Chapter 3
Old Trees and the Meaning of 'Old'

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3.1   Introduction

While the mere presence of 'old' trees does not automatically indicate old-growth conditions (see Chap. 2 by Wirth et al., this volume), it is fair to say that many old-growth forests contain a high number of trees close to their maximum longevity. Besides definitional aspects, tree longevity *per se* is a key demographic parameter controlling successional dynamics of species replacement, stand structure and biogeochemical cycles (see Chap. 5 by Wirth et al., this volume). This chapter takes a dendroecological perspective on tree longevity. The first part will explore differences in longevities between different life forms and will ask to what extent trees differ from herbs and shrubs and among each other (Sect. 3.2). The second part will discuss the mechanisms underlying the death of cells, tissues and whole plants (Sect. 3.3). It will be shown that the concept of death is problematic in the context of clonal plants, and that the inevitable presence of external mortality agents may bias our perception of biological limits of longevity.

3.2   Longevity of Conifers and Angiosperms

"After an individual becomes established, it must persist" (Weiher et al. 1999). The question remains: for how long? Undoubtedly, the oldest living beings on our planet are trees. The oldest trees look back on an individual history of almost 5,000 years, whereas most herbaceous plants persist for only a few years and some annuals die in the course of weeks. Apparently, longevity is highly variable among plants.

Reconstructing the age of an old tree is far from trivial because ring formation can be suppressed in stress periods or rings may be doubled in interrupted growing periods. In such cases, age determination requires the dendrochronological technique of cross-dating. As shown in Fig. 3.1, this simple method allows the
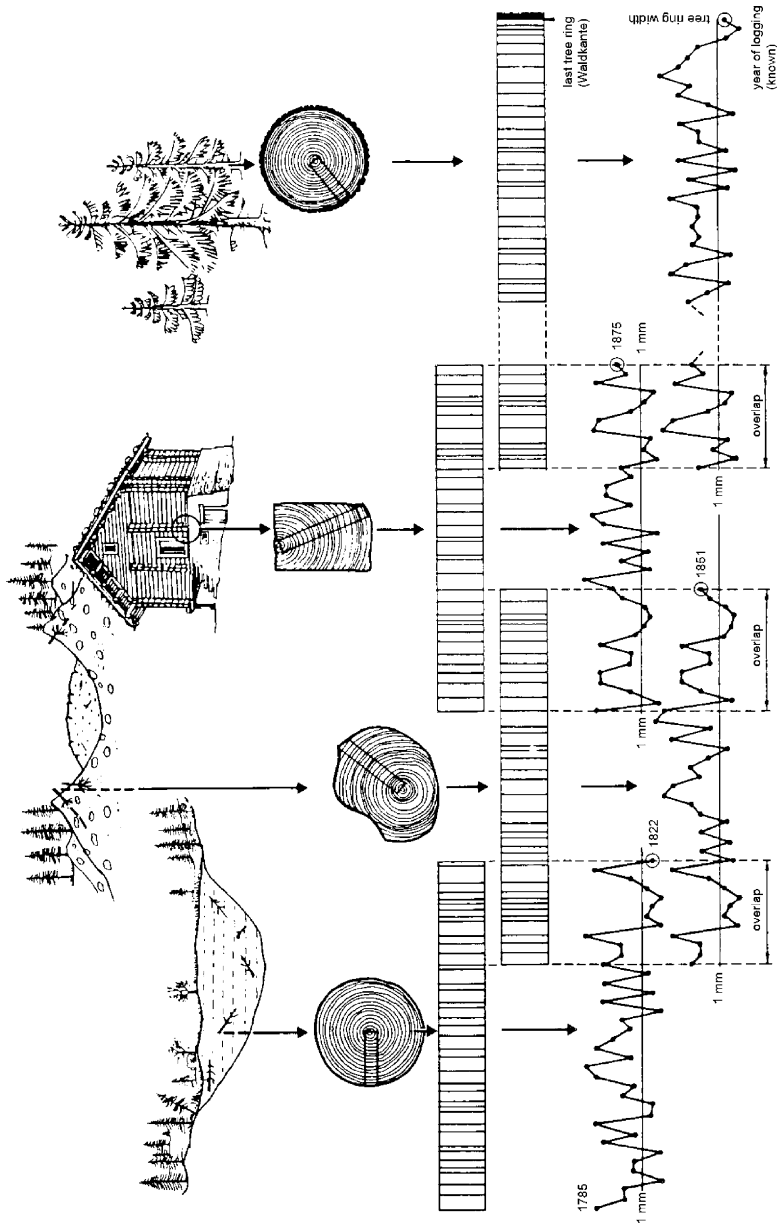
Fig. 3.1 Principle of dendrochronological cross-dating. The key to evaluating the calendar date of the last ring on a stem disk is the irregular distribution of extreme years, the so called pointer years (Schweingruber et al. 2006)

determination of felling dates of ancient woods as well as the age determination of living trees.

