Wood Quality and its Biological Basis

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Wood Quality and its Biological Basis

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Preface

Wood is undoubtedly the most versatile raw material available to man. It is burnt as fuel to provide energy (accounting for about 70% of all wood harvested), shaped into utensils and implements of various kinds, used as a cost-effective structural engineering material, converted into fibres for most paper production, and put to newer uses as a source of industrial chemicals. The steady increase in the demand for wood, resulting from a concomitant increase in its applications, means that pressure on forests is constantly increasing. The need to cut down trees for wood is in direct conflict with the need to preserve forests for the conservation of biodiversity and as sinks for carbon dioxide. It is therefore essential that forests are managed sustainably, if demand is to continue to be met without detriment to our environment. This can be achieved by developing new forests and replacing trees that are harvested, while at the same time ensuring that the trees that are grown produce wood of good quality.

The problem lies in the definition of wood quality. Wood which may produce pulp with good paper-making properties may not be suitable for use in construction, for example. The intrinsic variability of wood properties is also of concern in relation to quality. In the case of the paper industry, the pulping process is modified and the fibres are blended to produce a uniform end product. The construction industry relies on the grading of timber at the sawmill to select those timbers which are fit for purpose. Both processes have important economic implications.

For this reason, selection of seedlings for planting based on their potential wood properties should depend on their anticipated use. However, it is impossible to predict what the requirements might be 50–70 years later when the tree is ready for harvesting. Because of this, the pulp industry is beginning to look at fast-growing species, such as hybrid poplar, to be harvested in less than 10 years. The juvenile characteristics associated with the timber from these trees make them unsuitable for other high value purposes, except perhaps as veneers. There are good biological reasons why this juvenile wood develops and is required by saplings, but its presence is currently exercising the minds of wood scientists concerned about its inferior properties as a raw material.

The quality of wood results largely from the chemical and physical structure of the cell walls of its component fibres. This can be modified in nature as the tree responds to physical environmental stresses, such as wind acting on the growing tree. Internal stresses can accumulate, which are released

catastrophically when the tree is felled, rendering the timber useless, or at least reducing its value considerably. The quality of timber as an engineering material also depends on the structure of the wood and the way it has developed in the living tree.

Thus, tree improvement for quality cannot be carried out without an understanding of the biological basis underlying wood formation and structure. Wood is what it is because it is made by trees, and the question then is what are trees doing to wood? The primary aim in preparing this volume was to bring together the viewpoints of biologists and physical scientists, to cover the spectrum from the formation of wood to its structure and properties, and to relate these properties to industrial use. We have attempted to produce a book which is different from those concerned entirely with the biological or the engineering aspects of wood, and we hope that it will provide useful insights into both industrial and academic aspects of the subject.

We are grateful to all those who have contributed chapters.

J.R. Barnett
G. Jeronimidis

1 Tree growth and wood quality

Rodney Arthur Savidge

1.1 Cambial growth

1.1.1 Wood is a biosynthetic end product

Cambial (or secondary) growth comprises innumerable phenomena of biophysics, biochemistry and cell biology, and few of these phenomena are yet well understood (Savidge *et al.*, 2000; Savidge, 2001a). There has never been a dedicated resolve on the part of either forestry or biology to develop an in-depth understanding of how trees make wood. Consequently, progress has been a function of the piecemeal efforts of a few individuals and small groups. Under the pressure of increasing demands for wood and wood fibre associated with world population growth, and in the face of dwindling forest area containing increasingly juvenile stock, the need to have greater knowledge of the biological factors controlling wood supply, in terms of both quantity and quality, seems obvious. Moreover, the international climate-change community, evidently unaware of how little is understood about wood formation in trees, has identified forests as important sinks for draining off excess atmospheric carbon dioxide, the capacity of which can supposedly be readily increased (Savidge, 2001b).

Based on the different wood anatomies of conifers (softwoods) and hardwoods, softwood cambial growth gives the impression of being the less complex. Softwoods are also of worldwide distribution and importance, making consideration of their secondary growth a logical starting point for summarizing what is known about life processes underlying wood formation and the control of wood quality. Some aspects of hardwoods are considered later in this chapter.

