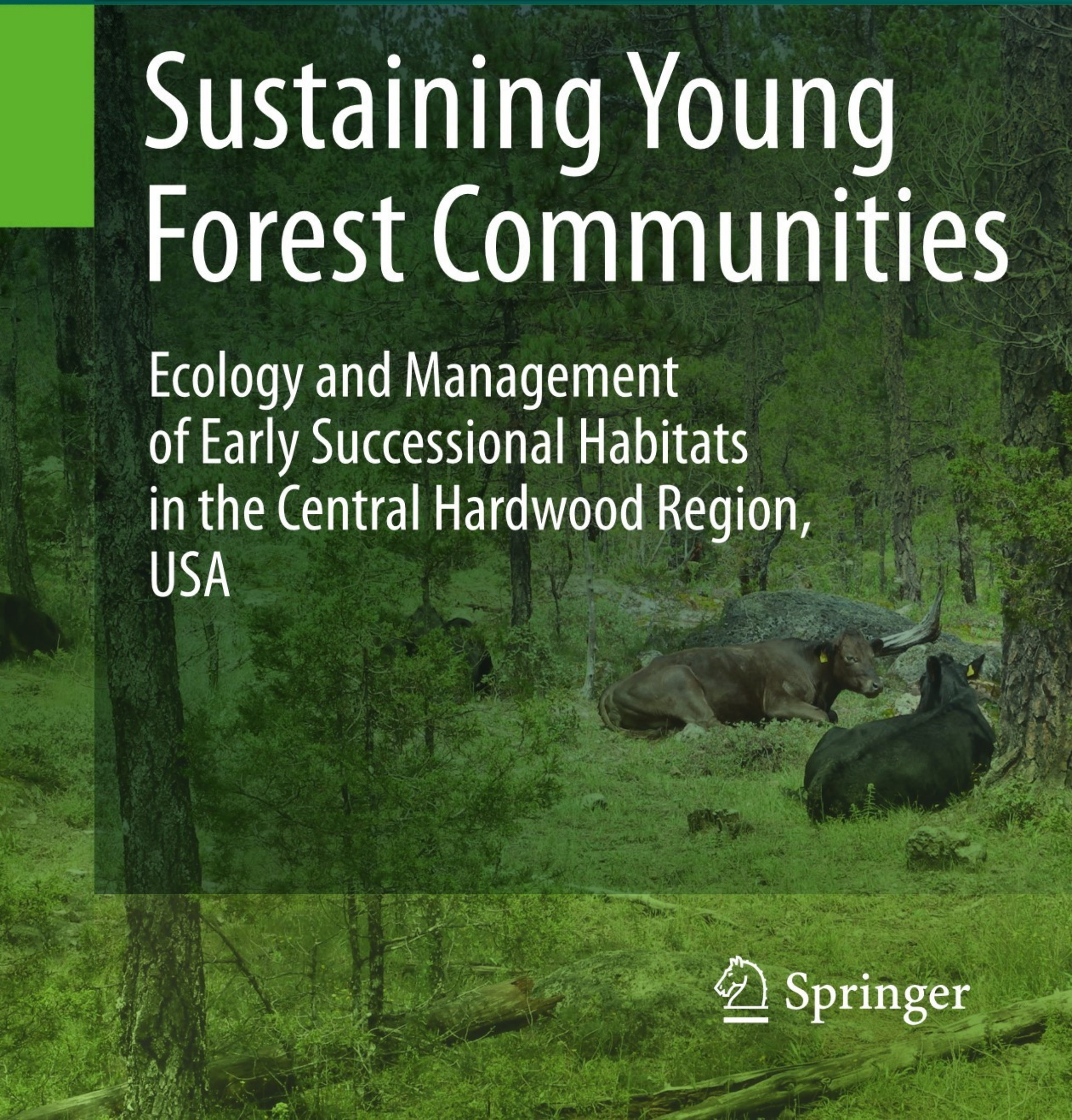
Managing Forest Ecosystems

Cathryn H. Greenberg
Beverly S. Collins
Frank R. Thompson III *Editors*

Sustaining Young Forest Communities

Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA



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Sustaining Young Forest Communities

Managing Forest Ecosystems

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Aims & Scope:

Well-managed forests and woodlands are a renewable resource, producing essential raw material with minimum waste and energy use. Rich in habitat and species diversity, forests may contribute to increased ecosystem stability. They can absorb the effects of unwanted deposition and other disturbances and protect neighbouring ecosystems by maintaining stable nutrient and energy cycles and by preventing soil degradation and erosion. They provide much-needed recreation and their continued existence contributes to stabilizing rural communities.

Forests are managed for timber production and species, habitat and process conservation. A subtle shift from *multiple-use management* to *ecosystems management* is being observed and the new ecological perspective of *multi-functional forest management* is based on the principles of ecosystem diversity, stability and elasticity, and the dynamic equilibrium of primary and secondary production.

Making full use of new technology is one of the challenges facing forest management today. Resource information must be obtained with a limited budget. This requires better timing of resource assessment activities and improved use of multiple data sources. Sound ecosystems management, like any other management activity, relies on effective forecasting and operational control.

The aim of the book series ***Managing Forest Ecosystems*** is to present state-of-the-art research results relating to the practice of forest management. Contributions are solicited from prominent authors. Each reference book, monograph or proceedings volume will be focused to deal with a specific context. Typical issues of the series are: resource assessment techniques, evaluating sustainability for even-aged and uneven-aged forests, multi-objective management, predicting forest development, optimizing forest management, biodiversity management and monitoring, risk assessment and economic analysis.

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Typical scene in the State of Durango where forests are managed by communities known as Ejidos: management is by selective tree removal, clear-felling is not allowed. Animals (ganado) are part of the multiple use system practiced there. (Photo by K. v. Gadow, autumn 2009)

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Preface

This edited volume addresses the rising concern among natural resource professionals that plants and animals associated with early successional habitats are declining in the Central Hardwood Region to undesirably low levels. The idea for this book was partially in response to a request by the USDA Forest Service's Southern Region, to the USDA Forest Service's Southern Research Station and partners, to identify top research synthesis needs, and to identify ecosystem restoration priorities for National Forests in the Southern Appalachians. Early successional habitat was identified as one of three top research synthesis needs. A full-day symposium, organized by the editors, at the 2010 Association of Southeastern Biologists conference in Asheville, North Carolina was the basis for this book. Our goal was to present original scientific research and knowledge syntheses covering multiple topics associated with early successional habitats. We strived for each chapter to include state-of-the-art, research-based knowledge and expert opinion, but also to identify research needs and discuss management implications for sustainable management in a landscape context.

Chapters were written by respected experts that include ecologists, conservationists, and land managers. The chapters provide current, organized, readily accessible information for scientists, the conservation community, land managers, students and educators, and others interested in the "why, what, where, and how" of early successional habitats and associated wildlife. Chapters cover concepts, management, plants and animals, ecosystem processes, and the future of early successional habitats. We provide a working definition of early successional habitats; examine where and why they occur over the landscape; and explore concepts related to their importance and sustainability. We examine the roles of natural disturbances, silviculture, and fire in creating and maintaining early succession habitats. We explore effects of these habitats on ecosystem processes and wildlife, and their role in producing forest food resources. We also explore management tools for early successional habitat, including use of novel places such as utility rights of way, and strategies for identifying priority species and implementing desired future conditions. The final chapter looks to the future, to project changes in forest age class diversity in relation to scenarios of land ownership, economics, demographics, and climate change. We attempted to provide a balanced view of past, current, and future scenarios on the extent and quality of early successional habitats within the Central Hardwood Region, and implications for ecosystem services and disturbance-dependant plants and animals.

