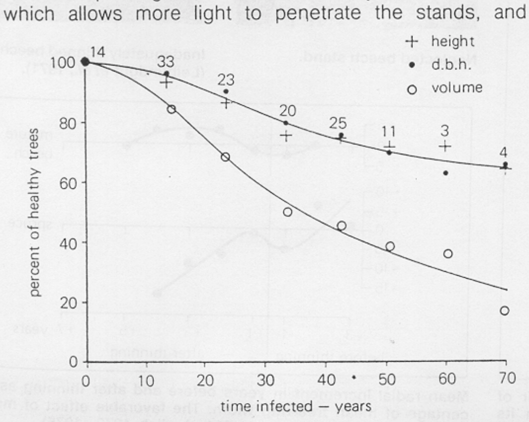
The longer the attack lasts, the more serious is its effect on stand vigor. This is evident both in reduced vertical growth and wood production (annual ring widths, volume). Seed production declines, another sign of reduced vigor, and so propagation of the trees is also adversely affected. Dead mistletoe shoots make a convenient point of entry for fungi. The resulting increase in rotten wood leads to greater structural instability, which makes the trees more vulnerable to storm damage. As a result the mortality rate again increases. The ultimate effect of mistletoe depends on the host—parasite relationship, the severity of the attack, the climatic and ecological conditions and the presence of harmful insects. However, generally speaking, the mortality rates are influenced by a combination of three primary factors; presence of mistletoe, insects and fungi.



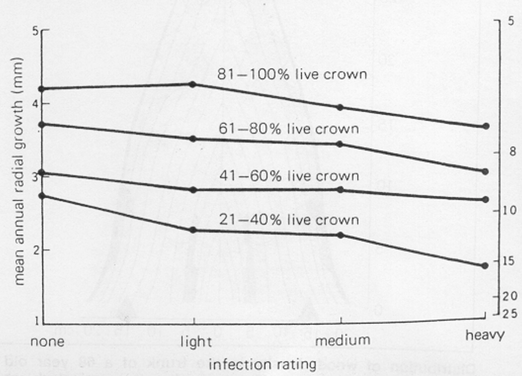
The devastating effect of mistletoe (*Arceuthobium vaginatum*) on vigorous Ponderosa pines within the last 20 years in the Grand Canyon, Arizona (Lightle and Hawksworth, 1973).

Ways of keeping the damage under control

Various measures are undertaken by foresters to reduce mistletoe damage and improve stand vigor. These include selective pruning, removal of severely affected trees, which allows more light to penetrate the stands, and reduction of shrubs in the underbrush. The effectiveness of these measures is clearly evident as crown size is correlated with the process of regeneration; the larger the crown, the more successful is seed production.



Relationship between relative height, d.b.h., and cubic foot volume of dominant and codominant Lodgepole pines and the time since the infection on the basis of 133 plot (Hawksworth and Hinds, 1964).



Relationship between radial growth, live crown ratio and dwarf mistletoe rating of red fir, 10 years after release (Scharpf, 1978).

The aim of forestry is to cultivate the forests in such a way as to achieve optimum production without disturbing ecological balances. Measures are taken to stimulate organic production while at the same time preserving or improving many other forest functions, such as providing recreational use and acting as a natural barrier to erosion etc.

Specific operations such as thinning, pruning and fertilization lead to increases in yield in the short term, and improved timber quality, in the long run. Although several studies have been carried out on the effects of such measures on individual trees and on whole stand growth, few generally applicable conclusions can be drawn, as there are wide discrepancies between the findings. As a result, little is known about the connection between forestry practices and tree ring structure.

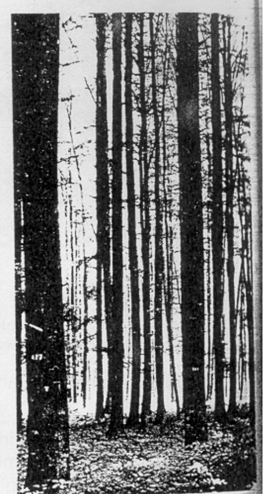
Thinning

The value of a commercial forest depends to a great extent on the effective use of thinning, but production can only be increased as far as site conditions permit. For example, on stony soil with poor nutrient supply only a slight improvement is possible, whereas large increases can be expected in stands on rich deep soils. Foresters look for more than enhanced growth, for this factor alone does not satisfy the demand for high quality wood in today's market. They therefore try to influence growth along certain lines by practices such as thinning, taking the following factors into account:

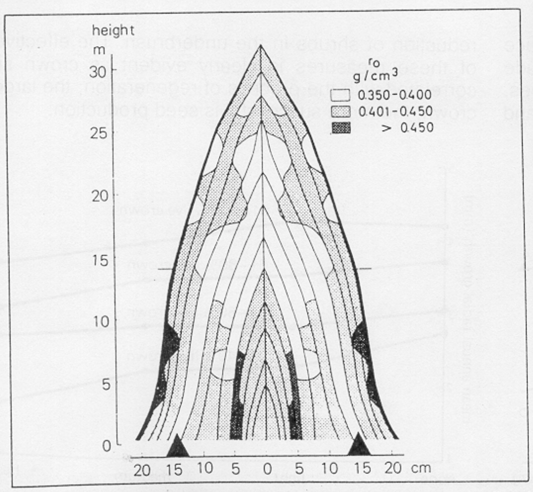
— production, i.e. establishing optimum conditions for growth.
— trunk quality, i.e. long straight trunks with only a few branches in the lower part and with regularly shaped crowns are preferred.
— stability of the stand, i.e. a tree species that can withstand heavy snowfalls, freezing rain and storms.

