The Ecology and Silviculture of Oaks

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Preface

> The earth is to be seen neither as an ecosystem to be preserved unchanged nor as a quarry to be exploited for selfish and short-range economic reasons, but as a garden to be cultivated for the development of its own potentialities for the human adventure.
>
> (René Dubos, 1976)[1]

This book is written for forest and wildlife managers, ecologists, silviculturists, environmentalists, students of those fields, and others interested in sustaining oak forests for their many tangible and intangible values. The focus is on the oaks of the United States. Although the approach is fundamentally silvicultural, it is based on the premise that effective and environmentally sound management and protection of oak forests and associated landscapes should be grounded in ecological understanding. Although the subject is inherently scientific and technical, we have striven to make it generally accessible by minimizing the use of technical jargon. Where technical terms are necessary for efficient expression of concepts, we have first defined them.

Much has been written about the ecology and silviculture of oaks. So much so that the related body of literature represents, in one sense, an informational 'embarrassment of riches'. The embarrassment derives primarily from the paucity of synthesis within and across two broad fields of study. The first is ecology, which is the scientific study of the processes and relations among organisms and between organisms and their environment including associated energy transformations. The second is silviculture, which is the art and science of producing, tending, and sustaining forests. Although the literature on North American oaks dates to the colonial period, most of it was written within the last 50 years, and a large proportion of that within the last 25 years. However, much of this literature resides in relatively obscure scientific and technical journals, proceedings of professional and scientific meetings, government publications, and other sources that are often difficult to locate and retrieve. But even with ready access to this disparate information, its synthesis into an holistic framework of knowledge is a daunting task. This book attempts to ease, if not eliminate, those problems.

Although ecology has become a household word, silviculture has not. Nevertheless, silvicultural practices have shaped the character of the landscape wherever oaks and associated forests occur, which includes much of the United States. Those practices often have produced negative public reactions and sometimes even deleterious ecological consequences. Increasing economic demand for oak wood nevertheless makes timber harvesting and its aftermath an ever more conspicuous feature of the landscape. Moreover, the distinction between designed silvicultural practices and purely exploitative logging practices is not always apparent, especially to the public.

[1]Symbiosis between the earth and humankind. *Science* 193(4252), 459–462 (1976).

Contemporary philosophies on how oak forests and associated resources should be managed range from narrowly preservationist or narrowly utilitarian to more inclusive and integrative multiple-value philosophies. One of the objectives of this book therefore is to present ecological and silvicultural concepts that can be used to address an array of problems defined by various perceptions of how oak forests should be treated. The current trend in managing forests and forested landscapes is away from a narrow focus on sustaining timber and other commodity outputs and towards a broader philosophy of sustaining desired ecological states. This shift in the forest management paradigm has been wrought by and is consistent with changing social values, scientific advances in ecology and society's increasing awareness of environmental problems and expressed concerns on how those problems affect us collectively and individually. Consistent with the new paradigm, this book is designed and intended not so much as a how-to-do-it management manual as it is a source of ideas on *how to think about oak forests as responsive ecosystems.* Armed with that understanding, we believe managers and conservators of oak forests will be better positioned to adapt to changing social values and simultaneously to build and act on co-evolving ecological and silvicultural information.

The book is divided into three sections. The first contains three chapters on the ecological characteristics and distribution of oak species and the various kinds of oak forests in the United States, differences among them and how they have been classified, their natural development, and the relation of oak forests to environment and related environmental concerns. The next two chapters on regeneration ecology provide the critical interface between oak ecology and silviculture. Understanding the regeneration ecology of the oaks is paramount to silviculturists because of widespread difficulties in regenerating and thus sustaining oak forests.

The second section comprises three chapters covering site productivity and stand development. An understanding of the productive capacity of oak forests is central to a broad spectrum of issues related to their management and potentialities, not only for timber but also for wildlife and other values. The chapters on stand development, self-thinning and stand density present concepts that are key to the application of silvicultural methods.

The third section comprises four chapters on silvicultural methods and the growth and yield of oak forests. Silivcultural methods include traditional even-aged and uneven-aged methods as well as non-traditional methods for multi-resource management and conservation. Regeneration methods are discussed in relation to the apparent regeneration strategies that have evolved in the oaks and how those strategies vary among oak-dominated ecosystems. The approach to regeneration thus is less prescriptive and more ecologically principled than that typically presented in silviculture textbooks and 'how-to' guides. Throughout the book, accepted common names of trees follow Little's (1979) *Check List of Native and Naturalized Trees of the United States.* Scientific names of trees and other organisms are listed in Appendix 1.

We express our appreciation and indebtedness to all the ecologists, foresters, wildlife biologists, soil scientists, entomologists, pathologists and others, past and present, who have contributed to our collective knowledge of the oaks. We are hopeful that this compilation will make some small contribution to a more ecosystem-centred approach to managing and conserving oaks in the many forests and plant communities in which they occur.

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Introduction

Conflicting Environmental Philosophies

Ecology is the scientific study of the interrelations among living things and their environment. Ecological knowledge effects an awareness of precarious interdependencies among the myriad organisms, large and minuscule, between organisms and non-living components of ecosystems, and the pervasive human impacts that threaten these relations. Ecology thus obviates our dependency on, and our relation to, natural processes and systems. Perhaps no science more so than ecology has generated more knowledge with implications relating to ethics, morality and human behaviour.

In contrast, silviculture is *the art and science of tending forests to meet human needs*. Because silviculture is usually directly involved in the extraction of biomass, it produces disturbances along with associated ecological side effects. Silviculture is thus based on the planned use of controlled and directed disturbances to achieve defined human objectives. Ideally, it should be based on scientific principles which ensure that specified silvicultural goals are consistent with preserving or improving a forest's ecological qualities, are compatible with its natural dynamic and thereby provide reasonable assurance of the forest's sustainability.

Like its parent discipline, forestry, silviculture evolved out of 17th century Europe in response to purely utilitarian needs, especially for the timber required for sustaining the large naval armadas required for projecting colonial power in the late 18th century. Paramount among these concerns in Britain and France was a ready supply of pine and oak for ship masts and hulls. However, in the United States, serious concern over a declining forest resource did not occur until the late 19th century. By then the forests of eastern United States had been decimated by exploitative logging. A small but politically influential group of conservationists feared the same would happen to the western forests. This prompted the setting aside of forest reserves in the early 1890s from what remained of the public domain in the west. In 1897, the Organic Act was passed, which specified that the purpose of the reserves was 'to improve and protect the forest within the reservation, or for the purpose of securing favourable conditions of water flows, and to furnish a continuous supply of timber for the use and necessities of citizens of the United States' (United States Congress, 1897). This landmark legislation specified that the forest reserves were intended for *managed use*, not for wilderness preservation. Following the recommendations of the American Forest Congress of 1905, the reserves were transferred from the Department of Interior to the Department of Agriculture. Known as the *Transfer Act*, it provided that funds from the sale of products or the use of land in the reserves be used for managing and developing the forest reserve system.

This change heralded the implementation of an ambitious programme of scientific forest management under the direction of Gifford Pinchot, the first Chief of the USDA Forest Service. At that time, forestry was virtually an unknown discipline in the United States and forestry curricula in US universities were just emerging. Although politically controversial in its day, the conservation movement was hailed by its founders as not only environmentally wise, but also economically beneficial (Pinchot, 1987).

Pinchot and the founders of the early forest conservation movement envisioned a scientifically based forestry that would not only provide conservation benefits but would also result in the economic stability of rural communities in forested regions. Such benefits would accrue, they argued, from the application of scientifically derived sustained yield principles, which would ensure for perpetuity the even flow of timber and other commodities originating from the forest (Pinchot, 1987). Because the scientific underpinnings of sustained yield were largely invested in silviculture, and because silviculture has historically been justified on economic grounds, silviculture philosophically straddled agronomy (i.e. growing trees as crops) and economics. However, modern silviculture has been broadened to include not only sustaining timber yields, but also sustaining non-commodity values including old-growth forests, biodiversity, wildlife habitat and aesthetics. In this wider context, silviculture assumes application to a panoply of values that transcend economic utilitarianism.

Despite the differences between the two disciplines, contemporary silviculture as it has been applied to most North American forests, remains naturally allied with and dependent upon ecology for much of its scientific underpinnings. The schism between silviculturists and some ecologists nevertheless runs deep. One source of this disunion emanates from the ecologists' traditional focus on studying ecological processes in ecosystems largely unaffected or minimally affected by humans and drawing conclusions therefrom. In contrast, silviculturists depend on scientifically based knowledge of *disturbance-mediated mechanisms* to control and direct forest ecosystem processes for human benefit. Recovery from such disturbances is predicated on the assumption that forests are inherently *resilient*, i.e. capable of rapidly returning to their previous or other silviculturally directed state.

The silviculturist's *anthropocentric view* of the forest is anathema to those who adhere to the *biocentric view*, which elevates nature to a position superior to human self-interest (Devall and Sessions, 1985; Chase, 1995; Ferry, 1995; Fox, 1995). The biocentrist's agenda is centred on maintaining 'natural' ecosystems, including forest, in states free from human interference, and the need for establishing the pre-eminence of those states. From that perspective, human-mediated disturbance is seen as a disrupter of fragile ecosystems and the intended order of things. Moreover, such disruptions can potentially produce species extinctions and other irreversible environmental effects. The biocentric view therefore holds that the best way to preserve nature, wherever some vestige of it remains, is to leave it alone (Devall and Sessions, 1985; Chase, 1995). Humans are viewed as just one of many organisms in the biosphere no more important than any other – and like all component organisms should be subordinate to the healthy functioning of the interactive whole, i.e. the ecosystem. Biocentrism is therefore egalitarian among organisms and premised on an inherent right to life of all species and life forms. By extension, maintaining ecosystems in their 'natural' state becomes a social imperative. A biocentrist thus may view silviculture, along with other human interferences in the development of forests, as ecologically threatening, if not ruinous. The biocentric interpretation of the 'message' from ecology is thus at irreconcilable odds with the interpretation from silviculture. Biocentrism nevertheless now occupies a position of social and political prominence (Chase, 1995).

The connections between ecology and silviculture none the less are apparent and important, especially when silviculture is applied to forests of natural origin. In that setting, silviculture by itself may not introduce new species or populations (i.e. new genetic material) from outside the forest. Human energy expenditures are often limited only to those required in cutting and removing trees. Such relatively non-intensive practices have characterized the silviculture applied to oak forests of the United States. There, oak silviculture has largely followed an *ecological model* whereby forests are managed by directing their continually changing states, or ecological successions, through manipulation of existing on-site vegetation and propagules. This approach relies on periodic timber harvesting and usually natural regeneration to maintain or periodically recreate desired ecological states. It contrasts with the more intensive *agronomic model* used in growing pine plantations and other monotypes. The latter approach usually depends on artificial regeneration, the introduction of new and 'improved' genotypes, exotic species, and other intensive and energy-expensive cultural methods like those used in agriculture, horticulture and agroforestry (growing trees intermixed with agricultural or horticultural crops). Nevertheless, the silvicultural methods that have been applied to oaks span the entire range of approaches from ecological to agronomic.

In the public's view, silviculture is an often confusing and controversial subject exacerbated by the claims of some environmentalists that it is an ecologically damaging enterprise that 'seeks to accept "tree farms" in place of natural forests … The usual approach … is to seek ever more intensive management, which spawns even more problems' (Devall and Sessions, 1985, p. 146). By comparison, there is seemingly little controversy and confusion over the reason to preserve something in its natural state free from human interference if it is otherwise threatened with extinction – even though the method or means of preservation may be debatable. Likewise, the reason for the cultivation and harvest of a corn field is easily understood and accepted because of its purely utilitarian value, and its physical origins borne of human endeavour. Socially, silviculture is a more complicated issue. It is vulnerable in appearance, conceptually and often physically, seen as conforming to neither preservation nor agronomy. It is neither fish nor fowl, yet is often identified as disruptive if not exploitative of nature.

To the non-silviculturist, application of the ecological model to silviculture may sometimes be difficult to distinguish from purely exploitative and environmentally damaging practices. However, such exploitation is not the intent of, nor does it constitute, silviculture. Silviculture is not synonymous with timber harvesting, yet is dependent upon it. The objective of modern silviculture is to create and maintain forests by design that produce material and nonmaterial benefits to humans without sacrificing their sustainability. Silvicultural intentions nevertheless are not ecologically infallible. A given silvicultural application, despite best intentions, may be inconsistent with ecological realities because of our incomplete knowledge and understanding of ecosystems. Poorly applied silviculture therefore can produce unintended and negative long-term ecological consequences. The possibilities for such outcomes impose serious responsibilities on silviculturists in the practice of their art and science.

When silviculture is applied to 'natural' ecosystems, the intent, some would say, is to improve on nature by tinkering with it. But the biocentrist would argue that humans cannot improve upon nature – a notion consistent with the theological view that 'man cannot improve upon God's handiwork'. And much ecological knowledge and theory is purported to support that perception. Perhaps it is the proximity of the existing 'near-natural' state to the intended silviculturally created state that concerns those whose sentiments might be to 'leave well enough alone'. The biocentrist might argue that silviculture promises only 'a kinder, gentler rape of the forest'. These views may be further bolstered by an awareness of the shrinkage of natural ecosystems globally and its consequences.

The fragmentation of today's landscape into discrete blocks of forests spatially detached from human development may further reinforce the perception of the separation of humans and forest. This outlook is reflected in the Latin origin of the word forest, *foris*, which means *outside.* This etymology suggests a human view of forests evolving from deep historical and psychological roots, and one in which forests are functionally disconnected from humans. Even as late as the 18th century, the forest was perceived as something 'beyond' the boundary of European culture (Bonney, 1996). Today, most of the US population resides in urban areas. There, sources of basic human-sustaining resources are physically distanced from and foreign to everyday experience. A perception of forests as functionally and spatially distant from humans may be further reinforced by the common acknowledgement that, in some cases, the physical separation of humans from nature is necessary to preserve rare or endangered species and habitats. It is generally accepted that such preservation is a democratically mandated function of government. The results are commonly and favourably experienced annually by millions of visitors to national and state parks, wildlife refuges, and designated wilderness areas in national forests and other federal lands. It is generally understood that the role of humans there is restricted to that of protector and spectator, but not interloper.

Contrasting with such models of the separation of humans and nature is the historical relation between humans and oaks, which are characterized by connectedness. From the oak's perspective, those connections have produced both beneficial and harmful effects. The ecological evidence, as later discussed, nevertheless indicates that sustaining and thus preserving many oak-dominated ecosystems will require human intervention. Humans and oaks have been closely associated throughout history. Before the arrival of Europeans, native Americans set fires, both accidentally and intentionally, which often burned out of control over enormous areas (Grimm, 1983; Pyne, 1982, 1997; Guyette *et al.,* 1999). Periodic fires were repeated over centuries in regions indigenous to the oaks, which includes much of North America. Their frequent occurrence created extensive areas of open-grown forests favourable to the survival of the relatively light-demanding but fire-tolerant oaks. It was a disturbance cycle that, in time and space, is unlikely to be repeated. Humans thus have had a prominent effect in shaping the nature and extent of the oak's habitat, and perhaps even its evolution. But those events have been largely relegated to history. Much of what today remains of the oak forests of the United States is a legacy of an earlier disturbance history that was partially, if not largely, dependent on fire.

Unlike the ecologist, the silviculturist has traditionally viewed forests from a utilitarian perspective that emphasized timber production. Accordingly, failure to harvest forests at their inherent sustainable capacity to produce wood (sustained timber yield) is deemed wasteful. A theological counterpart is seemingly expressed by the biblical admonition for man to exert dominion over the earth (Genesis 1:28). An economic analogue is expressed in Adam Smith's 1776 treatise on the inherent value of the individual pursuit of economic self-interest (Smith, 1870). Collectively, these beliefs and values, largely borne of the Enlightenment, have dominated the thinking and institutions of Western civilization for over 200 years.

Self-interest prevails among private forest owners today, whether ownership goals are economic or non-economic. To a lesser extent, economic objectives dominate the management of many publicly owned lands, including the national forests. In the past, agency mandates, operating budgets and incentives tied to timber sales, produced powerful inducements to emphasize timber production, albeit within calculated sustained yield limits. Only within the last few decades has this philosophy been seriously challenged. Such material utilitarianism reduces forests to collections of trees having only commercial value. Other values are consequently diminished. The

American conservationist, Aldo Leopold (1966, p. 251) expressed concern for this philosophy by asserting that '… a system of conservation based solely on economic self-interest is hopelessly lopsided. It tends to ignore, and thus eventually to eliminate, many elements in the land community that lack commercial value, but that are (as far as we know) essential to its healthy functioning.'

Silviculture: a Consilient Discipline

The practice of silviculture therefore is caught in a web of competing values arising from different philosophies, ranging from biocentrism to economic utilitarianism. Unlike ecology, silviculture is directly connected to social institutions and conventions apart from science. Lying within its parent discipline, forest management, it is subject to the legal and social constraints of environmental law and policy operating within democratic processes (at least in the United States and other democratic countries where silviculture is practised). Within the context of democracy, silviculture is therefore socially integrative, i.e. in its application it must consider values borne of diverse social and political interests.

Silviculture nevertheless lies at the core of forest resource management because its application results in direct physical action on the forest. This is also where fundamental scientific analysis is most needed. However, silviculture does not stand firmly by itself as a scientific discipline. This results in part from its strong connections to social and political institutions, and in part from its interdisciplinary qualities as a science. Within the biological domain of science, silviculture is most closely allied to ecology. However, it is also heavily dependent on plant physiology and genetics, plant pathology, entomology, and applied mathematics and statistics. Among the physical sciences, it borrows knowledge from geology, climatology, hydrology and soil science. It is also closely allied to other resource management disciplines including wildlife, fisheries, water and air quality management. Silviculture therefore is inherently scientifically integrative.

Silviculture consequently depends on linking knowledge and theories across many disciplines, both scientific and non-scientific, to form what Wilson (1998) terms '… a common groundwork of explanation'. If we accept that such linkages comprise *consilience*, we might consider that silviculture fits Wilson's context, i.e. it comprises *a hybrid domain of knowledge in which consilience is implicit*. Because of silviculture's socioeconomic connections, this consilience extends to other branches of learning including the social sciences and humanities. These connections can be represented by a series of concentric circles representing the social hierarchies within which silviculture exists. With silviculture at its centre, each ring of the social hierarchy bounds all the great areas of knowledge, including the biological, physical and social sciences as well as the humanities (Fig. I.1). This representation emphasizes the consilient nature of silviculture by placing it at the locus of all knowledge comprising its context. It represents an ideal, a unity of learning in which subjects that have been traditionally compartmentalized are breached in Wilson's words, to '… provide a balanced clearer view of the world as it really is … A balanced perspective cannot be acquired by studying disciplines in pieces but through pursuit of the consilience among them … The enterprise is important for yet another reason: it gives ultimate purpose to intellect' (Wilson, 1998, p. 13).