We sincerely thank all those who encouraged and aided in the development of this book. Each chapter was peer reviewed by at least two outside experts and all co-editors, and we thank these colleagues for their useful suggestions: David Buehler, Josh Campbell, Dan Dey, Todd Fearer, Mark Ford, Jennifer Franklin, Charles Goebel, Margaret Griep, MaeLee Hafer, Chuck Hunter, Todd Hutchinson, Mike Jenkins, Jennifer Knoepp, Darren Miller, Mark Nelson, Chris Peterson, Jim Runkle, Ge Sun, Mike Ryan, Sarah Schweitzer, Ray Semlitsch, Bill Stiver, Bentley Wigley, and Mariko Yamasaki. We also thank the Association of Southeastern Biologists for allowing us to host a conference symposium on this important topic. We especially thank each author for contributing, and for timely chapter revisions, making this book possible.

Contents

Chapter 1
Introduction: What Are Early Successional Habitats, Why Are They Important, and How Can They Be Sustained?

Cathryn H. Greenberg, Beverly Collins, Frank R. Thompson III, and William Henry McNab

Abstract There is a rising concern among natural resource scientists and managers about decline of the many plant and animal species associated with early successional habitats. There is no concise definition of early successional habitats. However, all have a well developed ground cover or shrub and young tree component, lack a closed, mature tree canopy, and are created or maintained by intense or recurring disturbances. Most ecologists and environmentalists agree that disturbances and early successional habitats are important to maintain the diverse flora and fauna native to deciduous eastern forests. Indeed, many species, including several listed as endangered, threatened, sensitive, or of management concern, require the openness and thick cover that early successional habitats can provide. Management of early successional habitats can be based on the "historic natural range of variation", or can involve active forest management based on goals. In this book, expert scientists and experienced land managers synthesize knowledge and original scientific work to address critical questions on many topics related to early successional habitats in the Central Hardwood Region. Our aim is to collate information about early successional habitats, to aid researchers and resource management professionals in their quest to sustain wildlife and plant species that depend on or utilize these habitats.

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1.1 Introduction

There is a rising concern among natural resource scientists and managers about decline of the many plant and animal species associated with early successional habitats, especially within the Central Hardwood Region (Litvaitis 1993, 2001; Thompson and DeGraaf 2001). Open sites with grass, herbaceous, shrub, or incomplete young forest cover are disappearing as abandoned farmland and pastures return to forest and recently harvested or disturbed forests re-grow (Trani et al. 2001). There are many questions about "why, what, where, and how" to manage for early successional habitats. Tradeoffs among ecological services such as carbon sequestration, hydrologic processes, forest products, and biotic diversity between young, early successional habitats and mature forest are not fully understood. Personal values and attitudes regarding forest management for conservation purposes versus preservation, or "letting nature take its course," complicate finding common ground regarding if and how to create or sustain early successional habitats.

In this book, expert scientists and experienced land managers synthesize knowledge and original scientific work to address critical questions sparked by the decline of early successional habitats. We focus primarily on habitats created by natural disturbances or management of upland hardwood forests of the Central Hardwood Region in order to provide in depth discussion on multiple topics related to early successional habitats, and how they can be sustainably created and managed in a landscape context.

1.2 Geographic Scope: The Central Hardwood Region

Broadleaved trees form the predominant forest cover type in parts of ten eastern states which Braun (1950) included in the Central Hardwood Region (Fig. 1.1). The boundaries of the region also are similar to ecoregions mapped by Bailey (1994) and bird conservation regions delineated by the US North American Bird Conservation Initiative (on the Breeding Bird Survey website (www.mbr-pwrc.usgs.gov/bbs/)). The canopy of mature upland forests is dominated by varying proportions of six broadleaf deciduous taxa. Oak (*Quercus*) and hickory (*Carya*), each represented by several species, are present in most stands. Yellow-poplar (*Liriodendron*) increases in importance east of the Mississippi River and usually dominates the canopy of moist sites in the Southern Appalachian Mountains, and maple (*Acer* spp.), beech (*Fagus grandifolia*), and birch (*Betula* spp.) occupy much of the canopy of forests in the northern and eastern parts of the region, particularly on the Allegheny Plateau. About 45% of the 130 million acres of forest land in this region is occupied by hardwood-dominated stands; mixtures of hardwoods and conifers account for an additional 5% (Smith et al. 2004). Conifers, primarily pine (*Pinus*), are minor components of many low-elevation stands on dry sites. The humid, continental climate of the region produces soil moisture regimes that are adequate for plant growth during much of the warm season, although minor water deficits can develop in late

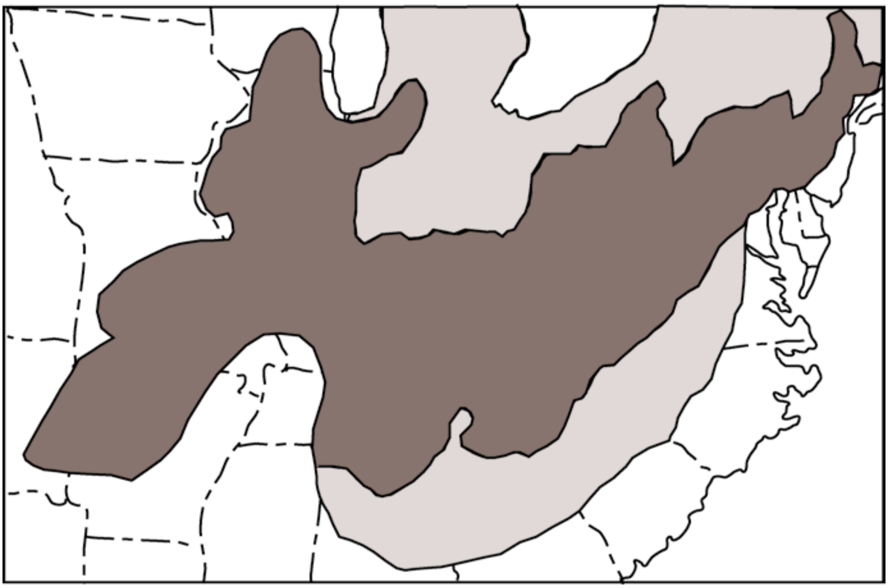

Fig. 1.1 Extent of the Central Hardwood Region in the eastern United States (dark shading). Transition to northern hardwoods occurs in the Lake States and to southern pines in the Appalachian Piedmont (light shading) (After Braun (1950))

summer. This characteristic climate (i.e., low soil moisture deficits and moderate levels of evapotranspiration) may be why forests of deciduous hardwoods dominate the Central Hardwood Region (Stephenson 1990). Detailed descriptions of forest composition and disturbance regimes characteristic of Central Hardwood Region subregions are provided in Chap. 2 (McNab).