Forest yield science uses a modified form of annual ring analysis; volume increments in individual trees or whole stands are measured periodically. It is easier to measure volume increases by measuring the diameter of the trunks at chest height and the height of the tree than by measuring annual rings in core samples. Variations from year to year are less significant than differences between sites and forestry methods. Only in a few European countries is growth increment measured by means of core samples.

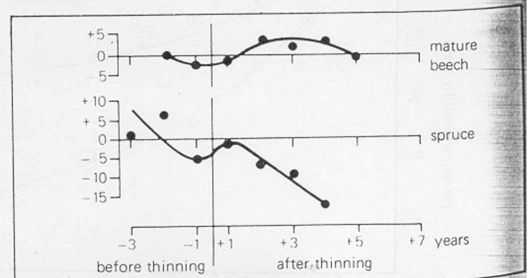
Neglected beech stand.



Inadequately thinned beech stand (Leibundgut *et al.*, 1971).



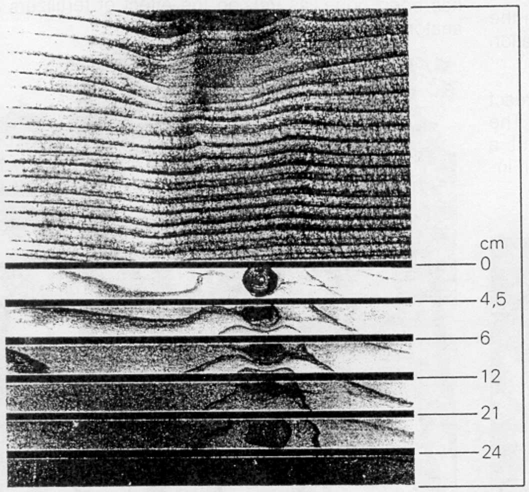
Distribution of wood density in the trunk of a 68 year old fir of approx. 40 cm diameter. 40 years after it germinated, when its diameter was about 30 cm, thinning was carried out and space was created for the tree to develop. For a short time density decreased but returned to normal within a few years (von Pechmann, 1974).



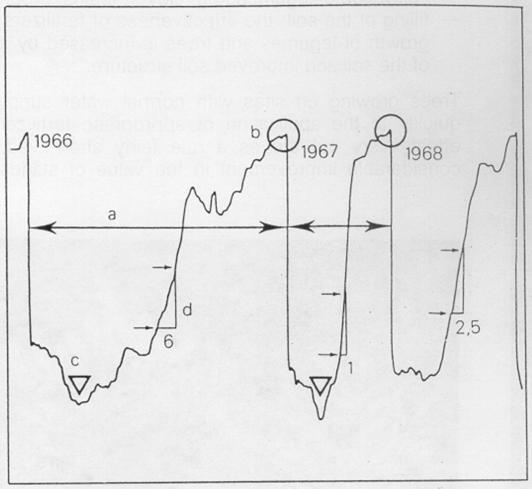
Mean radial increment in years before and after thinning as a percentage of mean tree-ring width. The favorable effect of moderate thinning lasts only a few years (Mitscherlich, 1970—1975).

Pruning

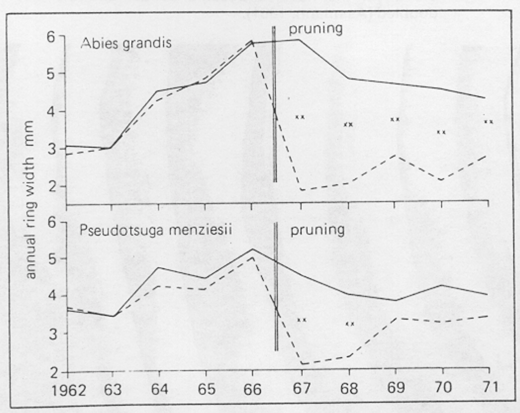
Pruning should improve the quality of the wood. Well-formed branches and long sections of trunk without branches increase the value of the timber. Many reports have been made on the practical and economic effects of pruning, e.g. Lepetre, 1957, Polge *et al.*, 1973, who studied the effects of pruning on tree ring structure. In 1971 core samples were taken from 16 trees with full crowns, growing in fairly open situations. The species used were *Pseudotsuga menziesii* and *Abies grandis*. Eight of the trees had never been pruned, 8 had had their branches reduced by 50% in 1966. The effects of this heavy pruning could be clearly seen in a reduction in ring width and a more gradual transition from earlywood to latewood. The maximum and minimum densities were slightly higher than normal. Only very heavy pruning has any lasting influence on growth; as long as the tree has a relatively large crown it can survive unfavorable conditions.

