THE BOTANICAL REVIEW

VOL. 67 APRIL–JUNE 2001 NO. 2

Sprouting in Temperate Trees: A Morphological and Ecological Review

PETER DEL TREDICI

Arnold Arboretum of Harvard University
125 Arborway
Jamaica Plain, MA 02130, U.S.A.

I. Abstract

Sprouting in trees, which results in the production of secondary trunks, is an induced response to injury or to a dramatic change in surrounding environmental conditions. This article reviews the forestry and ecology literature to produce an integrated view of the role of sprouting in both disturbed habitats and closed-canopy forests. Sprouting is a universal attribute of temperate angiosperm trees through the sapling stage of development but is much less common among gymnosperms. Four basic types of sprout morphologies are described: collar sprouts from the base of the trunk, sprouts from specialized underground stems (lignotubers

The Botanical Review 67(2): 121–140, April–June 2001

and rhizomes), sprouts from roots, and opportunistic sprouts from layered branches. In a survey of 68 species of trees native to northeastern North America, 41% were found to retain the ability to sprout from the collar into adulthood; 26% sprout from branch layers under natural conditions; and 25% have the capacity to form root suckers.

Sprouting in seedlings promotes their survival under a variety of stressful conditions, including suppression by canopy trees, herbivory, site exposure, and desiccation. In contrast, sprouting in mature trees extends the life span of the individual following damage and, in the case of root-suckering species, promotes the colonization of new ground. Although the sprouting of mature trees is more conspicuous than the sprouting of seedlings, its ecological significance is not as great.

As a broad generalization, species that grow in stressful sites or sites with frequent disturbances are likely to sprout more vigorously and to retain the sprouting ability longer than are species that grow in less stressful sites or sites with less frequent disturbance. Near the limits of a species' altitudinal or latitudinal range, the production of basal sprouts, root suckers, rhizomes, and/or branch layers allows trees to spread into adjacent areas, thereby circumventing the difficulties associated with seedling establishment.

II. Introduction

A tree can be defined as a plant that, when undisturbed, develops a single, erect woody trunk (Ng, 1999). A shrub, on the other hand, is a woody plant that, when undisturbed, branches spontaneously at or below ground level to produce multiple stems. In general, a tree will develop secondary trunks in response to injury to its primary trunk or root system, to displacement of its primary stem out of the normal vertical orientation, or to a dramatic change in surrounding environmental conditions (Hallé, 1999; Hallé et al., 1978; Putz & Sharitz, 1991; Sakai et al., 1995). As such, secondary trunk formation in trees—i.e., basal sprouting— is generally considered to be an induced response to exogenous environmental factors.

Much of what is known about sprouting in trees comes from the forestry literature on logging, a unique form of disturbance that involves the removal of the primary trunk of a tree without damaging the root system. Because logging has no precise natural analog—with the possible exception of beaver activity in North America—the forestry literature from temperate regions of the world provides very little information about the role that secondary sprouting plays in forests that have experienced disturbances other than logging. Only recently have ecologists begun to document the important role that sprouting plays in restructuring forests following non-logging disturbances, such as fire or wind (Cooper-Ellis et al., 1999; Everham & Brokaw, 1996), and to explore the evolutionary implications of sprouting (Bellingham & Sparrow, 2000; Bond & Midgley, 2001).

The purpose of this article is to review the basic morphology of sprouting in temperate trees and develop a classification system based on this information, to integrate the forestry literature on sprouting after logging with the ecological literature on sprouting following other types of disturbance, and to explore the ways in which morphology, physiology, and type of disturbance interact with one another to produce a given sprouting response, with a specific focus on trees native to northeastern North America.

III. Definitions

The development of form in trees is controlled by growth regulators that emanate from the distal tip of a shoot, through the loosely defined mechanisms of *apical dominance* and *apical control* (Brown et al., 1967; Zimmermann & Brown, 1974). In a precise physiological sense, the former term describes the temporary inhibition of the growth of axillary buds on a stem by an actively growing shoot tip, whereas the latter describes the regulation of overall tree shape by the terminal bud. Within the field of forestry, the term *apical dominance* is often used, albeit incorrectly, to describe the inhibition of secondary trunk development by the primary trunk. Although a few species of trees will naturally produce secondary trunks (Sakai et al., 1995), the vast majority of species will do so only when apical control is destroyed or blocked by some extrinsic factor. The basic effect of disturbance, in all of its forms, is to destroy the dominance of the primary stem and, with it, the hierarchical relationships that regulate the development of tree form. The term *sprouting,* as used in this article, describes the process whereby a tree develops secondary replacement trunks. Sprouting that occurs higher up on the stem or in the crown of erect trees, though not qualitatively different from basal sprouting, is not covered in this review because it does not lead to the production of secondary trunks.

Whether or not sprouting constitutes a form of clonal growth depends on which definition of the term one uses. In general, a clonal plant is one that naturally produces independent offspring by means of vegetative growth (Peterson & Jones, 1997; van Groenendael et al., 1997). Although this definition describes the situation for most herbaceous plants and many shrubs, it does not work well for trees, which typically allocate a high percentage of their total carbohydrate budget to the formation of a single, long-lived trunk (Ng, 1999; Zimmermann & Brown, 1974). For the purposes of this article, the term *clonal growth* is used to describe trees that produce secondary trunks a measurable distance away from the base of the primary trunk. This definition does not require that the secondary trunks be physiologically autonomous from the primary shoot/root system, only that they have the potential to become autonomous at some point in the future. In contrast to the term *clonal growth,* the term *sprouting* implies the persistence of the original root system and the replacement of a damaged trunk, independent of the potential for vegetative spread. Among trees, sprouting is more common than clonal growth.