Despite the complexities of silviculture's complete context, our intent in the following pages is to present a synthesis of the ecological and silvicultural knowledge of oak forests in the United States. It is not to resolve the environmental issues surrounding oak forests, which fall into the social, legal, political and managerial domains represented by the concentric circles surrounding silviculture in Fig. I.1. The silvicultural context is nevertheless broad, and not limited to narrowly defined economic or commodity-production objectives. Consistent with the view of silviculture

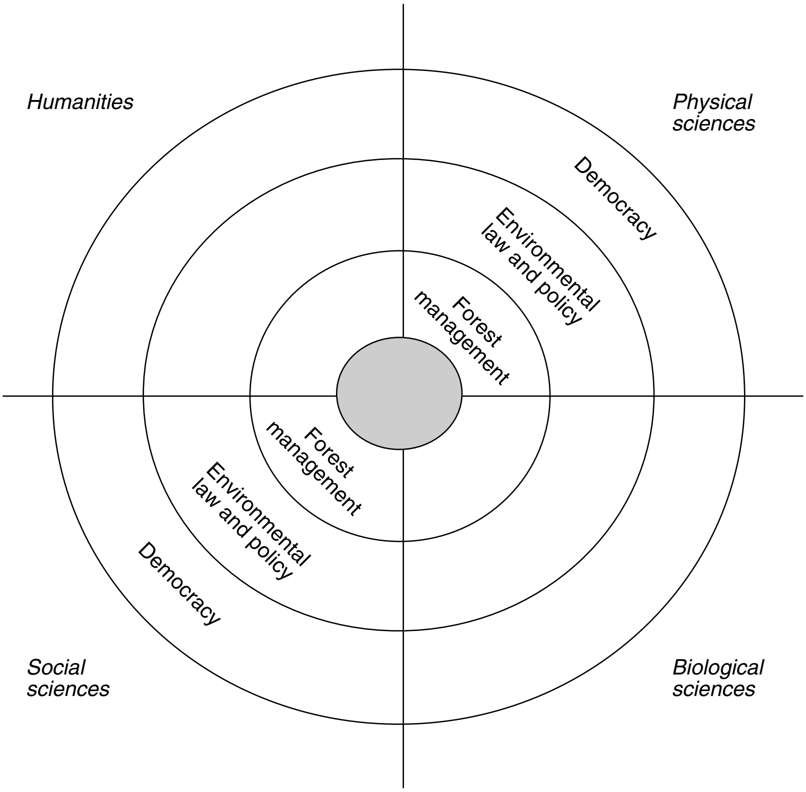

Fig. I.1. Silviculture's relation to other disciplines. Concentric circles represent the social hierarchy within which silviculture exists in a democratic society. With silviculture at its centre, each ring of the hierarchy bounds all the major areas of knowledge, including the biological, physical and social sciences, and the humanities.

as a consilient discipline, we view the role of the silviculturist as just one of many possible players in the management of oak forests. Unlike the biocentrist, we infer no moral imperative to create or maintain oak forests in specified states other than those that are perceived, as best we can discern, as sustainable, beneficial, and pleasing to humankind, and that provide habitat for the many plant and animal species naturally associated with oaks. We believe these goals are consistent with the philosophy of *land stewardship* and *wise use* as proposed by earlier generations of conservationists, from which the more recent philosophy of *ecosystem management* has evolved. Our intention is to present information that can lead to an understanding of, and solutions to, silvicultural problems related to oak forests. Moreover, we hope that this information fosters an informed and amiable dialogue and trust among foresters, land managers and owners, environmentalists, students and others interested in oak forests.

The subject therefore is presented from a silvicultural perspective. The approach comprises a comprehensive view of forests as providing important social, spiritual and economic needs. Such an approach requires anticipating and managing for change, both predictable and unpredictable. This notion is consistent with Botkin's (1990) call for a 'new management', wherein conservation and utilization of forest resources are compatible parts of an integrated ecosystem approach. It contrasts with the 'old management' in which conservation was too often subordinate to timber and other commodity production. The central concern of the new forest management, or *ecosystem management* (Salwasser, 1994), is the sustainability of forested ecosystems and associated human values in a continually changing mosaic of landscape patterns. The resulting management and silviculture therefore must accommodate the complexities of the inevitably and continually changing ecological states that comprise a forested landscape. It also recognizes that such changes occur with or without human interference, and that we have both potentialities and limitations in controlling these changes.

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1

Oak-dominated Ecosystems

Introduction

> A truly ecological perspective recognizes that humans and their activities are part of nature, and that enhancing all aspects of their lives – including their surroundings – begins with cooperation between individuals, based on mutual trust … Rather than halting or reversing disturbances, we should embrace change. Rather than excluding man from the garden, we should welcome his cultivation of it.
>
> (Alston Chase, 1995)

From earliest times, oaks have held a prominent place in human culture. Their uses have included wood for fuel, acorns for hog fodder and flour meal for human consumption, bark for tanning, wood strips for weaving baskets, charcoal for smelting ore, timbers for shipbuilding, mining timbers, railroad ties, pulpwood for paper, and lumber and laminates for furniture, panelling and flooring. Through the mid-19th century, oak was the wood of choice for shipbuilding in Europe and America. For that reason, oak forests and even individual trees were treated as critical national assets. During the Revolutionary War, the poor condition of the British fleet, which lacked replacements and repairs due to shortages of suitable oak timbers, may have contributed to the war's outcome (Thirgood, 1971). In the 17th century, alarm over the depletion of timber supplies, especially oak, prompted passage and enforcement of laws mandating the protection, culture and establishment of forests in several European countries. In turn, those events influenced the development of scientific silviculture, as we know it today.

Modern as well as ancient man has benefited from the oak's relation to wildlife. Wherever oaks occur as a prominent feature of the landscape, wildlife populations rise and fall with the cyclic production of acorns. Numerous species of birds and mammals are dependent on acorns during the food-scarce autumn and winter months. Even human cultures have relied on oaks as a staple food. Acorns were an important part of the diet of Native Americans in California before the 20th century (Kroeber, 1925) (Fig. 1.1). Today, the ecological role of oaks in sustaining wildlife, biodiversity and landscape aesthetics directly affects the quality of human life.

The demand for wood products from oaks nevertheless continues to increase and compete with other less tangible values. Some have proposed that forests, including those dominated by oaks, are best allowed to develop naturally, free from human disturbance. What should the balance be among timber, wildlife, water, recreation and other forest values? Is there some middle ground that adequately sustains multiple goals? Informed answers and perspectives require an understanding of the ecology of oaks and the historical role that humans have had in that ecology, especially the comparatively recent role of humans in the 'protection' of oak forests from fire. A prerequisite to such understanding is a general knowledge of the oak's geographical occurrence, taxonomic diversity, adaptations to diverse environments, and the historical changes in its environment.

Fig. 1.1. Native American collecting acorns as shown in *Hutchings' California Magazine* in 1859. Acorns were a staple food of most California tribes before the end of the 19th century. They were gathered in conical woven baskets, which could hold a bushel or two of the nuts. Although the acorns of many species were eaten, favoured species were California black and California live oaks (Pavlik *et al.*, 1991). After removing the shell (pericarp), acorns were ground into a flour, leached of tannins by soaking in running water, and then used to make a variety of foods including porridge and bread. Acorns were so highly valued that they sometimes provoked inter-tribal 'acorn wars'. They were also widely utilized as food by Native Americans in the eastern United States. (Courtesy of the Bancroft Library, University of California, Berkeley.)

The Taxonomy of Oaks

Taxonomically, the oaks are in the genus *Quercus* in the family *Fagaceae* (beech family). The *Fagaceae* probably originated in the montane tropics from which its members migrated and diverged into the current living genera by the late Cretaceous period (about 60 million years ago) (Axelrod, 1983). By that time, mammals and birds had only recently evolved. Rapid speciation of oaks commenced in the middle Eocene epoch (40–60 million years ago). This was in response to the expansion of drier and colder climates, and subsequently to increased topographic diversity in the late Cenozoic era (< 20 million years ago) and fluctuating climates during the Quaternary period (< 2 million years ago) (Axelrod, 1983).

Their fruit, the acorn, distinguishes the oaks from other members of the beech family (e.g. the beeches and chestnuts). With one exception, all plants that produce acorns are oaks. The exception is the genus *Lithocarpus*, which includes the tanoak of Oregon and California. Although represented by only one North American species, *Lithocarpus* is represented by 100–200 species in Asia (Little, 1979). *Lithocarpus* may be an evolutionary link between the chestnut and the oak (McMinn, 1964; cf., Miller and Lamb, 1985, p. 200).

Worldwide there are about 400 species of oaks, and they are taxonomically divided into three groups: (i) the red oak group (*Quercus* section *Lobatae*[1]); (ii) the white oak group (*Quercus* section *Quercus*[2]); and (iii) the intermediate group (*Quercus* section *Protobalanus*[3]) (Tucker, 1980; Nixon, 1997). All three groups include tree and shrub species. The red oaks and white oaks include evergreen and deciduous species, whereas the intermediate oaks are all evergreen. The red oaks are found only in the Western Hemisphere where their north–south range extends from Canada to Colombia. In contrast, the white oaks are widely distributed across the Northern Hemisphere. The intermediate group comprises only five species, all of which occur within southwestern United States and northwestern Mexico. Many of the world's oaks occur in regions with arid climates, including Mexico, North Africa and Eurasia, where they are often limited in stature to shrubs and small trees. About

[1] Subgenus *Erythrobalanus* in earlier classifications.
[2] Subgenera *Lepidobalanus* and *Leucobalanus* in earlier classifications.
[3] Subgenus *Protobalanus* in earlier classifications.

80% of the world's oaks occur below 35° north latitude and fewer than 2% (six or seven species) reach 50° (Axelrod, 1983).

The most reliable distinction between the white oaks and red oaks is the inner surface of the acorn shell. In the white oaks it is glabrous (hairless) or nearly so, whereas in the red oaks it is conspicuously tomentose (hairy or velvety) (Tucker, 1980). In the intermediate group, this characteristic is not consistent among species. The leaves of the white oaks are usually rounded and without bristle tips whereas the leaf lobes of the red oaks are usually pointed and often bristle-tipped. To many silviculturists, ecologists and wildlife biologists, the most important difference between the white oaks and red oaks is the length of the acorn maturation period. Acorns of species in the white oak group require one season to mature whereas species in the intermediate and most of the red oak group require two seasons. The white oaks and intermediate oaks are characterized by the presence of tyloses (occlusions) in the latewood vessels (water-conducting cells) whereas tyloses are usually absent in the red oaks. These vessel-plugging materials confer greater decay resistance to the wood of the white and intermediate oaks than the red oaks. Other morphological features that differentiate the three groups and species within them are presented in various taxonomic treatments (e.g. Tucker, 1980; Jensen, 1997; Manos, 1997; Nixon and Muller, 1997) and field identification guides (e.g. Miller and Lamb, 1985; Petrides, 1988; Petrides and Petrides, 1992). These sources also include range maps. In addition, the *Silvics of North America*, Vol. 2 (Burns and Honkala, 1990) provides information on the silvics and geographic ranges of 25 oaks.

Of the more than 250 oak species occurring in the Western Hemisphere, the largest number occurs in Mexico and Central America. About ten species occur in Canada. For the United States species, the most complete and authoritative taxonomic treatment of the oaks is in the *Flora of North America North of Mexico*, Vol. 3 (Flora of North America Editorial Committee, 1997), which lists 90 species of oaks native to the continental United States. However, we follow the taxonomic nomenclature of Little's (1979) *Checklist of United States Trees* because of its widespread use in North American forestry literature. This checklist recognizes 58 native oak species plus nine varieties. Of these, about ten species are shrubs or shrub-like forms. More than 80 hybrids also have been described (Little, 1979; Tucker, 1980).

The Geographic Distribution of US Oaks

Species ranges and groupings

The oaks are widely distributed across the United States (Fig. 1.2). According to Little (1979), about 40 species and varieties occur east of the 100th meridian and about 30 species and varieties occur to the west. Only two species, chinkapin oak and bur oak, are common to both regions. Bur oak extends to the northwest whereas chinkapin extends to the southwest beyond the 100th meridian. The western oaks fall into three geographically distinct groups. One group is comprised of the west Texas oaks (nine species and varieties), and a second includes the southwestern oaks (16 species) that occur in New Mexico, Arizona, Utah, Colorado and Nevada. A third group is comprised of the Pacific Coast oaks (about 13 tree species plus several shrubby species) occurring largely in California, Oregon and Washington.

Within the United States, numbers of oak species vary regionally. Based on a count of the number of oak species that occur within 6000 square mile areas, oak species 'richness' reaches a maximum of 20 species in the southeast (Aizen and Patterson, 1990) (Fig. 1.3). There, the ranges of several narrowly distributed North American oak species overlap with the ranges of several widely distributed species. Although the range of an oak species is positively correlated with its acorn size, the reason for this is unknown (Aizen and Patterson, 1990).

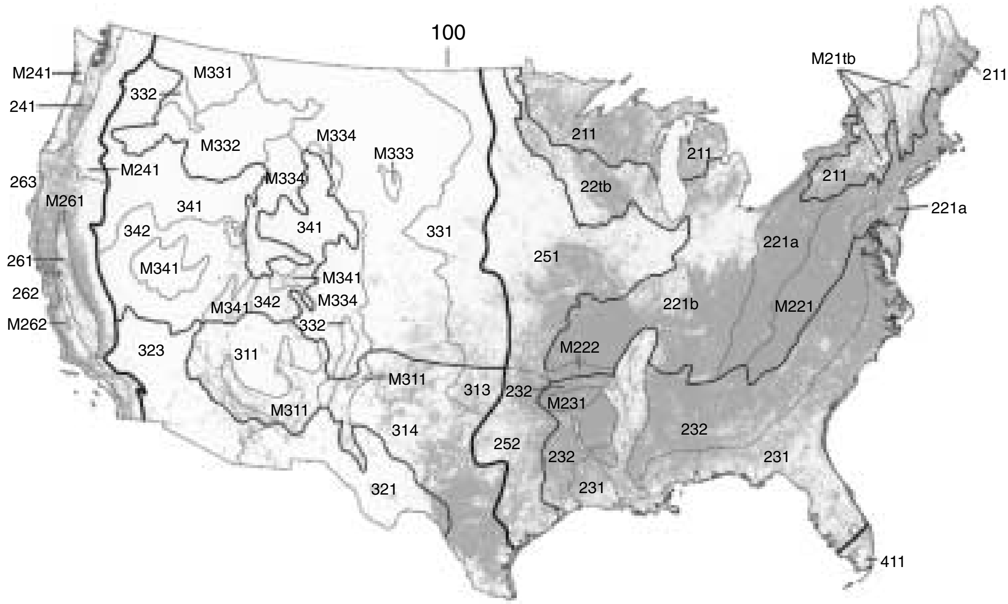

Fig. 1.2. The distribution of oaks in conterminous United States. The shaded areas represent the aggregated vegetation cover types within which oaks frequently occur as important species at a scale of 1 km^2. The 100th meridian demarcates the approximate division between eastern and western oaks. Generated from Advanced Very High Resolution Radiometer satellite images (1990) and an associated system of land cover classification (USDA Forest Service, 1993; Powell *et al.*, 1994). Ecoregion boundaries are from Bailey (1997). See Tables 1.2 and 1.3 for index to numbered ecoregions and oak species found in each. (Map compiled by W.D. Dijak, USDA Forest Service, North Central Research Station, Columbia, Missouri.)

Forest cover types (or simply cover types) are combinations of tree species that tend to spatially reoccur at stand-level scales (e.g. < 100 acres). The resulting categories are thus silviculturally useful in differentiating among different kinds of oak stands. Categorization of United States forests based on defined cover types was begun by the Society of American Foresters in 1929. There are 145 defined cover types in the United States and Canada (Eyre, 1980). These include 31 with 'oak' in the cover type name or in the list of species that define the type (Appendices 2 and 3). Of these, 23 oak types occur east and eight occur west of the 100th meridian. In addition, many of the non-oak cover types include one or more oak species as common associates.

The geographic extent of individual cover types ranges from tens of millions of acres (e.g. the white oak–black oak–northern red oak cover type of the eastern US) to relatively restricted areas (e.g. the northern pin oak cover type of the upper Lake States and the Mohr oak cover type of Texas and Oklahoma). Other types such as the live oak type of the South and the bur oak cover type in the Great Plains occur within long narrow belts associated with coastal plains and river corridors, respectively. Many of the western oak cover types, especially those in California, form belts that follow the Coastal and Sierra Nevada mountain ranges and foothills surrounding the Central Valley.

Oaks occur in environments ranging from extremely wet and humid (e.g. the overcup oak–water hickory cover type of southern flood plains), to mesic (moist) upland forests receiving 50 or more inches of precipitation per year (e.g. the yellow–poplar–white oak–northern red oak cover type), to Mediterranean climates that receive 10 inches or less precipitation per year (e.g. the blue

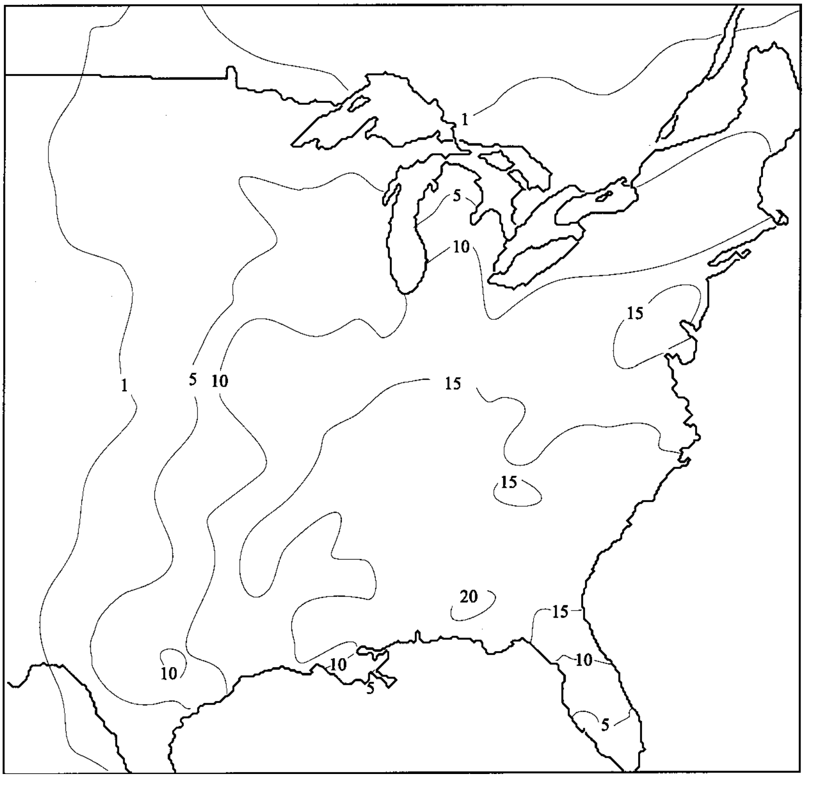

Fig. 1.3. The geographic distribution of numbers of oak species in eastern United States and Canada. The isolines were drawn from a grid comprised of 78 × 78 square mile cells within which the number of oak species were counted based on Little's (1971, 1977) range maps. The greatest concentration of oak species (15 to 20) occurs in the southeastern United States where the ranges of several narrowly distributed species overlap the ranges of several widely distributed species. (Redrawn from Aizen and Patterson, 1990, used with permission.)

oak–digger pine cover type). Oaks occur in even drier climates where they form shrub vegetation such as the chaparral of southern California and the semi-desert scrub woodland vegetation of the interior southwest. Western cover types such as the canyon live oak cover type include closed-canopy stands in the northern part of their range and savanna-like woodlands in the south. Oak forests therefore range from closed canopy upland and lowland forests with trees greater than 120 ft tall to xeric (droughty) scrublands dominated by dwarf trees and shrubs.