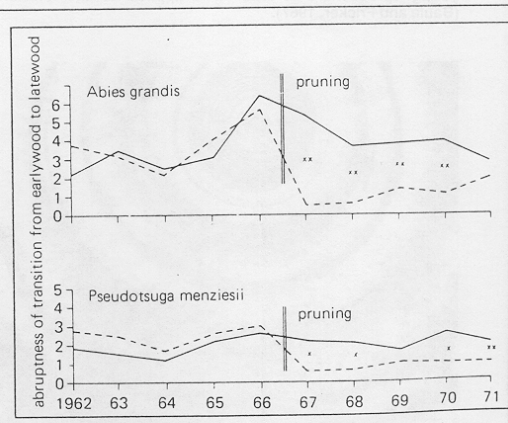


Improvement in the quality of the timber as a result of pruning. If the place where a branch is removed is quickly covered by new tissue, the wood fibres run more or less straight within about 2 cm of the scar. In the case illustrated here all signs of a branch having been removed had disappeared within 6 years (Lenz, unpublished).



Features of the density curve used to determine the effects of pruning.
(a) tree ring width
(b) maximum density
(c) minimum density
(d) abruptness of transition from earlywood to latewood (Polge *et al.*, 1973).





Effects of heavy pruning on ring formation in *Pseudotsuga menziesii* and *Abies grandis* (Polge *et al.*, 1973).

Tree ring width decreases immediately after pruning but gradually returns to normal.
__ average of 8 control samples
--- average of 8 pruned trees
xx significant differences.

Increase in density from earlywood to latewood occurs more rapidly after pruning. As ring width increases the transition becomes more gradual once more. (Polge *et al.*, 1973).

Mitscherlich, 1970—1975; Polge et al., 1973.

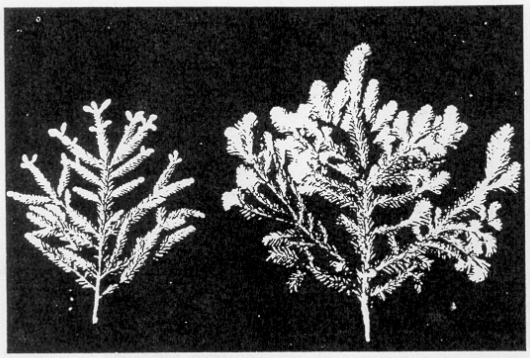
Fertilization and soil improvement

As with all forestry measures, soil improvement is intended to raise the vigor of weak stands and increase organic production. In cases where the soil is exhausted or poor in nutrients and the exact conditions are known, appropriate measures can be taken to improve it. These include:

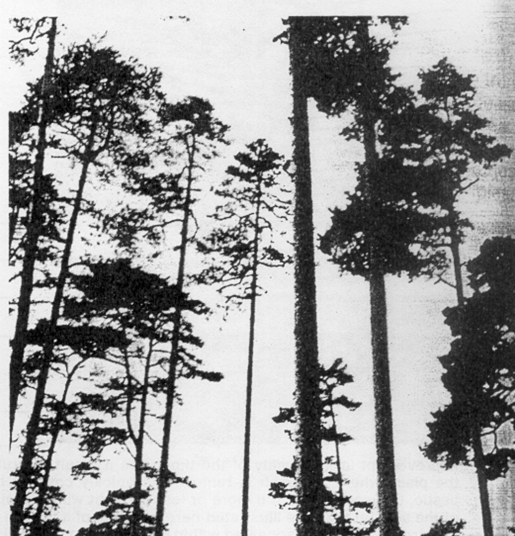
- application of fertilizers such as lime, potash, phosphates and nitrogen.
- cultivation of legumes, e.g. clover, lupins, broom.
- tilling of the soil; the effectiveness of fertilizers on the growth of legumes and trees is increased by aeration of the soil and improved soil structure.

Trees growing on sites with normal water supply react quickly to the application of appropriate fertilizers. The effects vary but are as a rule fairly short-lived, but a considerable improvement in the value of stands or individual trees can be achieved by means of fertilizers in conjunction with soil cultivation and general forestry measures as described above. Whether such measures are economically worthwhile, however, depends primarily on the cost and effectiveness of the fertilizer and the production costs and selling price of the timber.