1.3 What Are Early Successional Habitats?

Like most things ecological, there is no concise definition of early successional habitats. Early ecological studies and adoption of the term "succession" were based in part on secondary succession of abandoned farm fields (i.e., "oldfield succession"). In the southeastern USA, oldfields are first colonized by "pioneering" grasses and forbs, then gradually by pines or hardwoods, until closed forest develops (Clements 1916; Keever 1950, 1983; Odum 1960). Over time, the term "early successional" has taken on a broader meaning, to include recently disturbed forests with absent- or open-canopy and, often, transient, disturbance-adapted or pioneer species (many of them also found in old fields). Unlike oldfields, these recently disturbed forests generally do not undergo major shifts in woody species composition (Lorimer 2001). Similarly, we use the term "habitat" in this volume, as it is commonly used and understood in recent wildlife literature, to denote "a set of specific environmental features that, for a terrestrial

Plate 1.1 Examples of different types of early successional plant communities. From *left to right*: recently abandoned farmland, reclaimed surface mine, scrub-shrub, and recently harvested forest

animal, is often equated to a plant community, vegetative association, or cover type" (Garshelis 2000; but see Hall et al. 1997). We use 'early successional habitats' to refer to sets of plant communities, associations, or cover types for multiple wildlife species.

Vegetation structure in early successional habitats can range from scattered trees or snags to no canopy cover, or from an open, grass-forb understory to thickets of shrubs and vines (Plate 1.1). Abandoned farmlands, grassland, shrub-scrub, recently harvested forest, heavily wind-, fire-, or ice-damaged forests, and even ruderal habitats such as roadsides, utility rights-of-way, and restored coalfields are all early successional habitats from this functional perspective (e.g., Thompson and DeGraaf 2001). Plant composition and micro-physical structure differ considerably among these diverse early successional habitat types, and can be dominated by grasses, forbs, shrubs, seedlings, woody sprouts, or a patchy mix of herbaceous and developing woody cover. However, all have two structural attributes in common: they have a well developed ground cover or shrub and young tree component and they do not have a closed, mature tree canopy.

Recently disturbed, regenerating upland hardwood forests may not, strictly speaking, be "successional," in terms of species turnover, but they do change greatly in structure over time. Many hardwood tree species resprout after damage or harvest, such that there may be little change in woody species composition between the progenitor forest, the young regenerating forest, or the mature forest decades later. In these common cases, longer-term changes are due to change in physical structure and potential shifts in the relative abundance of species, rather than species loss and establishment over time (Lorimer 2001). In some cases, non-native species colonize following disturbance, further altering the original forest composition (Busing et al. 2009). In this volume, Loftis et al. (Chap. 5) discuss dynamical changes in structure and woody species composition, and Elliot et al. (Chap. 7) discuss herbaceous layer response to different silvicultural or natural disturbances and across moisture or fertility gradients associated with topography and physiographic regions or subregions.

Another characteristic of early successional habitats is that they are created by intense or recurring disturbances and are transient if not maintained by disturbance. Different types and intensities of natural disturbances (such as wind- or ice storms,

Plate 1.2 Examples of variation in the structure of early successional habitats in the upland hardwood forest of the Central Hardwood Region. From *left to right*: an experimental gap in the first season following its creation; ice storm damage; hot prescribed burn

wildfire, or outbreaks of pathogens) or forest management practices (such as two-age harvests, clearcuts, group selections, or hot prescribed burns) can create early successional habitats ranging from homogeneous structure with no trees to highly heterogeneous structure with scattered standing trees, multiple windthrows, or standing boles with broken tops. The scale of early successional habitats can also range from canopy gaps to thousands of hectares (Plate 1.2).

Historical and current patterns of frequency, intensity, and scale of natural and anthropogenic disturbances that create early successional habitats vary across the Central Hardwood Region. For example, catastrophic hurricanes occur at 85–380 year intervals in upland hardwood forests of the mid-Atlantic and southern New England (Lorimer and White 2003). The proportion of the landscape in young forest in this region might have varied from 40% to 50% after a severe hurricane to <3% as the forest matured (Lorimer and White 2003). In contrast, further inland where the likelihood of catastrophic wind damage is small, the proportion of early successional habitats due to wind disturbance was likely low (1–3%) and maintained by canopy gaps from single-tree death (estimated at <1% annually) (Runkle 1990) and infrequent windstorms (Lorimer and White 2003). Widespread, frequent burning was used by Native Americans and (later) by European settlers to maintain an open understory and improve conditions for travel and game or livestock for about 14,000 years, and decades of fire suppression has contributed to today's decline of early successional habitats and a shifting forest composition (Lorimer 1993; Brose et al. 2001). This variation in disturbances over time and across the landscape certainly created "nonequilibrium" or irregularity in the availability of early successional habitats, and populations of plants and animals that utilize them also likely waxed and waned in response to their availability.

In this volume, White et al. (Chap. 3) discuss how types, intensities and frequencies of natural disturbance vary across the Central Hardwood Region, and implications of these disturbances for patterns and probabilities of early successional habitats being created or maintained. Spetich et al. (Chap. 4) discuss the historic role of fire in creating and maintaining early successional habitats, and how fire suppression policies of recent decades have reduced their extent in the Central Hardwood Region.

1.4 Why Are Early Successional Habitats Important?

Most ecologists and environmentalists agree that disturbances and early successional habitats are important to maintain the diverse flora and fauna native to deciduous forests of the Central Hardwood Region (Brawn et al. 2001). Patches of early successional habitat play a pivotal role in forest dynamics as foci for tree regeneration and maintaining disturbance-dependent plant species. Hunter et al. (2001) recognized 128 bird species associated with grasslands, shrub-scrub, savannah and open woodlands, or forest gaps in eastern North America. Indeed, many species, including several listed as endangered, threatened, sensitive, or of management concern, require the openness of reduced or absent overstory, tall grasses, or thick shrub cover that early successional habitats can provide (Hunter et al. 2001; Litvaitis 2001; Thompson and Degraaf 2001).

Disturbances across the landscape and through time create habitat heterogeneity and affect the spatial and temporal availability of food resources in a forest matrix (Thompson and Willson 1978). Different disturbance types and intensities shape the size, structure, and distribution of early successional habitat patches, which may be key factors for maintaining populations of wildlife species that depend on them. Canopy gaps or small patches of recently disturbed, young forest may be sufficient for some species, whereas others require larger areas (Thompson and DeGraaf 2001). Mobile species may be able to utilize a landscape of connected or recurring smaller patches, whereas species with limited dispersal ability may require larger or less ephemeral patches. Some disturbance-adapted bird species may require grass-dominated early successional habitats (e.g., Field Sparrows (*Spizella pusilla*) or Grasshopper Sparrows (*Ammodramus savannarum*)), whereas others require brushy areas (e.g., Eastern Towhees (*Pipilo erythrophthalmus*)); open areas with the presence of nesting cavities (e.g., Eastern Bluebird (*Sialia sialis*)); or high elevation early successional habitats (e.g., Chestnut-sided Warblers (*Dendroica pensylvanica*) and Golden-winged Warblers (*Vermivora chrysoptera*)). Thus, defining high- or low-quality early succession habitat must be tempered by the species or suite of species that require specific structural conditions.