A selection of the maximum ages of some of the oldest trees (see Table 3.1) shows that the availability of data on tree longevity, determined by cross-dating, is not evenly distributed across the world. The list suggests that tree longevity itself is not strictly related to the climate. The hot spot of tree longevity is located in the mountain ranges of western North America, where many species reach an age of 2,000 years. In contrast, the Canadian boreal forest is characterised by remarkably short maximum longevities. Here, conifers rarely exceed an age of 400 years. The biogeochemical relevance of these differences in longevity is shown in the model study presented in Wirth et al. (see Chap. 5 by Wirth et al., this volume). However, low longevities are not a feature of boreal forests in general, as some larches in the Eurasian subalpine zones and the boreal taiga are over 1,000 years old. The Eurasian Stone pines (*Pinus cembra* and *Pinus sibirica*) can probably also reach that age, but relevant dendrochronological data are missing. Spruces, firs, and deciduous trees do not exceed a maximum lifespan of 500 years. In this context, it is interesting to note that the oldest *artificial* tree, a cross-dated tree ring sequence composed of different individuals of central European living and subfossil oaks and pines is 12,460 years old (Friedrich et al. 2004).

Information on the maximum longevity of shrubs is very limited, but it seems that they are generally shorter-lived than trees (Schweingruber 1995) and dwarf-shrubs (see below). The oldest known shrubs grow in Siberia. Hantemirov et al. (2003) found an 840-year-old *Juniperus sibirica*. Dendrochronological analyses in a dry temperate *Quercus pubescens* forest in the Swiss Jura mountains revealed that the age of the root stocks of several shrub species capable of resprouting is usually much higher than the age of the shoots. For *Cornus sanguinea* the ages of the root stock and the shoots were 35 years and 5 years, respectively; for *Ribes alpinum* the relationships was 62 vs 10 years; and for *Lonicera xylosteum* 48 vs 12 years.

More is known about the maximum longevities of dwarf shrubs. According to Kihlman (1890), Callaghan (1973) and Schweingruber and Poschlod (2005), the oldest individuals may reach maximum ages of up to 200 years (Table 3.2). Even a small, delicate plant such as *Dryas integrifolia* has been found to live for at least 145 years. In general, individuals of dwarf shrubs older than 50 years are not rare in subalpine and sub-Arctic environments.

Within the group of herbs, the age of the whole plant can be determined only in species that form a taproot – this being the only structure where all rings are preserved. In clonally growing rhizomatous plants, counting of annual rings in the rhizomes allows the age of currently present tissues to be determined, but not the age of the whole plant. The maximum ages of tap-rooted herbs are well known for western Europe (Schweingruber and Poschlod 2005). As for the dwarf shrubs, the herbaceous species with highest longevities grow in the subalpine and alpine zone. We found 50 annual rings in *Trifolium alpinum*, 43 in *Draba aizoides*, 40 in *Minuartia sedoides* and 32 in *Eritrichium nanum*. The maximum age of the majority of tap-rooted herbaceous plants in the lowlands is between 1 and 6 years.

Table 3.1 Selection of maximum (extreme) tree ages. Sources: Old-list, Rocky Mountain Tree-Ring Research (http://www.rmtrr.org/oldlist.htm), and tree-ring data-bank (http://www.wsl.ch), Dendrochronological laboratories of P. Gassmann, Neuchatel, Switzerland, and H. Egger, Boll, Switzerland

Species	Location	Maximum age (years)
Pinus longaeva	Wheeler Peak, Nevada, USA	4,844
Pinus longaeva	Methusela Walk, California, USA	4,789
Fitzroya cupressoides	Chile	3,622
Sequoiadendron giganteum	Sierra Nevada, California, USA	3,266
Juniperus occidentalis	Sierra Nevada, California, USA	2,675
Pinus aristata	Central Colorado, USA	2,435
Pinus balfouiana	Sierra Nevada, California, USA	2,110
Juniperus scopulorum	Northern New Mexico, USA	1,889
Pinus balfouriana	Sierra Nevada, California, USA	1,666
Pinus flexilis	South Park, Colorado, USA	1,661
Thuja occidentalis	Ontario, Canada	1,653
Pinus balfouriana	Sierra Nevada, California, USA	1,649
Taxodium distichum	Bladen County, North Carolina, USA	1,622
Thuja occidentalis	Ontario, Canada	1,567
Pinus flexilis	Central Colorado, USA	1,542
Juniperus occidentalis	Sierra Nevada, California, USA	1,288
Pinus albicaulis	Central Idaho, USA	1,267
Pseudotsuga menziesii	Northern New Mexico, USA	1,275
Juniperus occidentalis	Sierra Nevada, California, USA	1,220
Lagarostrobus franklinii	Tasmania, Australia	1,089
Pinus albicaulis	Alberta, Canada	1,050
Larix decidua	Valais, Alps[a]	1,081
Thuja occidentalis	Ontario, Canada	1,032
Cedrus atlantica	Atlas, Morocco[b]	1,024
Pinus edulis	Northeast Utah, USA	973
Pinus ponderosa	Wah Wah Mountains, Utah, USA	929
Pinus monophylla	Pine Grove Hills, Nevada, USA	888
Pinus albicaulis	Western Alberta, Canada	882
Pinus ponderosa	Central Utah, USA	843
Pinus nigra	Vienna, Austria[c]	833
Picea engelmannii	Western Alberta, Canada	780
Pinus cembra	Alps, Austria[d]	775
Larix sibirica	Ovoont, Mongolia	750
Pinus ponderosa	Northwest Arizona, USA	742
Pinus mugo ssp. *uncinata*	Pyrenees, Spain[e]	732
Larix lyalli	Western Alberta, Canada	728
Pinus ponderosa	Black Hills, South Dakota, USA	723
Pinus monophylla	White Pine Range, Nevada, USA	718
Pinus cembra	Carpathians, Romania[f]	701
Picea glauca	Klauane Lake, Yukon, Canada	668
Abies magnifica var. shastensis	Klamath Mountains, California, USA	665
Pinus siberica	Tarvagatay Pass, Mongolia	629