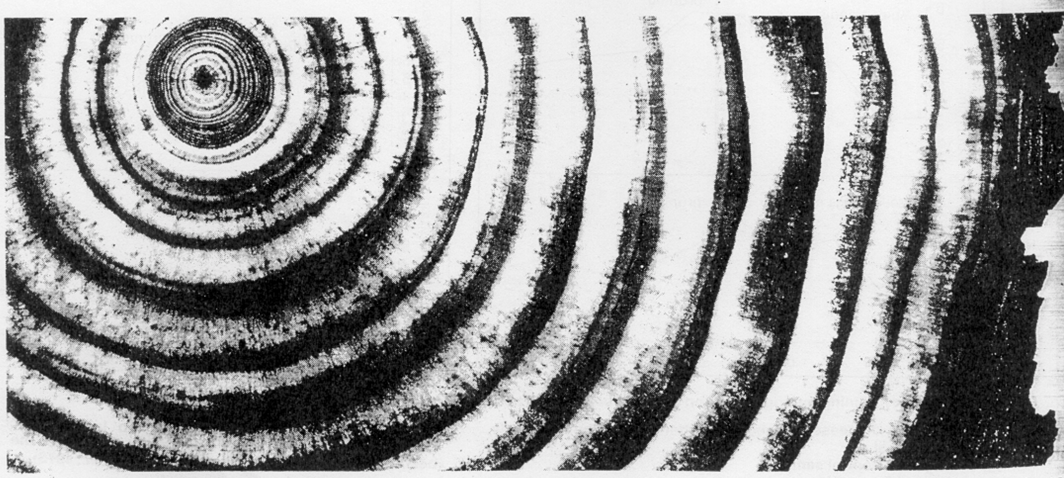
Much has been written about the physiological, pedological, technical and forest yield aspects of fertilizers and soil improvement (Baule and Fricker, 1967). Little work has been done, as yet, on the effect of fertilizers on the anatomical structure of tree rings.



Effect of application of fertilizer on needle and shoot growth in young spruces. No fertilizer was applied to the left-hand shoot (Baule and Fricker, 1967).



Effect of an application of nitrogen to pines in the Black Forest (left — no fertilizer). After the application of the fertilizer to the 190-year-old trees, the needles became denser and the tree ring widths doubled (Assmann, 1961).

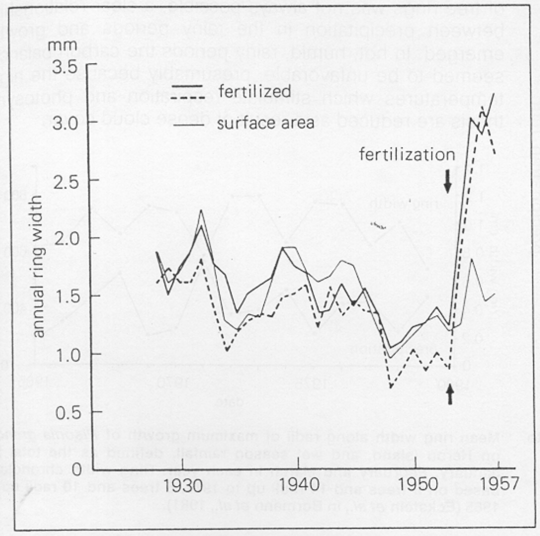


Effect of the application of fertilizer on the cambial activity of Pinus radiata on a poor site on New Zealand. The reaction began 3 years after the fertilizer was applied (Kozlowski, 1971).

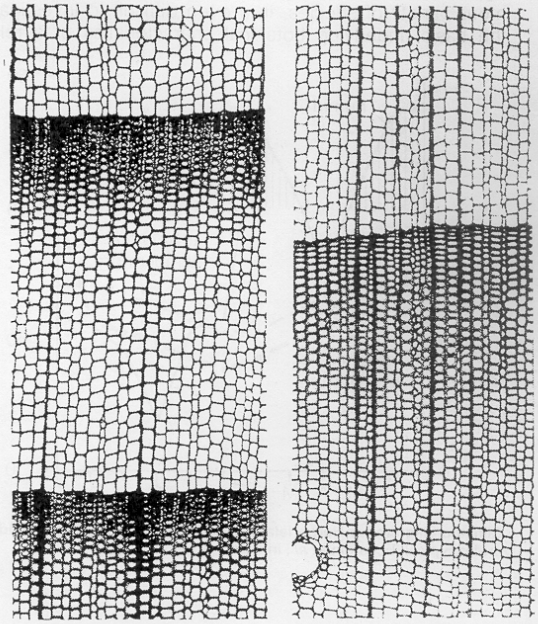
The following example describes the effects of application of fertilizer (von Pechmann, 1960). A 63—year-old spruce growing on variegated sandstone was treated with nitrogen and phosphate fertilizer (between 1953 and 1955). As early as one year after the first application changes could be seen in the annual ring structure:

- the width, especially of the earlywood increased greatly.
- the latewood density was lower than in the previous year.
- the density sank from 0.475 g/cc to 0.412 g/cc and the compression strength showed a parallel reduction from 513 kg/cm^2 to 410 kg/cm^2