1.1.2 Zonation

Under the microscope, the actively growing cambium of a conifer exhibits several developmental zones. The cambial zone (CZ, Fig. 1.1A) is seen to comprise two cell types, ray and fusiform cambial cells. The former are approximately isodiametric whereas the latter are many times longer than wide when measured across either their radial or tangential axes of symmetry. Through periclinal cell divisions, both ray and fusiform cambial cells produce radial files of daughter cells, adding inwardly to the pre-existing wood and outwardly to the pre-existing phloem (Fig. 1.1A). New fine structural details of the periclinal division as it occurs in conifers following cryofixation were
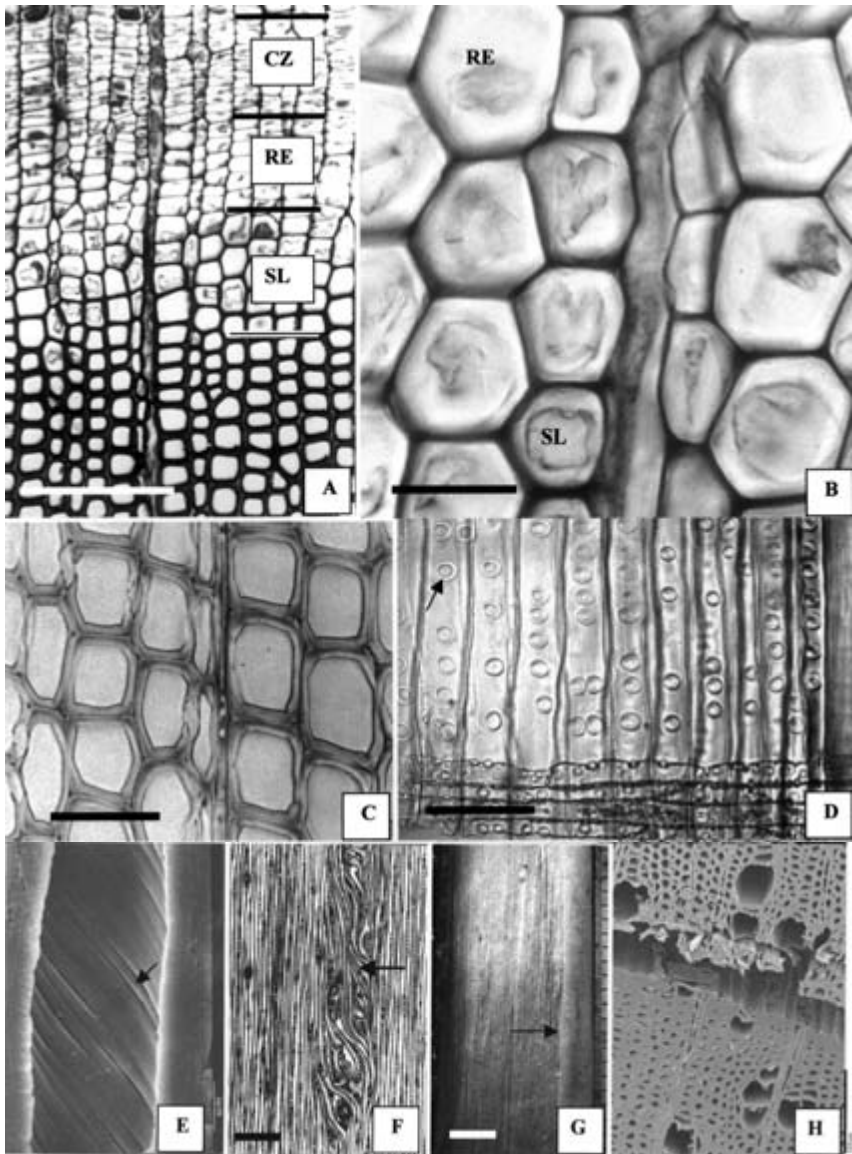
Fig. 1.1 (A) Cross section of the region of active wood formation in *Pinus contorta*. CZ, cambial zone; RE, zone of primary wall radial expansion; SL, zone of secondary wall formation and lignification, with mature tracheids below. A ray bisects the field of view. Bar = 100 μm. (B) Higher magnification of A showing the region transitional between the RE and SL zones, with a ray bisecting the field. Bar = 20 μm. (C) Cross section of wood of *Abies balsamea*. The compound middle lamella and tripartite secondary wall are evident, as are bordered pits. A ray bisects the field. Bar = 40 μm.