Pinus jeffreyi	Truckee, California, USA	626
Picea glauca	Aishihik Lake, Yukon, Canada	601
Pinus strobiformis	San Mateo Mountains, New Mexico, USA	599
Taxus baccata	Jura, Switzerland[a]	550
Picea abies	Jura, Switzerland[a]	576
Picea glauca	Norton Bay, Alaska, USA	522
Fagus sylvatica	Abruzzi National Park, Italy	503
Fagus sylvatica	Jura, Switzerland[a]	500
Abies lasiocarpa	Southern Yukon, Canada	501
Quercus petraea	Jura, Switzerland[a]	480
Acer pseudoplatanus	Jura, Switzerland[a]	460
Picea abies	Alps, Switzerland	455
Quercus petraea	Bern, Switzerland[g]	428
Quercus robur	Jura, Switzerland[a]	400

[a]Personal communication, P. Gassmann
[b]Personal communication, J. Esper
[c]Personal communication, M. Grabner
[d]Personal communication, K. Nicolussi
[e]Personal communication, U. Buentgen
[f]Personal communication, I. Popa
[g]Personal communication, H. Egger

3.3 What Limits the Life Span of a Tree?

Different aspects of ageing have been discussed in a number of reviews. A summary is given in Schweingruber and Poschlod (2005). Most studies to date focus on physiological aging processes and refer to parameters at the level of cells, tissues or organs, while processes relevant at the level of the whole plant are usually ignored (Thomas et al. 2003; Zentgraf et al. 2004; Schweingruber et al. 2006).

3.3.1 Programmed Cell Death

The process of secondary growth in trees involves the continuous formation and death of cells. Programmed cell death creates a diverse array of cell longevities. Taking the xylem as an example, tracheids and vessels formed very early in the growing season may live for only a few days, while the same cell types formed later may survive for months. In general, however, all water-conducting tissues die at the end of the growing season. Non-conducting fibres normally die after cell-wall thickening is finished. Their lifespan is short and rarely exceeds 1 year. In contrast, most parenchyma cells are longer-lived. Axial and vertical parenchyma cells in the sapwood may live for several years. The maximum age of living ray cells in *Robinia pseudoacacia* is 4–6 years and up to 130 years in *Sequoiadendron giganteum*.

Table 3.2 Selection of maximum ages of dwarf shrubs according Kihlman (1890), Callaghan (1973) and Schweingruber and Poschlod (2005)

Species	Location	Maximum age (years)
Rhododendron ferrugineum	Subalpine belt, Alps, Switzerland	202
Dryas octopetala	Banks Island, Canada	45
Loiseleuria procumbens	Subalpine belt, Alps, Switzerland	110
Vaccinium vitis-idaea	Heathland, Finland	109
Salix myrsinithes	Tundra, Kola, Russia	99
Arctostaphylos alpina	Tundra, Kola, Russia	84
Empetrum nigrum	Tundra, Kola, Russia	80
Helianthemum nummularium	Subalpine belt, Alps, Switzerland	66
Globularia cordifolia	South exposed rock, Switzerland	60

Trees face the problem that they can grow taller only by progressively putting on new cell layers around the entire surface of the stem. Over the years, this leads to the accumulation of a massive body of woody tissue, which, if containing live, respiring parenchyma cells (usually around 7% and 16% of the sapwood volume in conifers and hardwoods, respectively; White et al. 2000) would inevitably drain the energy resources of the tree even under the most favourable growing conditions due to the fact that the surface of assimilating foliage increases more slowly with size than the wood volume. To overcome this problem, old parenchymatic cells die and excrete fungicidal phenolic substances (Fig. 3.2). This protects the interior dead woody tissues from microbial decomposition, which is important in maintaining the mechanical stability of the tree [Fig. 3.3; but see Thomas (2000) for trees without true heartwood]. Often, this chemical impregnation of the heartwood goes along with a discoloration allowing us to distinguish macroscopically the coloured heartwood from the pale "living" sapwood.

The design of a tree crown is largely the product of cladaptosis, the die-back of twigs and branches. The process of cladaptosis is crucial for a trees ability to forage for light. It enables the tree to abscise branches that run into a negative carbon balance due to self-shading and light competition with neighbours. Some species, such as oaks and poplars, show a weak and almost unlignified zone at the base of the twigs, which acts as a predetermined breaking point (Fig. 3.4). Other species actively form a barrier zone at the base of their twigs to cut the twigs off from the water supply. As a consequence they dry up and drop off after a few months or years.