Closely related to the concepts of clonal growth and sprouting is the term *vegetative reproduction* (or *regeneration*), which covers the wide variety of mechanisms that plants have evolved for asexual reproduction (de Kroon & van Groenendael, 1997; Harper, 1977). The term *reiteration,* used in the field of tree architecture, has a narrower definition than does vegetative regeneration and covers any shoot arising on any part of a tree that repeats the basic model of that tree (Hallé, 1999; Hallé et al., 1978). Because the term *reiteration* is used to describe the functionally distinct processes of crown development and secondary trunk formation, however, it is not used in this article. Relying heavily on the concepts of clonality and reiteration, Jenik (1994) has reviewed the full range of potential sprout morphologies in tropical as well as temperate woody plants, but he does not cover the ecological implications of the various sprout morphologies that he describes. Peterson and Jones (1997) have also reviewed the issue of clonality in woody plants, focusing specifically on the issues of competition and physiological integration among the ramets of a clone.

The ecological implications of sprouting in woody plants have recently been reviewed (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). These articles examine how the frequency and intensity of disturbance independently affect both the morphology and the physiology of the sprouting response. They also propose models for describing the long-term evolutionary and the short-term ecological implications of the sprouting strategy (the "persistence" niche) versus the seeding strategy (the "recruitment" niche) in a variety of distinct habitats.

IV. The Morphology of Sprouting

The forestry literature is replete with systems for classifying sprout growth, intended to quantify the quality and extent of "advance regeneration" in the forest understory. The simplest systems are based on the size of the stem that is sprouting, the number of sprouts produced, and the location of sprouts in relation to the trunk (Leffelman & Hawley, 1925; McIntyre, 1936). Although these practical systems achieve their intended goal of predicting future forest structure, they do not deal directly with the actual morphology of the sprout or the ecological factors that promote one type of sprouting over another. More recently, ecologists have developed a variety of classification systems that describe the sprout growth of mature trees following catastrophic disturbance (Cooper-Ellis et al., 1999; Everham & Brokaw, 1996), of suppressed seedlings growing in the forest understory (Hara, 1987), and of trees growing on stressful sites near the limits of their natural range (Koop, 1987). The classification system used in this article relies on the work of previous authors and describes four basic types of sprout morphologies displayed by temperate trees.

A. COLLAR SPROUTS

For the vast majority of trees, the greatest potential for the production of secondary trunks is localized at the *collar,* a term that is generally defined as the point on the seedling axis where the root and the shoot systems come together (Sutton & Tinus, 1983). This definition is morphologically imprecise, given that the stem and root systems come together at the hypocotyl region of the seedling, a portion of the stem that rarely produces buds in temperate trees (Groff & Kaplan, 1988). A review of numerous plant anatomy and forestry texts failed to locate a precise morphological description of the term *collar.* Although this situation was somewhat unexpected, it is understandable, given that the collar is a secondary structure that does not develop until a trees is several years old.

Only by studying the earliest stages of collar formation in first-year seedlings can one hope to understand the structure of the mature collar. Such detailed morphological/anatomical work has only been done on a few species, most of which develop specialized sprouting structures (e.g., lignotubers) at an early age: *Eucalyptus* sp. (Carr et al., 1984), *Ginkgo biloba* (Del Tredici, 1992), *Sequoia sempervirens* (Del Tredici, 1998b), *Quercus suber* (Molinas & Verdaguer, 1993), and *Arbutus unedo* (Sealy, 1949). An indirect source of anatomical information about collar development comes from observing the growth of buds on the trunks of mature trees, which sprout out in response to damage to the primary stem or root system (Church & Godman, 1966; Sakai et al., 1995; Wilson, 1968; Zimmermann & Brown, 1974).

Combining the data from these two sources, it is possible to develop a generalized scenario for collar development in temperate trees: in angiosperms, and a few gymnosperms, the collar originates from stem tissue immediately above the cotyledonary node. During the initial stages of collar formation, meristems in the axils of the two cotyledons develop into buds and develop with a direct connection to the vascular cylinder. These cotyledonary buds, in turn, give rise to accessory buds in the axils of their scale leaves, eventually producing a distinct cluster of buds at each of the cotyledonary nodes. Over time, bud proliferation spreads up the stem to include axillary buds produced during the first season of growth. An identifiable collar is formed when these separate bud clusters fuse into a more or less continuous band at the base of the trunk.

In mature trees the collar develops at or just below ground level and is readily identifiable by the presence of numerous suppressed buds that protrude out from the trunk. Suppressed buds are on the collar and the trunk and are distinguished from dormant buds on the twigs of a tree by virtue of the fact that the former are growing slowly, just enough to keep pace with the radial growth of the trunk, whereas the latter will generally die if they fail to sprout out within a year or two of their formation (Sakai et al., 1995; Wilson, 1968; Zimmermann & Brown, 1974). From the morphological perspective, suppressed collar buds are loosely covered with rudimentary leaf and scale primordia, whereas dormant twig buds are tightly covered with overlapping bud scales (Church & Godman, 1966; Kozlowski, 1971; Sakai et al., 1995). When the bark is removed from the collar, the traces of suppressed buds are clearly visible as conical protrusions on the surface of the exposed xylem. Suppressed buds branch freely from accessory buds, giving rise to clusters of buds that, in cross section, are supported by V-shaped bands of vascular tissue that connects to the pith at their point of origin (Sakai et al., 1995; Wilson, 1968; Zimmermann & Brown, 1974). In general, suppressed buds grow in length an amount equal to the width of the annual ring, thus keeping them near the surface of the trunk.

Typically there is a strong density gradient of suppressed buds along the trunk of the tree, with a maximum concentration at the collar that decreases as one moves up the trunk. The suppressed buds that are high up on the trunk are known as *epicormic buds,* which are morphologically identical to collar buds but functionally distinct because they produce new branches rather than new trunks (Kozlowski, 1971; Zimmermann & Brown, 1974). The pronounced swelling at the base of the trunk that often accompanies collar development is the result of carbohydrate storage that functions to support the growth and proliferation of suppressed buds throughout the life of the tree as well as to facilitate their development into leafy shoots following traumatic disturbance (Bellingham & Sparrow, 2000; Pate et al., 1990; Sakai et al., 1995). Very little is known about the factors that control the development of suppressed buds and determine how long they can remain viable. In some species, the collar retains its sprouting ability into old age, whereas in others it loses this capacity relatively early in life.