recently reported (Rensing *et al.*, 2002). Younger cambium in terminal parts of trees and older cambium at the bases of aged trees generally have shorter fusiform cells than cambium in the intervening stem region. Fusiform cell length is a major factor in determining the final length of conifer tracheids (or *fibres*); consequently, the longer fibres in uncultivated aged trees are found in the middle-aged region of the stem.

On the inner periphery of the CZ, cell-division activity is supplanted by enlargement of CZ daughter cells by expansion of the primary cell-wall surface area. It occurs primarily in the radial direction, creating a zone of radially expanding and expanded primary-walled cells (RE, Fig. 1.1A). Although cell division and expansion both contribute to overall increase in tree girth, expansion – thought to be driven by turgor pressure and facilitated by auxin-promotion of cell-wall loosening – is the primary means of moving the CZ centrifugally (Savidge, 1996).

During, but usually near the completion of each cell's primary-wall expansion, a decision is made to either initiate or not the development of bordered pits (Fig. 1.1D). Those RE cells undergoing bordered-pit development subsequently begin producing secondary-wall lamellae and lignin, thus generating the secondary-wall forming layer (SL), a zone of still-living cells (Figs 1.1A–D).

1.1.3   Bordered-pit development

Bordered-pit numbers are typically highest in earlywood and decline to negligible frequency in the last-produced latewood tracheids of each annual ring. Bordered pits are usually confined to radial walls, although they occur naturally in tangential walls, particularly of latewood tracheids at low abundance (Panshin & de Zeeuw, 1980). Tangential wall bordered pits have been induced to develop experimentally in large numbers by manipulating auxin concentration (Leitch & Savidge, 1995).

Both the cell biology and biochemistry underlying bordered-pit development remain uncertain, but it is clear that the process involves a series of successive

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Fig. 1.1 (continued) (D) Radial section of *P. resinosa* developing earlywood, with mature latewood on the far right. The arrow points to a bordered pit at an early stage of development of its over-arching border. The bar (50 µm) is in a ray tracheid having smaller diameter bordered pits. (E) SEM view of a compression wood tracheid showing separations in the microfibrillar matrix of the S2 layer (arrow). The bar at lower right is 4 µm. (F) Tangential section of *Picea glauca* showing a microdomain (arrowed) of tracheids with upward to left orientation relative to the surrounding elements. Bar = 200 µm. (G) Radial view of *Betula alleghaniensis* showing a juvenile core that changes abruptly, at the arrowed location, to a different wood. Bar = 15 mm. (H) Cross section at the arrowed point in G showing the interface between the corewood (lower) and the exterior wood (above). The bar at lower right is Bar = 10 µm.

and quite profound modifications to the compound middle lamella between adjoining RE cells, as can be seen in Fig. 1.1D. The spatial correspondence of the borders in adjoining cells is clear evidence that some form of intercellular communication occurs (Savidge, 2001a). After the circular site, or margo, of the pit-to-be has become visible and the torus (not found in bordered pits of all species but common in the Pinaceae) has begun to form in an RE cell, birefringent putatively cellulosic highly oriented microfibrils begin to be deposited exclusively around the circumference of each margo. This localized deposition of circularly oriented crystalline microfibrils continues, around and around, progressing gradually inward while winding upward towards an imaginary line at the centre and perpendicular to the plane of the margo. Thus, the over-arching pit border is formed, leaving an aperture usually about half the diameter of that of the margo. During its formation, the over-arching border can be isolated as a discrete ring (Savidge, 2000a); however, other evidence indicates that over-arching borders of discrete bordered pits are actually interconnected by thin microfibrillar strands (Savidge, 1996).