Breeding bird density and richness generally are higher in disturbed habitats, including treefall gaps (Blake and Hoppes 1986; Greenberg and Lanham 2001), intensively burned forest (Greenberg et al. 2007a), and recently harvested young forests, particularly if some tree canopy is retained (e.g., Annand and Thompson 1997; Whitehead 2003). Many bat species use early successional habitats to forage for insects (e.g., Loeb and O'Keefe 2006). The density of many salamander species declines in recently disturbed early successional habitats (e.g., deMaynadier and Hunter 1995), but the abundance of some reptile species increases in response to the same conditions (e.g., Greenberg 2002). Indeed, many wildlife species forage opportunistically for insects and fruit in resource-rich young forest patches (Greenberg et al. 2007b).

In this volume Greenberg et al. (Chap. 8) discuss the ample availability of food resources, including native forest fruit, browse, and arthropod and small mammal prey for wildlife in recently disturbed upland hardwood forest. Franzreb et al. (Chap. 9) examine the relationship between availability of early successional (small-diameter) forest and population trends of 11 focal bird species associated with "scrub-shrub" forest structure. Loeb and O'Keefe (Chap. 10) discuss how young forest patch size, shape, distribution, and connectivity, as well as vegetation structure, influence use by different bat species in relation to roost sites, mature forest, and water sources. Moorman et al. (Chap. 11) synthesize information to provide an overview of amphibian and reptile response to forest disturbance and the creation of early successional habitats. Lanham et al. (Chap. 12) present a case for considering utility rights-of-way and other "novel" places as an option for managing bird and butterfly species associated with early successional habitats.

As noted earlier, all early successional habitats are ephemeral. For example, young upland hardwood forest reaches the stem exclusion stage within 10 or 15 years of harvest, when the density of young tree stems can exceed 20,000–25,000 stems/ha, and canopy closure reduces light availability at the forest floor (Dessecker and McAuley 2001). Habitat suitability for different wildlife species changes with changing forest structure; for example, there is rapid turnover of songbird species during this period (Thompson and DeGraaf 2001). Decline of Ruffed Grouse (*Bonasa umbellus*) also is attributed to paucity of the stem exclusion age class (6–15 years) in forests of the Central Hardwood Region (Dessecker and McAuley 2001); this age class declines with forest maturation and the absence of new disturbances. Disturbances are required to create early successional habitats and to maintain a forest with a mosaic of age classes and a structural heterogeneity that increases plant and animal diversity at local, landscape, and regional scales (Askins 2001, Shifley and Thompson, Chap. 6).

Ecosystem processes and services provided by forests, such as carbon storage and water resources, are altered by creating early successional habitats. In this book, Vose and Ford (Chap. 14) examine post-disturbance changes in water quality and quantity, and recovery over time in relation to forest management practices, woody species composition, and climate. Keyser (Chap. 15) examines how creating early successional habitats and forest regrowth affect carbon storage and sequestration at stand and landscape levels.

1.5 How Can Early Successional Habitats Be Sustained?

One approach to maintaining early successional habitats is to base forest management on the "historic natural range of variation" (Lorimer and White 2003). This requires us to determine a reference point or time period; understand both the natural range of variation and what is 'unnatural' (for example should pre-settlement clearing and burning by Native Americans be considered natural?); and be prepared to implement management actions toward the historical variation. For example, prescribed fire may be needed because wildfires are not allowed to burn the acreages they would have historically.

Alternative strategies for creating and maintaining early successional habitats include a proactive approach. We could 'look forward' by identifying desired future conditions or goals, such as amounts and characteristics of early successional habitats needed to maintain viable populations of dependant plants and animals, and create them accordingly. Chapters in this volume explore management tools for determining how much early successional habitat is needed, and how and where to create and sustain it on the landscape. Shifley and Thompson (Chap. 6), use long-term, landscape-level Forest Inventory and Analysis data to simulate management scenarios designed to create a "shifting mosaic" of age classes and sustain a target proportion of the landscape in a young forest condition. Warburton et al. (Chap. 13) focus on strategies being used to identify priority species and specific recovery goals, develop spatially explicit blueprints of desired future conditions, and implement them by creating early successional habitats to sustain target populations through regional initiatives, ventures, cooperatives, and State Wildlife Action Plans. This book concludes with a chapter using empirical forest forecasting models to project 50 year change in forest types and age distributions in relation to scenarios of land ownership, economics, demographics, and climate change (Wear and Huggett, Chap. 16).

1.6 Conclusions

Overall, our aim in this book is to collate information about early successional habitats, to aid researchers and resource management professionals in their quest to sustain wildlife and plant species that depend on or utilize these habitats. We focus primarily on early successional habitats generated by natural or anthropogenic disturbance in upland hardwood forests, which are the predominant ecosystem in the Central Hardwood Region. This focus is in part because of the rising concern over the decline of plant and animal species associated with early successional habitats in this region, and because large areas of upland hardwood forest are in public lands where, compared to privately owned lands, land management decisions can be influenced more easily by conservation concerns. Using information in this book, resource management professionals may elect to look to the past to guide management by the natural range of variation in disturbance types and frequencies, and the area and conditions of early successional habitats they created. Or, they might look forward to create conditions based primarily on an objective to sustain biodiversity and species associated with early successional habitats through future decades.

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Chapter 2
Subregional Variation in Upland Hardwood Forest Composition and Disturbance Regimes of the Central Hardwood Region

William Henry McNab

Abstract Oaks and hickories characterize the Central Hardwood Region, with its temperate, humid climate and deep soils. Several xerophytic species characterize stands on xeric sites; mesic sites usually have greater diversity of oaks and hickories and include maple, ash, beech, and yellow-poplar. Ice and wind storms are common disturbances across the region; wildland fires ignited by lightning are uncommon and generally confined to small, stand-size areas. Variable environmental conditions, topography, and forest species compositions from the eastern Appalachians to the western Ozarks can require different silvicultural prescriptions to create early successional habitats, even in stands of similar appearance.

2.1 Introduction

Extensive temperate deciduous broadleaf forests are present in only three areas on earth: central Europe, eastern Asia, and the eastern USA (Rohrig and Ulrich 1991). These areas have a moderately humid, continental climate with ample summer rainfall and severe winters (Whittaker 1975). In the USA, deciduous forests dominated primarily by upland hardwoods (with minor amounts of coniferous species) occur mainly from latitudes 35° to 40°, between grasslands on the west and forests with a higher proportion of conifers on the north and south (USDA Forest Service 1967). Historically referred to as the Central Hardwood Region, these forests are among the most compositionally and structurally complex vegetative assemblages in eastern North America (Braun 1950; Barbour and Billings 2000). Embedded within this region are equally complex bottomland deciduous forests associated with some of the largest river systems in the