3.3.2 Whole Plant Longevity – Internal Versus External Factors

There is little literature about the endogenous processes controlling the longevity of whole plants (Ricklefs and Finch 1995) and, if discussed, the focus is either on genetic components or on the mere quantification of mortality rates as a demographic parameter.
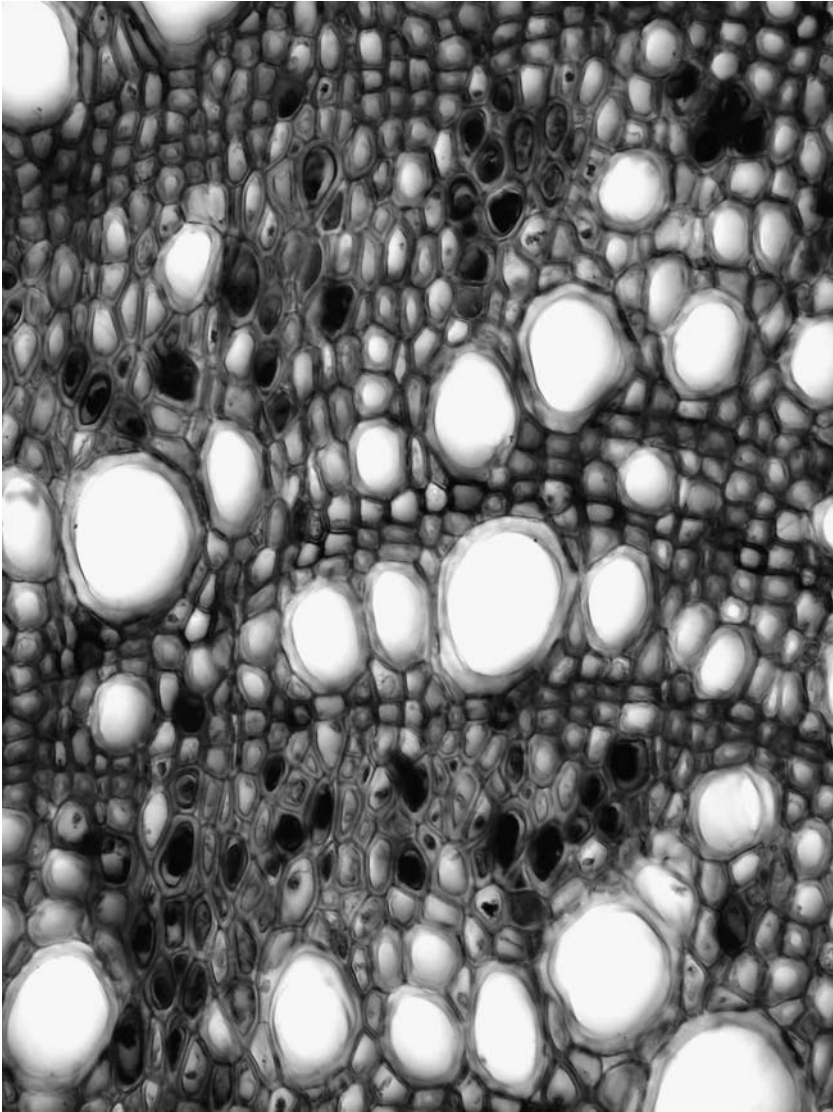
Fig. 3.2 Microscopic section through the heartwood of the dwarf shrub *Eriogonum jamesii*. Axial parenchyma cells contain dark substances, probably phenols

For herbs (with taproots – see above) the data allow us at least to distinguish between annual and perennial species (Schweingruber and Poschlod 2005). In addition, this latter study demonstrated that the life span of most herbs is definitely restricted to a few years, because the genetic potential excludes the possibility of reaching longevities in the order of decades (Fig. 3.5).
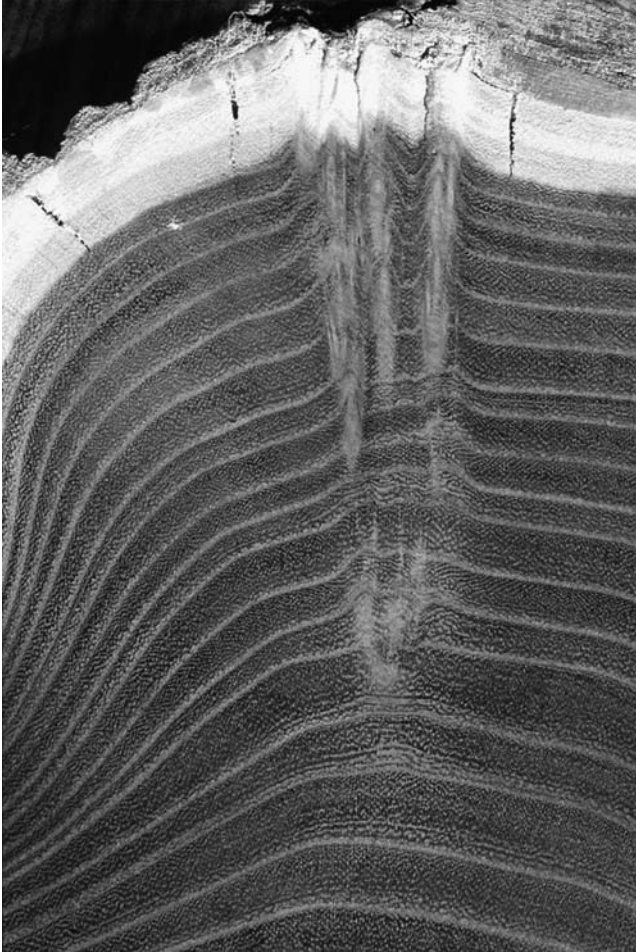
Fig. 3.3 Sapwood and heartwood in the xylem of a *Robinia pseudoacacia* stem. All cell types in the dark part (heartwood) of the stem are dead and contain phenolic, fungicide substances. Water transport and storage of assimilates occur in the light part (sapwood). Axial and vertical (ray) parenchyma cells are living