The precise location of sprouts on the primary trunk can be of critical importance in determining their future development. If the sprouts originate above ground level, they will be dependent on the primary trunk and root system for water and mineral nutrients and, later in life, will be highly susceptible to disease or decay-related problems that originate with the decaying primary trunk (Roth & Hepting, 1943, 1969; Wilson, 1968). If the sprouts originate at or below ground level, however, they will be in direct contact with the soil and will have an opportunity to develop adventitious roots from the buried portions of their stems and to become autonomous from the parent trunk (e.g., *Castanea dentata:* Matoon, 1909; Paillet, 1984; *Euptelea polyandra:* Sakai et al., 1995).

It is important to keep in mind that sprouts which arise from the collar of a mature tree are considered to be ontogenetically juvenile relative to the mature parts of the tree (Borchert, 1976; Fontanier & Jonkers, 1976). One sign of this juvenility, as measured in greenhouse experiments, is a sprout's enhanced capacity to form adventitious roots in comparison with cuttings taken from shoots in the crown of the same tree. This trait, as indicated above, can have important ecological implications. Other so-called juvenile traits of collar sprouts include strong vertical orientation, indeterminate growth, the production of large, variably shaped leaves, and the retention of dead leaves (Borchert, 1976; Del Tredici, 1998a). From the physiological perspective, the collar of a tree can be considered a specialized organ of regeneration and rejuvenation.

Collar formation and suppressed bud development appear to be a universal characteristic of temperate angiosperm trees, at least through the sapling stage of development. Conifers, on

Table I

Sprouting characteristics of trees of northeastern North America

Species name[a]	Effective collar-sprouting stage[b]	Branch layers	Root suckers
	Bottomland species		
Acer negundo	Sapling		Yes
A. rubrum	Adult	Yes	
A. saccharinum	Adult	Yes	
Betula nigra	(Sapling)		
Celtis occidentalis	Sapling		
Chamaecyparis thyoides (G)	Sapling	Yes	
Diospiros virginiana	Adult		Yes
Fraxinus nigra	(Sapling)		
F. pennsylvanica	Sapling		
Ilex opaca	Sapling	Yes	
Larix laricina (G)	Seedling	Yes	
Liquidambar styraciflua	Sapling		Yes
Magnolia virginiana	(Sapling)	Yes	
Morus rubra	(Sapling)	Yes	Yes
Nyssa sylvatica	Sapling		Yes
Platanus occidentalis	Sapling		
Populus balsamifers	Sapling	Yes	Yes
P. deltoides	Adult		Yes
Quercus bicolor	Adult		
Q. macrocarpa	Adult		
Q. palustris	Adult		
Salix nigra	Sapling	Yes	
Thuja occidentalis (G)	Seedling	Yes	
Ulmus americana	Sapling		
U. rubra	Sapling		Yes
	Mesic species		
Abies balsamea (G)	Seedling	Yes	
Acer pensylvanicum	(Sapling)	Yes	
A. saccharum	Adult		
Betula allegheniensis	Sapling		
B. lenta	Sapling		
B. papyrifera	Sapling		
Carpinus caroliniana	Adult		
Carya cordiformis	Adult		Yes
C. glabra	Adult		Yes
C. lacinosa	Adult		
C. ovata	Adult		Yes
C. tomentosa	Adult		
Cornus florida	Adult	Yes	
Fagus grandifolia	Sapling	Yes	Yes
Fraxinus americana	Sapling		
Juglans cinerea	Sapling		
J. nigra	Sapling		
Liriodendron tulipifera	Adult		
Magnolia acuminata	Adult		
Ostrya virginiana	Adult		
Picea glauca (G)	Seedling	Yes	
P. mariana (G)	Seedling	Yes	

Table I (*continued*)

Species name[a]	Effective collar-sprouting stage[b]	Branch layers	Root suckers
	Mesic species (*continued*)		
P. rubens (G)	Seedling	Yes	
Pinus banksiana (G)	Seedling		
P. resinosa (G)	Seedling		
P. strobus (G)	Seedling		
Populus grandidentata	Sapling		Yes
Prunus serotina	Adult		
Quercus alba	Adult		
Q. coccinea	Adult		
Q. muehlenbergii	Adult		
Q. prinus	Adult		
Q. rubra	Adult		
Q. velutina	Adult		
Sassafras albidum	Sapling		Yes
Tilia americana	Adult		
Tsuga canadensis (G)	Seedling	Yes	
	Xeric species		
Juniperus virginiana (G)	Seedling		
Pinus rigida (G)	Sapling		
Populus tremuloides	Sapling		Yes
Prunus pensylvanica	(Sapling)		Yes
Quercus stellata	Adult		
Robinia pseudoacacia	Adult		Yes

[a] Species selection, nomenclature, distribution, and habitat preferences from *Silvics of North America* (Burns & Honkala, 1990). (G), gymnosperm.

[b] Sprouting data based on Burns & Honkala, 1990; parentheses indicate data based on personal observations. Seedlings have a basal diameter <2 cm; saplings, 2–15 cm; and adults, >15 cm.

the other hand, are generally considered to be weak collar sprouters, seldom sprouting vigorously once they grow beyond the sapling stage (Table I). There are a few exceptions to this rule among the conifers, most notably the genera *Sequoia* and *Cunninghamia* in the Taxodiaceae and *Taxus* and *Torreya* in the Taxaceae (Burns & Honkala, 1990; Del Tredici, 1998b). As a broad generalization, the author has observed that conifer species which produce two cotyledons possess cotyledonary buds and develop collars that sprout, whereas species which produce more than two cotyledons generally lack cotyledonary buds and functional collars and typically do not sprout (see Butts & Buchholz [1940] for conifer cotyledon numbers). The primary exception to the above rule are a few fire-adapted pines that lack cotyledonary buds but are capable of sprouting at the base of the trunk from axillary buds above the cotyledonary node (Keeley & Zedler, 1998; Little & Mergen, 1966; Stone & Stone, 1954).