Some oaks, such as Georgia oak and McDonald oak are confined to very small geographical ranges and a narrow range of habitat conditions. Others such as white oak are widely distributed and occur over a broad range of climates and habitat conditions. A species' flexibility in occupying different habitats is implicit in the definition of *species niche*. The term denotes *the specific set of environmental and habitat conditions that permit the full development and completion of the life cycle of an organism* (Helms, 1998). The oaks occupy many niches because of the wide range of environmental conditions within which they can collectively occur. However, the niche of an individual species is more limited. Niche differentiation among the oaks and associated species is often evident from the way species segregate along environmental gradients such as the soil moisture gradient (Fig. 1.4). Oaks also differ in their *ecologi-*

cal amplitude, i.e. the range of habitat conditions that a species can tolerate (Allaby, 1994). The ecological amplitude of a species often forms a bell-shaped curve when illustrated diagrammatically (Fig. 1.4). However, some species, such as bur oak, occur in both bottomlands and dry uplands but are nearly absent at intermediate points along the moisture gradient (Curtis, 1959; Johnson, 1990).

The species composition of forests is continually changing as a result of forces both internal (autogenic) and external (allogenic) to the forest. Changes are often gradual and frequently result in the replacement of one tree species by another in the process of ecological succession. The vegetation and other organisms within the forest thus effect autogenic change. For example, shade-tolerant species growing beneath the main forest canopy may gradually replace dominant species of lesser shade-tolerance that are unable to regenerate under their own shade. In contrast, allogenic change occurs as a result of changes in climate, defoliation by exotic insects and pathogens, the movement of soil by wind and water, or from other forces originating outside the forest. Autogenic and allogenic factors sometimes jointly affect the direction and rate of succession. Moreover, disturbances such as windthrow, insect and disease outbreaks, and timber harvesting can accelerate succession or alter its direction.

Although the oaks are relatively intolerant of shade, species vary substantially in this attribute. In some habitats, oaks are vulnerable to successional replacement by more shade tolerant species. Compared to many of their competitors, oak seedlings grow more slowly during their first few years after initial establishment. When young oaks are overtopped and heavily shaded by other vegetation, few survive for very long. On the other hand, the oaks tend to be relatively drought tolerant, and often survive in habitats that limit the development of species of lesser drought tolerance. Oaks also can produce vigorous

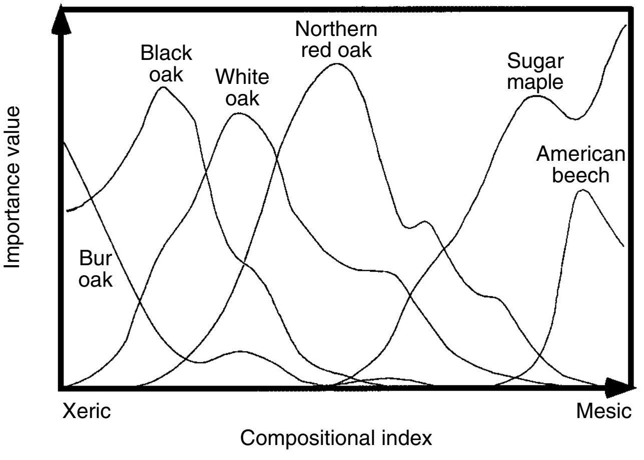

Fig. 1.4. Changes in the relative importance of six tree species in the upland forests of southern Wisconsin in relation to the regional soil moisture gradient. Species' importance is quantitatively expressed by an *importance value*, which is an index of species' importance based on its frequency of occurrence, density and basal area relative to other species within a stand. Although there is much overlap among species' importance value curves, no two species behave exactly the same way with respect to the moisture gradient. The length of the gradient spanned by a species' range of importance values together with the shape of its importance value curve reflects its *niche* with respect to the gradient. Importance value curves also define the *ecological amplitude* of a species, i.e. the range of conditions it can tolerate and the magnitude of its importance in relation to the gradient under the prevailing (i.e. relatively undisturbed) stand conditions. The moisture gradient shown is inferred from the species composition of a series of relatively undisturbed stands (see Curtis, 1959). (Adapted from Curtis, 1959, used with permission.)

sprouts that often outgrow competitors. The balance of these factors thus determine the relative permanence of oaks within a given cover type.

In the eastern half of the United States, oaks are often relatively permanent members of cover types on drier sites. In the absence of disturbance, many of the pine and oak–pine cover types occurring on dry habitats are successional to oaks because the oaks are somewhat more shade tolerant than the pines. This successional pattern creates silvicultural problems in maintaining pure pine stands in the south and other regions where oaks and pines co-occur (Burns and Barber, 1989). In bottomlands and mesic uplands, shade-tolerant or faster growing species often successionally displace the oaks. Such displacement creates silvicultural problems in perpetuating oaks in these forests.

The relative permanence of an oak species within a given cover type (i.e. its resistance to successional replacement by other species) is likely to be highly variable if the cover type spans a broad range of environments. For example, the white oak cover type occurs across a wide range of site conditions from dry to moist. Whereas the type tends to be relatively permanent on dry sites, it is successional to other types on the more mesic sites. Cover type designations, although useful, largely fail to consider these and other ecological factors that determine changes in species composition and how those changes vary spatially (e.g. in relation to climate and site quality), and temporally (e.g. in relation to plant succession and disturbance). Consequently, two or more stands representing a single cover type may represent quite different ecologies with respect to the successional status of oaks, physical environment, understorey vegetation, forest regeneration, fauna and other factors.

Forest inventories and satellite imagery have been used to describe the geographic distribution of forest types in the United States (e.g. Fig. 1.5). These maps identify broad cover type groups that are aggregates of the stand cover types described above. Four groupings widely used to delineate oak forests at the regional scale are: the *oak–hickory group*, the *oak–pine forest group*, the *oak–gum–cypress group* (bottomland forests), and the *western hardwood group* that includes the western oaks as a subset (Fig. 1.5). However, the names commonly applied to the resulting species aggregations can be misleading. For example, hickory is absent throughout much of the northern part of the range delineated as oak–hickory (Fig. 1.5). Moreover, other forest cover types dominated by oaks are also included within the delineated oak–hickory area. The term 'oak–hickory' nevertheless is widely used in reporting forest resource statistics at the regional level even though it is an ecologically imprecise term. Oaks also occur as ecologically and silviculturally important components of many non-oak forests (e.g. pine forests and maple–beech–birch forests).

In the eastern United States the oak–hickory, oak–pine and the oak–gum–cypress cover type groups collectively covered 187 million acres or 52% of the timberland[4] in 1997. That is an increase from 162 million acres and 45% of eastern timberland in 1953 (USDA Forest Service, 2000). At 124 million acres, the oak–hickory group is the largest cover type in the United States. The western oaks are also significant geographically and ecologically. Western hardwood forests (including oaks, tanoak, red alder and aspen) cover 43 million acres or 12% of western forestland. Oaks comprise about 23% of the cubic volume of growing stock trees in the eastern United States and about 1% in the western United States (USDA Forest Service, 2000).

Distribution of oaks by hierarchically classified ecoregions

Climate and landform strongly influence the distribution of oaks. Locally, the distribution of oaks is influenced by factors such as physiography, soil moisture and geology.

[4] Timberland is forest land that is producing, or is capable of producing, more than 20 feet^3 acre^{-1} year^{-1} of industrial wood crops under natural conditions, and that is not withdrawn from timber use, and that is not associated with urban or rural development. Currently inaccessible and inoperable areas are included.

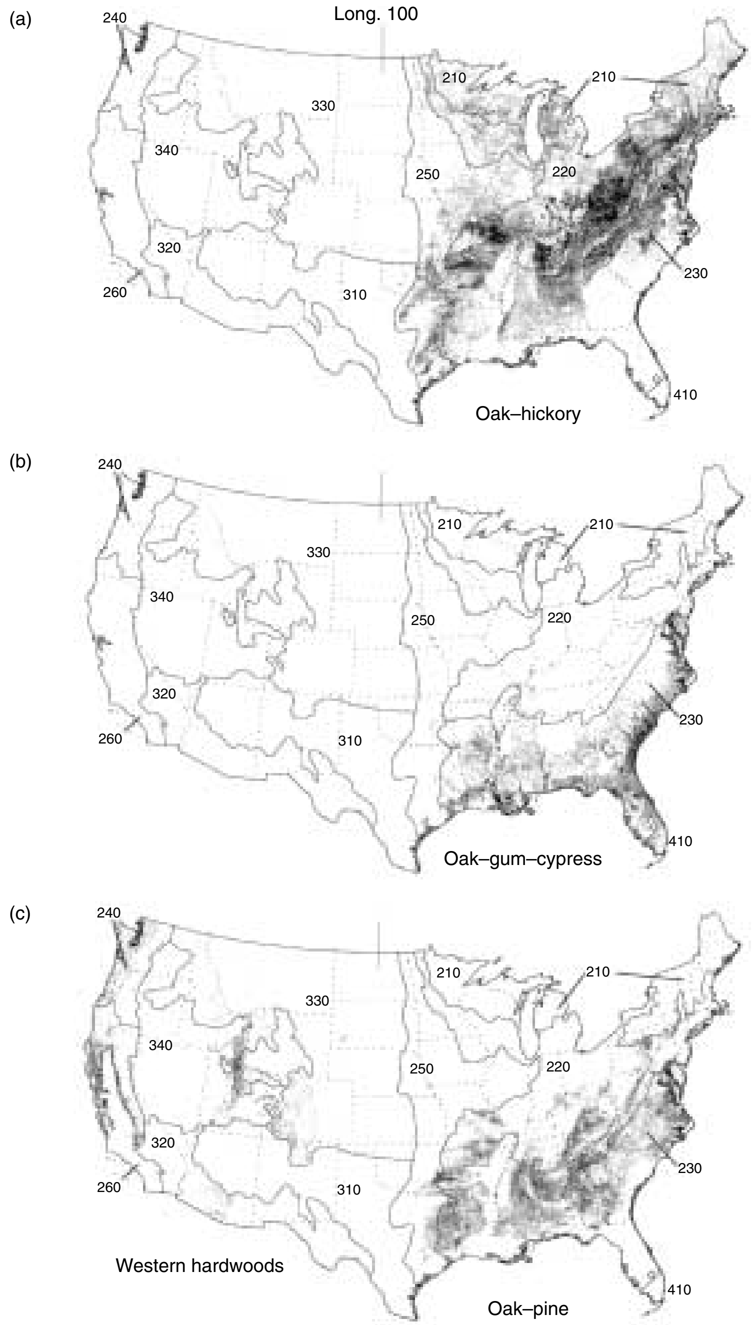

Fig. 1.5. The major areas of oak–hickory, oak–pine, oak–gum–cypress, and western hardwoods (shaded areas) by state and ecoregion Divisions. In the western US, the map shows the composite western hardwood group that includes oaks, tanoak, red alder, cottonwood and aspen. Numbered ecoregion boundaries on the map are from Bailey (1997) and are summarized in Tables 1.2 and 1.3. Generated from Advanced Very High Resolution Radiometer satellite images at a scale of 1 km^2 (1990) and an associated system of land cover classification (USDA Forest Service, 1993; Powell *et al*., 1994). (Map compiled by W.D. Dijak, USDA Forest Service, North Central Research Station, Columbia, Missouri.)

These and other factors have been used to structure a hierarchical ecological classification system (McNab and Avers, 1994; Bailey, 1995, 1997, 1998). This system recognizes the increasing detail necessary to explain the spatial arrangement of forests at increasingly smaller spatial scales (Table 1.1). It thus provides an objective basis for the regional delineation of ecosystems into successively smaller and more homogeneous units.

The hierarchical ecological units range in size from continents to a few acres. The larger units are often referred to as ecoregions; the smallest units are often equivalent to forest stands. *Domains*, *Divisions* and *Provinces* form the larger ecoregions (Table 1.1). These are climatic and climatic–physiographic regions that cover millions to tens of thousands of square miles. Provinces are further subdivided into smaller units termed *Sections*, *Subsections*, *Landtype Associations* (LTAs), *Ecological Landtypes* (ELTs) and *Ecological Landtype Phases* (ELTPs). These units range in size from thousands of square miles for Sections to less than 10 acres for some Ecological Landtype Phases. Ecological Landtypes and Ecological Landtype Phases are important silviculturally because they often correspond to individual stands, which are the objects of silviculture.

The oaks occur in all three Domains (major climatic regions) of the 48 contiguous states: Humid Temperate, Dry and Humid Tropical (Bailey, 1997). The latter occurs only in the southern tip of Florida. The three Domains are further subdivided into 11 climatic Divisions. Within each Division, mountainous areas with elevational zonation of vegetation are also identified. Although oaks naturally occur in all 11 of the Divisions, within each Division the distribution of the four major oak forest types is closely related to Division boundaries (Fig. 1.5; Tables 1.2 and 1.3).

Table 1.1. Hierarchy of ecological units used to classify forest ecosystems in the United States.[a]

Ecological unit	Scale (reference size)[b]	Delineating factors[c]
Domain	Millions to tens of thousands of square miles (subcontinent)	Macroclimate, ocean temperature and currents, geomorphology
Division	Millions to tens of thousands of square miles (multi-state)	Geomorphology, climate
Province	Millions to tens of thousands of square miles (multi-state, state)	Geomorphology, climate
Section	1000s of square miles (state, multi-county, National Forest)	Geomorphology, climate, vegetation
Subsection	10s to 100s of square miles (multiple counties, National Forest Ranger District)	Geomorphology, climate, vegetation
Landtype association	10s to 1000s of acres (landscape, watershed)	Landforms, species composition of overstorey, soil associations
Ecological landtype	10s to 100s of acres (multiple stands)	Landform, natural vegetative communities, soils
Ecological landtype phase	1 to 10s of acres (stand)	Soils, landscape position, natural vegetative communities

[a] Adapted from McNab and Avers (1994), Bailey (1995) and Cleland *et al.* (1993); see also Figs 1.2, 1.5 and 1.6.
[b] Indicates a familiar unit of comparable size for reference purposes. This reference unit is not used to delineate the ecological unit.
[c] Some of the factors used to distinguish among ecological units at a given level. Classification complexity typically increases with decreasing unit size.

Table 1.2. The ecoregion domains, divisions and provinces in the eastern conterminous United States where oaks are found and the principal species occurring in each. Ecoregions from Bailey (1995). Division and province boundaries are shown in Fig. 1.2.

Division	Province
200 Humid Temperate Domain	
210 Warm Continental	211 Mixed deciduous coniferous forests
M210 Warm Continental Mountains	M211a Mixed forest–coniferous forest–tundra, medium
	M211b Mixed forest–coniferous forest–tundra, high
10 oak species:	*bear, black, bur, chestnut, chinkapin, n. pin, n. red, scarlet, swamp white, white*
220 Hot Continental	221a Broadleaved forests, oceanic
	221b Broadleaved forests, continental
M220 Hot Continental Mountains	M221 Deciduous or mixed forest–coniferous forest–meadow
	M222 Broadleaf forest–meadow
22 oak species:	*basket, bear, black, blackjack, bur, cherrybark, chestnut, chinkapin, n. pin, n. red, overcup, pin, post, scarlet, shingle, Shumard, s. red, swamp chestnut, swamp white, water, willow, white*
230 Subtropical	231 Broadleaved–coniferous evergreen forests
	232 Coniferous–broadleaved semi-evergreen forests
M230 Subtropical Mountains	M231 Mixed forest–meadow province
31 oak species:	*Arkansas, bear, black, blackjack, bluejack, bur, Chapman, cherrybark, chestnut, chinkapin, Durand, Georgia, laurel, live, myrtle, Ogelthorpe, n. red, Nuttall, overcup, pin, post, scarlet, shingle, Shumard, s. red, swamp chestnut, swamp white, turkey, water, white, willow*
250 Prairie	251 Forest-steppes and prairies province
	252 Prairies and savannas province
20 oak species:	*black, blackjack, bluejack, bur, chinkapin, Durand, live, n. pin, n. red, overcup, laurel, pin, post, s. red, shingle, Shumard, swamp chestnut, swamp white, water, white*
400 Humid Tropical Domain	
410 Savanna	411 Open woodlands, shrubs and savanna
	412 Semi-evergreen forests
	413 Deciduous forests province
4 oak species:	*Chapman, live, laurel, myrtle*
Intrazonal Regions	
	R Riverine forest

The 11 ecoregion Divisions within the conterminous United States are further subdivided into 44 Provinces (Fig. 1.2). Provinces are delineated based on broad vegetation groups and related regional landforms. Oak forests and woodlands commonly occur in 23 Provinces (Tables 1.2 and 1.3). Province boundaries are useful in delineating oak distributions in some parts of the United States. For example, Province boundaries correspond with the spatial distribution of the oak forests and woodlands encircling California's Central Valley. Province boundaries also separate the oak–pine forests of the Piedmont (Province 232) from the wetter oak habitats of the Coastal Plain and the lower Mississippi flood plain (Province 231 and

Table 1.3. The ecoregion domains, divisions and provinces in the western conterminous United States where oaks are found and the principal species occurring in each. Ecoregions from Bailey (1995). Division and province boundaries are shown in Fig. 1.2.

Division	Province
200 Humid Temperate Domain	
240 Marine	241 Mixed forests
M240 Marine Mountains	M241 Deciduous or mixed forest–coniferous forest–meadow M242a Forest–meadow, medium M242b Forest–meadow, high
3 oak species:	*Oregon white, California black, canyon live*
260 Mediterranean	261 Dry steppe 262 Mediterranean hardleaved evergreen forests, open woodlands and shrub 263 Redwood forests
M260 Mediterranean Mountains	M261 Mixed forest–coniferous forest–alpine meadow M262 Mediter. woodland or shrub–mixed or conif. forest–steppe or meadow M263 Shrub or woodland–steppe–meadow
13 oak species:	*blue, California black, California scrub, canyon live, coast live, Dunn, Engelmann, interior live, island live, McDonald, Oregon white, turbinella, valley*
300 Dry Domain	
310 Tropical/ Subtropical Steppe	311 Coniferous open woodland and semideserts 312 Steppes 313 Steppes and shrubs 314 Shortgrass steppes
M310 Tropical/ Subtropical Steppe Mountains	M311 Steppe or semidesert–mixed forest–alpine meadow or steppe
16 oak species:	*Arizona, canyon live, Chisos, Dunn, Emory, Gambel, Gray, Havard, Lacey, lateleaf, Mohr, sandpaper, silverleaf, Toumey, wavyleaf, turbinella*
320 Tropical/ Subtropical Desert	321 Semideserts 322 Oceanic semideserts 323 Deserts on sand
M320 Tropical/ Subtropical Desert Mountains	M321 Semidesert–shrub–open woodland–steppe or alpine meadow M322 Desert or semidesert–open woodland or shrub–desert or steppe
22 oak species:	*Arizona, chinkapin, Chisos, Dunn, Durand, Emory, Gambel, Graves, gray, Havard, Lacey, lateleaf, live, Mexican blue, Mohr, netleaf, post, sandpaper, silverleaf, Toumey, turbinella, wavyleaf*
330 Temperate Steppe	331 Steppes 332 Dry steppes
M330 Temperate Steppe Mountains	M331 Forest-steppe–coniferous forest–meadow–tundra M332 Steppe–coniferous forest–tundra M333 Steppe–coniferous forest M334 Steppe–open woodland–coniferous forest–alpine meadow
2 oak species:	*bur, Gambel*
340 Temperate Desert	341 Semideserts 342 Semideserts and deserts
M340 Temperate Desert Mountains	M341 Semidesert–open woodland–coniferous forest–alpine meadow
3 oak species:	*Gambel, turbinella, wavyleaf*

Riverine Forest). Province boundaries are also useful in separating the regions where oaks occur from those where they do not.