The presence of a spherical organelle tightly appressed to the plasma membrane, such that the side in contact with the membrane is flattened, may be the explanation for how the margo and over-arching border arise (Savidge, 2000a). Contact between the cell membrane and the flattened organelle is envisaged to prevent microfibril deposition occurring within the area of the margo and, if the organelle contains lytic enzymes (as supposed from its evidently vacuolar origin – Bethke *et al.*, 1998; Savidge, 2000a), it could concomitantly serve to hydrolyze non-cellulosic constituents of the underlying compound middle lamella. The upper, domed surface of the membrane-bound organelle would obviously also serve as template for the formation of the circular over-arching border.

1.1.4   Secondary-wall lamellae

After the onset of bordered-pit development, general secondary-wall polysac-charide deposition commences, followed by the initiation of lignification in the middle lamella, most conspicuously at cell corners. By the completion of these processes, three secondary-wall layers appear to be present when viewed under the light microscope (Fig. 1.1C), although electron microscopy indicates that each layer actually comprises a number of sub-lamellae. This structure has profound implications for wood properties and utilization, and it is described in detail in Chapters 2 and 4. The chemical structure of the wall is the subject of Chapter 3. [The problem of dimensional stability in wood ultimately reduces to its chemistry, in particular the relative abundances of different chemical bonds to resist stress and stabilize the macrostructure. What is really needed in this area is a detailed understanding of the chemical reactions occurring during wood formation and how they are controlled.]

1.1.5 Microfibrils and lignin

The essential events underlying differentiation of a cambial derivative into a woody element are microfibril deposition and lignification. Considerable research has been conducted into both over the last century, but at the level of biochemistry much remains to be discovered about how these processes proceed (Lewis & Sarkanen, 1998; Atalla, 1998; Delmer, 1999; Brett, 2000; Savidge, 2000a; Savidge & Förster, 2001). To do justice to the continuing uncertainty, it would probably be correct to say that most research so far attempted has suffered from a lack of clear definition, insufficient material for investigation and/or a lack of resolution. Compounding the overall problem, no substantial and therefore convincing synthesis of cellulose *in vitro* using a cell-free biological system has yet been achieved, despite a number of reports on putative *cellulose synthase* genes (Delmer, 1999; Brett, 2000; Taylor *et al.*, 2000; Williamson *et al.*, 2001; Desprez *et al.*, 2002).

A common conclusion from many scientific investigations has been that microfibril orientation is determined by the orientation of cortical microtubules (Chaffey *et al.*, 2000), but no shortage of additional investigations has presented data indicating the contrary. Many have noted a lack of correlation between the two orientations (e.g. Sugimoto *et al.*, 2000a,b; Bichet *et al.*, 2001). It has also been suggested that microfibril production must precede cortical microtubule orientation (Fisher & Cyr, 1998). Indeed, some evidence indicates that there may be no need for microtubules at all during microfibril deposition (Savidge & Barnett, 1993).

Although the field of microtubule–microfibril correlation analysis seems to be at an impasse, there is substantial experimental evidence indicating that the orientation of cortical microtubules is altered by the phytohormone environment (Blancaflor & Hasenstein, 1995; Wenzel *et al.*, 2000). *Microfibril* has become synonymous with cellulose, but xyloglucan and glucomannan microfibrils – easily confused with cellulose microfibrils when merely imaged at the structural level – are well-known constituents of secondary-wall layers and, arguably, are as important as cellulose in determining many of the properties of wood (Jones, 1971; Wilkie, 1985; Brett, 2000). Could the explanation be that some micro-fibril polymerizations are, and others are not, linked to cortical microtubules?

The biochemistry of lignification is supposedly far better understood than the formation of microfibrils, but the reality is that it also remains an open question, far from completely understood (Lewis & Sarkanen, 1998; Savidge & Förster, 2001).

1.1.6 Protoplasmic autolysis

Biological control of protoplasmic autolysis during xylogenesis has received little attention. It should be noted that sapwood is not, in contrast to popular perception, a dead tissue. A large proportion of cambial derivatives which

become incorporated into sapwood actually remain living, for example as ray and axial parenchyma, and as non-autolyzed fibres, those cells dying only years later in association with heartwood formation (Savidge, 1996). Hardwood fibres tend to be ambivalent in pursuing a programme of cell death, but tracheary elements (i.e. tracheids and vessel members) in both conifers and hardwoods seem to be committed to apoptosis occurring within at least a year, and usually within a month, after the elements have otherwise differentiated. As the newly matured and protoplasmically autolyzed woody elements become distanced from the CZ, water begins flowing from one element to another through bordered pits and, in the case of hardwoods, through the perforation plates separating vessel members. Thus, water is distributed throughout the tree. It is probable that the living component has a role in resisting the onset of decay, and it is well established that diurnal and phenological changes in chemistry are normal to the sapwood, a result of their metabolism.