B. SPROUTS FROM SPECIALIZED UNDERGROUND STEMS

As opposed to collar sprouts, the sprouts produced by specialized underground stems typically emerge some distance away from the primary trunk. This spatial separation tends to reduce competition between the primary trunk and the sprout and to facilitate the autonomous development of the sprout later in life. Among temperate trees, two types of specialized underground stems have been described. The first is the lignotuber, which develops from suppressed buds at the cotyledonary node of seedlings. Over time the cotyledonary buds, along with axillary buds higher up on the stem, proliferate to produce a basal swelling that protrudes out from the stem and may or may not have a downward orientation (Carr et al., 1984; Del Tredici, 1992). The lignotuber continues to expand throughout the life of the tree and eventually forms a large basal burl with a high carbohydrate content.

Functionally speaking, the lignotuber is a site for the production and storage of suppressed buds, the storage of carbohydrates, and the production of adventitious roots, all attributes that facilitate rapid resprouting following traumatic injury (Canadell & Zedler, 1994; Christensen, 1985; James, 1984; Pate et al., 1990). On steep slopes, lignotubers can also function as a type of clasping organ that anchors the plant to rocky substrates (Del Tredici et al., 1992, 1998b; Sealy, 1949). *Tilia americana,* like many other members of the genus, is the only tree native to northeastern North America that forms a true lignotuber.

A second type of specialized underground stem is the rhizome with distinct nodes and internodes, which grows out from the base of the trunk and produces aerial stems some distance away from its parent. Drought-adapted species in the genus *Quercus* from southeastern and western North America often produce rhizomes, as does *Q. virginiana,* which grows along the Atlantic coastal plain (Muller, 1951; Tiedemann et al., 1987). In the Northeast, *Prunus virginiana* is the only tree (or large shrub) that produces rhizomes (Schier, 1983).

In general, both lignotubers and rhizomes are adaptations that allow trees to survive the occurrence of frequent disturbance, especially herbivory and fire. Their sprouts, because they typically emerge from below ground, have a strong potential to form adventitious roots and to develop into autonomous ramets. It should be noted, however, that some lignotuber-producing shrubs can sprout continuously for up to 25 years in the absence of fire or any other identifiable form of disturbance (Mesleard & Lepart, 1989), an observation suggesting that basal sprouting may have more to do with the nature of the shrub growth form than with adaptations to specific environmental factors, such as fire.

C. SPROUTS FROM ROOTS

In many angiosperm trees, the root system is capable of producing shoots, known as *root suckers.* The phenomenon is well documented in the ecological, horticultural, and forestry literature. Among gymnosperms, root sprouting is extremely rare, having only been documented in a two tropical species (Burrows, 1990; Wong, 1994). From the anatomical perspective, the tree roots of angiosperms produce two basic types of shoot buds, the first being additional buds that are formed from the deep tissues (endogenously) of young, uninjured roots. Like suppressed collar buds, additional buds grow just enough every year to keep up with the diameter growth of the root, and they typically branch to form prominent bud clusters. Reparative buds, in contrast, are formed near the surface of the root (exogenously) in response to senescence or injury (Bosela & Ewers, 1997). Among the trees of eastern North America, *Sassafras albidum* and *Populus tremuloides* produce both types of buds, whereas *Fagus grandifolia* produces only reparative buds and *Liquidambar styraciflua* only additional buds (Bosela & Ewers, 1997; Kormanic & Brown, 1967).

Most root-suckering shrubs—e.g., *Rhus typhina* (Luken, 1990), *Rhus glabra* (Gilbert, 1966), and *Xanthoxylum americanum* (Reinartz & Popp, 1987)—produce new stems spontaneously, as part of their normal development. Most trees, on the other hand, do not begin suckering until the primary trunk has experienced some form of traumatic damage. Although the presence of a healthy trunk does not seem to inhibit the production of root buds per se, it often suppresses their development into aerial shoots through a physiological process that is somewhat comparable to the phenomenon of apical dominance in shoot systems (Burns & Honkala, 1990; Farmer, 1962). In general, the roots that link individual stems can remain functional for many years, with nutrients and water shared among ramets (DeByle, 1964; Jones & Raynal, 1986; Peterson & Jones, 1997; Reinartz & Popp, 1987; Zahner & DeByle, 1965). A characteristic morphological feature of root suckers is a pronounced thickening of the portion of the root distal to their point of origin, whereas the proximal portion of the root leading to the parent tree shows no such thickening and eventually dies (Kormanic & Brown, 1967).

The most widely studied root-suckering trees, and the source of most of our information about the subject, are *Populus tremuloides*, the quaking aspen, which can form gigantic clones, covering up to 43 hectares in the arid Rocky Mountain region of Utah (Mitton & Grant, 1996). Interestingly, under the moister, forested conditions of eastern North America the clone size of the same species is generally much smaller, reaching a maximum of 1.5 hectares, presumably due to the increased competition with other, more shade-tolerant vegetation as well as with adjacent aspen clones (Kemperman & Barnes, 1976).

Observations on cultivated trees growing in full sun indicate that the more light a root-suckering species receives, the more likely it is to produce sprouts in the absence of injury to the primary trunk and that these stems will develop into mature trees (Del Tredici, 1995). On the other hand, shady conditions in a closed forest generally suppress the production of root suckers or inhibit their development beyond a meter in height. For most species, light is not necessary for root-sucker initiation, but it is essential for subsequent growth. For many temperate trees, especially those native to mesic habitats, root suckering appears to be primarily a reparative response that only secondarily results in clonal growth. Frequent fires and heavy logging are two types of disturbance that favor the spread of root-suckering species over non-root-suckering ones (Burns & Honkala, 1990).