In contrast to the coarser levels of the classification hierarchy (Domains through Subsections), which have been delineated nationally, classification of the ELT and ELTP levels is incomplete across much of the oak range. Even though classification systems down to the ELT or ELTP have been developed for millions of acres, they include only a small fraction of the total area of oak forests.

ELTs or ELTPs are usually mapped in the field based on differences in soils, physiography and vegetation (including herbs and shrubs). The species composition of the herbaceous layer is often used to distinguish among different ELT or ELTP units because of the fidelity of some herbaceous species ('indicator' species) to specific biophysical conditions. Accordingly, the presence or absence of one or more indicator species can be used to differentiate among otherwise similar ELTs or ELTPs. Shrubs are also sometimes used as indicator species.

Compared to the herbaceous layer, the composition of the tree layer often recovers slowly from disturbances. Moreover, the tree component may not recover to its pre-disturbance composition. Joint consideration of physical and biological factors and their interactions provide a basis for identifying ecologically homogeneous land units that are silviculturally relevant and useful in delineating management units (Barnes *et al.*, 1982).

Ecological classification provides a broader ecological context for understanding why oaks occur where they do, and how those occurrences change with time, disturbance and other factors. At the broadest scale the oak forests of the United States can be divided into four eastern and two western groups based on species associations, ecological conditions and successional relations (Fig. 1.6).

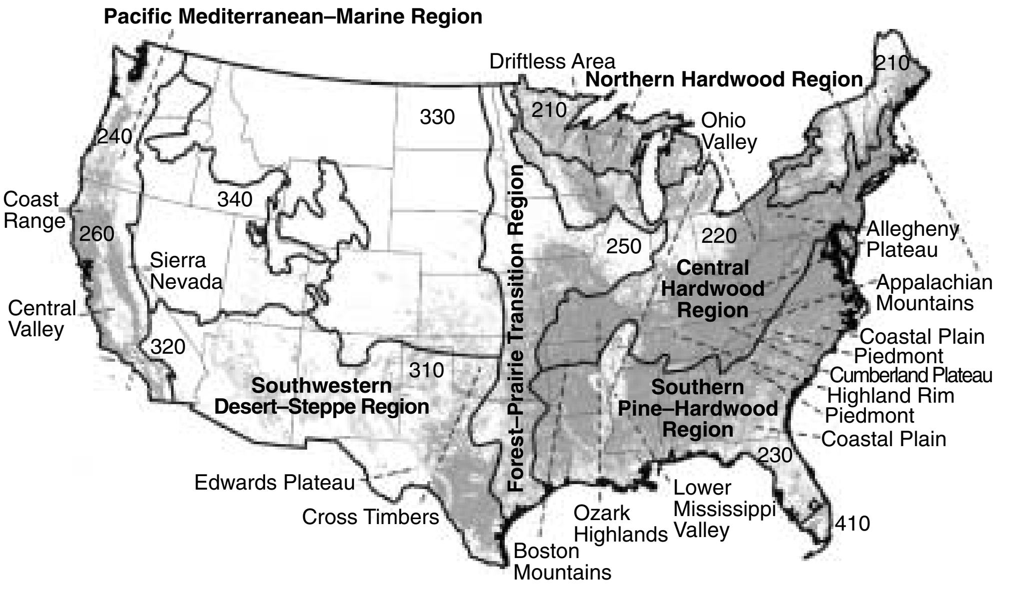

Fig. 1.6. The six regions where oaks commonly occur: Northern Hardwood Region; Central Hardwood Region; Southern Hardwood–Pine Region; Forest–Prairie Transition Region, Southwest Desert–Steppe Region; and Pacific Mediterranean–Marine Region. Numbers correspond to Ecoregion Divisions (Figs 1.2 and 1.5) (Bailey, 1997). Not considered by the above regional groupings are the ranges of Gambel and bur oak, which extend into *Division* 330, and the ranges of Gambel, turbinella and wavyleaf oaks, which extend into *Division* 340. The shading shows the distribution of oaks from Fig.1.2.

Boundaries between regions follow Division boundaries in the hierarchical ecological classification system. These regional groupings are useful ecologically and silviculturally because they identify areas with broadly similar macroclimates and species associations. Regional differences in the application of silvicultural methods are closely related to corresponding differences in species composition, environmental factors and other ecological conditions. The six forest regions are described below in relation to the Domains, Divisions and Provinces of the hierarchical ecological classification system described in the preceding section. However, the regional designations do not explicitly identify the lowland and riparian forests occurring within them. There, along the major rivers and streams within the Southern Pine–Hardwood Region, the oaks attain their greatest size and growth.

Eastern Oak Forests

The Northern Hardwood Region

Geographic extent

The Northern Hardwood Region includes the northern halves of Minnesota, Wisconsin, Michigan and much of the northeastern United States including New Hampshire, Vermont and Maine in their entirety. It includes two ecoregion Provinces: Mixed Deciduous–Coniferous Forests Province (211) and Mixed Forest–Coniferous Forest–Tundra, High Province (M211b) within the Warm Continental Division (Figs 1.2 and 1.6; Table 1.2). The Region extends 1300 miles from west to east and covers 123 million acres, about three-quarters of which is forested.

Braun (1972) called this area the Hemlock–White Pine–Northern Hardwood Region. She recognized two major subsections, the Great Lakes–St Lawrence and the Northern Appalachian Highlands. The western and eastern portions of the Northern Hardwood Region share many of the same species, but they differ ecologically and silviculturally (Godman, 1985). Those differences are due in part to the influence of the Appalachian Mountains in the eastern part of the Northern Hardwood Region.

More than 1.5 million non-industrial private forest owners own approximately half of the forests in the Northern Hardwood Region. Corporate and other private owners hold an additional 25% (Birch, 1996). There are 11 national forests in the region (primarily in the Lake States) that cover 6.5 million acres.

Climate, physiography and soil

Precipitation typically ranges from 24 to 45 inches per year although as much as 70 inches occurs in some mountainous areas in the eastern part of the region. Snowfall of 60 to 100 inches per year is common throughout the region. More than 100 inches of snowfall occurs at some of the higher elevations, and snowfall exceeds 400 inches in some locales near the Great Lakes. Mean annual temperature ranges from 35° to 52°F (2 to 11°C) and the growing season lasts from 100 to 160 days (Fig. 1.7) (McNab and Avers, 1994).

The region is characterized by low relief with numerous lakes, depressions, morainic hills, drumlins, eskers, outwash plains and other glacial landforms. Variation in the depth and type of glacial deposits and associated heights of water tables are important factors in the identification of silviculturally relevant ELTPs (Fig. 1.8). Elevations in the mountainous areas range from 1000 to 4000 feet with individual peaks exceeding 5000 feet. Valleys in the mountainous areas include outwash plains and lakes resulting from glaciation (Bailey, 1995). Soils have formed in diverse organic and mineral materials including peat, muck, marl, clay, silt, sand, gravel and boulders in various combinations. At lower elevations in New England and along the Great Lakes, Spodosols are common. Inceptisols and Alfisols dominate at lower elevations elsewhere. In the mountainous zones the soils are primarily Spodosols (Bailey, 1995).

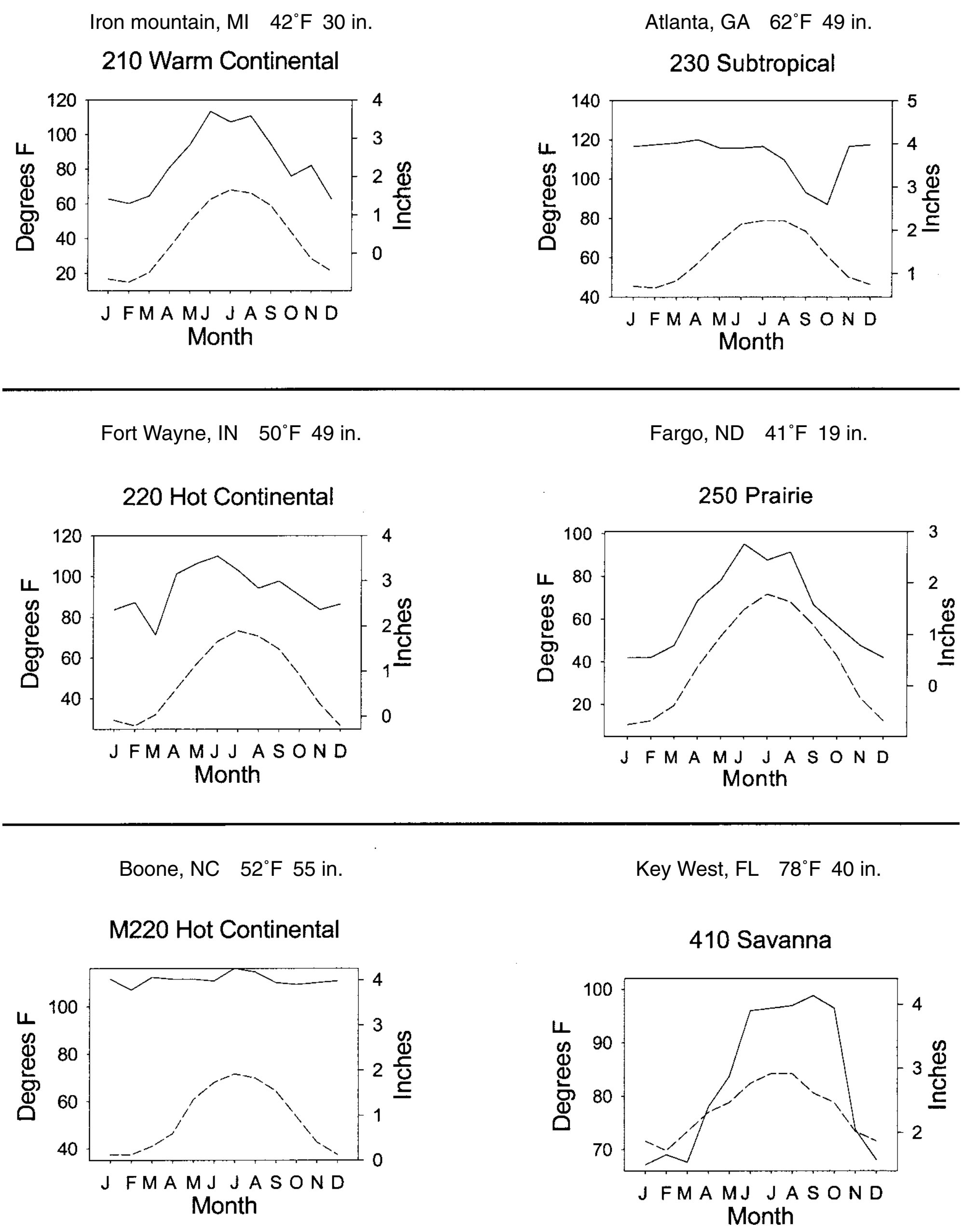

Fig. 1.7. Representative climates for selected ecoregion Divisions in the eastern United States. Mean monthly precipitation is shown by the solid lines (right axis) and temperature by dashed lines (left axis). Mean annual values are given above each graph. Division boundaries are shown in Figs 1.2 and 1.5. (Ecoregion and climatic data from Bailey, 1995.)

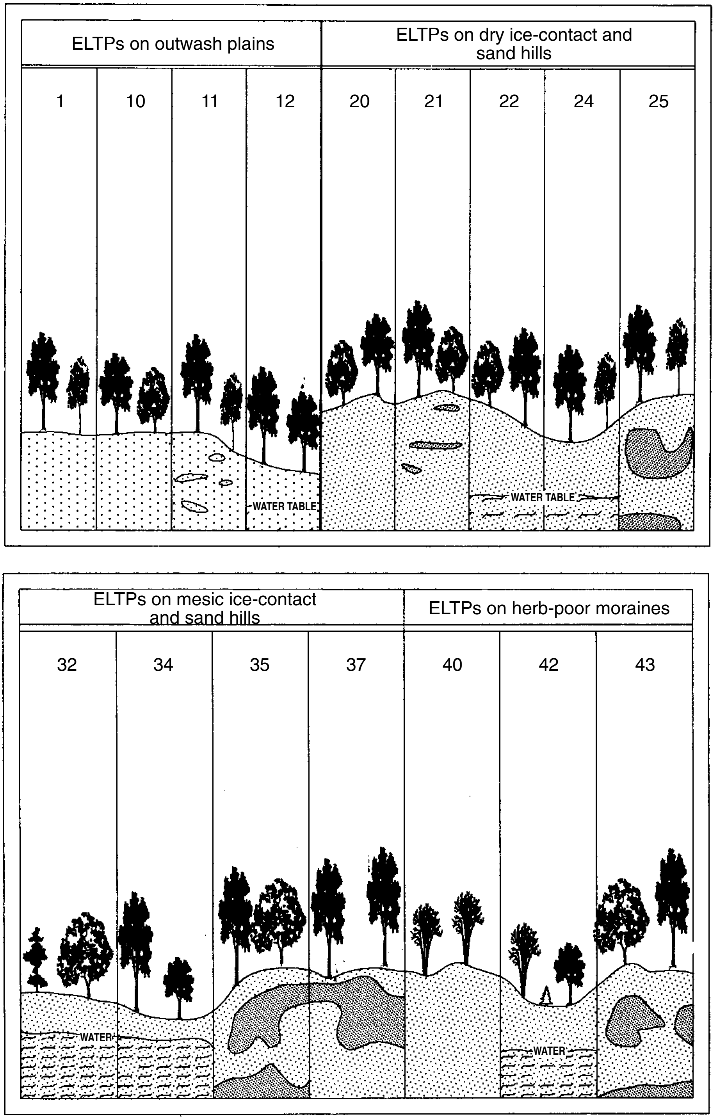

Fig. 1.8. Ecological landtype phases (ELTPs) for the upland forests of the Huron–Manistee National Forests in the lower peninsula of Michigan (*Province* 211: *Mixed Deciduous–Coniferous Forests Province*). Site productivity generally increases with increasing ELTP value. ELTP 1: Northern pin oak/white oak – *Deschampsia* type; ELTP 10: Black oak/white oak – *Vaccinium* type; ELTP 11: Black oak/white oak – *Vaccinium* type with loamy sand to sandy loam bands in substrata; ELTP 12: Black oak/white oak – *Vaccinium* type with perched water table at 6–15 ft; ELTP 20: Mixed oak/red maple – *Trientalis* type; ELTP 21: Mixed oak/red maple – *Trientalis* type with loamy sand to sandy loam bands in substrata; ELTP 22: Mixed oak/red maple – *Trientalis* type with perched water table at 6–15 ft; ELTP 24: Mixed oak/red maple – *Trientalis* type with perched water table at 3.5–6 ft; ELTP 25: Mixed oak/red maple – *Trientalis* type with coarse loamy substrata; ELTP 32: Northern red oak/red maple – *Viburnum* type with perched water table at 6–15 ft; ELTP 34: Northern red oak/red maple – *Viburnum* type with perched water table at 3.5–6 ft; ELTP 35: Northern red oak/red maple – *Viburnum* type with fine loamy substrata; ELTP 37: Northern red oak/red maple – *Desmodium* type with sandy loam over fine loamy substrata; ELTP 40: Sugar maple/beech – *Maianthemum* type; ELTP 42: Sugar maple – *Maianthemum* type with perched water table at 6–15 ft; ELTP 43: Sugar maple/northern red oak – *Maianthemum* type with fined texture substrata. (Adapted from Cleland *et al.*, 1993.)

Forest history

The forests of the Northern Hardwood Region were strongly influenced by the aboriginal people who lived there. For thousands of years before the arrival of Europeans, Native Americans used fire and land clearing to shape the forest to meet their needs. Accounts of early European settlers indicate that Native Americans burned large portions of the landscape each year (Pyne, 1982). Dry fuels in the late spring before 'greenup' and again after leaf fall during 'Indian summer' provided favourable conditions for burning. Fires often eliminated forest understorey layers, which in turn encouraged the growth of edible berries and increased forage that attracted edible wildlife. A combination of fire and tree cutting or girdling also was used by Native Americans to create and maintain openings for cultivated crops (Pyne, 1982). Maintaining an open understorey condition by burning also helped defend Indian villages from surprise enemy attacks. Repeated burning helped maintain large areas of oak savannas and barrens. Topography greatly influenced the spatial distribution of fires, and the frequency and intensity of burning were lower on wet or mesic sites and at higher elevations. This produced a landscape mosaic of diverse species composition.

The land clearing and burning practices used in New England were carried westward by settlers who immigrated to the Lake States. Oaks were known as indicators of fair to good conditions for agriculture. Oak forests therefore were often girdled, felled and burned in preparation for agriculture. Over time, enormous areas in the Northern Hardwood Region were cleared for agriculture. Ultimately, however, it was logging that had the greatest impact on the region's forests.

Logging gradually accelerated with the influx of Europeans to New England in the 17th century. Demands for forest products were initially modest in the developing agrarian society. Local timber harvesting supplied wood for homes, barns, fences, heating and cooking, and making potash and tannin. Forests were considered more an impediment to agriculture than a valued resource. However, this changed with industrialization during the 19th century (Williams, 1989).

The industrialization of America provided the capacity and economic incentive to exponentially increase lumber production from less than 1 to nearly 45 billion board feet between 1800 and 1900. That lumber, which was principally white pine and other softwoods, came primarily from the Northern Hardwood Region. In 1839, 30% of the nation's lumber (on a value basis) came from New York. Combined, New York, Pennsylvania, New Jersey and New England produced two-thirds of the nation's lumber. As supplies of white pine dwindled in the eastern part of the region, timber production moved westward. Although New York reached peak production in 1849, the northeastern states together had by then dropped to half of the national lumber output. The shift in lumber production from the Northeast to the Lake States occurred between 1840 and 1860. Lake States harvest reached a peak of 10 billion board feet annually in 1889. Relatively level terrain, easy access and high demand facilitated the rapid rise in timber harvesting across the Lake States. By 1940, Lake States production dropped below a billion board feet as the timber industry moved south (Williams, 1989).