1.1.7   Cambial fusiform cell length and orientation

Fusiform cambial cells usually, but not invariably, give the appearance of being stretched in a direction more or less parallel to the long axis of the stem (or branch, or root). Fibre elongation in hardwoods is promoted by the phytohormone class known as gibberellins (Stant, 1961; Eriksson *et al.*, 2000), and these presumably also influence the elongated character of fusiform cambial cells in all species (Savidge, 1985; Kijidani *et al.*, 2001). Gibberellin promotion of fusiform cambial cell elongation remains to be unequivocally demonstrated, however. Continuing basipetal transport of auxin through the cambium was found to maintain the fusiform nature of cambial cells, preventing them from shortening and becoming septate axial parenchyma (Savidge, 1983; Savidge & Farrar, 1984). As shown in Fig. 1.1F, microdomains of disoriented cells sometimes arise within otherwise oriented populations, and the control mechanisms underlying microdomain formation, although still poorly understood, are believed to be at the heart of spiral, wavy and interlocked grain formation in trees (Savidge & Farrar, 1984).

1.2   Perennial cambial growth

1.2.1   Episodic but variable cambial growth

Wood can be seen as an engineering material, an aggregate of fibres and fines, or as a mass of different chemical substances and voids in combination, but more fundamentally wood is a biological end product generated during cambial growth over successive years. Cambial growth is episodic, restricted in temperate zones to the warm spring and summer months when photoperiod is long, and limited to periods of water availability in the tropical zones (Savidge, 1993). The outcome of each growth episode can be envisaged simplistically as the

formation of an inverted cone, or layer, of durable, supportive woody elements deposited upon the pre-existing structure. Each new layer of wood at the commencement of its formation becomes chemically cemented to the woody elements of the preceding layer through covalent bonding between lignin, polysaccharides and other substances. Consequently, wood when green usually is a seamless, continuously reinforced material, although there are exceptions (Fig. 1.1G). Vertical or rotational shear-slip at the boundary between increments (Fig. 1.1H) is encountered only following stresses sufficiently severe to crush or otherwise deform the weaker earlywood elements.

1.2.2   Tapering to the point in form and function

Every tree tapers to minute apical meristems supporting primary (or extension) growth. Cambium arises immediately basal to sites of primary growth; thus, cambial age and therefore the time available to increase the girth of the corresponding axis necessarily vary along the axis. Sites of primary growth are the locations within the tree having the highest concentrations of nutriment. Consequently, both solute concentration and water-potential gradients extend longitudinally over stem and branch axes. In other words, the intrinsic environment experienced by individual cambial cells will vary from one point to the next, even when the extrinsic environment of the whole tree is maintained constant within a controlled growth chamber.

The reality of chemical and physical gradients extending longitudinally, and also circumferentially and radially, in the cambial region is surely the key factor determining the variable nature of wood (Savidge, 1996, 2001a). In the final biological analysis, individual elements of wood constitute phenotypes arising through interactions between each cambial derivative's genotype and its subcellular environment (Savidge, 1996, 2000a). The cambial genotype throughout a tree can be assumed to be constant, but because the physical and chemical environments experienced by cambial cells vary at different locations, the nature of gene expression and the resulting end products reasonably can also be expected to vary. Thus, although perhaps not welcome information for wood-processing industries, within the framework of the biological sciences it is entirely to be expected that the nature of wood must inevitably vary over the tree.