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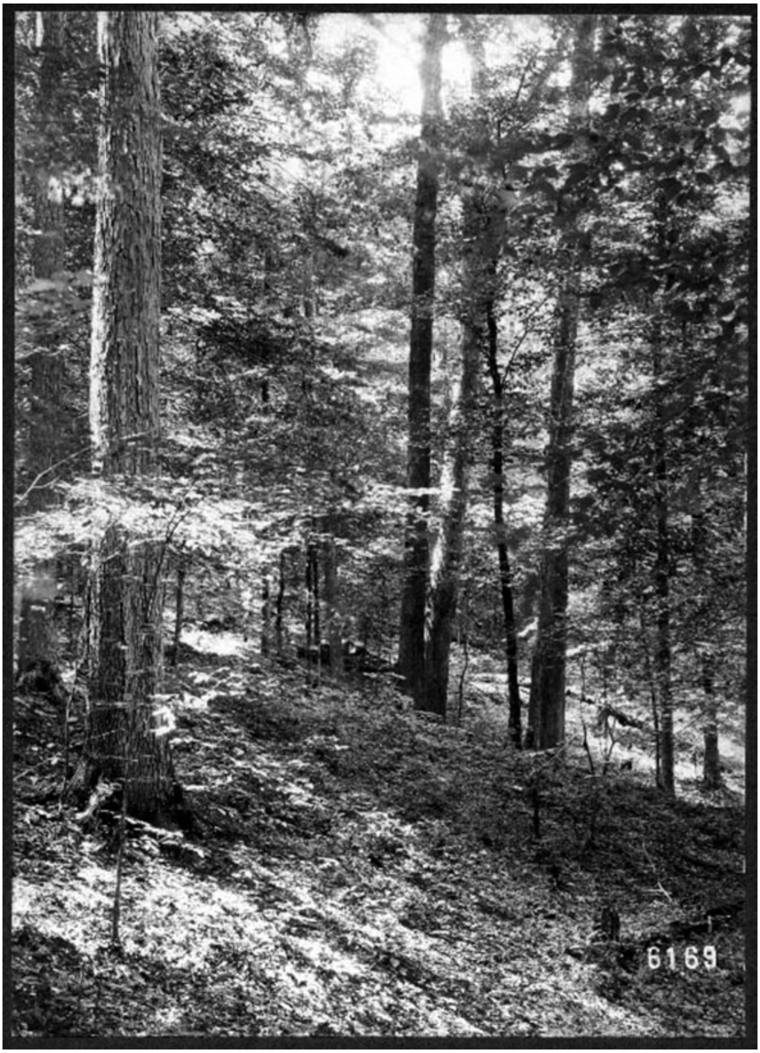

Plate 2.1 Oaks and hickories typically dominate the canopy of mature forests on middle and upper slopes in the Central Hardwood Region, such as this stand on the Cumberland Plateau, in Scott County, Tennessee (US Forest Service photo by F.E. Olmsted, 1901. Source: US Forest Service Photograph Collection, #P9801, D.H. Ramsey Special Collections, UNC-Asheville)

USA, including the Ohio, Wabash, Cumberland, and Tennessee Rivers (Braun 1950). The Central Hardwood Region covers over 40 million ha of the central USA.

Two general associations of canopy species are apparent in upland forests of the Central Hardwood Region: xerophytic associations of dry sites and mesophytic associations of moist sites. Stands on dry sites (ridges, upper and middle slopes) are characterized by a high proportion of oaks (*Quercus*) and hickories (*Carya*) in the canopy (Plate 2.1). On moist sites (coves and lower slopes), however, oaks and

Plate 2.2 A 55-year old stand of almost pure yellow-poplar that regenerated on an old-field site in a mesic cove of the Southern Appalachian Mountains, in Union County of northeastern Georgia (US Forest Service photo by C.A. Abell, 1930. Source: US Forest Service Photograph Collection, #P9876, D.H. Ramsey Library Special Collections, UNC-Asheville)

hickories are less abundant and the canopy may be shared with red maple (*Acer rubrum)*, white ash (*Fraxinus pennsylvanicum*), beech (*Fagus grandifolia*), sugar maple (*A. saccharum*) or occasionally dominated by few mesophytic species after severe disturbance (Plate 2.2) (Schnur 1937; Braun 1950). Although the region is dominated by upland hardwoods several species of conifers, such as red cedar (*Juniperus virginiana*) and Virginia pine (*Pinus virginiana*), may be present as minor components in stands on dry sites, particularly after disturbance. Many stands have three or more vertical strata: the overstory canopy, usually 24 m or more in height; a midstory of shade tolerant species; and a low shrub layer that usually includes advance regeneration of overstory species (Braun 1950). Abundance of advance regeneration and new seedlings depends strongly on the severity and timing of natural disturbances, which vary on a gradient of intensity from relatively frequent mortality of single canopy trees to infrequent catastrophic stand replacing events (White et al., Chap. 3). Considerable knowledge is available on the ecology, regeneration, and response of upland hardwood stands to silvicultural manipulations (Barrett 1980; Hicks 1998; Loftis et al., Chap. 5).

In this chapter, I describe the extent of the Central Hardwood Region and composition of arborescent vegetation in relation to environmental gradients, and briefly review the major types of disturbance across the region. Although I use canopy tree composition and its association with soil moisture availability to subdivide the region, other authors have chosen to use equally appropriate methods of stratification, such as ecoregions, as a basis of analysis for their chapters. This chapter provides an overview of the Central Hardwood Region that will supplement and link material presented throughout the book.

2.1.1 Distribution of Upland Hardwood Forests

The Central Hardwood Region has been delineated with general agreement (Schnur 1937; Braun 1950; USDA Forest Service 1967; Hicks 1998; Barbour and Billings 2000; Fralish 2003) (Fig. 1.1). This region is bordered on the north by forests with fewer oaks and more northern hardwoods (e.g. beech, sugar maple) and conifers (e.g. eastern white pine [*P. strobus*], eastern hemlock [*Tsuga canadensis*]) that transition to the Northern Hardwood Region (Braun 1950). To the south, southern yellow pines such as loblolly (*P. taeda*) Virginia, and shortleaf (*P. echinata*) increase in importance and oaks decrease as forests transition to the Southern Pine Region in the Piedmont (Eyre 1980; USDA Forest Service 1967). Conifers or hardwood-conifer mixtures may occur because of local conditions. For example, stands of red spruce (*Picea rubens*) occupy small areas of high mountain tops in West Virginia (>1,000 m) North Carolina (>1,400 m), where altitude presents environmental conditions similar to boreal conditions of southern Canada. As with other major forest regions in the eastern USA, (e.g. Southern Pine, Hemlock-Northern Hardwood) the Central Hardwood Region may be defined by its canopy composition of deciduous upland hardwoods (Braun 1950; Eyre 1980), and particularly by the predominant oak-hickory forest cover type (Barrett 1980; Hicks 1998; Fralish 2003).

The Central Hardwood Region also can be described by its climate. Whittaker (1975) reported an association of temperate deciduous forests with average temperature range between 3°C and 20°C and annual precipitation from about 1,125 to 1,225 mm. Stephenson (1998) explained the distribution of deciduous hardwood forests by actual evapotranspiration and water supply: "(1) annual precipitation (water supply) must be greater than 600 mm, (2) annual potential evapotranspiration (energy supply) must be greater than 600 mm, and (3) the seasonal timing of available water and potential evapotranspiration must be such that at least 600 mm of both occur simultaneously." In general, the Central Hardwood Region is associated with a climate in which precipitation is about equivalent to potential evapotranspiration and deficiencies of precipitation are offset by stored soil water during the mid to late frost-free season of most years.