The genetic predisposition of whole plant death is difficult to evaluate in long-lived trees, because it would require long-term common garden experiments that would by far exceed human longevity. The collection of maximum tree ages given in Table 3.1 is rather arbitrary. Moreover, the available data probably underestimate maximum longevities. So-called "age hunters" tend to search for trees with particularly thick stems, but we know very well that size is an unreliable predictor for tree age. Quite on the contrary, maximum tree ages are much lower on sites with optimal environmental conditions. Dendrochronologists have often found

Fig. 3.4 Branches with scars of dropped twigs on *Quercus robur*. Crown formation is based on the existence of this process of cladaptosis

the oldest trees on marginal sites, where trees survive close to their ecological limit, e.g. in swamps or on shallow soils near the timberline. Such a negative relationship between site quality and longevity can be found in both 'annual' herbs and perennial trees. The 'annual' *Linum catharticum* completes its life cycle in 1 year only at optimal sites, but needs 3 years in the subalpine zone. The giant tree *Sequoiadendron giganteum* may grow for more than 3,000 years without any sign of senescence in its natural habitat in the Rocky Mountains, with ring widths remaining on average below 1 mm for centuries. In contrast, the same tree species grown in European plantations in a wet oceanic climate on deep soils has an average ring width of about 1 cm, but becomes very susceptible to wind storms. Thus, mortality seems to be correlated with size rather than absolute age.

Determination of maximum longevity becomes impossible in trees that reproduce clonally, such as poplars, willows and hornbeam. In these species, new ramets continue to sprout long after the initial stumps has decayed away. Even where the founder module is still present in the population of ramets, molecular methods may be required to actually identify it. This is illustrated by two examples: in the Canadian boreal forest, black spruce (*Picea mariana*) spreads vegetatively by
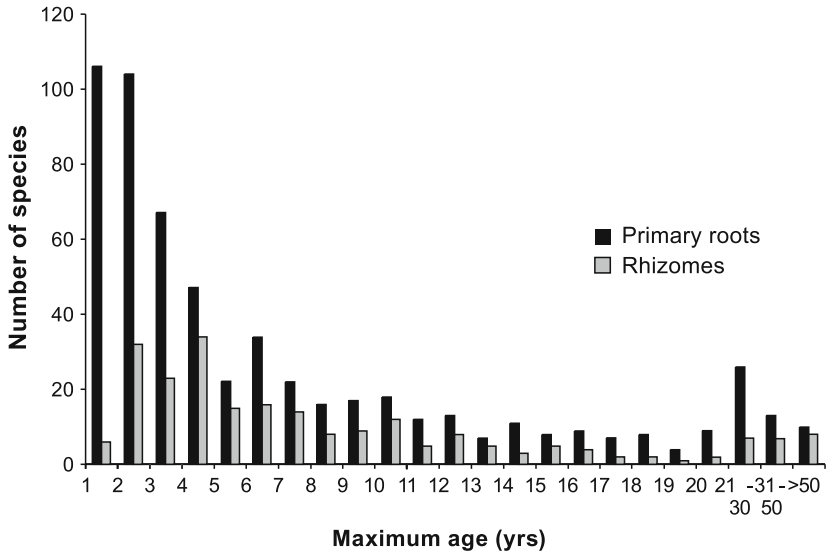
Fig. 3.5 Maximum ages of central European herbs and dwarf shrubs. *Black columns* Number of species with taproots roots (total of 603 species), *grey columns* species with rhizomes (total of 232 species); 63% of the species with taproots have a limited age between 1 and 6 years, and only of 8% of the plants have a lifespan that exceeds 20 years (Schweingruber and Poschlod 2005)

branch layering. A dendrochronological analysis revealed that a genet having regenerated from seeds after a forest fire may reach an age of at least 300 years (Legère and Payette 1981). However, molecular studies showed that a larger genet could even reach 1,800 years (Laberge et al. 2000). The oldest genet on earth is a polycormon of *Lomatia tasmanica* in Western Australia spread over 1.2 km^2. Charcoal buried next to fossilised leaves with the same genome as the contemporary trees was dated as being at least 43,600 years old (Lynch et al. 1998).

It remains an open question whether trees are in principal immortal or whether their genetic constitution limits their lifespan as is the case for herbaceous plants with taproots. The example of *Lomatia tasmanica* in fact suggests that clonal tree species are almost immortal. However, even for non-clonal trees we are unable to know for sure whether they would not live forever (or at least for much longer), if they were protected from disturbances and diseases. While we know very little about the endogenous controls of longevity, there are countless studies on how various external agents such as fire, wind, flooding, herbivory, pathogens, pollutants, etc. speed up senescence and reduce the lifespan of trees. In the following we can only briefly touch on this topic, and we do so only to emphasise that the influence of external mortality factors biases our view of tree longevity.