Although white pine was the preferred species, oaks and other hardwoods were utilized locally where they were abundant. Oaks were in less demand by the logging industry. Because of their high density, oak logs could not be floated down rivers as easily as white pine and required overland transportation to avoid losses (Williams, 1989). Over time, repeated timber harvesting removed the trees of greatest economic value leaving behind stands of inferior quality and composition. Farmers emigrating westward subsequently completed the land clearing.

As a preferred fuelwood, the oak's utilization for that purpose significantly affected the region's forests during the early agricultural period. A colonial family used 20–60 cords of wood annually for heating and cooking. Although the per capita volume of wood used for fuel decreased over time, the total volume increased because of a growing population. In 1880, more than half of America's energy needs were still met with fuelwood (Whitney, 1994).

Iron furnaces in the region were fired with hardwood charcoal. Less than 1% of the fuelwood burned from 1800 to 1930 was used to produce charcoal for iron smelting, but large areas of forest surrounding iron furnaces were greatly affected (Whitney, 1994). A typical 18th-century smelting operation consumed 100 acres of forest annually to produce charcoal. Because forest regrowth could be repeatedly harvested for this purpose every 25 years, about 2500 acres of forest were required to sustain production of the ironworks. By the late 19th century, charcoal production for large ironworks required annual harvests of 1000–2000 acres, and some large companies owned 100,000 acres of forest adjacent to their smelters for that purpose (Whitney, 1994). The large clearcuts surrounding the ironworks radically changed the age structure of the forests and also influenced their species composition.

Harvesting hardwoods for fuel favoured the development of hardwood sprouts and increased the relative proportion of hardwood trees in areas that were not converted to agricultural land (Whitney, 1994). During the last half of the 19th century, many cleared acres marginally suited to agriculture were abandoned and subsequently reverted to forest. During the latter half of the 20th century, the combination of abandoned agricultural lands and natural regeneration of cutover lands resulted in large increases in timber volumes throughout the region. In New England, forest volumes increased by 16% between 1970 and 1982 (cubic foot basis) (Seymour, 1995). The increase was predominantly in hardwoods that as a group increased in volume by 24%. The increase in oak volume (16%) was low relative to other hardwoods. In 1992, net annual growth in the Northern Hardwood Region remained at more than twice the annual harvest (Powell *et al.*, 1994).

Oaks as components of the region's forests

The forests of the Northern Hardwood Region today are dominated by more than half a dozen recognized northern hardwood forest types comprising various combinations of sugar maple, red maple, beech, paper birch, yellow birch and eastern hemlock. Although northern red oak typically occurs as a minor component within these types, it sometimes forms pure or nearly pure stands (Fig. 1.9A). Wherever it occurs, it is a valuable and desirable species for timber, acorn production and species diversity. White, black, northern red and chestnut oaks also occur in the southern portions of the region.

Oaks are thus a relatively small component of northern hardwood forests. They are most abundant and attain their best development in the southern parts of the region including New York, Massachusetts, northern Pennsylvania, and central and southern Minnesota, Wisconsin and Michigan. There the oak and mixed-hardwood forests grade into the oak–hickory forests of the Central Hardwood Region. In both New England and the Lake States, about 11% of the forestland is classified as oak–hickory or oak–pine. These forest types include 17 billion cubic feet of growing stock (inclusive of oaks and associated species). Throughout the Northern Hardwood Region, sugar maple, red maple and aspen are the most abundant hardwoods. Conifer forests (red and eastern white pines, spruce and balsam fir) also exceed oak in acreage and volume (Powell *et al.*, 1994).

Oaks often reach their greatest density on sites that have been repeatedly disturbed by fire, timber harvesting and other events. After burning or timber harvesting, oaks originating from vigorous seedling sprouts and stump sprouts often dominate stands. However, in the absence of disturbance the oak forests of the Northern Hardwood Region are usually successional to other hardwoods on all but the poorest sites. On the poorer sites, oaks are often relatively permanent members of the forest.

A

B

Fig. 1.9. (A) A 130-year-old stand of northern red oak in the Northern Hardwood Region of northern Wisconsin (*Province* 211: *Mixed Deciduous–Coniferous Forests Province; Southern Superior Uplands Section*). The absence of oak reproduction and a sparse sub-canopy of shade tolerant red and sugar maples are indicators of what is likely to eventually replace the oaks in the absence of disturbance. (B) Xeric northern pin oak–white oak/*Deschampsia* type (see Fig. 1.8) on deep outwash sand in the northern lower peninsula of Michigan (*Province* 211: *Mixed Deciduous–Coniferous Forests Province; Northern Great Lakes Section*). This oak stand is mixed with jack pine; oak site index is ≤50 ft. (USDA Forest Service, North Central Research Station photographs.)

There, oaks frequently invade and successionally replace established pine stands (Seymour, 1995). The loss of the American chestnut to chestnut blight fungus in New England oak forests began in the early 1900s (Fig. 1.10). This increased the relative importance of oaks because oaks often captured the growing space vacated by dying American chestnuts.

Today, the single-tree selection method of silviculture is often applied to northern hardwood forests dominated by shade tolerant species such as sugar maple. This practice focuses on maintaining stands of high quality trees while largely relying on the natural regeneration of shade tolerant species to sustain the silvicultural system. Although this system favours the develop-

Fig. 1.10 A standing dead American chestnut (minus bark). Chestnut was a common associate and dominant member of eastern oak forests throughout the Appalachians from Maine to Alabama and westward to Missouri. The chestnut blight, which decimated the species throughout its range, permanently altered the ecology of eastern oak forests. The blight was first identified in New York in 1904. Fifty years later it spanned the entire natural range of chestnut. Oaks and associated hardwoods quickly captured the growing space vacated by dead and dying chestnuts. (USDA Forest Service, North Central Research Station photograph.)

ment of high quality oaks in stands where oaks are already present, regenerating oaks beneath the relatively closed canopies of selection forests is usually difficult in this region. On the poorer sites, oaks may develop beneath a pine overstorey and eventually displace the less shade tolerant pine through natural succession or the exposure of oak reproduction in the understorey to full light after timber harvest. On deep sandy soils of the upper Lake States, stands of northern pin, black and white oaks, often mixed with jack pine, form relatively stable forest types of low productivity (Fig. 1.9B).

The Central Hardwood Region

Geographic extent

The Central Hardwood Region includes the predominantly deciduous broadleaf forests of Central United States. The region lies entirely within the Humid Temperate Domain. The region includes the two Hot Continental Divisions (Divisions 220 and M220), and intergrades with the eastern part of the Forest–Steppes and Prairies Province (251) of the Prairie Division (250) (Figs 1.2 and 1.6; Table 1.2). The Hot Continental Division is subdivided into two provinces: Broadleaf Forests, Oceanic (221a); and Broadleaf Forests, Continental (221b). The Hot Continental Mountains Division (M220) also is divided into two provinces: Deciduous or Mixed Forest–Coniferous Forest–Meadow (M221), and Broadleaf Forest–Meadow (M222).

The Northern Hardwood Region, the Southern Pine–Hardwood Region, the Forest–Prairie Transition and the western edge of the Appalachian Mountains bound the Central Hardwood Region. The Central Hardwood Region extends 1200 miles from southwest to northeast and covers approximately 220 million acres; about half the region is forested. Approximately three-quarters of the forest area in the Central Hardwood Region is in non-industrial private ownership. Within that ownership, most holdings are 50 acres or smaller (Birch, 1996). There are seven national forests in the region comprising about 4 million acres distributed across the southern half of the region in Arkansas, Missouri, Illinois, Indiana, Ohio, Kentucky and Tennessee.

Climate, physiography and soil

The climate in the Central Hardwood Region is hot continental with warm summers and cold winters. Mean annual temperature ranges from 40 to 65°F (4–18°C), with the warmer temperatures in the south.

Annual precipitation ranges from 20 inches in the northwest to 65 inches in the southeast and reaches as much as 80 inches on some Appalachian peaks (Fig. 1.7). Precipitation occurs throughout the year, but tends to be somewhat greater in spring and summer. Droughts may occur during the summer when evapotranspiration is high. Frost-free periods range from 100 days in the northern Appalachians to 220 days in the southern part of the region (Bailey, 1995).

Topography is diverse in this region. Elevations in the Appalachian Highlands (province M221) range from 300 to 6000 ft with as much as 3000 ft of local relief. Further west (province 221a), the hills and low mountains of the dissected and uplifted Appalachian Plateau (including the Allegheny and Cumberland Plateau) range from 1000 to 3000 ft in elevation. In the western half of the Central Hardwood region (province 221b), most of the land is rolling but varies from extensive, nearly level areas to areas like the Ozark Highlands where relief reaches 1000 ft. Most of the northern portions of this province were glaciated with the exception of the driftless area of southwestern Wisconsin and adjacent states. Major soils are Alfisols, Inceptisols, Mollisols and Ultisols (Bailey, 1995).

Forest history

The utilization and exploitation of forests in the Central Hardwood Region has passed through various historical phases (Hicks, 1997). Even before the arrival of Europeans, humans influenced the nature and extent of the region's forests (Whitney, 1994). The use of fire to control vegetation by Native Americans significantly influenced the extent and character of presettlement forests (Pyne, 1982; DeVivo, 1991; Olson, 1996). These human-caused alterations of the landscape continued for thousands of years before the arrival of Europeans (Hicks, 1997). After settlement by Europeans, human impacts on the forest expanded and intensified. Burning, grazing, exploitative timber harvesting and clearing of forests for agriculture occurred on an unprecedented scale. These practices occurred about 200 years earlier in the eastern part of the Central Hardwood Region than in the western part. Historically, different human disturbances were further confounded by intrinsic ecological differences among oak forests within the various ecoregion provinces. Each subregion of the Central Hardwood Forest has its own unique combination of disturbance history, climate, physiography, soils, species associations and successional possibilities. This complicates generalizing the application of silvicultural methods to oak forests across the region.

As in the Northern Hardwood Region, the loss of American chestnut to chestnut blight increased the relative proportion and importance of oaks throughout the region. Shortly after 1900, the disease became epidemic and within 40 years it had invaded the entire natural range of the chestnut (Kuhlman, 1978). The loss represents one of the greatest recorded changes in a natural population of plants caused by an introduced organism (Liebhold *et al.*, 1995). The chestnut comprised 25% of the eastern hardwood forest that covered 200 million acres. In the Appalachians, it was the most ecologically and economically important tree species (Kuhlman, 1978). There and in other regions, it grew faster and taller than associated oaks. Before the blight, chestnut was especially important in moist upland forests where it sprouted vigorously and often increased in dominance after logging. In 1900, half the standing timber in Connecticut was chestnut, which was largely comprised of young stands of stump sprout (coppice) origin (Smith, 2000). Although American chestnut provided only about 1% of the nation's hardwood lumber even at the peak of its importance, its loss (beginning in the early 1900s) had a significant impact on local economies in the Appalachians. There its nuts and bark (for tannin) provided scarce cash income, and its wood was valued for a variety of uses (Youngs, 2000).

The practice of silviculture in the Central Hardwood Region dates back to the genesis of North American forestry in the late 19th century (Fernow, 1911; Pinchot, 1987). From then until the 1960s, the major emphasis was on uneven-aged silviculture (Roach, 1968). During the 1960s, the emphasis shifted to even-aged silviculture, especially clearcutting, and this emphasis persisted for about 20 years (Roach and Gingrich, 1968; Johnson, 1993a). Where applied, hardwood silviculture in the region usually follows the 'ecological model', which relies on the existing forest vegetation and its natural regeneration capacity. Silvicultural prescriptions are usually focused on controlling stand structure and species composition using cutting methods such as those recommended by Roach and Gingrich (1968). This approach contrasts with the more intensive 'agronomic model' of silviculture based on artificial regeneration, the introduction of improved genotypes, use of herbicides and fertilizer, prescribed burning, and other intensive cultural methods like those commonly used in the silviculture of pine monotypes in the south and elsewhere.

Where applied, silviculture in the Central Hardwood Region has usually focused on growing high quality sawtimber. During the course of stand management (but before final harvest of even-aged stands), this requires 'leaving the best' and 'cutting the worst' at each harvest. In even-aged silviculture, each timber harvest concentrates on removing small, sub-canopy trees and poor quality trees in the main canopy, with concomitant attention to species composition. Similarly, in uneven-aged silviculture, timber removals are concentrated on poor quality trees, but cutting occurs across a wide range of diameter classes in order to create and maintain the uneven-aged stand structure. In both systems the objective is the improvement of the quality and the economic value of the residual stand.

Today, only a small fraction of the forests of the Central Hardwood Region receive systematic silvicultural treatment. This is largely due to the pattern of forest ownership, which is characterized by numerous small tracts owned by private individuals. Many forest owners are uninterested in silviculture or lack information on its benefits (Bliss *et al.*, 1994, 1997; English *et al.*, 1997). Consequently, the systematic application of silviculture has largely been limited to industrial forests and public lands.

The predominant methods of timber harvesting on private lands are probably commercial clearcutting and other forms of high-grading. Not to be confused with silviculturally prescribed methods, these methods consist of harvesting all trees with commercial value without regard to regeneration needs and future stand condition. Such malpractice typically leaves stands of highly variable residual stocking comprised of trees of poor vigour, low quality and undesirable species composition. These practices persist and continue to impact negatively on the quality of the region's forests. Nevertheless, annual forest growth for the region exceeds annual harvest, and total standing volume of timber has increased steadily since the 1950s (Powell *et al.*, 1994).

Oaks as components of the region's forests

The predominant oaks are black, white, scarlet, chestnut, post, northern red, southern red and bur oak (Fig. 1.11). These species typically occur in various combinations with hickories, sassafras, flowering dogwood, blackgum, black cherry, red maple, and other upland oaks and deciduous tree species. The Ozark Highlands Section of the region, which covers southern Missouri, and parts of northeastern Oklahoma, northern Arkansas and southwestern Illinois, comprises one of the largest contiguous areas dominated by the oak–hickory association in the Central Hardwood Region. Many oak–hickory forests of today may have originated from extensive fire-maintained oak savannas of the presettlement period; these formed closed canopy forests when fires were suppressed (Johnson, 1993a; Olson, 1996).

The oak cover types of the Central Hardwood Region include various combinations of oaks, hickories and other tree

Fig. 1.11 A mature black–northern red–white oak stand on a good site in the Central Hardwood Region of southeastern Ohio (*Province* 211a: *Broadleaved Forests, Oceanic Province*). (USDA Forest Service, North Central Research Station photograph.)

species that vary geographically (Appendix 2). Although hickories are common and persistent members of this forest type, they seldom represent more than a small proportion of trees in the main canopy of a mature forest (Braun, 1972). Oak–hickory forests develop on relatively dry sites where oaks persist as dominant members of the forest through successive disturbance events. This persistence is facilitated by the oaks' drought tolerance and by light intensities in dry ecosystems that are sufficient for the regeneration of the relatively shade-intolerant oaks (Bourdeau, 1954; Carvell and Tryon, 1961; Abrams, 1990).

Oaks and hickories are found together on the drier sites throughout the region and comprise a commonly occurring species association. These forests dominate the landscape in the western part of the region. Elsewhere, oaks and hickories as a group commonly occur on dry ridges and south-facing slopes. On the more mesic sites, oaks are often interspersed with other hardwoods. Slope position and aspect strongly influence the spatial distribution of these forests and are thus useful in defining ELTPs in much of the region (Figs 1.12 and 1.13).

From southern Illinois eastward and in northern Arkansas, the more mesophytic forests of the Central Hardwood Region generally include more complex species mixtures than found in drier oak forests (Fig. 1.14). Although oaks commonly share dominance with non-oaks on these sites, in the absence of recurrent fire and grazing the oaks are often successionally displaced by more moisture-demanding and more shade tolerant non-oaks (Jokela and Sawtelle, 1985; Lorimer, 1985, 1989; Nowacki *et al.*, 1990; Abrams, 1992). Understoreys of these stands are typically lacking in oak reproduction, especially large oak seedling sprouts. Over time, the dominance of oaks decreases while the proportion of non-oaks increases. The latter include various combinations of maples, American beech, black cherry, white ash, American basswood and yellow-poplar. Timber harvesting may accelerate the successional replacement of the oaks (Abrams and Nowacki, 1992).

Diverse mixtures of hardwoods are common throughout the Ohio Valley, the Cumberland Plateau and Highland Rim areas of Tennessee and Kentucky, the Appalachian and Allegheny Plateau of

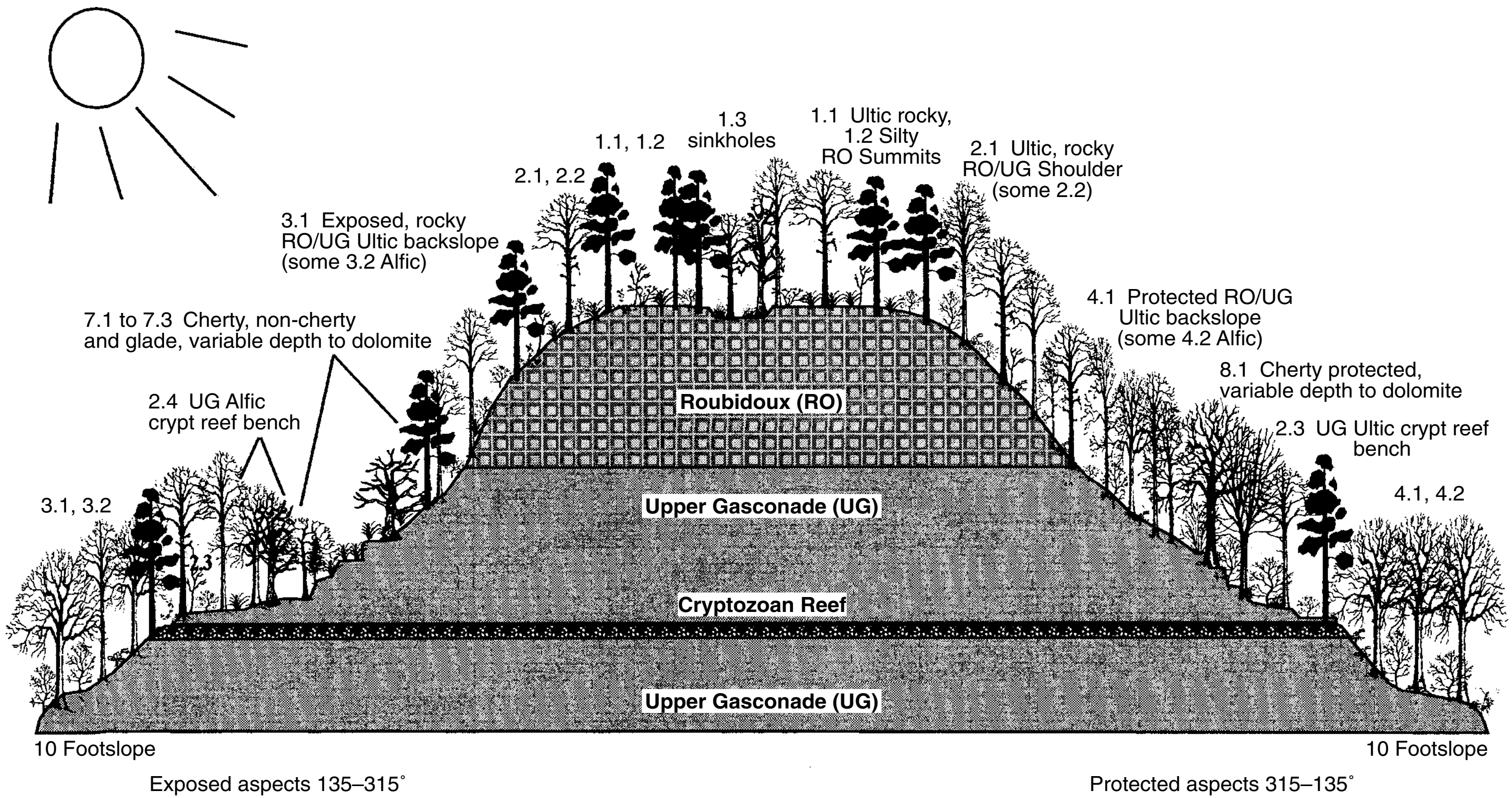

Fig. 1.12. Ecological landtype phases (ELTPs) for the Ozark Highlands of Missouri (*Province* 221b: *Broadleaved Forest, Continental Province; Ozark Highlands Section*, upland ELTPs in the Current, Eleven Point and Black River Landtype Associations). Aspect, landform and bedrock geology are factors in the classification system. ELTP 1.1, 1.2, 1.3, 2.1, 2.3 and 3.1: pine–oak/*Vaccinium* dry ultic (chert) woodland; ELTP 2.2 and 3.2: mixed oak–pine/*Desmodium*, *Vaccinium* dry-mesic alfic (chert) woodland; ELTP 4.1: mixed oak–hickory/dogwood/*Desmodium* dry-mesic ultic (chert) forest; ELTP 4.2: mixed oak (white, red) dogwood dry-mesic alfic (chert) forest; ELTP 7.1: post oak (blackjack oak, pine) bluestem xeric chert woodland; ELTP 7.2: red cedar–hardwood/redbud dry dolomite woodland; ELTP 7.3: bluestem, Missouri coneflower dolomite glade; ELTP 8.1: mixed oak–sugar maple/redbud dry-mesic dolomite forest; ELTP 10: mixed oak (white)/dogwood dry-mesic alfic (chert) footslope forest. (From Nigh *et al*., 2000, used with permission.)