The above may give the impression that cambial growth, though variable, always occurs, and certainly the concept of annual rings and the physiologically unsubstantiated interpretations given to them by the field of dendrochronology reinforce that supposition. On the other hand, cambial growth in conifers is commonly suppressed at the bases of a tree's lower live branches, as well as at the bole base, in old trees (Meredieu & Caraglio, 2002). Moreover, pronounced taper does not necessarily always attend morphogenesis of perennial woody plants having cambium. Lateral roots, for example, typically extend through soil for many metres nevertheless maintaining quite small diameters over the

distance, little or no cambial growth attending their primary growth. Vines also are quite capable of focusing their energy and biomass allocation on extension growth, although cambial growth does occur to a limited extent particularly near the base of the vine. Many hardwood species when grown in tight quarters allocate minimal resources to secondary growth, instead growing in height to produce long slender stems. Considering the differences between roots, vines and trees, there appears to be a connection between the occurrence of cambial growth and the need of the stand-alone tree to biosynthesize sufficient structural support to resist the force of gravity.

1.3   Wood quality in perspective

1.3.1   Defining wood quality

Wood *quality*, as understood within both dictionary and practical contexts, has to do with the degree of excellence – in relation to some preconceived applica-tion(s) – of each log, piece of wood or woody fibre under consideration. Because quality assessment is multi-faceted and depends on the intended application, there is no absolute measure. Quality assessment by the woodsmen who fell and process the trees and by the mill workers who decide how logs should be used involves experienced observation and snap-judgment integration of particular features, based largely on subjective experience.

1.3.2   Measuring wood quality

Some aspects of quality, such as wood density, cellulose, lignin or extractive contents, can be repeatedly analyzed and quantitatively expressed with high accuracy and precision, although always within the proviso that the estimate may be accurate only for the sample actually measured and within the method employed. Other measures, such as fibre length, cell-wall thickness, microfibril angle, bordered-pit number and percentages of the various types of woody elements coexisting in a wood are more problematic. Upon repeated random sampling and measurement of the same preparation, a Gaussian distribution is predictably obtained, and the magnitude of the standard deviation may provide equally or more important information than the mean value. However, that information essentially is no more than a confirmation of what can be readily seen when viewing a section of wood in the compound light microscope (Fig. 1.1). Immense variation exists within wood. In other words, the sub-micrometre pre-cision of microscopic imaging and associated measuring of small samples of wood readily and consistently reveals that so-called *accurate* estimates on wood samples obtained through physical and/or chemical analytical procedures in fact are low resolution, relatively crude simplifications. They do little justice to the immense variation existing in wood, from nanometre to higher scales.

1.3.3   Wood quantity versus wood quality

Wood quantity and quality can be contemplated independently of one another, at least in an abstract sense. Whereas wood *quantity* is concerned with the total amount of wood (measured as diameter, length, volume, weight or any combination thereof) and can be expressed numerically with accuracy and precision, quality assessment frequently involves subjective estimations. However, both have their origin in the cambial region, and the dimensions of the bole usually have a major influence on quality as well as quantity, particularly at the applied level. For example, clear or knot-free wood is obtained from larger diameter trees; lumber dimensions in the mill are decided on the basis of log length and diameter; slow-grown conifers with smaller diameter stems have more dense and therefore stronger woods than those of fast-grown trees; and more dense and therefore higher yielding pulps come from fast- as compared to slow-grown hardwoods. In other words, fundamental research projects focusing on the control of cambial growth, allocation of photosynthate and nutrients to cambium, metabolism in the cambium, water potential relations across, along and around the cambial sheath, and cambial cell biology in general have direct relevance to understanding wood quality as well as wood quantity (Larson, 1969).

1.3.4   Stem dimensions and quality

Stem dimensions are a function not only of how quickly height and girth increase during any one episode of growth, but of how many growth episodes have occurred. A massive millenary redwood or a 140-year-old straight-stemmed American chestnut (Figs 1.2A and B, respectively) generally would be expected to have high quality boles. On the other hand, as Figs 1.2C and D show, despite their ages, the boles of a century-old eastern white pine or of an 800-year-old white spruce might fail most quality tests, excepting perhaps those of specialist wood artificers. Thus, aging, although usually an enhancing factor, is of itself no guarantee that the wood in a tree will be of high quality in relation to the more common uses of wood.