Based on the simple observation that ecological factors limit the existence of single trees, we have to accept the old idea that trees often die by exhaustion or starvation (Molisch 1938), e.g. due to a lack of light (Fig. 3.6) or energy (i.e. summer temperatures; Fig. 3.7) or a shortage of water (Bigler et al. 2006). This
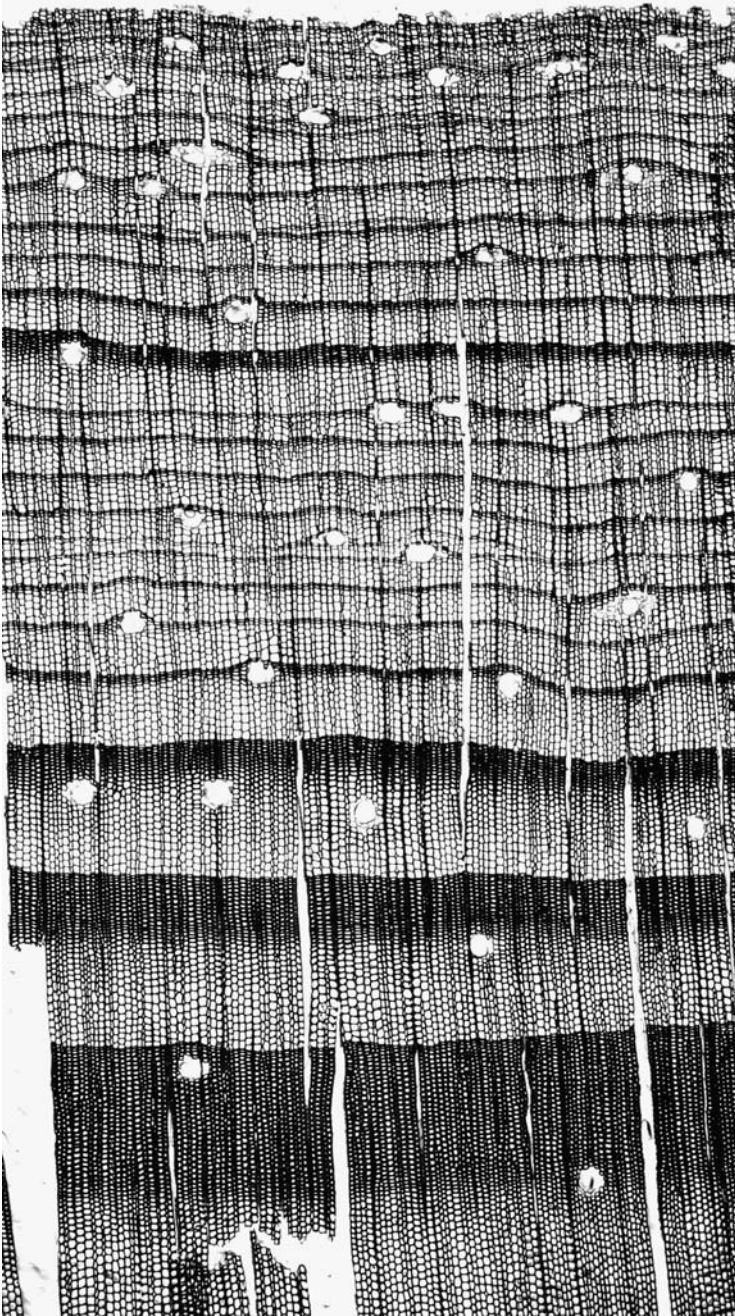
Fig. 3.6 Starvation due to light shortage. Competitive beeches have suppressed the crowns of pines (*Pinus sylvestris*) and induced their death. The starving period is indicated by the narrow rings with small latewood and the enhanced frequency of resin ducts in the pre-lethal period

Fig. 3.7 Dying at the beginning of the Little Ice Age between 1430 and 1450 AD. Stands of larches (*Larix sibirica*) died at the timberline in the Polar Ural. The stumps have remained and have been dated dendrochronologically (Shiyatov 1992)

may lead to false conclusions about the longevity of species. For example, maximum longevities reported in the literature for the Eurasian *Betula pendula* range between 120 and 140 years (Nikolov and Helmisaari 1992). However, Schulze et al. (2005) recently found individual trees older than 300 years. One reason for the low literature estimates may be that birches, as typical pioneer trees, tend to be outcompeted by tall-statured late-successional species already after about 100 years. Thus, the majority of birches dies early as a result of light starvation and not because they have reached their biological limit. Older individuals may simply have been overlooked. Another example was already mentioned above: old trees are very rare in the Canadian boreal forest. However, this is determined not only by the biological age limit of the tree species, but also by the circumstance that in the North American boreal forest lethal crown fires recur on average every 100 years (see Chap. 13 by Bergeron and Harper, this volume, and Wirth 2005). Toxic substances, for example, sulphur dioxide from anthropogenic pollution sources can kill trees, but we have also found that the reaction to poisonous agents depends on the species and may vary even between individuals. Trees at the borderline of the catastrophic sulphur contamination in the downwind area of Norilsk (Siberia) clearly show species-, individual-, and site-dependent mortality: larches (*Larix sibirica*) in all ecological situations were dead, whereas spruces (*Picea obovata*) and birches (*Betula pendula*) growing at the same ecological sites were either dead, or had reduced foliage or even looked healthy. Spruces in the most intensive contaminated regions survived as dwarfs in moist riverbeds between healthy looking sedges (Schweingruber and Voronin 1996, see Fig. 3.8).