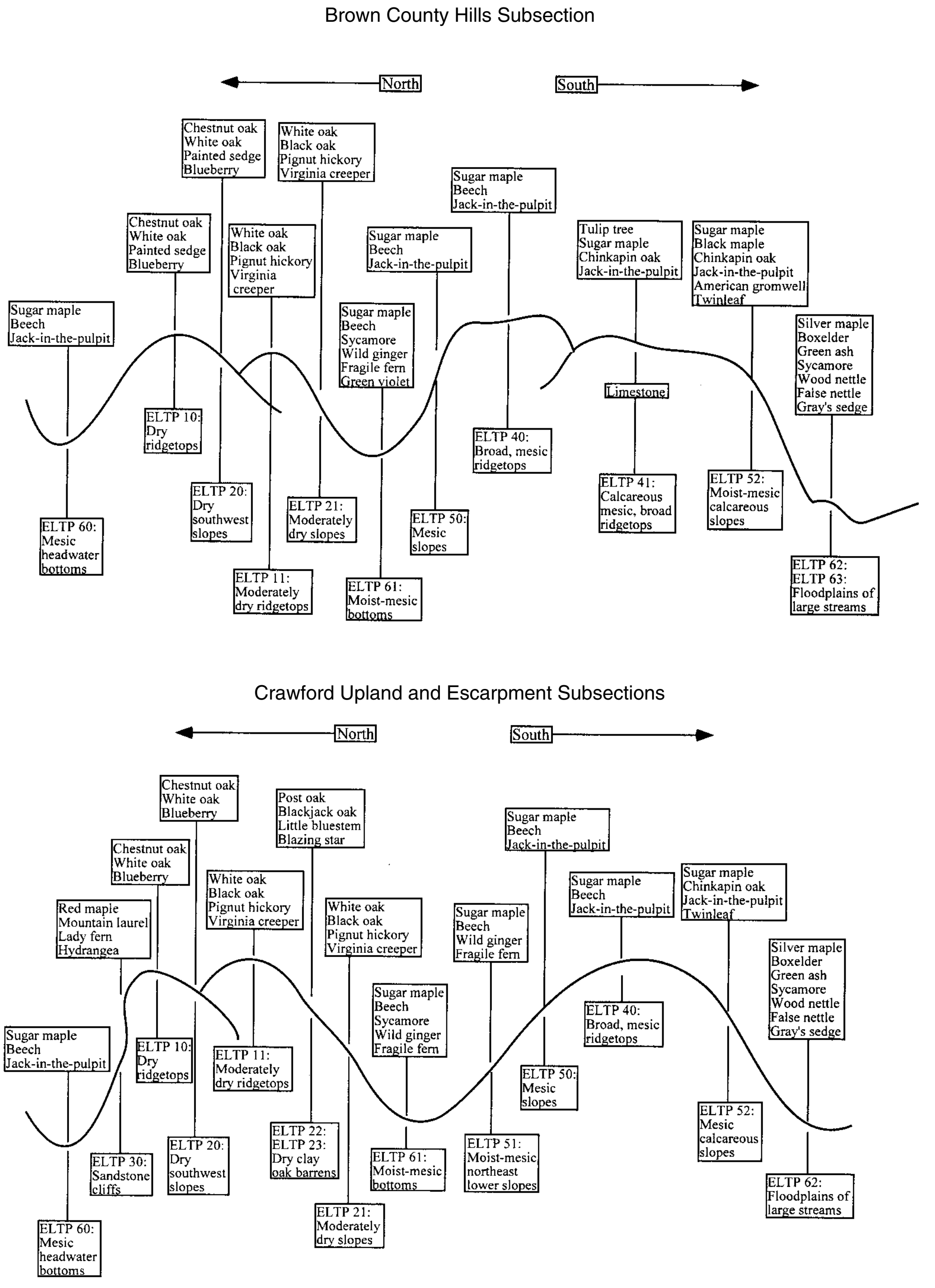

Fig. 1.13. Ecological landtype phases (ELTPs) for the forests of the Brown County Hills, Crawford Upland and Escarpment Subsections of southern Indiana (*Province* 221b*: Broadleaved Forests, Continental Province; Interior Low Plateau, Shawnee Hills Section*). Oaks and pines typically dominate the exposed (hotter) aspects whereas sugar maple, American beech, yellow-poplar and other shade tolerant hardwoods dominate the protected (cooler) aspects. (Adapted from Van Kley *et al.*, undated.)

Fig. 1.14. A large white oak (47 inches dbh) in Dysart Woods in southeastern Ohio (*Province* 221a: *Broadleaved Forests, Oceanic Province*). This 55-acre old-growth oak forest is dominated by white and northern red oaks and is the largest known remnant of the original mixed mesophytic forest of the Central Hardwood Region in southeastern Ohio. (USDA Forest Service, North Central Research Station photograph.)

western West Virginia and western Pennsylvania, the southern Lake States, and other parts of the region. Specific combinations of canopy dominants often form distinct geographic species groupings. Examples include the beech–maple forests of central Indiana and eastern Ohio, the maple–basswood–northern red oak forests of the driftless area of southwestern Wisconsin, and the black cherry–ash–yellow-poplar forests of the Allegheny Plateau of Pennsylvania. Toward the eastern end of the region, eastern white pine and eastern hemlock may be locally important members of mixed hardwood forests. Mixtures of oak and mesophytic species also occur in northern Arkansas in the Broadleaf Forest–Meadow Province (M222) (Fig. 1.2; Table 1.2) (Braun, 1972). However, unlike the mixed mesophytic forests further to the east, yellow-poplar is absent. These are the most mesophytic forests in the western end of the region. Some of these combinations are formally recognized as cover types (Eyre, 1980); others form mixtures that are only locally distinguished silviculturally.

It is within these mesic, mixed hardwood stands that northern red oak, one of the most commercially valuable tree species of the region, reaches its best development. It is also within these forests that the oaks are also the most difficult to regenerate silviculturally (Carvell and Tryon, 1961; Arend and Scholz, 1969; Trimble, 1973; Loftis, 1988; Johnson, 1993b, 1994a,b). Mesophytic mixed hardwood forests generally occur where oak site index (chapter 4) is ≥65 ft at an index age of 50 years.

Oak–pine mixtures occur most frequently in the southern and eastern parts of the region and are closely correlated with fire and succession in old fields, heavily disturbed hardwood stands, and pine plantations. Oak–pine mixtures represent an early- to mid-stage in the succession toward oak–hickory or mixed hardwood forests. In the absence of fire or other disturbances, oak–pine forests may change successionally from predominantly shortleaf pine, pitch pine or Virginia pine to hardwoods as the more shade tolerant hardwoods replace the intolerant pines (Cunningham and Hauser, 1989; Sheffield *et al.*, 1989; Smith *et al.*, 1989; Orwig and Abrams, 1994). The oak–pine mixtures are important for maintaining biodiversity as well as economic timber production (Phillips and Abercrombie, 1987; Cooper, 1989; Kerpez and Stauffer, 1989; Leopold *et al.*, 1989). Consequently, there is increasing interest in methods to create and maintain oak–pine forests (Waldrop, 1989). Specific combinations of oaks and pine vary with subregion and site quality. Because the pines tend to be associated with the driest (xeric) sites, the associated oaks often include species such as post oak and blackjack oak. On somewhat less xeric sites, pines are commonly associated with black, white, scarlet, southern red or chestnut oaks. In the extreme northwestern part of the region in Minnesota and Wisconsin, jack pine and northern pin oak commonly occur together.

Stands of eastern redcedar are closely affiliated with the oak–pine mixtures. Eastern redcedar is a common invader of old fields and glades (Lawson, 1990). It may eventually form dense pure stands if succession is allowed to progress unimpeded by disturbance. However, such stands are short-lived. As the redcedar matures and forms canopy gaps conducive to hardwood or pine regeneration, stands may succeed to oak–pine and oak–hickory mixtures.

The Southern Pine–Hardwood Region

Geographic extent

The Southern Pine–Hardwood Region includes broadleaved forests, conifer forests and various hardwood–pine mixtures. The region includes the two Subtropical Divisions (230 and M230) of the Humid Temperate Domain (Figs 1.2 and 1.6; Table 1.2). The region covers approximately 270 million acres of which 60% are forested. The extent of the Southern Pine–Hardwood Region is best illustrated by the joint ranges of the oak–pine and oak–gum cypress forest types (Fig. 1.5B and C). The region extends 1300 miles from eastern Texas to Virginia and occurs in a band extending 200–400 miles inland from the coast. At its northern boundary, the Southern Pine–Hardwood Region meets the Central Hardwood Region.

Nearly 90% of the forest area in this region is privately owned. Four million non-industrial private forest owners control about 60% of all timberland. About 45% of this ownership is comprised of tracts smaller than 100 acres (Birch, 1996). The 25 national forests in the region comprise 9 million acres of timberland (Powell *et al.*, 1994).

Climate, physiography and soil

Annual precipitation in the region ranges from about 40 to 60 inches and is well distributed throughout the year. Mean annual temperature ranges from 60 to 70°F (16 to 21°C) and the growing season from 200 to 300 days (Bailey, 1995) (Fig. 1.7).

The Southern Pine–Hardwood Region includes four major physiographic regions: the Piedmont (Province 232), the Coastal Plain (Province 231), the Interior Highlands (Province M231) and the lower Mississippi Valley (Riverine Intrazonal Province (R)) (Fig. 1.2). Gentle slopes characterize 50–80% of the area. Elevations range from sea level to 600 ft in the Coastal Plain, 300–1000 ft in the Piedmont, and up to 2600 ft in the Ouachita Mountains of the Interior Highlands. Numerous low-gradient streams, lakes, swamps and marshes characterize the flat Coastal Plain. The wet habitats along the Coastal Plain, the Mississippi Valley and other major rivers support bottomland forest types that are largely absent from the Piedmont and Interior Highlands.

The principal soil groups are Ultisols, Spodosols, Vertisols and Entisols, all of which tend to be low in fertility. Exceptions are the Inceptisols, which occur in the alluvial bottoms of the Mississippi River (Bailey, 1995).

Forest history

Here, as in other regions, fire greatly impacted the early forests. Fire was an essential tool for maintaining agricultural openings, eliminating brush and hardwood reproduction from pine forests, and increasing forage for grazing. Native Americans regularly burned the forests where they lived. Increased burning associated with European settlement increased the proportion of pine in the region relative to earlier periods (Pyne, 1982; Skeen *et al.*, 1993). Fire was combined with land clearing to open the hardwood forests of the south for agriculture. Even today, forest burning is a prominent practice throughout the region.

In the Piedmont and alluvial river bottoms, vast areas were cleared for agriculture before industrial logging peaked in the region (Sargent, 1884; Hodges, 1995).

Logging and the production of naval stores began on a small scale in the 1600s. But by 1880, forests accessible by water and close to population centres were heavily cut over. Charles Mohr noted the rapidity at which the cypress swamps were being logged in some localities and the apparent lack of forest regeneration. He observed that 'the large number of logs harvested shows clearly with what activity the destruction of these treasures of the forest is being pushed; and the reports, as of heavy thunder, caused by the fall of the mighty trees, resounding at short intervals from near and far, speak of its rapid progress' (Sargent, 1884). However, Mohr also noted that immense areas of pine forest remained unaffected by logging and that many former hardwood forests that were earlier cleared for agriculture had reverted to pine after their abandonment.

The South did not become the centre of the US logging industry until shortly after logging peaked in the Lake States in 1890. By 1900, lumber production in the South exceed that of the Lake States and by 1910 the South produced half of all US lumber. The movement of large lumber companies to the Southern Pine–Hardwood Region coincided with technological advances that increased the speed with which logs could be removed from the woods and transported to the mills (Williams, 1989). Steam powered stationary skidders and loaders were mounted on boats and railcars. As rail lines were extended into the southern forest, logging trains followed and systematically removed virtually all timber within the long reach of a cable skidder mounted on a rail car. The joint enterprise of rail construction and logging greatly accelerated the harvest of southern pines (Williams, 1989).

By 1925 southern lumber production began to decline and western production increased. Following the Great Depression, timber production in the South never returned to the levels of 1910–1930, and the bulk of US timber production moved west. The subsequent establishment of southern paper mills coupled with successful fire prevention and a reduction in open-range grazing accelerated the reforestation of one million cutover acres. This gave rise to the South's 'third forest' which today again produces a greater volume of wood than any other region of the United States.

Oaks as a component of the region's forests

The oak forests in this region can be divided into upland and lowland types. Were it not for the complex spatial intermingling of upland and lowland forests, they could be treated as two ecologically distinct regions. The upland and bottomland oak forests of the region differ substantially in species composition, ecology and the application of silvicultural practices.

The Southern Pine–Hardwood Region today includes about 172 million acres of timberland. Of the broadly defined oak forests recognized in national inventories, the oak–hickory group occurs on 55 million acres or one-third of the region's timberland. Oak–gum–cypress and oak–pine each occur on an additional 16% of the timberland. Thus, oak forests collectively cover more than 60% of the region. Loblolly-shortleaf pine and longleaf-slash pine make up most of the remaining forest acreage. A more detailed cover type classification (Eyre, 1980) recognizes 63 cover types that occur within the region (Walker, 1995) – 15 of those include oaks as primary species, and several others include oaks as important associated species (Appendix 2).

Southern silviculture has largely focused on pine, especially on industrial forestlands. There, intensive silviculture is commonly practised to maximize timber and wood fibre yields through site preparation, planting genetically improved seedlings, frequent thinning, prescribed burning, and the use of fertilizers, herbicides and pesticides. However, annual softwood removals are nearly equal to annual growth and may soon exceed annual growth (Walker, 1995).

The importance of pine in the Piedmont is related to the region's history – the historical sequence of lumbering, land clearing and farming deforested large areas that were abandoned before 1930 and burned frequently. This disturbance favoured the establishment of pine forests, which greatly increased in acreage relative to other species. Oaks and other hardwoods occur in most natural southern pine stands, and on these sites they increase in importance through succession. Fire suppression, silvicultural thinnings and partial harvests often accelerate this trend (Skeen *et al.*, 1993).

The large oak–hickory acreage in the region, the increasing hardwood volumes in pine–hardwood mixtures, and the nearly full utilization of the annual pine growth in the region has recently shifted the utilization of the region's forests towards the hardwoods. Much of this change has resulted from the utilization of hardwood chips for paper production and composite products. Chips can be made from low quality, small diameter (>4 inches) hardwoods. This technology created new markets for the abundant low-quality trees that previously had been considered a silvicultural liability. However, this utilization capability has also raised concerns about the potential for overutilization of hardwoods, especially well formed, small hardwood trees that comprise the future hardwood growing stock for solid hardwood products. The region's oak–hickory forests attain their best development along the border separating the Southern Pine–Hardwood Region and the Central Hardwood Region.

Closely related to the oak–hickory forests are mixtures of oak and pine (Fig. 1.15). These mixed forests are increasingly recognized for their importance in maintaining forest biodiversity and their historical importance in the region. The oak–pine type, which occurs on 16% of the timberland of the region, rates high in aesthetic appeal and species richness compared to even-aged pine stands. However, relatively little is known about the long-term management and productivity of oak–pine mixtures for lumber, fibre or other values. In the absence of disturbance, the oaks tend to successionally displace the pines and harvesting the pine often accelerates the process.

Fig. 1.15. A black oak–white oak–shortleaf pine stand in the Ozark Highlands of Missouri (*Province* 221b*: Broadleaved Forests, Continental Province; Ozark Highlands Section*). (USDA Forest Service, North Central Research Station photograph.)

Southern bottomland hardwoods commonly include 11 species of oaks (cherrybark, Delta post, laurel, Nuttall, overcup, pin, Shumard, swamp chestnut, water, white and willow oaks) (Hodges, 1995). These oaks occur in mixture with other bottomland species along the major rivers of the Coastal Plain as well as the lower reaches of the Mississippi, Arkansas, Missouri, Ohio and Wabash Rivers (Fig. 1.16). In total, southern bottomland hardwoods cover more than 27 million acres (16% of the region's timberland) and are physiographically and ecologically distinct from surrounding upland oak–hickory, oak–pine and pine forests.

Fig. 1.16. A cherrybark oak–sweetgum bottomland stand near the Tombigbee River in Alabama (*Province* 232*: Coniferous-Broadleaved Semi-evergreen Forests Province*). (USDA Forest Service, Southern Research Station photograph.)