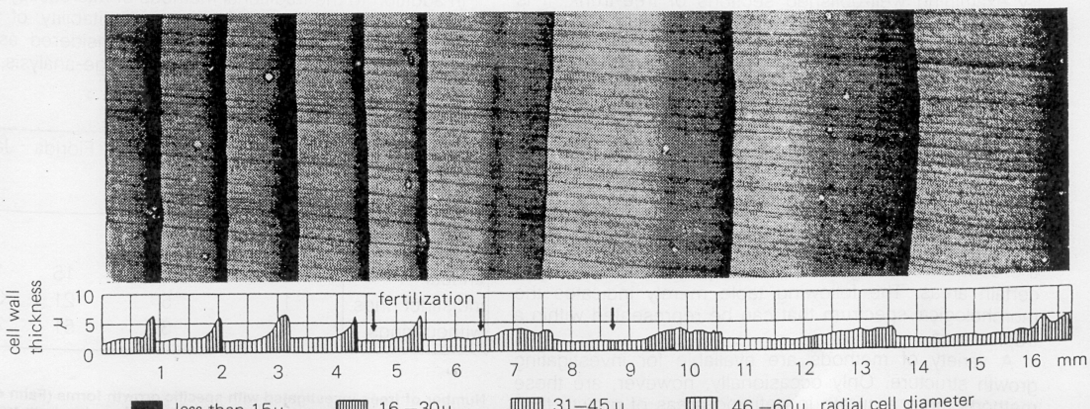
It seems that cambial activity had been stimulated by the nitrogen. It follows that the yield of forests on acid soils with poor nutrient supply can be increased by the cultivation of nitrogen-assimilating plants, e.g. lupin, on the site.



Effect of fertilization with nitrogen on annual ring width in spruce on a site with poor nutrient supply in Germany; the ring width increases (von Pechmann, 1960).



Earlywood-latewood transition in spruce before (left) and after (right) application of fertilizer. The transition becomes more gradual (von Pechmann, 1960).



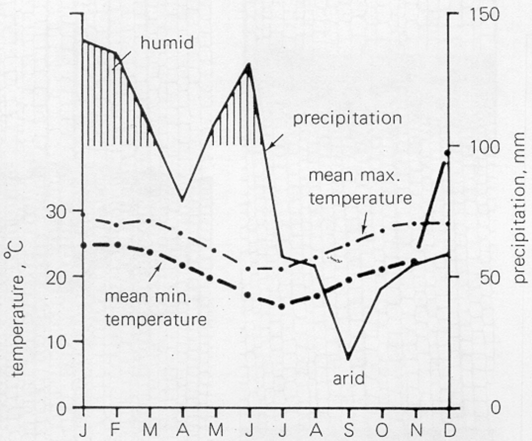
Tree-ring structure of a 63-year-old spruce on a site with poor nutrient supply before and after application of fertilizer. Widths of earlywood, latewood and the whole ring increase. The density difference between earlywood and latewood, and the average latewood density decrease (von Pechmann, 1960).

Assmann, 1961; von Pechmann, 1960.

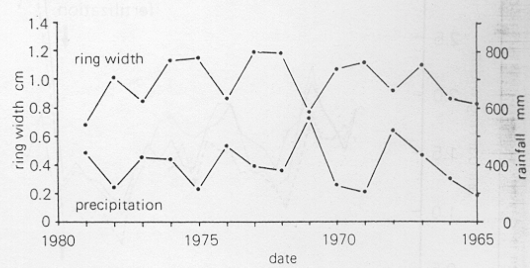
Study of yield in tropical forests

As has already been shown (p. 109), traditional methods of dendrochronology are completely unsatisfactory when determining yield characteristics such as tree age and radial and volumetric growth in tropical forests. It is not surprising, therefore, that relatively few dendrochronologists have studied tropical trees. Considering the enormous variety of species, it is even difficult to investigate the basic underlying botanical characteristics of a relatively small area. It is not uncommon to find 200 types of tree species growing on one hectare of land. It can be regarded as a challenge, therefore, to work on growth rings in certain tropical regions. Eckstein *et al.* (1981) and Worbes (1985) showed that such work could be successful by a study carried out in a seasonal tropical climate.

Using 70 cross-sections taken from the trunks of 20 *Pisonia grandis* trees Eckstein *et al.* tried to establish the relationship between ring width and meteorological factors. Although the definition, counting and measurement of tree rings was not always possible, a clear relationship between precipitation in the rainy periods and growth emerged. In hot, humid, rainy periods the carbon balance seemed to be unfavorable, presumably because the high temperatures which stimulate respiration and photosynthesis are reduced as a result of dense cloud cover.



Climatic diagram for Heron Island. The yearly change from humid to arid is typical (Eckstein *et al.*, in Bormann *et al.*, 1981).



Mean ring width along radii of maximum growth of *Pisonia grandis* on Heron Island, and wet season rainfall, defined as the total for January, February and March in each year. Ring width chronology based on 8 trees and 14 radii up to 1971, 6 trees and 10 radii up to 1965 (Eckstein *et al.*, in Bormann *et al.*, 1981).

Methods of determining growth

Studying cross-sections of the trunk

By examining well-polished sections of tree-trunk, it is possible to judge whether a tree is forming definable, incremental growth. What had appeared to be definable annual growth when core samples were taken, was often found to be localized, one-sided trunk growth when cross-sections were studied. Often tangential bands of parenchyma cells or ill-defined tangential pigmented zones can be distinguished from rhythmic incremental limits only on closer examination. Only rarely can distinct rings be seen all around the trunk. Even then, it is possible that several rings have been formed in the same year. Various authors have tried to build up a picture of the dendrochronological applicability of some species in certain areas. The following table merely indicates the morphological spectrum that can be represented within a tropical area.