D. OPPORTUNISTIC SPROUTS

This final category covers sprouting that occurs only when specific environmental conditions are met. Layered sprouts develop from low-hanging lateral branches that produce adventitious roots where they come into contact with the soil. Eventually these branches form vertical shoots that can develop into autonomous trunks when the parent branch rots away. Typically the diameter of the branch distal to the point of root formation is much greater than that of the proximal portion. When cultivated as an open-grown specimen, virtually any tree has the potential to produce branch layers whenever low-hanging lateral branches come into contact with the soil (Koop, 1987; Rackham, 1986). Under forested conditions, where trees typically shed their lower branches, layering is rare. Layering is common in conifers growing on exposed sites where the harsh conditions promote the retention of lower branches (Kajimoto, 1992; Larson et al., 2000; Marr, 1977; Timell, 1986) and on sunny, wet sites where the soil conditions facilitate the development of adventitious roots (e.g., *Larix larcina* and *Thuja occidentalis:* Burns & Honkala, 1990; Curtis, 1946).

Multistemmed, understory trees that are adapted to low light levels also commonly form layers, especially when their branches are pinned to the ground by the fallen trunks and branches of canopy trees. Such layers in the western vine maple, *Acer circinatum*, become autonomous when the original branch connection rots away (O'Dea et al., 1995). Hibbs and

Fischer (1979) found that such layers in the eastern *Acer pensylvanicum* accounted for only 3% of the total population. The authors conclude that layering in this species functions as a mechanism more to survive suppression than to increase population size. Koop (1987) reached this same conclusion based on extensive observations on European tree species.

Trunk sprouts arise from buds on the horizontal trunks of leaning or partially uprooted trees, especially when they are growing on open sites with wet, peaty soils or on forested sites with moist soils and heavy shade. Such trunks can produce adventitious roots as long as some portion of their primary root systems remains functional (Koop, 1987). Although the vertical trunk sprouts that develop may or may not be autonomous, the whole complex can be considered a form of clonal growth. Several of the species for which this phenomenon has been documented are conifers (Curtis, 1946; Del Tredici, 1998b), but it also can also occur in moisture-loving angiosperms such as *Salix nigra* (Burns & Honkala, 1990). No absolute morphological distinction between branch layers and trunk sprouts exists; rather, they represent a continuum of sprouting from stem tissue above the collar.

V. Resource-Allocation Issues

The morphological classification system outlined above says little about the physiology of sprouting in trees. Working with a Japanese species, *Euptelea polyandra,* Sakai and his colleagues have demonstrated that sprouting involves at least two basic resource-allocation strategies (Sakai & Sakai, 1998; Sakai et al., 1995, 1997). The first type, exemplified by species referred to as "resprouters," involves the translocation of carbohydrate reserves from underground portions of the trunk and/or root system to support rapid sprouting following serious damage to the aboveground portions of the plant (Bellingham & Sparrow, 2000; Canadell & Zedler, 1994; Pate et al., 1990).

The second strategy, which Sakai and his colleagues call "resource remobilization," is exemplified by the behavior of *Euptelea polyandra,* which grows naturally on steep, unstable slopes in central Japan. Under field conditions, *Euptelea* spontaneously produces suppressed buds at the base of its trunk which sprout out at a relatively early age in response to ground-surface disturbances that cause a partial uprooting of the primary stem. This secondary sprouting typically leads to the development of a multitrunked form in which each stem develops its own adventitious root system that reanchors the tree to the unstable substrate. Through a series of cutting experiments involving three species, the authors demonstrated that successful resprouting in *Euptelea* requires the remobilization of resources from older, aboveground stems. Specifically, they found that the removal of aboveground stems dramatically reduced sprouting in *Euptelea* in comparison with *Quercus serrata,* which, with its fleshy, carbohydrate-rich roots, resprouted vigorously following trunk removal.

Among the trees of eastern North America, it seems probable that some trees that are typically multitrunked, such as *Betula populifolia* and *Ostrya virginiana,* utilize the resource-remobilization strategy when sprouting. Kays and Canham (1991) provide experimental evidence for resource remobilization in *Betula populifolia,* which typically forms multitrunked specimens when its primary trunk is displaced from the vertical orientation as a result of snow loading. In their study of the effects of trunk removal on the sprouting behavior, *B. populifoia* showed the highest mortality among four species studied, regardless of the time of year of cutting. The fact that *B. populifolia* spontaneously forms a basal burl similar to that produced by *Euptelea* provides further support for the idea that it utilizes the resource-remobilization strategy (Stone & Cornwell, 1968). Resource remobilization provides a plausible explanation for the seemingly paradoxical observation that many species of birch develop the "clump form" despite being poor sprouters following logging (Burns & Honkala, 1990; Solomon & Blum, 1967). Circumstantial evidence for resource remobilization in *Ostrya virginiana* comes from an experiment in which more than 3000 trees were cut, leaving stumps that varied in height from 0 to 150 cm (Diller & Marshall, 1937). The authors found that the percentage of *O. virginiana* stumps resprouting after cutting increased from 15% for stumps cut at ground level to 87% for stumps cut 1 m above ground level.

VI. The Ecology of Sprouting

A. SEEDLING AND SAPLING SPROUTS

From the ecological perspective, the issue of when sprouting occurs in the life cycle of a tree is more significant than is the morphological origin of the sprout. Sprouting in seedlings promotes their survival under a variety of stressful conditions, including suppression by canopy trees, herbivory, site exposure, pathogens, and desiccation. In contrast, the major effect of sprouting in mature trees is the prolongation of the life span of the individual following disturbance and, in the case of root-suckering species, the colonization of new territory. Although the sprouting of mature trees is more conspicuous than the sprouting of seedlings, its ecological significance is not as great.

The critically important role that seedling sprouting plays in forest development has been documented by both foresters and ecologists. Among North American oaks, for example, the majority of "seedlings" growing in the forest understory have died back to the ground repeatedly. What looks at first to be a young seedling often turns out to have a collar that is 10–20 years old. In the forestry literature, a true seedling is defined as a plant in which the age of the shoot is the same age as the collar (Hara, 1987). Seedlings with collars that are older than the shoots they produce are classified as seedling sprouts, and, in the older literature, are arbitrarily defined as coming from stems <5 cm in diameter (McIntyre, 1936).