Although bottomland forests are relatively flat, elevational differences of only a few feet alter soil formation processes, soil moisture regimes and species composition. Thus, changes in species composition are often associated with relatively minor differences in physiography (Fig. 1.17). Moreover, floodplain physiography can quickly and frequently change as a result of scouring and deposition of sediments. These factors, coupled with the high tree species diversity of bottomland forests, complicate classifying forest types and developing silvicultural prescriptions appropriate to each. Up to 70 tree species occur in southern bottomland forests (Putnam *et al.*, 1960), and species mixtures often change over short distances within stands. Consequently, species associations are difficult to classify meaningfully into more than a few broad types. Although Eyre (1980) listed 14 bottomland cover types (six named for oaks), Hodges (1995) reduced the number to three types (cottonwood–willow, baldcypress–tupelo, mixed bottomland hardwoods), and the USDA Forest Service usually reports only two types (oak–gum–cypress, elm–ash–cottonwood) in regional summaries.

The Forest–Prairie Transition Region

Geographic extent

Within the United States, the Forest–Prairie Transition Region extends from southern Texas northward to Minnesota and North Dakota (Fig. 1.6). The region coincides with two ecoregion provinces: Forest–Steppes and Prairies (251) and Prairies and Savannas (252) within the Prairie Division (250) (Fig. 1.2, Table 1.2). The region includes Braun's (1972) Grassland or Prairie Region, Forest–Prairie Transition and Prairie Peninsula Sections, which fall within her Oak–Hickory Forest Region.

As its name implies, the Forest–Prairie Transition Region is transitional between the eastern forests and the prairies and dry woodlands of the *Dry Domain* to the west. On its eastern border, the region adjoins the Northern Hardwood Region, the Central Hardwood Region and the Southern Pine–Hardwood Region. The Forest–Prairie Transition Region spans 1400 miles in latitude and varies in width from as little as 100 miles along the Canadian border to 600 miles between eastern Nebraska and western Indiana. The region includes approximately 191 million acres, about 7% of which are forested. Between Canada and Oklahoma, forests cover 5% of the landscape with most of the remainder devoted to tilled cropland or pasture. The forest cover increases to 13% in parts of Oklahoma and Texas. Most of the forestland in the Forest–Prairie Transition Region is privately owned. Although there are three national grasslands within the region, only 15,000 acres of national forest land (in central Missouri) are included.

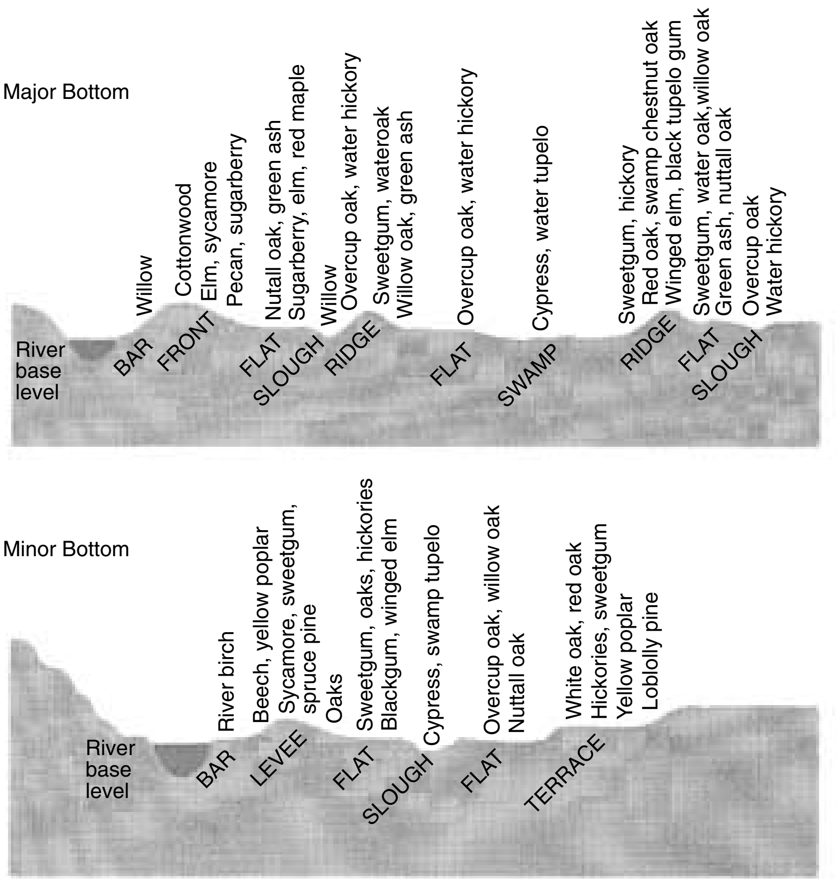

Fig. 1.17. The topographic distribution of southern bottomland oaks and associated species in major and minor stream valleys of the Southern Pine–Hardwood Region (*Province* 232: *Coniferous-Broadleaved Semi-Evergreen Forests Province*). (Reprinted from Hodges and Switzer, 1979, by permission of Society of American Foresters, Bethesda, Maryland. Not for further reproduction.)

Climate, physiography and soil

Precipitation within this vast region varies from less than 20 inches per year in the north to 55 inches along the gulf coast of Texas. One-half to two-thirds of the precipitation typically falls during the growing season and snowfall is common north of Texas. From north to south, mean annual temperature ranges from 36° to 70°F (2 to 21°C) with corresponding growing seasons ranging from 111 to 320 days (McNab and Avers, 1994) (Fig. 1.7). Throughout the region precipitation is largely offset by evapotranspiration, creating soil moisture conditions in many localities that are marginal for tree growth.

Most of the region comprises gently rolling plains, although high rounded hills occur and steep bluffs border some river valleys. Elevations range from sea level to 2000 ft. Local relief is less than 165 ft throughout most of the region, but it reaches 500 ft in the Flint Hills of Kansas (McNab and Avers, 1994). Soils are predominantly Mollisols although Vertisols occur on the prairies, and Alfisols occur on savannas and within the Mississippi Valley (Bailey, 1995).

Forest history

Native Americans who were largely nomadic inhabited the region for at least 10,000 years. Crops were cultivated as early as 1000 years ago. A few large Native American communities developed in the major river valleys. One of these was Cahokia (near present-day St Louis), which flourished between AD 1000 and 1400 with an estimated population of 25,000. The forests in the region were an important resource for both nomadic people and larger permanent communities. The demise of Cahokia may have been caused by the exhaustion of the surrounding forests that were used for fuel and for the construction and maintenance of a 2-mile-long perimeter wall around the city (Lord, 1999).

Frequent fires were essential to the maintenance of prairie and savanna vegetation in many parts of the Forest–Prairie Transition Region, and Native Americans burned the grasslands and woodlands where they lived. Grazing and trampling by herds of bison and other ungulates also were important in maintaining prairies and preventing the encroachment of forests and other woody vegetation. By mid-19th century, European settlers began farming the prairies and draining prairie wetlands. The latter produced some of the nation's most productive agricultural lands.

Trees were largely confined to riparian corridors, steep slopes and scattered savannas. With the exclusion of fire and the elimination of free-ranging ungulates, forests frequently encroach upon abandoned fields and pastures. In 1884, Sargent (1884) stated that, 'Dakota, with the exception of its riverlands and the small territory between the north and south forks of the Cheyenne River, is practically destitute of timber. The bottoms of the principal streams contain extensive groves of hardwood.' In Iowa he observed that 'since the first settlement of the state the forest area has increased by the natural spread of trees over ground protected by fire, and by considerable plantations of cottonwood, maples, and other trees of rapid growth made by farmers to supply fuel and shelter'. Further south, in Texas, Charles Mohr noted, 'The timber growth immediately west of the Brazos is stunted and scanty; large areas of grass land intervene between the scrubby woods until all at once ligneous growth disappears and the seemingly boundless prairie, in gently undulating swells expands before the view on all sides' (Sargent, 1884).

Since that time, farms have been established on virtually all the lands suitable for row crops or forage production (McNab and Avers, 1994). Depending on the farm economy, the forested acreage has decreased or increased as forests and woodlands were cleared to create more farm land, or as marginal farm land reverted to forest through tree planting or abandonment.

Oaks as components of the region's forests

The best forest development in this region occurs on its eastern border where it abuts the Northern Hardwood Region, the Central Hardwood Region and the Southern Pine–Hardwood Region. Of the 7% of the Forest–Prairie Transition Region that is forested, three-quarters is classified as oak–hickory or oak–pine. Few of the savannas that formerly occupied the transition zone between forest and prairie exist today.

The prairie fires that historically restricted the extent of the region's forests have been replaced by agricultural practices that now limit most forests to riparian areas or to slopes unsuitable for forage or other crops (Fig. 1.18). Before the mid-19th century, fire was the primary regulator of the distribution of tree species in the region. Narrow bands of forest along streams and ravines, sometimes called gallery forests, provided refuges for trees from the frequent fires that burned across the prairie. Oaks dominated many of these forests. With the advent of farming in this region, the frequency of wildfires was greatly reduced. This allowed the gallery forests to expand into untilled areas that were formerly covered by native grasses (Abrams and Gibson, 1991). However, the invading woody species were generally species such as American elm, hackberry and eastern redcedar rather than oaks. The

A

B

Fig. 1.18. (A) Aerial view of the distribution of forests in the Forest–Prairie Transition Region *(Province* 251: *Forest-Steppes and Prairies Province*) of northwestern Missouri. Throughout much of this ecoregion, forests are largely restricted to narrow belts occupying steep slopes along rivers and drainages interspersed with agricultural lands. (B) Forested bluffs dominated by oaks (background) along the Missouri River in central Missouri fronted by cultivated bottomland fields. Before settlement by Europeans, these bottomlands were covered by lowland forests dominated by American elm, silver maple, green ash, eastern cottonwood, bur oak and pin oak. (USDA Forest Service, North Central Research Station photographs.)

reduction in wildfires also allowed those species to increase in abundance within existing forests that were formerly dominated by oaks, especially on the more mesic sites. In much of this region, frequent fires are required to prevent the displacement of the oaks by other species (Penfound, 1968; Abrams, 1988; Abrams and Gibson, 1991).

Oak–hickory forests extend from the Central Hardwood Region westward across eastern Oklahoma and into northern Texas (Fig. 1.5A). From east to west the forests become increasingly scrubby and open. An exception is the relatively dense oak forest of the Cross Timbers Region. In Texas, the Cross Timbers comprise two bands of scrubby oak woodland extending 175 miles southward from the Oklahoma border. These bands are 20–50 miles wide and separated by the Fort Worth Prairie. Forest cover occurs along outcrops of sandy soils of greater porosity than adjacent prairie soils (Braun, 1972).

The Cross Timbers were prominent landmarks for westward travellers who otherwise traversed relatively open landscapes (Dyksterhuis, 1948). Although the heavier forest cover in the Cross Timbers area of Texas is somewhat evident from Fig. 1.6, the two distinct strips of woodland are not distinguishable at the resolution shown. Post oak and blackjack oak are the dominant tree species and account for 60% and 20% of the trees, respectively. Except in floodplains, these oaks seldom exceed 12 inches in diameter and 30–45 ft in height. At one time, the herbaceous vegetation in the Cross Timbers was probably similar to that of the surrounding prairie, but grazing during the last century has greatly altered the species composition of the herbaceous layer (Dyksterhuis, 1948).

The Cross Timbers vegetation extends northward through Oklahoma and eventually disappears in southern Kansas. Except for the Cross Timbers Region, the upland woodlands of eastern Oklahoma were formerly post–blackjack oak savannas maintained by frequent fires. Grazing and a reduction in burning have since reduced grass cover and facilitated the establishment of dense tree reproduction in many areas; post and blackjack oaks dominate most stands. Although the average basal area of these forests historically has been relatively low, in the absence of burning it has increased from 49 ft^2 $acre^{-1}$ in 1957 (Rice and Penfound, 1959) to 80 ft^2 $acre^{-1}$ in 1993 (Rosson, 1994).

From Kansas northward there are few forests, but where they do occur, oaks often dominate (Figs 1.2 and 1.6). Many of the oak forest types and conditions occurring in the Central Hardwood Region extend westward through the central portion of the Forest–Prairie Region. The central part of the region is capable of supporting forest vegetation and is successional to forest in areas protected from cultivation. However, because agriculture is the dominant land use, forests are usually restricted to riparian corridors, wet areas, steep slopes and highly erodible lands, or other sites unsuited to agriculture. Nevertheless, oaks and other hardwoods often develop into commercially valuable stands in those parts of the region lying within Illinois, Iowa, northern Missouri and eastern Kansas.

Bur oak is the dominant oak species in the northern reaches of the Forest–Prairie Transition Region. It is the only major oak species with a natural range that extends across western Minnesota and into the Dakotas. Bur oak is well adapted to this region because its deep taproot makes it resistant to drought and able to invade prairie grasslands (Johnson, 1990). Its thick bark makes it highly resistant to fires that eliminate most other woody species. Bur oak also thrives on moist alluvial bottoms that support dense hardwood forests in the northern portion of the Forest–Prairie Transition Region. Here, the bur oak type covers approximately 2% of the land area and is the principal forest type. Cottonwood, quaking aspen and American elm are other abundant hardwoods in the northern part of the Forest–Prairie Transition Region.

Western Oak Forests

The Southwestern Desert–Steppe Region

Geographic extent

The Southwestern Desert–Steppe Region includes the scattered oak forests of Arizona, New Mexico, southern Utah, west Texas and southwest Oklahoma (Figs 1.2, 1.6; Table 1.3). Although the range of Gambel oak extends northward as far as southern Wyoming, the oaks there are a small component of the vegetation. Forests and woodlands cover about 20% of the area, but only 7% of this is considered productive forest. Soil moisture deficiencies limit the distribution of oaks and other plant life throughout the region. Oaks occur as scattered trees and in open woodlands. Their distribution within the region is often limited to discontinuous elevational zones that provide the required regime of precipitation and temperature.

The region lies entirely within the Dry Domain and comprises parts of three Divisions: Tropical/Subtropical Steppe (310), Tropical/Subtropical Steppe Mountains (M310) and Tropical/Subtropical Desert (320). Included are six ecoregion Provinces: Coniferous Open Woodland and Semideserts (311), Steppes and Shrubs (313), Shortgrass Steppes (314), Steppe or Semidesert–Mixed Forest–Alpine meadow or Steppe (M311), Semideserts (321), and Deserts on Sand (323) (Fig. 1.2; Table 1.3).

The Southwestern Desert–Steppe Region extends 1200 miles from northwestern Arizona to the Gulf of Mexico in southern Texas. It varies from 300 to 700 miles in width, and encompasses roughly 250 million acres including the Mojave Desert, the Sonoran Desert, the Painted Desert, the Colorado Plateau, the southern Rocky Mountains, Texas High Plains and the Edwards Plateau. Within the region, oak forests are widely scattered and cover only a small fraction of the landscape (Fig. 1.2). The federal government or Native Americans own two-thirds of the forests and woodlands in Arizona and New Mexico, but in Texas and Oklahoma most are privately owned (Powell *et al.*, 1994).

Climate, physiography and soil

A defining characteristic of this region is a rate of surface evaporation that exceeds precipitation. The climate varies from dry to desert. Annual precipitation ranges from less than 10 inches to 30 inches (Bailey, 1995). Even in areas with greater precipitation, high rates of evaporation limit moisture availability. Average annual temperature ranges from 40 to 70°F (4 to 21°C). Although temperatures decrease with increasing elevation, mean monthly temperatures generally exceed 32°F (0°C) (Fig. 1.19). Elevation ranges from sea level along the southern Texas Gulf Coast to 7000 ft in the Colorado Plateau; some mountain peaks are substantially higher. Soils are variable throughout the region and include Mollisols, Aridisols and dry Entisols (Bailey, 1995).

Forest history

As in other regions of the United States, Native Americans customarily burned the forests and woodlands where they lived. Lightning was also a common cause of combustion. These fires maintained an open understorey in the extensive ponderosa pine forests of higher elevations. In 1880 alone, about 75,000 acres burned – which accounted for 0.1 to 1% of the woodland within the settled area (Sargent, 1884).

Beginning in the mid-19th century, European settlers were drawn to the region by opportunities for mining and livestock production. Lands were not suitable for agriculture, and the great land clearing that decimated the eastern oak forests did not occur here. However, logging, grazing and changes in fire regimes changed the species composition of forests and woodlands. In recent decades, the suppression of fires has increased the amount of tree reproduction, especially conifers, and decreased grasses and forbs growing beneath forest canopies (Long, 1995).

Throughout the region, oaks have historically had little commercial value. In 1884, Sargent (1884) described the forests in and around New Mexico: 'The deciduous trees of this entire southwestern region, often of considerable size, are generally hollow, especially the oaks; they are of little value for any mechanical purpose, although affording abundant and excellent fuel.' Then, as now, ponderosa pine was the principal timber species.