A variety of methods are available for investigating growth structure. Only occasionally, however, are these methods more accurate in defining areas of growth than what can be achieved when examining trunk cross-sections with the naked eye.

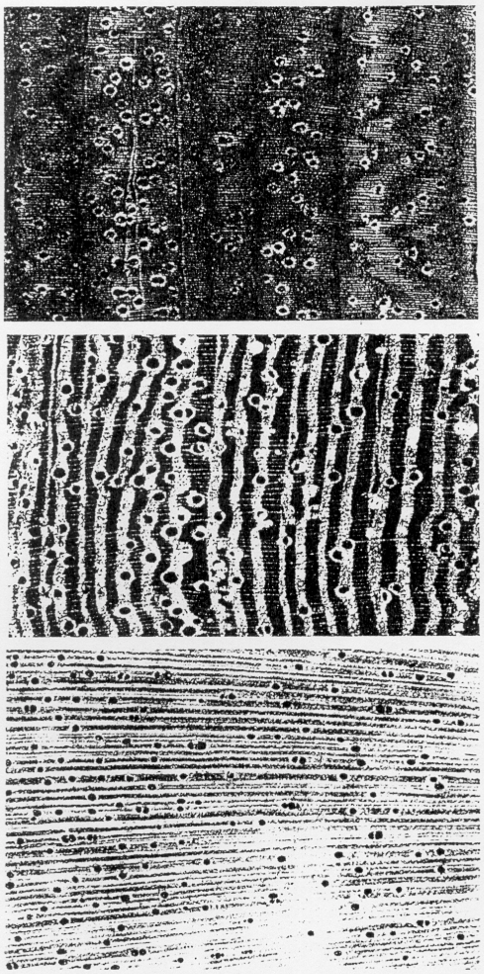
In addition to the traditional methods of microscopy and mechanical-physical examination, the suitability of the following newer methods should be considered as to their suitability: X-ray densitometry, image-analysis, or optical photometry.

	Tropical rain forest Africa	Aride Zone Savannah Africa	Florida	Java
distinct rings not necessarily annual	16	20	15	10
indistinct rings	1	5	21	32
without rings	7	3	51	21

Number of trees investigated with specific growth forms (Fahn *et al.*, 1981). Trees with and without rings are to be found in both tropical zones with a consistently wet climate as well as those with a seasonal climate (Eckstein *et al.*, in Bormann *et al.*, 1981).

Age determination of trees in plantations of known age

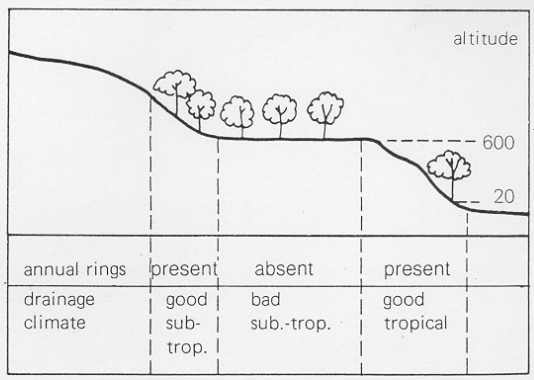
Deciding whether growth rings are formed annually or not is easiest if the exact date of planting is known as thus tree age can be compared with growth structures in cross-sections taken from the trunk. Of the many tropical species — and there may be as many as 7000 — there are only about 100 being cultivated intensively which are suitable for study by dendrochronologists. It will never be possible to reproduce accurately the natural conditions of the tropical forest in plantations, because only a few varieties can be grown in the test areas and these are often conifers growing outside their natural habitat. Moreover, cultivation of trees in these test areas is very different from the growth conditions which prevail in the dense forest. But in spite of all this, investigations concerning growth structure carried out in such areas have great advantages: the relationship between the actual age of the tree, annual climate and site and the morphology of growth can be examined. In one such investigation in Brazil it was found that the same variety of tree under the same climatic conditions, but on different sites, formed rings on one site, but not the other.



Cross-sections of tropical woods.
Top: *Dalbergia retusa* with distinct areas of growth and possibly even annual rings.
Middle: *Milletia laurentii* with continuous, tangential growth areas but no annual ring formation.
Bottom: *Ochroma lagopus* without any rhythmic growth structures (Gottwald, 1958).

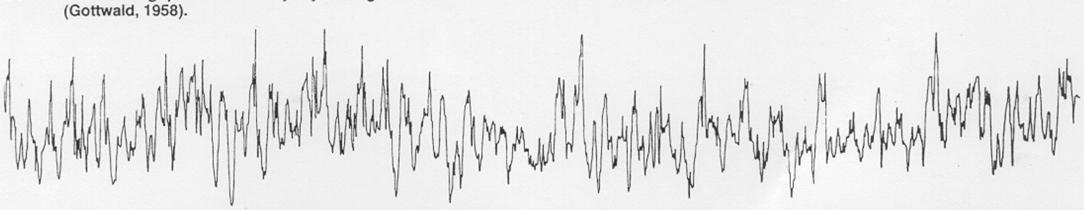
Determination of growth by dendrometers and markings

Dendrometers give information about growth. A simple tape dendrometer records the extent of radial growth whereas dendrometers with the facility to make daily recordings are capable of providing information about chronological growth rhythm. The relationship to the structure can be established only if chemical substances are injected into the layers of cambium in the trunk with needles. When the relevant tree sections are examined at a later stage, it is possible to ascertain the stage of development that the xylem had reached at a given point in time. (Fahn *et al.* 1981.)