In one study of the ratio of seedling sprouts to true seedlings among seven tree species growing in the forest understory in the Missouri Ozarks, Liming and Johnson (1944) found that 77.9% of the "seedlings" were actually resprouts (n = 4800). Merz and Boyce (1956) found that 74% of the oak seedlings they sampled were of sprout origin (n = 100); and Ward (1966), working in Pennsylvania, found that 58% of the hardwood seedlings growing in an undisturbed, 53-year-old forest were resprouts (n = 12,000). Ward also found that following logging many true seedlings were converted to seedling sprouts as a result of increased exposure to sunlight and not as a result of mechanical damage. This conclusion was corroborated by Crow (1992), who studied a six-year-old cohort of *Quercus rubra* seedlings growing under a variety of site conditions and found that resprouting occurred in 22% of the seedlings when no overstory was present, in 20% of seedlings under a partial overstory, and in 13% of those under a complete overstory. Hara (1987) conducted a detailed study of seedling sprouts of 22 tree species growing in a mature Japanese beech forest (*Fagus crenata*) and carefully described the range of morphology displayed by seedling sprouts for each species, as well as their age and size distributions. He concluded that sprouting generally increases seedling longevity, thereby increasing their chances for eventual success in filling canopy gaps.

Powell and Tryon (1979) ranked eight of the common hardwoods of eastern North America according to their capacity to produce seedling sprouts and found that *Quercus alba* and *Prunus serotina* produced the highest percentage of seedling sprouts (relative to the number of unsprouted seedlings) and *Acer saccharum* the lowest. In the second-growth forests of southeastern Pennsylvania, Hough (1937) reported that *Acer saccharum, Fraxinus ameri-*

cana, Ostrya virginiana, and *Prunus serotina* all produced seedling sprouts in response to both natural and logging-related damage. Perala (1974) found a high frequency of sprouting (60–100%) among eight of nine species of northern hardwood saplings after a prescribed burn. *Tilia americana* and *Quercus rubra* produced the greatest amount of stem dry weight after five years of growth; *Acer saccharum* and *Betula alleghaniensis* (which sprouted at a frequency of only 11%) produced the least. In a detailed study of the ecology of *Prunus serotina,* Auclair and Cottam (1971) determined that resprouting allowed seedlings and saplings to survive long-term suppression (up to 60 years) in the forest understory. A later study by Auclair (1975) determined that the resprouting response in *P. serotina* seedlings reached its highest level in the understory of oak stands with high basal area and that these sprouts were eventually effective at colonizing canopy gaps created by the death of mature trees.

In one of the few physiological studies of seedling sprouts, Kruger and Reich (1993a) found that coppiced *Quercus rubra* saplings (4–12 years old) growing in an undisturbed forest in Wisconsin possessed higher leaf photosynthetic rates and stomatal conductances than did the uncoppiced controls. In further greenhouse experiments, Kruger and Reich (1993b) determined that coppiced seedlings (2 years old) had higher relative growth rates and a lower ratio of leaf area to root-surface area than did the uncoppiced controls.

Sprouting can also play a significant role in allowing a species to persist in the face of pathogen infestations. A well-known example in northeastern North America is chestnut blight–infected *Castanea dentata,* which has been producing new sprouts from old collars for up to 90 years. The young sprouts usually produce new adventitious root systems as well as new collars, which allow them to become autonomous from their parent root system (Matoon, 1909; Pailett, 1984). In essence, the blight has converted a dominant canopy tree into a perpetual, albeit gigantic, "seedling sprout." In the absence of blight, the sprouting capacity of chestnut seedlings and saplings probably developed as a strategy to survive suppression in the understory as well as periodic fires (Matoon, 1909; Zon, 1904). In this regard, it is important to note that the majority of the American chestnut sprouts in today's forest originated from plants that were seedlings or saplings at the time of the blight's arrival in the 1920s and 1930s, not from mature trees (Paillet, 1988).

B. SPROUTING OF MATURE TREES IN RESPONSE TO LOGGING

The ancient art of coppice forestry, which involves the repeated cutting and resprouting of individual trees, is one of the best sources of information on secondary trunk formation in mature trees. The goal of coppice forestry is to produce a sustainable supply of relatively small diameter stems on short rotation that can be used for fuel and for construction (Peterken, 1996; Smith et al., 1997). Coppicing typically involves cutting trees down close the ground, thereby inducing the production of basal sprouts, which are allowed to grow for 5–30 years before being cut down again. If done systematically, coppice woodlands can remain productive for several centuries, with individual stumps tolerating multiple generations of cutting before they deteriorate (Peterken, 1996; Rackham, 1986; Smith et al., 1997). In the deciduous forests of eastern North America, extensive logging has occurred over the past several hundred years. Coppice forestry was practiced during much of this time but began to fall out of favor in the late 1800s, when the demand for small-diameter wood products began to drop off (Whitney, 1994). The older forestry literature makes it clear, however, that many of the woody angiosperm trees native to the region (collectively known as *sprout hardwoods*) performed well under a short-rotation, coppice management system (Leffelman & Hawley, 1925; Little, 1937; Matoon, 1909; McIntyre, 1936).

The vast majority of angiosperm trees respond to traumatic injury or breakage with the sprouting of suppressed buds immediately below the point of damage. In general, buds closest to the point of damage, be they on the branches or the trunk, show the most vigorous growth, an indication that basal sprouting is generally an induced response, the primary purpose of which is to replace the damaged trunk. With few exceptions, most angiosperm trees with trunks <10–15 cm produce numerous collar sprouts after logging (Burns & Honkala, 1990). Typically, the majority of these sprouts (75–90%) die off within five to ten years, leaving only the most vigorous or the most firmly attached sprouts (Johnson, 1975, 1978; McIntyre, 1936; Wendel, 1975). Unlike seedling sprouts, the sprouts produced by larger trees, regardless of morphological origin, require high light in order to develop into effective replacement stems.