Oaks as components of the region's forests

Forests and woodlands cover only a small portion of the total area in the region, and the oaks comprise only a small percentage of that. In Arizona and New Mexico, only 15% of the land base is forested. Only 3% of the area of those two states can produce more than 20 ft^3 of timber per acre per year,

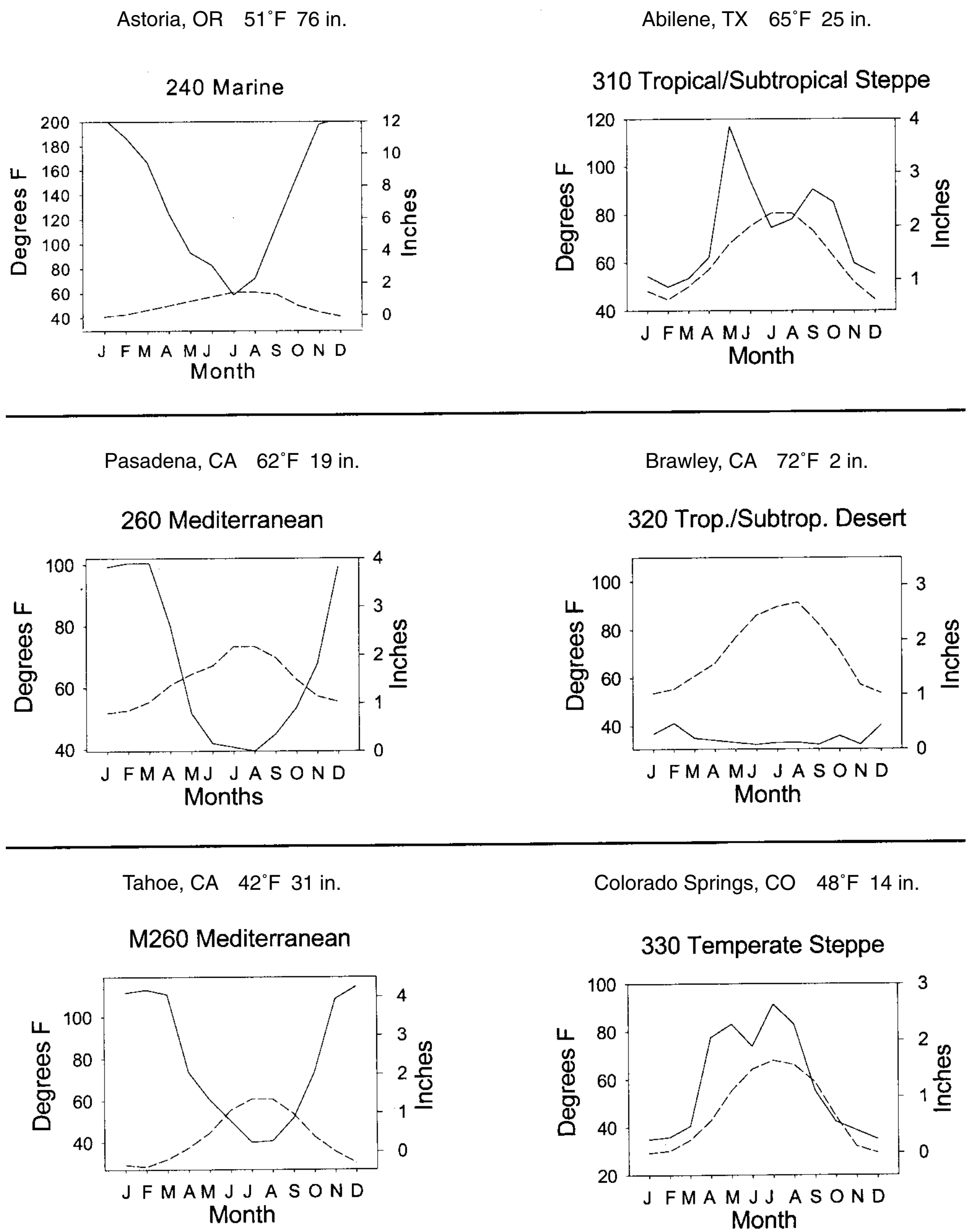

Fig 1.19. Representative climates for selected ecoregion Divisions in the western United States. Mean monthly precipitation is shown by the solid lines (right axis) and temperature by dashed lines (left axis). Mean annual values are given above each graph. Periods of drought are indicated where the precipitation line falls below the temperature line (e.g. as in Division 260). Division boundaries are shown in Figs 1.2 and 1.5. (Ecoregion and climatic data from Bailey, 1995.)

and virtually none of that is oak forest. Commercial forests include ponderosa pine (75%), Douglas-fir (13%), spruce–fir (9%) and aspen (3%). The only recognized oak cover type here is western live oak (Appendix 3) (Eyre, 1980). It occurs at elevations from 4000 to 6000 ft in the foothills and lower mountain slopes of Arizona and New Mexico. At higher elevations, the western live oak cover type gives way to ponderosa pine and pinyon–juniper, with oak–conifer mixtures occurring in the transition. At lower elevations the western live oak type yields to an open growth of shrubby evergreen oaks. Mesquite and desert vegetation typically occurs below that. Characteristic species of the western live oak type include Emory, Arizona white, Mexican blue and silverleaf oaks (Eyre, 1980) (Fig. 1.20). Ajo oak, Dunn oak, grey oak and Havard oak also occur in Arizona and New Mexico.

At the eastern end of the Southwestern Desert–Steppe Region towards the High Plains and Edwards Plateau of west-central Texas, precipitation increases and oaks become more prominent. The Mohr (shin) oak forest type covers more than 8 million acres in Texas where it develops best under 20–25 inches of precipitation annually (Eyre, 1980). However, that amount of precipitation represents the upper end of the range for the region (e.g. see Fig. 1.19, Division 310). Other oaks that occur in west-central Texas include Arizona white, blackjack, bur (marginally), chinkapin, Durand, Emory, Havard, Lacey, live, sandpaper, Texas and Texas live oaks.

The Pacific Mediterranean–Marine Region

Geographic extent

The Pacific Mediterranean–Marine Region includes the oak forests and woodlands of California, Oregon and Washington (Fig. 1.6). The region lies within the western portion of the Humid Temperate Domain and includes the Mixed Forest–Coniferous Forest–Alpine Meadow Province (M261) and the Mediterranean Woodland or Shrub–Mixed Coniferous Forest–Steppe or Meadow Province (M262) within the Mediterranean Mountains Division (M260) (Fig. 1.2). Oaks also occur within the Coast Ranges of California, which includes the Mediterranean Hardleaved Evergreen Forest,

Fig. 1.20. Emory oak woodland in the Peloncillo Mountains of southwestern New Mexico, Coronado National Forest, New Mexico (*Province* M321: *Semideserts Province*). (USDA Forest Service, Rocky Mountain Research Station photograph.)

Open Woodlands and Shrubs Province (262) and the Redwood Province (263). At its northern extent, the Pacific Mediterranean–Marine Region also reaches the Mixed Forest Province (241) of the Marine Division (240) in Oregon and Washington. The Pacific–Mediterranean–Marine Region also includes California's Central Valley (province 261) and the mountainous zones of Washington and northern Oregon (M261) where oaks are not abundant.

The Pacific Mediterranean–Marine Region extends nearly 900 miles from Washington to southern California but less than 200 miles from the Pacific Ocean to the eastern slopes of the Sierra Nevada Mountains. Although the region covers about 75 million acres, the oaks are limited to relatively narrow elevational zones.

In California, Oregon and Washington, slightly less than half the timberland is publicly owned (Powell *et al.*, 1994). In contrast with the eastern United States, most of the privately owned timberland in this region is held by corporations rather than by non-industrial private owners (Birch, 1996). However, the ownership of oak forests and woodlands does not follow this trend; about three-quarters of that acreage is in non-industrial private ownership (Thomas, 1997).

Climate, physiography and soil

Climate is strongly influenced by the Pacific Ocean and by the Coast and Sierra Nevada Ranges, which dominate the physiography of the region. Elevations range from sea level to more than 14,000 ft. In the mountain ranges, increasing elevation is associated with decreasing temperatures and variation in precipitation. For a given elevation, precipitation is generally greater on western slopes than on eastern slopes. Latitude also influences climate so that a given climatic zone occurs, from north to south, at progressively higher elevations. However, mountainous topography creates climatic irregularities and discontinuities, and the distribution of oaks and associated tree species varies accordingly.

Most of the precipitation occurs during the autumn, winter and spring. Annual precipitation generally ranges from 10 to more than 60 inches in the ecological provinces where oaks occur. Temperature extremes and moisture stress are reduced near the coast where fog supplements precipitation and the ocean reduces fluctuations in temperature. Elsewhere the region's Mediterranean climate is characterized by 2 to 4 months of drought during the summer (Table 1.3, Fig. 1.19). Low precipitation generally occurs at lower elevations and on the east faces of mountain ranges. Soils include Ultisols, Alfisols, Mollisols, Entisols and Inceptisols (Bailey, 1995).

Forest history

The historical importance of oaks is recorded in ancient bedrock mortars that were used by Native Americans to grind acorns into flour. Acorns were a staple food of Native Americans in this region, and Biswell (1989) suggests that oaks were so important to their diet that they burned oak woodlands to both encourage oak reproduction and to facilitate acorn gathering. Although human-caused fires have been historically associated with the oaks of the region for thousands of years, there is uncertainty about what proportion of the landscape was regularly affected by humans. During the post-settlement period of 1850–1950, the mean interval between fires in the oak–pine forests of the foothills of central California was 8 years (Stephens, 1997).

Commercial logging in the region has largely focused on the conifers. In 1884, Sargent (1884) stated:

> The forests of California, unlike those of the Atlantic States, contain no great store of hardwoods. The oaks of the Pacific forests, of little value for general mechanical purposes, are unfit for cooperage stock. No hickory, gum, elm, or ash of large size is found in these forests, California produces no tree from which a good wine cask or wagon wheel can be made. The cooperage business of the state, rapidly increasing with the development of grape culture, is entirely dependent upon the forests of the Atlantic region for its supply of oak.

Sargent further noted that large quantities of chestnut oak (*sic* tanoak), once common in the northern Coast Range of California, are 'now becoming scarce and in danger of speedy extermination' due to utilization by the tanning industry. Sargent's reference to the oaks of Oregon and Washington is slightly less disparaging. In the Willamette Valley, he noted that Oregon white oak woodlands were becoming re-established after reductions in fire frequency. Along the Yakima River in Washington, he noted that Oregon white oaks were limited to 15 ft in height and 6 inches in diameter.

The logging industry on the Pacific Coast was established in the 18th century under Hispanic influence. Through the middle of the 19th century the relatively small industry served markets in South America, Australia and the Pacific Rim (Williams, 1989). The gold rush of 1849 and the completion of the transcontinental railroad opened additional markets, but the increase in lumber production in this region occurred gradually, beginning about 1900 when the large timber companies and railroads moved west after exhausting the ready supply of timber in the Lake States. Increases in timber production in the region continued into the Great Depression, but output eventually dropped by 75%. By 1950, however, annual timber production in the West exceeded 16 billion board feet annually, which was greater than that produced in other regions of the United States. Today lumber production in this region lags significantly behind that of the south. Harvest of hardwood growing stock has remained nearly constant since 1976, but the volume of hardwoods harvested annually is only about 5% of the region's total.

Historically, oak forests were little affected by commercial logging, but locally they were widely utilized for firewood and fence posts. Ranchers and farmers had the greatest influence on the oak woodlands of the foothills and lower slopes as a consequence of clearing them for agriculture and grazing. Sargent (1884) noted:

> The permanence of the mountain forests of California is severely endangered, moreover, by the immense herd of sheep, cattle, and horses driven to the mountains every year, at the commencement of the dry season, to graze. From the foothills to the highest alpine meadows, every blade of herbage and every seedling shrub and tree is devoured.

In California, oak woodlands were reduced from an estimated 10–12 million acres to about 7 million acres today (Thomas, 1997). The oak woodlands are predominantly owned by farmers and ranchers, and between 1945 and 1970 the primary loss of woodland acreage resulted from conversion to rangeland. Invasion of non-native grasses and the suppression of fire have created problems in maintaining oak woodlands and savannas (see Chapter 9 for details of savanna restoration and management). More recently, the greatest losses of oak woodland have resulted from suburban residential development (Bolsinger, 1988). This has given rise to concern for property damage from the wildfires historically associated with the oak woodlands.

Oaks as components of the region's forests

Most of the region's oak forests and woodlands occur in California where they account for approximately one-quarter of the wooded acres. Oaks surround California's Central Valley in the foothills of the Sierra Nevada, Cascade and Klamath Ranges (Figs 1.5 and 1.6). Although oaks were formerly abundant within parts of California's Central Valley (province 261), their distribution has been greatly reduced there (Griffin, 1977). Oaks also occur on the western slopes of the Coast Ranges in central and southern California. The range of Oregon white oak extends northward into central Oregon and Washington in the Willamette Valley and the Puget lowlands between the Cascade and Coast Ranges. Included are 18 species of oak trees and shrubs plus additional hybrids (Bolsinger, 1988; Thomas, 1997). Eight oak species that reach tree size are abundant: California black, blue, interior live, coast live, canyon live, valley, Oregon white and Engelmann oaks (Plumb and McDonald, 1981).

Western oak forests are often categorized as either timberland (forests suitable for commercial wood production and capable of producing at least 20 ft^3 $acre^{-1}$ $year^{-1}$ of merchantable volume), or woodlands (sites of lower productivity primarily utilized for forage and firewood). In California, only about 1 in 4 acres of hardwood forest qualifies as timberland. Oak woodlands are sparsely covered with trees compared to oak timberlands. The statewide volume of oaks in woodlands and in timberlands is nevertheless nearly equal because the acreage of woodlands is approximately three times that of timberlands (Table 1.4). Three-quarters of the oak woodlands are grazed and these account for about one-third of California's total forage (Thomas, 1997). Only about 500,000 board feet of hardwood lumber was produced in California in 1992 (Ward, 1995).

The combined effects of temperature and precipitation (which latitude, elevation, slope and aspect affect) regulate the distribution of oaks. In the Pacific Mediterranean–Marine Region, many oak forests and woodlands are restricted to elevational zones in the transition between grassland and chaparral at lower elevations and coniferous forest at higher elevations. Mean temperatures within the region increase with decreasing latitude, and the oaks occur at higher elevations at lower latitudes. Due to the interaction of climate and mountainous topography, the distribution of oaks in this region is more geographically restricted than in the eastern United States.

Several classification schemes have been proposed for the complex vegetation relationships that occur in the Pacific Mediterranean–Marine Region (e.g. Griffin, 1977; Paysen *et al.*, 1980, 1982; Barbour, 1988; Allen, 1990) (Fig. 1.21). Eyre (1980) recognized five oak cover types and two additional types where oaks commonly occur in mixtures with other species (Appendix 3). The Oregon white oak type is found in the northern portion of the Pacific Mediterranean–Marine Region from northern California to Vancouver Island. This type occurs at lower elevations (0–3900 ft) and primarily in inland valleys or lower slopes between the Coast Ranges and the Cascade or Sierra Nevada Ranges (Eyre, 1980). The type makes its best development in the vicinity of the Willamette Valley where closed-canopy Oregon white oak stands developed from former oak savannas when periodic ground fires were excluded (Thilenius, 1968). The species also occurs in mixtures with other hardwoods and conifers including California black oak, canyon live oak, ponderosa pine and Douglas-fir (Appendix 3).

Table 1.4. Standing oak volumes in California timberlands and woodlands. Although oaks make up 63% of the total volume of California's hardwoods, oak timberlands (commercial forest lands) comprise only 8% of the 50 billion cubic feet total volume (softwoods plus hardwoods on California timberlands).[a]

Species	Volume in timberlands (million ft^3)	Volume in woodlands (million ft^3)	Total (million ft^3)	Species total as a proportion of all oaks (%)
California black oak	2,254	277	2,531	32
Canyon live oak	1,302	731	2,033	26
Blue oak	1	1,112	1,113	14
Coast live oak	126	755	881	11
Oregon white oak	211	389	600	8
Interior live oak	45	508	553	7
California white (valley) oak	34	164	198	3
Engelmann oak	0	10	10	0
Total oak	3,973	3,946	7,919	100
Total hardwoods (all species)	7,661	4,855	12,516	–

[a] Adapted from Shelly (1997) and Bolsinger (1980, 1988).

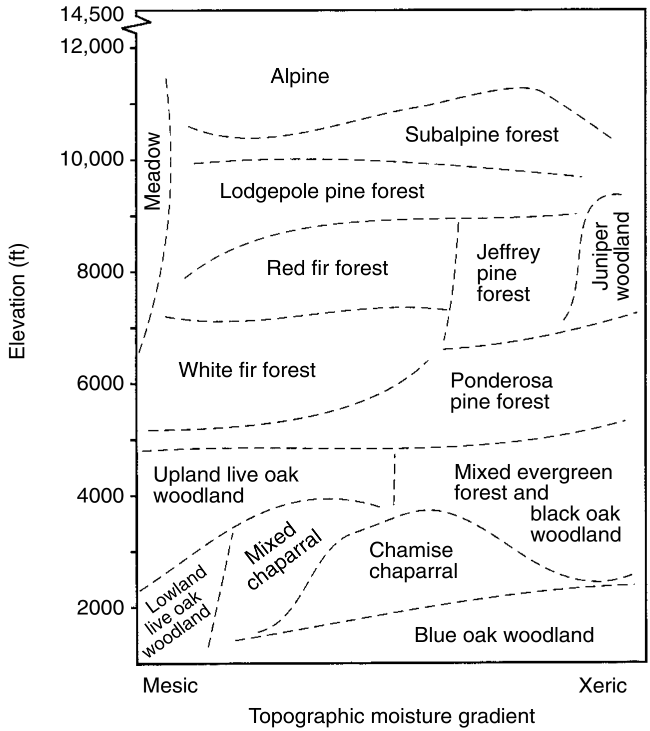

Fig. 1.21. Relation of oak forests to elevation, moisture gradients and other forest types found in the Pacific–Mediterranean–Marine Region of California (Ecoregion *Provinces* 261, 262, 263 and M261). Oak forests and woodlands are usually found above the chaparral zone and below the ponderosa pine zone. (Redrawn from Barbour (1988) and Vankat (1982).) Reprinted with permission of Cambridge University Press.)

California black oak attains a greater volume (Table 1.4) and is distributed across a greater area than the other California oaks (Plumb and McDonald, 1981). The California black oak type occurs from central Oregon to the Mexican border across elevations ranging from 200 to 8000 feet with corresponding annual precipitation of 25–85 inches annually. Best development of the forest type occurs in the northern half of California in the Klamath and Cascade Mountains and the Coast and Sierra Nevada Ranges. There the forest type is found at elevations between 1500 and 3000 ft with corresponding annual precipitation between 30 and 50 inches (Eyre, 1980). After disturbance, this species maintains itself through sprouting to form even-aged stands. On suboptimal sites it is successional to other forest types. Associated species include other oaks, ponderosa pine, Douglas-fir and Pacific madrone (Appendix 3).

Canyon live oak occurs from the Willamette Valley to the Baja Peninsula and east into Arizona at elevations from near sea level in the north to 9000 feet in the south (Eyre, 1980). It comprises about one-quarter of California's oak volume and is second only to California black oak in this regard (Table 1.4). Canyon live oak forms pure stands on very steep slopes and dry canyon bottoms. Elsewhere it occurs in mixture with Douglas-fir, ponderosa pine and other conifers. The species is shade tolerant when young and often maintains itself in relatively stable communities (Eyre, 1980).

The blue oak–digger pine forest type surrounds California's Central valley at elevations between 500 and 5000 ft, although blue oak occasionally extends to the valley floor (Fig. 1.22). This forest type occurs between the valley grasslands and the montane forests above, where it can

Fig. 1.22. Blue oak woodland in the Sierra Nevada Range (*Province* M261*: Dry Steppe Province*). (USDA Forest Service, North Central Research Station photograph.)

endure a meagre 10 inches of annual precipitation (Eyre, 1980). Forest cover ranges from 30 to 80% with canopy heights between 15 and 50 ft. Associated species include California live oak, interior live oak, valley oak and California black oak (Barbour, 1988). At low elevations blue oak and valley oak mixtures develop savanna communities. Valley oak savannas extend into the Central Valley where they make their best development on alluvial soils (Griffin, 1977).

The California coast live oak forest type (sometimes referred to as southern oak woodland) occurs on the west side of the Coast Range in the southern two-thirds of California. It extends inland on north-facing slopes of narrow valleys and other cool sites. This type occurs at elevations of up to 3000 ft in the northern part of its range and to 5000 ft in the southern portion. Although it can form pure, closed canopy stands, it is considered a woodland type and commonly occurs in savannas comprised of scattered oaks or in mixture with conifers (Appendix 3). California coast live oak is long-lived, moderately shade tolerant, and forms relatively permanent woodlands. When trees reach about 8 inches dbh they are also highly resistant to fire (Eyre, 1980).

The ecological importance of California's oak woodlands and timberlands is receiving increased attention (Pillsbury *et al.*, 1997). Although their value for commercial products is low, their importance to wildlife, water quality, aesthetics, soil protection, recreation and fuelwood is widely acknowledged (Helms and Tappeiner, 1996). A principal silvicultural problem related to the oak woodlands of the Pacific Mediterranean–Marine Region is ensuring that the regeneration of oaks is sufficient for replacing trees periodically lost to natural mortality and timber harvesting.

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