Pinus eliotti **plantation. On well-drained sites trees only form annual rings when a water shortage exists in dry periods of short duration.**

Density diagram of a tropical deciduous tree. Neither in the cross-sections nor in the density diagrams can seasonal growth fluctuations be distinguished from annual rings.



Fahn et al., 1981; Gottwald, 1958.

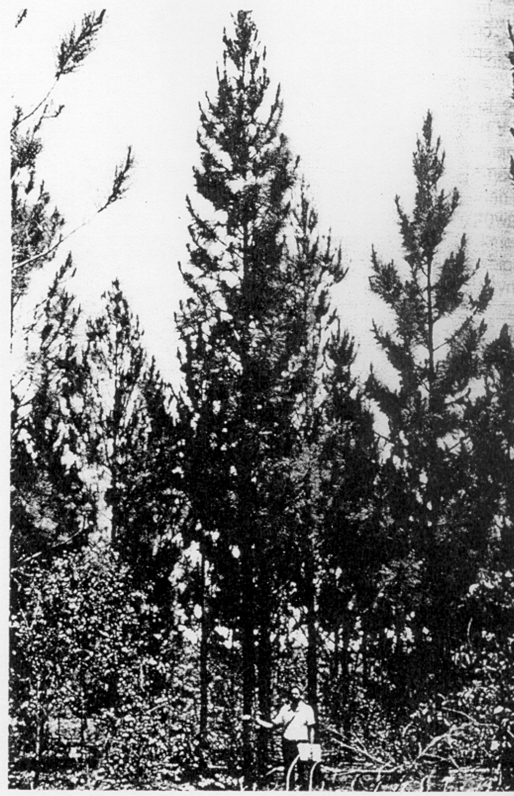
The density of wood is one of its most important technological features. It is influenced by biological, physical and chemical characteristics and a relationship exists between such things as cell wall thickness, cell size, compression strength, breaking load, modulus of elasticity and lignin content. It is often the case that density determines the suitability or otherwise of a particular wood for a particular purpose, which is the reason why radiodensitometric analysis is so important in research into wood technology. It is hardly surprising that even in the early days such studies (Green, 1965, Hughes 1968, Keller 1968, Phillips 1966, Sanderson *et al.*, 1960) raised technological questions, an even more frequent occurrence in later research.

Little mention has been made in this book of tropical woods, an omission which will now be rectified by referring to some relevant material from the work of such authors as Plumtree (1984). Pines native to the Caribbean and Central America (*Pinus caribaea, Pinus patula*) are cultivated extensively in tropical regions today and are very important to forestry.

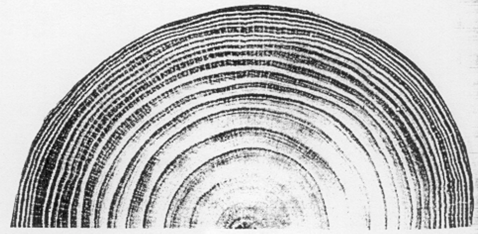
Radiographic analysis is made more difficult by the presence of resins which can make up to 60% of the total weight. After they have been extracted the irregularities in density can be seen clearly in the density curves. On subtropical sites annual rings are present with maximum densities often in the middle of the rings. The proportion of latewood is very high as a rule. The average density of the wood is therefore higher than that of pine-wood in temperate zones (0.5—0.7 g/cm^3). The width of the annual rings in trees grown on plantations is striking. In the center it is not unusual for them to measure 2—3 cm, decreasing rapidly towards the outside. The ageing process is completed significantly faster under these conditions than in cooler or more arid zones.

Ring width, average ring density and cross-sectional areas vary in a characteristic way. These reactions, similar from species to species, seem to be partly controlled by climate. For example, Plumtree (1978) discovered that the annual volumetric growth and dry matter content in *Pinus patula* increased with heavy rainfall.

To ensure the optimal use of wood from conifers growing on tropical plantations it is important to know something about annual rings and density structures within the tree. So Plumtree (1978, 1984) drew up density profiles for *Pinus Caribaea* along several radii and at several different heights. By extrapolation he succeeded in determining the density variations using suitable mathematical methods.