From the forester's perspective, the major advantages of stump sprouts are their rapid growth rate during their first few years of life and their reliable replacement of the existing forest structure. Site conditions, the age of the stump, the timing of cutting, and the species involved all affect the growth rate of the sprouts, which can average 0.5–1 m a year for the first ten years of life (Burns & Honkala, 1990; Cook & Sharik, 1998; Johnson, 1975; Roth & Hepting, 1969). One study of oak sprouting after clear-cutting (*Quercus coccinea, Q. prinus,* and *Q. velutina*) found that the percentage of stumps producing sprouts increased with decreasing site quality and that sprouting stumps were generally smaller, younger, and slower growing during the ten years before clear-cutting than were those that did not sprout (Ross et al., 1986).

Practically speaking, a major problem with stump sprouts is the increased probability that they will suffer from heart rot, which spreads directly from the cut trunk to the sprout. To avoid this problem, foresters recommend cutting stumps as low to the ground as possible, in order to stimulate the growth of buds from the collar instead of the trunk (Wendel, 1975). Similarly, stumps that had been burned after logging produced sprouts of lower origin than did unburned stumps, with a reduced susceptibility to heart rot (Roth & Hepting, 1943, 1969). In general, lower-origin sprouts are more firmly attached to the stump, less susceptible to heart rot, and more likely to develop a new, adventitious root system. Regardless of the height of the cut stump, some species have a strong tendency to sprout from the top of the stump, near the edge of the cut surface, whereas other species tend to sprout mainly from the collar. In general, trees cut during the dormant season tend to produce more numerous and more vigorous sprouts than do trees cut during the growing season (Burns & Honkala, 1990; Smith et al., 1997).

Every species of tree shows a characteristic relationship between the size and/or age of a stump, the probability that it will sprout, and the number of sprouts that it will produce. The forestry literature indicates that following logging some trees possess the ability to produce vigorous sprouts well into old age (e.g., *Quercus* sp.: Cook & Sharik, 1998; *Castanea dentata:* Matoon, 1909; Zon, 1904), whereas others lose the ability to sprout relatively early in life (e.g., *Betula alleghaniensis:* Solomon & Blum, 1967). A comparison of two maples shows that stump-sprouting percentages for *Acer saccharum* drop off at diameters between 10 and 15 cm, whereas those for *Acer rubrum* increase up to diameters of 25 cm and then decrease with increasing stump diameters (MacDonald & Powell, 1983; Solomon & Blum, 1967). Among a variety of oak species with trunks >15 cm, sprouting percentages decline with increasing stump diameter and/or age. However, overall sprouting percentages among oaks, even at large diameters, are very high compared with those of other tree species (Cook & Sharik, 1998; Johnson, 1978; Sander, 1971; Wendell, 1975).

Based on data in the forestry literature, it can be generalized that all temperate angiosperm trees will sprout vigorously and in high percentages from stumps between 5 and 15 cm in diameter. The majority of species will continue to sprout vigorously at stump diameters up to

25–30 cm, but in lower percentages than they do in smaller diameters. Beyond 30 cm, the number of non-oak species that are capable of successful sprouting drops off precipitously. Although the causes of this drop-off are not fully understood, it is clear that genetic, physiological, and anatomical factors limit the life span of suppressed buds.

Table I summarizes the sprouting characteristics of the common trees of northeastern North America, based on the data presented in Burns and Honkala (1990). It should be noted that larger-sized trunks (>25 cm) often sprout vigorously after logging but die within a few years, even under conditions of full sun (Roth & Hepting, 1969; Wendel, 1975). This observation suggests that the lack of successful sprouting among older trees may have more to do with the inability of a given bud to form a structurally sound, rot-free connection to the vascular system of the stump than it does with a lack of bud viability (Wilson, 1968). It also suggests that sprouting studies based on a single year of observation do not present an accurate picture of the long-term implications of the sprouting response.

C. SPROUTING OF MATURE TREES IN RESPONSE TO NON–LOGGING DISTURBANCES

How trees respond to various types of non-logging-related disturbances depends on the dynamic interaction between the species in question, the habitat in which it is growing, and the type of disturbance (Barnes et al., 1998; Bond & Midgley, 2001; White & Pickett, 1985). Although ecologists working in fire-prone, Mediterranean-type climates have long recognized the important role that sprouting plays in forest development (Canadell & Zedler, 1994), scientists working in mesic temperate forests have been slow to acknowledge the ecological importance of sprouting. Indeed, much of the literature on disturbance and regeneration in temperate forests deals with the growth of seedlings and saplings and makes no mention of sprouting in mature trees (Peterson & Pickett, 1995; Runkle, 1985). Fortunately, this situation has begun to change, and at least one forest-succession model has recently been modified to account for sprouting capacity as an important life-history trait (Loehle, 2000).

In undisturbed forests with relatively small light gaps, many tree species will produce basal sprouts in the absence of any obvious damage or disturbance. Depending on the species involved, its position in the forest profile, and its proximity to a light gap, such sprouts may or may not develop into secondary trunks. *Fagus japonica* is a large canopy tree that typically forms long-lived, multistemmed "stools" under closed-canopy conditions in central Japan (Ohkubo, 1992). Although basal sprout initiation in *F. japonica* is independent of disturbance, the development of these sprouts into secondary trunks is dependent on the presence of light gaps (Ohkubo et al., 1996).

This same type of spontaneous basal sprouting has been observed in two other canopy trees growing in an undisturbed, mixed forest in northern Japan: *Magnolia obovata* and *Tilia maximowicziana*. For both of these species, the number of basal sprouts was found to be directly dependent on the diameter at breast height (DBH) of the parent stem and independent of their proximity to light gaps (Sonoyama et al., 1997). For understory species growing in the same forest, in contrast, both the production of basal sprouts and their subsequent development into secondary trunks were dependent on the formation of a light gap. In general, the multistemmed nature of many understory trees is a manifestation of the important role that basal sprouting plays in allowing them to persist under shaded conditions as well as to increase their leaf-surface area following canopy disturbance (Harcombe & Marks, 1983; Hibbs & Fischer, 1979). For trees growing on sites near the limits of a species' latitudinal or altitudinal range, where seedling establishment is often problematic, sprouting of all types becomes an increasingly significant phenomenon (Koop, 1987; Marr, 1977; Mitton & Grant, 1996).