Biological degradation caused by mammals, insects, nematodes and fungi affects different species in different ways (Thomas and Sadras 2001). A morphological expression of the different sensitivities towards herbivory of pathogen

Fig. 3.8 Death due to anthropogenic pollution near a smelter in Central Siberia (Norilsk). Extremely high SO_2 content in the air leads to selective tree death. The most sensitive species are larches (*Larix sibirica*); spruces (*Picea obovata*) and birches (*Betula pendula*) are less sensitive. Within Siberian spruce there are also intra-specific differences in sensitivity: some individuals die, but some manage to survive high doses of toxic gases

attack is the formation of barrier zones (Schweingruber 2001, see Fig. 3.9). Longitudinal barriers are, for example, weak in birch and ash, but very effective in beech and maple (Dujesiefken and Liese 1991).

A few years ago there was a great hope that tree-ring curves would allow the prediction of individual lifespan. Indeed, there is strong evidence that the risk of mortality is negatively correlated with growth and that the shape of this relationship differs between trees with low and high shade tolerance (Kobe et al. 1995). However, it is too simple to assume that a reduced growth period in adult trees

Fig. 3.9 Formation of a barrier zone after mechanical wounding of the cambial zone. The zone below the wound was laterally compartmentalised by the formation of a toxic barrier zone. Fungal decay occurs only in the part below the wound, all other parts are protected by the barrier zone. *Arctostaphylos uva-ursi*. 40x

would indicate senescence. Very narrow ring sequences simply indicate a transient period of starvation and, as such, are a reversible feature of tree growth (Fritts 1976). Moreover, tree death may occur abruptly or gradually. Rapid death has often been observed in shade-intolerant species, whereas shade-tolerant species literally

Fig. 3.10 Mammoth trees (*Sequoiadendron giganteum*) represent tremendous carbon stocks and may live for 3,000 years
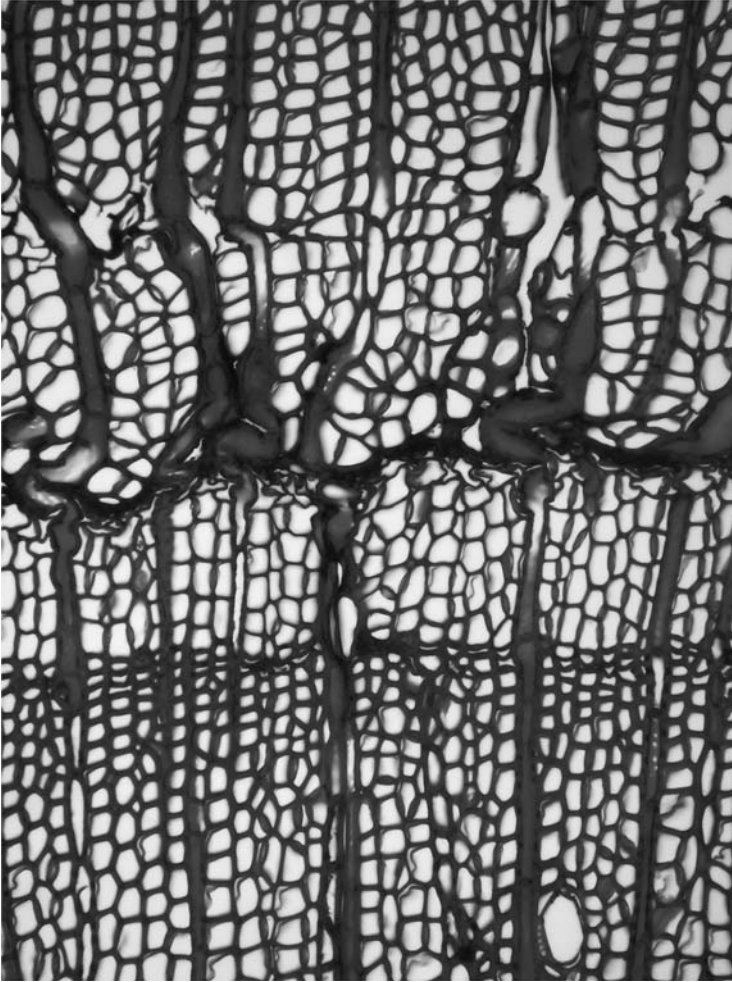
Fig. 3.11 Frost ring. The reaction to extreme low temperatures at the beginning of the growing season at the end of June 1601 in the Polar Ural was the formation of a frost ring. *Larix sibirica* (100x)

shrink to death on a branch-by-branch basis over decades to centuries. This variability in behaviour makes it impossible to use tree ring sequences to infer estimates of tree longevity or even to predict the expected duration until death.