2.1.2 Environment of the Central Hardwood Region

The continental climate of the Central Hardwood Region is classified as humid-temperate (Bailey 1995), with long hot summers and cold winters. Mean annual temperature in most of the region ranges from 11°C to 16°C. The frost-free season ranges from about 120 days in the north to almost 200 days in the south.

Annual precipitation ranges from less than 750 mm near the Great Plains to more than 1,100 mm in mountainous areas, with more than half falling in the growing season. Throughout this region, potential evapotranspiration during the early to middle growing season is about equal to the precipitation

West of the Mississippi River, elevations in the Central Hardwood Region range from about 100 m in major river valleys to over 800 m in the Ouachita Mountains, which are part of the Ozark Plateau, an extensive area in Arkansas and Missouri underlain by limestone, sandstone, and shale bedrock. East of the Mississippi River, elevation ranges from 100 m in the northeastern part of the Central Hardwood Region to over 2,000 m in the Southern Appalachian Mountains of North Carolina. Topography on level-bedded limestone and sandstone formations in central Kentucky and the Highland Rim of Tennessee ranges from gently rolling to dissected and hilly. The Appalachian Plateau, from central Pennsylvania to northern Alabama, grades from a dissected plateau to high hills and subdued mountains underlain by shale, sandstone, coal, and some limestone. Eastward, the folded and faulted shale, sandstone, and limestone bedrock of the Ridge and Valley province form long sandstone capped ridges separated by valleys underlain by limestone. East of that province are the highly weathered, steep Blue Ridge Mountains and the hilly Piedmont, both of which are underlain by igneous and metamorphic rocks. Overall, the highly variable topography and geologic substrate of the Central Hardwood Region have a greater effect on the distribution of species at smaller, landscape scales than on limiting the broader regional extent of the oak-hickory cover type throughout the central USA.

Soils of the Central Hardwood Region are varied and include four orders with extensive distributions. Ultisols are present across about half the region, from Arkansas and southern Missouri, central Tennessee, and Kentucky southeastward to the Piedmont and north into Pennsylvania. These soils are acidic, generally low in fertility, have high clay content in the subsoil and low amount of moisture storage capacity, and often are eroded as a result of past land use. Inceptisols are young soils that are present on steep terrain of the Appalachian and Cumberland Mountains, West Virginia, Pennsylvania, and southwestern Indiana. Alfisols usually form over calcareous rock formations and are present in northern Missouri, northwestern and central Kentucky and much of Indiana, Ohio, and southern Michigan. With sufficient soil moisture, Alfisols can be highly productive. Mollisols are the principal soil order in northern Missouri and much of Illinois, where the “Prairie Peninsula” extends eastward from the Great Plains into the Central Hardwood Region. Although soil orders are variable across the region, properties such as solum thickness of the A and B horizons and texture are among the most important factors affecting species composition and productivity of stands on both dry and moist sites.

Much of the central part of the region north of the Ohio River, including most of Illinois, has been influenced by one or more periods of glaciation, the most recent being the Wisconsin, which reached its peak about 20,000 years before present. Forward movement of the ice sheet created a smoothed landscape while its retreat left a layer of till of varying thickness and local variation caused by end moraines. Soils are generally deep and fertile in the northern part of the glaciated area.

Soils on flat terrain in the southern parts of Ohio, Indiana, and Illinois generally have poor internal drainage, resulting in wet conditions in winter and dry conditions in summer. An indirect effect of glaciations in the northern part of the region was deposition of wind-blown loess, which ranges in thickness from less than 0.5 to over 5 m.

Major, landscape-scale, natural disturbances throughout the Central Hardwood Region are associated mostly with wind (Everham and Brokaw 1996) and ice storms (Lemon 1961), and somewhat less by fire. Wind storms, mainly tornados, are more likely to occur in the western parts of the region (Fig. 3.3). Ice storms tend to be more common in the Appalachian Mountains and in the north (Fig. 3.3). Drought is a subtle form of natural disturbance that affects species composition of stands, particularly on moist sites, in the low-elevation parts of the Central Hardwood Region. Although wildland fires ignited by lightning occur throughout the region, the humid climate and highly urban and agricultural landscape limit their numbers to fewer than 300 annually and total area burned of about 4,500 ha (www.nifc.gov/fire_info/lightning_human_fires, accessed 12 Jan 2011). However, anthropogenic fires, set by Native Americans and later European settlers, were common throughout much of the region until the past several decades (Spetich et al., Chap. 4). Two historic sources of natural disturbances to forests in the eastern part of the Central Hardwood Region include elimination of American chestnut (*Castanea dentata*) as a canopy species during the 1920s and the differential effects among species from defoliation by gypsy moth (*Lymantria dispar*). White et al. (Chap. 3) provide more detailed information on the type and extent of disturbances.

2.1.3 Subregions of the Central Hardwood Region

Several species of oaks are in the canopy of most upland stands in the Central Hardwood Region, particularly on sites that are drier than average; mesophytic species increase on upland sites that are wetter than average (Braun 1950). The east–west precipitation gradient, variable bedrock formations with differing geologies and associated soils, and variable topography combine to form four smaller subregions of more uniform vegetation composition within upland forests: (1) Western Dry Subregion, (2) Transition Dry-Mesic Subregion, (3) Central Mesic Subregion, and (4) Eastern Mesic Subregion (Fig. 2.1). These subregions are similar to geographical areas delineated by Braun (1950), as oak-hickory, western mesophytic, mixed mesophytic, and oak-chestnut, respectively. Although forests are generally dominated by oaks, species composition varies in relation to moisture gradients at the subregion and stand scales.

Much of the information in the following paragraphs was extracted with little change from descriptions of large ecosystems termed major land resource areas (Natural Resources Conservation Service 2006); arborescent species composition was condensed from Braun (1950). The climatic regime of each subregion is presented as a water balance diagram for a representative location that combines annual variation in temperature and precipitation (Stephenson 1998). Potential evapotranspiration and actual evapotranspiration were estimated using the function developed by the US Geological Survey. Thirty year normal temperature and