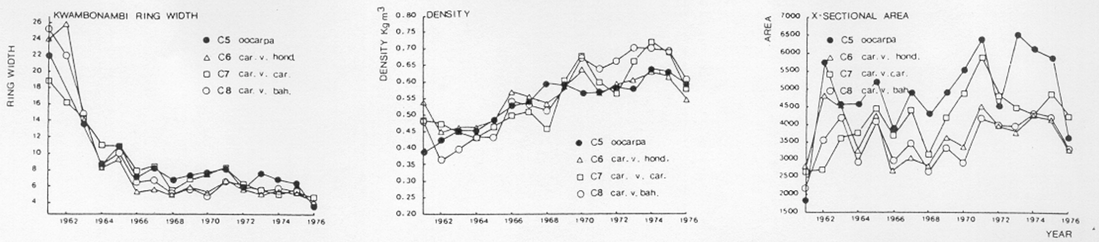


***Pinus caribaea* var. hondurensis. 7 year-old trees in a plantation on Melville Island, Northern Territory, Australia (Plumtree, 1984).**

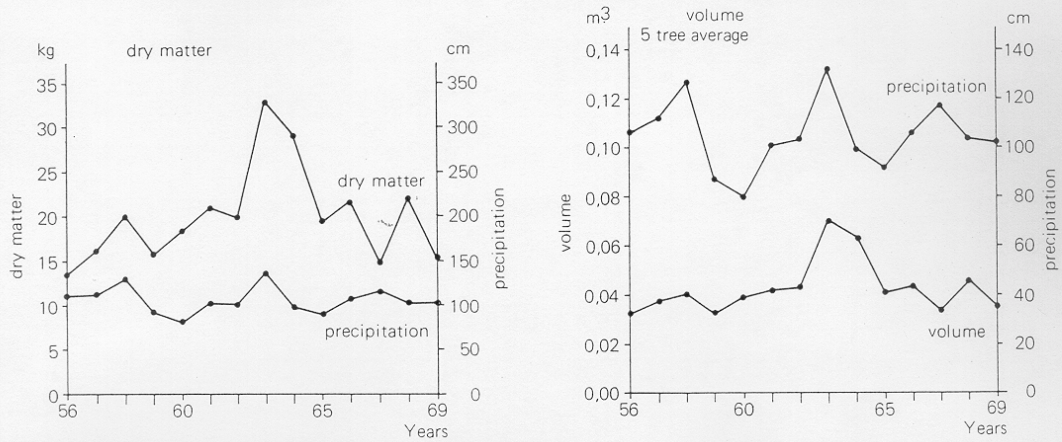


Cross-section through a 18 year-old Pinus caribaea growing in an area of afforestion in Cuba. The annual ring width decreases rapidly towards the outside as a result of crowding on all sides from other trees. Characteristic of all tropical trees are the large number of intra-annual density fluctuations, the high proportion of latewood and the high average wood densities. In the example shown they are about 0.7 g/cm^3 (Specimen J. F. Hughes).

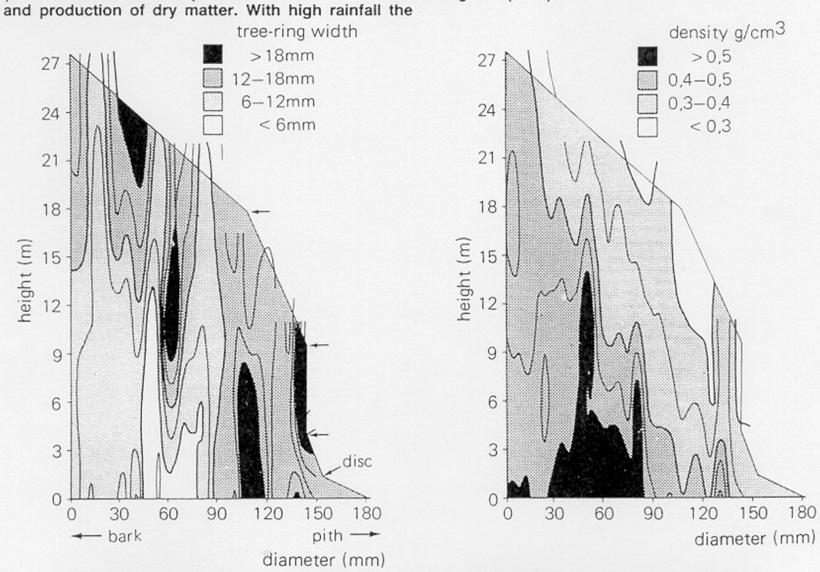
Plumtree, 1984; Sauvala, 1982



Annual variation in width of tree rings, mean density and cross-sectional area of pines in an afforestation in Uganda, Africa. The ring width decreases very rapidly; by the fourth year it is only one third of what it was in the first. Density increases with decreasing ring width. Annually changing ecological conditions are reflected principally in cross-sectional area (Plumtree, 1974).



Relationship between annual rainfall and wood characteristics with importance to forestry in *Pinus patula* in an afforestation in Uganda (Plumtree, 1978). There seems to be a positive correlation between annual rainfall and production of dry matter. With high rainfall the production of wood is lightly stimulated. The relationships between cross-sectional growth and rainfall are partly positive (1963), partly negative (1967).



Contour diagram of *Pinus patula* trunks from Uganda. With the aid of densitometric photographs of trunk sections, taken at different tree-heights, the relationship between tree ring width and density for the entire trunk was extrapolated. Ring widths are usually greater in the centre of the tree (right side of diagram) than those on the periphery of the trunk. Densities along the pith in the centre of the trunk are less than those at the outside. The highest values are to be found in the lower, outer sections of the trunk (Plumtree, 1978).