In summary, the large range of longevities realised by trees makes it likely that a genetic predisposition in general determines longevity, but the real lifespan will always be modified by the environment. Thus, separating 'nature and nurture' in their effect on longevity will remain a difficult task.
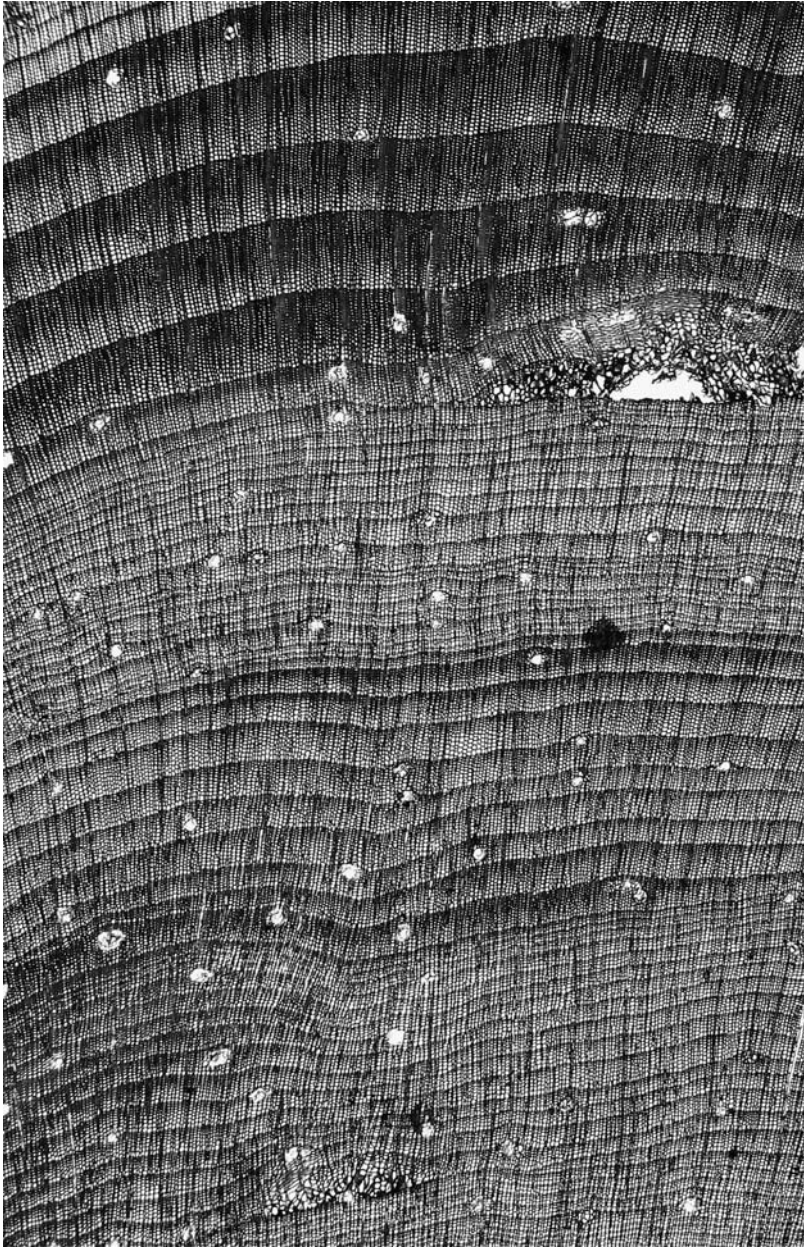
Fig. 3.12 The reaction to an extreme change in the position of a branch after being hit by a stone was the formation of a callus and compression wood. *Pinus mugo*. (20x)

Fig. 3.13 People celebrating under the canopy of an old lime (Fischbach und Masius 1879)

3.4   Concluding Remarks

Within the plant system, and within the range of life forms, trees are very special. Thanks to their high longevity, trees may accumulate enormous amounts of bio-mass. The largest tree on earth, a *Sequoiadendron giganteum* contains 1,470 m^3 wood with a dry weight of 800 tons. One single tree contains approximately 400 tons carbon. These 'biological monsters' would not exist if they were not perfectly designed to resist extreme mechanical stress (Fig. 3.10).

The potential age of physically existing trees exceeds that of all other life forms. Old trees tend to be perfectly adapted to specific sites. In Europe, many old larches and stone pines at the alpine timberline germinated at the beginning of the Little Ice Age in the thirteenth century. They have survived many stress periods and are now benefitting from the current warming period. Since these 'living fossils' maintain the potential to regenerate generatively and, in many cases, also vegetatively, these trees are an indispensable genetic resource. Old trees do not lose their capacity to respond to the environment. Variations in the size of their cells and in the width of their tree rings demonstrate that even millennium-old trees maintain their biological sensitivity and their potential to react to environmental stress and favourable periods. Expressions of this reaction potential are e.g. scars, callus formation (Fig. 3.11), reaction wood (Fig. 3.12) and growth variations such as abrupt growth changes and pointer years.

Thanks to their longevity and their sustained sensitivity, old trees represent important archives of past climates. Dendrochronological techniques allow the reconstruction of annual climatic patterns and the occurrence of extreme weather events at both local and global level. In doing so, they provide a means of placing

the contemporary man-made climate warming into a historical context (Fritts 1976; Schweingruber 1995; Fig. 3.11).

Old trees have always fascinated people. Gollwitzer (1984) has summarised the evidence for the human fascination with old trees, which goes back at least 3,000 years: old trees were the seats of the gods. They stood at the centre of world religions and embodied myths. People celebrated and mourned under the canopy of old trees (Fig. 3.13). During the period of enlightenment in the seventeenth century, people began to study trees scientifically. Today, we still have not solved the puzzle of why trees become as old as they are. Only one thing is certain: the circumstance that so many tree species have gone extinct tells us that even trees do not live forever – as palaeontology shows us (Zimmermann 1959).

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