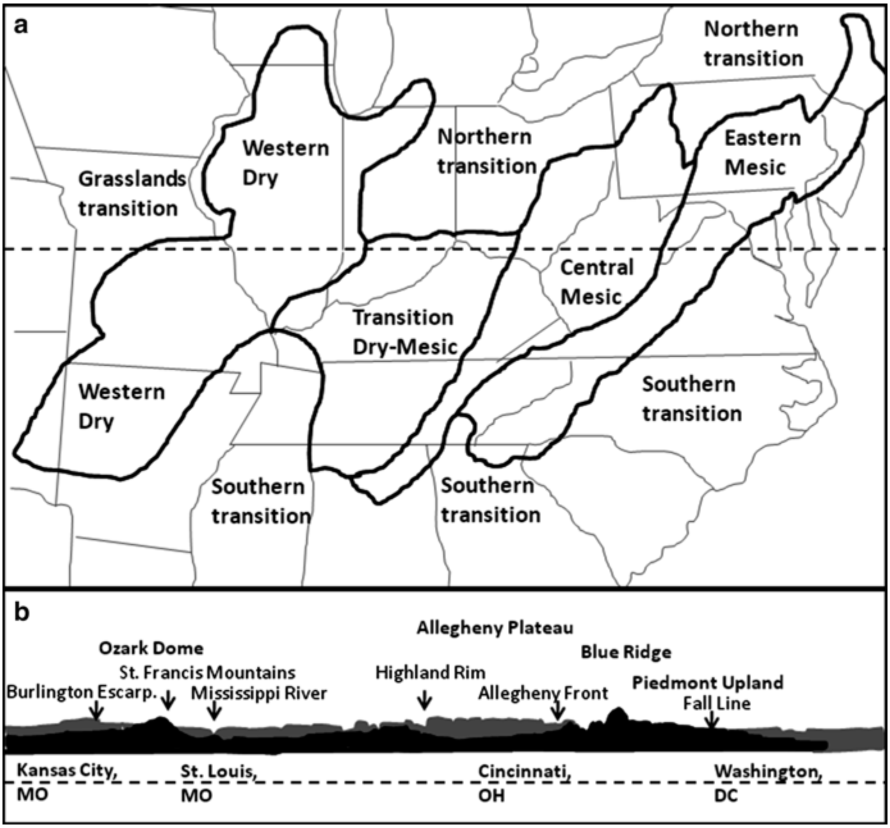

Fig. 2.1 (**a**) The Central Hardwood Region, its subregions, and transitions to adjoining subregions (From Braun 1950), and (**b**) profile of physiography along a transect (*dashed line*) from Kansas City, Missouri to Washington, DC and corresponding with the dashed transect line in (**a**) (from Lobeck 1957)

precipitation (1961–1990) were obtained from www.worldclimate.com. Soil field capacity of 200 mm was used for all locations.

2.1.3.1 Western Dry Subregion

This subregion extends in a broad diagonal band from northwestern Arkansas through south-central Missouri, and includes much of Illinois, which was about 60% prairie and oak savannah at the beginning of European settlement (Anderson 1970). The average annual temperature ranges from about 11.6°C to 15.5°C; the frost free season ranges from 175 to 245 days. Average annual precipitation ranges from about 1,000 to 1,150 mm, almost 60% falls during the growing season. Most of this subregion is a nearly smooth peneplain that was glaciated in the northern part (in Illinois) but not in the south, where it is slightly dissected by small streams.

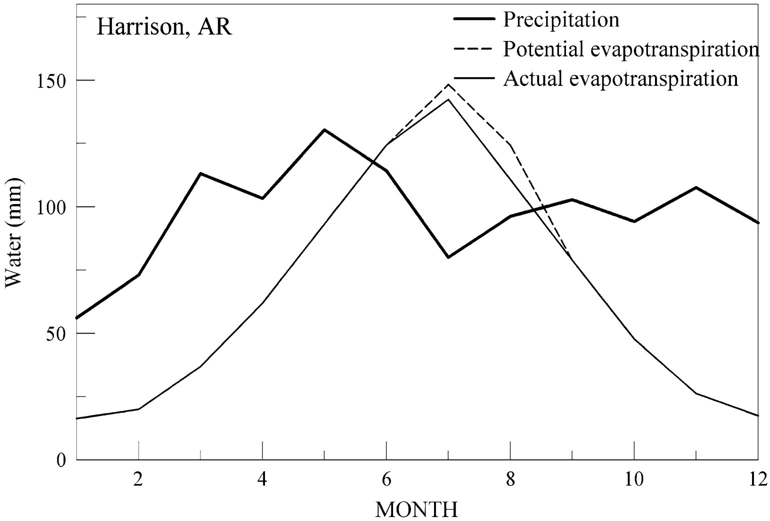

Fig. 2.2 A soil moisture deficit begins to develop in parts of the Western Dry Subregion during June in response to decreased summer precipitation as shown by a water balance diagram for Harrison, Arkansas

Elevation ranges from about 180 to 510 m. The Burlington Escarpment (Fig. 2.1) rises nearly 100 m above the peneplain and separates the Salem and Springfield Plateaus in southwestern Missouri. Bedrock geology is mostly sedimentary formations although intrusive granites are present in the St. Francis Mountains area of the Ozark Dome (Fig. 2.1), a large Precambrian uplifted and eroded region. Loess deposits range from several centimeters to almost a meter in thickness, with the greatest depth in the northern and eastern parts of the subregion. Soils are primarily Alfisols or Ultisols that have formed in material weathered from cherty limestone.

Tree species found in mesic ravines and gorges of this region include beech, northern red oak (*Q. rubra*), white oak (*Q. alba*), chinkapin oak (*Q. muehlenbergii*), sweetgum (*Liquidambar styraciflua*), winged elm (*Ulmus alata*), American elm (*U. Americana*), white ash, sugar maple, bitternut hickory (*C. cordiformis*), and basswood (*Tilia americana*). Dry site species on ridges and slopes include black oak (*Q. velutina*), white oak, shortleaf pine, scarlet oak (*Q. coccinea*), shagbark hickory (*C. ovata*), and in southern areas of the subregion, post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), and southern red oak (*Q. falcata*). Before European settlement, much of this subregion in Illinois was a mosaic of open woodlands and tallgrass prairie maintained by frequent fire (Spetich et al., Chap. 4).

A water balance diagram for Harrison, Arkansas, in the northwest corner of the state near Missouri and the transition to the Great Plains, shows precipitation does not meet evapotranspiration requirements beginning in June and continuing during the growing season through October (Fig. 2.2). Water required for evapotranspiration, but not supplied by precipitation, is obtained from stored soil moisture. In a normal year, about 35% of available soil moisture remains at the end of the growing season. The steep decline in summer precipitation, particularly for July, is typical of climates associated with grasslands (Vankat 1979). Windstorms, particularly tornados, and drought are the main types of natural disturbance. Fire set by humans was also an important disturbance prior to the early 1900s (Spetich et al., Chap. 4).

2.1.3.2 Transition Dry-Mesic Subregion

This subregion includes much of the western and central parts of Kentucky and central Tennessee, and is a transition between the drier subregion to the west and mesic area to the east. The landscape is a plateau with low, rolling hills, upland flats, and narrow valleys. Steep slopes are present in the Nashville Basin and bordering the Coastal Plain on the west. Limestone is present in many areas, particularly the fertile Bluegrass Region of Kentucky (Fig. 2.1), which was an oak savannah before European settlement. The average annual temperature ranges from about 11.1°C to 15.5°C; the frost free season ranges from 185 to 235 days. Average annual precipitation ranges from about 1,100 to 1,600 mm. Precipitation is generally well distributed annually, but the monthly maximum occurs during late winter and early spring; the minimum occurs in fall. Bedrock geology is mostly Ordovician to Mississippian age limestone and dolomite. Thick clay covers much of the bedrock and areas of karst occur where clay is not present. Loess deposits of varying thickness cover much of the bedrock on uplands and ridges. Soils are mostly Alfisols, Inceptisols, and Ultisols that are deep to very deep, generally well drained, and loamy or clayey texture.