   Although the many wood-quality problems attending taper appear to be unavoidable during the youth of the stand-alone tree, trees when approaching their maximum height tend to lose taper, secondary growth continuing especially in the crown after primary growth has been reduced to production of new leaves or needles with little associated extension growth (Fig. 1.2). Thus, the problem of taper finds a solution in time, and the primary controlling factor ultimately is the vision forest management can muster in its long-term planning.

1.3.5   G×E control of wood quality

There are both genetic and environmental reasons for time not being the sole determinant of stem dimensions (Savidge, 1996, 2000a, 2001a). The genetic
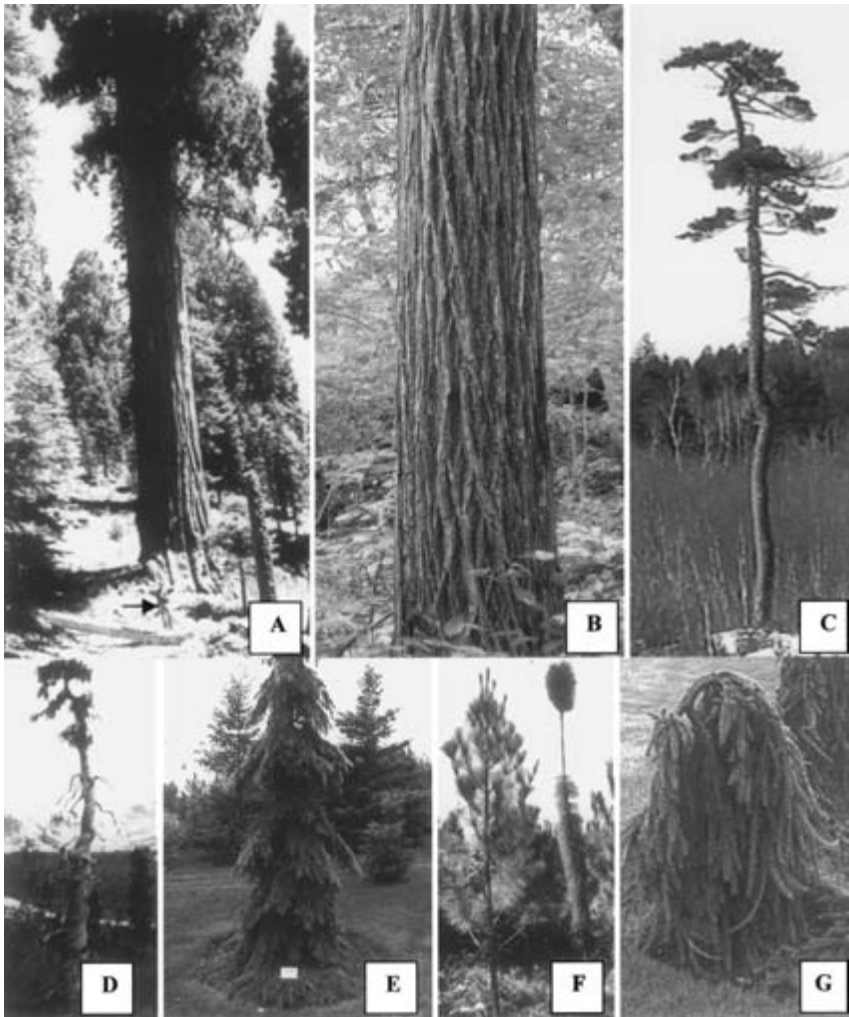
Fig. 1.2 (A) Mature *Sequoiadendron giganteum* bole in Mountain Home Demonstration State Forest, California. For scale, a man at the base of the tree is arrowed. (B) A young *Castanea dentata* bole of good form, Mount Uniacke, Nova Scotia. (C) *Pinus strobus*, typical of the trees rejected by loggers throughout New Brunswick, Canada. (D) *Picea glauca* var. *albertiana*, severely spiral grained, near Mount Nansen, Yukon Territory, Canada. (E) *P. glauca* phenotype in the New Brunswick Botanical Garden. (F) Normal branched and foxtailed *Pinus caribea* (reproduced with FAO permission from Kozlowski & Greathouse, 1970). (G) Another interesting *Picea glauca* phenotype in the New Brunswick Botanical Garden.