Some of the more important tree species of mesic sites in this subregion include beech, yellow-poplar (*Liriodendron tulipifera*), northern red oak, sugar maple, black walnut (*Juglans nigra*), and slippery elm (*U. rubra*); dry site species are white oak, northern red oak, shagbark hickory, black oak, pignut hickory (*C. glabra*), sassafras (*Sassafras albidum*) and, on basic soils, chinkapin oak. A water balance diagram for Columbia, Tennessee, shows a small deficit of precipitation developing in early summer that remains about constant until fall (Fig. 2.3). July precipitation increases sharply from the amount received in June, a trend which differs markedly from that of the adjoining Western Dry Subregion. Fire was less common here compared to neighboring subregions (Fig. 3.3). Drought is a recurring natural disturbance throughout this subregion; wind storms are more common in the north.

2.1.3.3 Central Mesic Subregion

This subregion extends from central Pennsylvania to northern Alabama (Fig. 2.1) and includes much of the Appalachian Plateau, which consists of the Allegheny Plateau and Mountains in the north and the Cumberland Plateau and Mountains in the south (Fenneman 1938; Bailey 1995). Its eastern and western boundaries are marked by abrupt changes in topography identified as the Allegheny Front and Highland Rim, respectively (Fig. 2.1). Elevations range from about 300 m along the western edge to over 1,200 m in the Allegheny Mountains. Topography in much of this subregion is

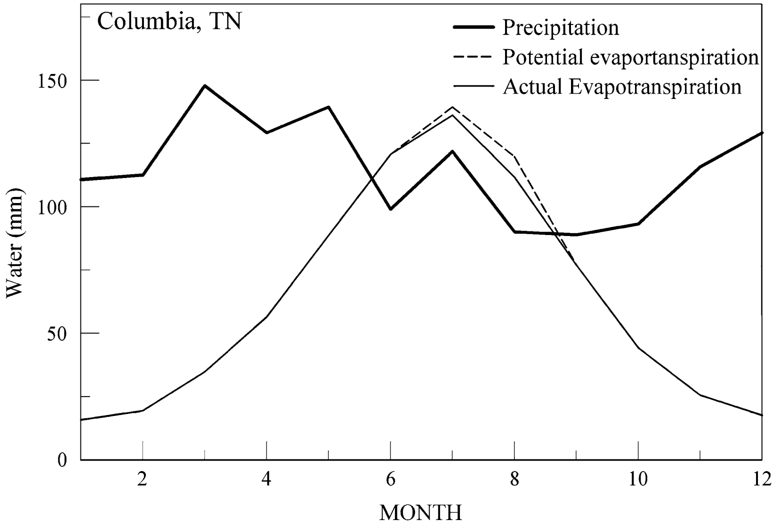

Fig. 2.3 As illustrated in a water balance diagram for Columbia, Tennessee, increased precipitation during July is the primary reason that soil moisture deficits are small in the Transition Dry-Mesic Subregion of the Central Hardwood Region

highly dissected plateau with steep side slopes between narrow ridge tops and mountains of moderate to high relief. The average annual temperature ranges from about 7.2°C to 15.6°C; the frost free season is variable depending on elevation and latitude, and ranges from 120 to 225 days. Average annual precipitation ranges from about 900 to 1,500 mm, and may exceed 1,900 mm in the mountains; about half occurs during the early growing season. Bedrock geology is mostly sedimentary formations of sandstone and shale, with small areas of limestone and coal in Virginia and Alabama. Ultisols form most of the soils in the undulating to rolling landscape of the Cumberland Plateau; shallow to deep and well drained to excessively drained Inceptisols are typical in areas of steep sandstone or shale residuum.

Canopy species composition is more varied here than in the other subregions and on mesic sites includes white oak, northern red oak, yellow-poplar, beech, sugar maple, buckeye (*Aesculus* spp.), black walnut, slippery elm, bitternut hickory and white ash; species on dry sites usually include white oak, chestnut oak (*Q. prinus*), black oak, shagbark hickory, pignut hickory, and redbud (*Cercis canadensis*). Stands of red spruce are present on the highest mountains in central West Virginia. A water balance diagram for Farmers, Kentucky, on the western edge of the subregion, shows a trend of actual evapotranspiration similar to the adjacent transition dry-mesic subregion to the west, but with very slight deficit of soil moisture as a result of the high July precipitation (Fig. 2.4). Ice storms are the most important type of natural disturbance, especially in the northern part of the subregion. Spetich et al. (Chap. 4) suggest that Native American use of fire was a common type of disturbance in this subregion that likely affected the regeneration dynamics of American chestnut, which was a component of many upland hardwood stands on non-calcareous soils,

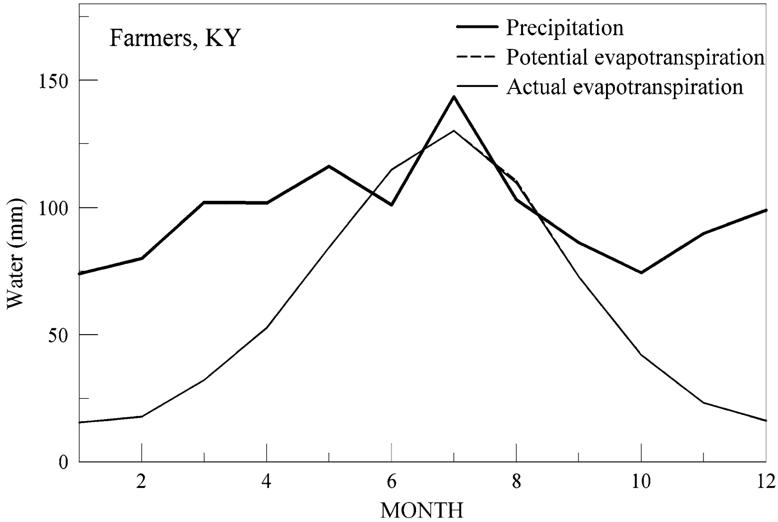

Fig. 2.4 Potential and actual evapotranspiration are almost equal in many parts of the Central Mesic Subregion, as shown by this water balance diagram for Farmers, Kentucky

before it was eliminated as a canopy species by the chestnut blight (*Cryphonectria parasitica*) in the early 1900s.

2.1.3.4 Eastern Mesic Subregion

Two large areas of differing physiology are included in this subregion: the low topography of the Ridge and Valley and higher peaks of the Blue Ridge Mountains (Fig. 2.1). Both of these areas extend from eastern Tennessee and western North Carolina through western Virginia into eastern Pennsylvania. Elevation ranges from about 30 m in the north to over 2,000 m in the southern mountains. Average annual temperature ranges from about 7.8°C to 15.6°C; the frost free season averages about 180 days, but is variable depending on elevation and latitude and ranges from 135 to 235 days. Average annual precipitation ranges from about 1,000 to 1,500 mm, and exceeds 2,500 mm along parts of the southern Blue Ridge escarpment in western North Carolina. Precipitation is generally evenly distributed annually with slightly reduced amounts in the fall. Ridge and valley bedrock geology consists of alternating beds of limestone, dolomite, shale, and sandstone; ridge tops are topped with resistant sandstone and the valleys have been eroded into less resistant shale and limestone. Southern Appalachian Mountain bedrocks consist mainly of Precambrian metamorphic formations of gneiss, schist, and small areas of amphibolites. The dominant soil orders are Inceptisols, Ultisols, and Alfisols, which are shallow to very deep, moderately well-drained to excessively drained and loamy or clayey.

Composition of the canopy in this subregion is almost as varied as in the central mesic subregion. Common mesophytic species of low to middle elevation stands are