In a detailed study of the dynamics of *Prunus serotina* in the disease-ravaged forests of Wisconsin (Auclair, 1975; Auclair & Cottam, 1971), basal sprouting was found to be widespread among all size classes but most pronounced in the sapling category. Among 40 sampled stands, mean resprouting percentages were 35.4% for seedlings, 79.7% for saplings, and 72.2% for trees. The authors determined that basal sprouting allowed plants to survive suppression and put them in better condition for future release when a gap was created by the death of a nearby canopy tree.

Most of the literature that deals with the role of fire in the forests of northeastern North America focuses on various species of oak. Brown (1960) found that the density of several species of oaks (*Quercus alba, Q. velutina,* and *Q. coccinea*) and *Prunus serotina* increased dramatically in burned versus unburned areas in comparison with species that are considered to be weak sprouters. Similarly, Swan (1970) found that oaks and other species native to the oak woodlands of central New York State were better at surviving naturally occurring fires than were the so-called northern hardwoods, as measured by the lower mortality of mature trees, the higher percentage of sapling sprouting, and the higher average number of sprouts per sapling. An exhaustive review of the ecology of *Quercus rubra* (Crow, 1988) concluded that its present distribution is closely linked to past fires.

The literature on the effects of hurricanes, both real and simulated, on forest regeneration suggests that the collar and trunk sprouting of mature trees plays a major role in the years immediately after the event, when light levels are highest, but that their contribution becomes less important as decay weakens them or as rapidly growing seedlings overtop them (Cooper-Ellis et al., 1999; Everham & Brokaw, 1996). In a hurricane-prone bottomland forest in South Carolina, Putz and Sharitz (1991) found that resprouting of canopy trees affected both the immediate processes of forest recovery and the long-term processes that determine future forest composition. In an old-growth forest plot in southern New Hampshire that was not salvage logged following the famous hurricane of 1938, only a few scattered trees that sprouted back after the storm survived long enough to become part of the replacement canopy (Henry & Swan, 1974).

VII. Conclusion

Virtually all temperate angiosperm trees possess the ability to resprout through the sapling stage of development (<15 cm DBH), and many retain this capacity into adulthood (>15 cm DBH). The ability to resprout can be interpreted as an "insurance policy" in which trees invest as a hedge against future damage. The investment comes in the form of energy required for the production and maintenance of a bank of suppressed collar buds as well as a reserve of carbohydrates necessary to support their rapid growth following disturbance. By way of analogy, some species appear to invest in a 25-year insurance policy and others take out a 100-year option.

Table I presents data on the 68 species of trees native to northeastern North America (Burns & Honkala, 1990): all of these species possess the ability to sprout as seedlings; 84% of the species (all angiosperms and two conifers) can sprout as saplings (basal diameter >2 cm <15 cm); 41% of them retain the sprouting capacity into adulthood (basal diameter >15 cm); 26% of the 68 species form branch layers under natural, forested conditions; and 25% have the capacity to form root suckers either spontaneously or after logging. If one excludes the 13 conifers from the analysis, 51% of the angiosperms retain the ability to sprout into adulthood; 18% of them form branch layers; and 31% form root suckers. It is worth noting that 78% of angiosperm trees have the capacity to sprout as adults, to root sucker, or to form branch layers, clearly indicating that vegetative regeneration is a crucial part of their survival strategy. Among gymnosperms, the situation is the reverse: only 15% produce collar sprouts as saplings and none sprout as adults; none produce root suckers; and 62% can form branch layers.

VIII. Summary

1. The formation of secondary trunks by trees is an induced response to injury or to a dramatic change in surrounding environmental conditions.
2. Sprouting is a universal attribute of temperate angiosperm trees through the sapling stage of development. Sprouting is uncommon among gymnosperms.
3. The ability of seedlings to resprout following damage greatly enhances their survival in both disturbed habitats and closed-canopy forests.
4. Following severe damage, the number of sprouts a tree produces undergoes a natural self-thinning process, such that only a few survive to become secondary trunks.
5. Sprout growth and sprout longevity are greater in sun than in shade.
6. For most trees with trunks >15 cm DBH, the percentage of stumps that successfully resprout after logging generally decreases with increasing DBH.
7. Basal sprouts that form adventitious roots have the potential to develop into autonomous ramets and to live longer than do sprouts that are only connected to their parent trunk.
8. In most trees, the carbohydrate reserves that support sprouting are primarily stored in below-ground structures. In a few species that are typically multistemmed, the carbohydrate reserves that support sprouting come primarily from above-ground stems.
9. Root-suckering species tend to lose the ability to produce collar sprouts at younger ages than do species that do not root sucker.
10. Branch layering is a common phenomenon in conifers growing in exposed, stressful sites.
11. In undisturbed temperate forests, the sprouting of mature canopy trees does not typically play an important role in forest development. For understory trees, basal sprouting is an important mechanism for promoting both survival under closed-canopy conditions and vegetative expansion when a canopy gap develops.
12. Species that grow in stressful sites or sites with frequent disturbances are likely to sprout more vigorously and retain the sprouting ability longer than are species that grow in less stressful sites or those with less frequent disturbances.
13. Sprouting reduces the genetic diversity within a population by increasing the number of identical stems, especially in the case of root-suckering, rhizomatous, and branch-layering species.
14. On exposed sites or near the limits of a species range, the production of basal sprouts, root suckers, rhizomes, or branch layers allows trees to spread into adjacent areas, thereby circumventing the difficult process of seedling establishment.

IX. Acknowledgments

The author wishes to thank the staff of both the Harvard Forest in Petersham, Massachusetts, and the Arnold Arboretum in Boston, Massachusetts, for their support during the writing this article. The author also thanks the following individuals for their critical reading of the manuscript: Nick Brokaw, Robert Cook, David Foster, Glen Motzkin, John O'Keefe, David Orwig, Audrey Barker Plotkin, Terry Sharik, and Barry Tomlinson.

X. Literature Cited

Auclair, A. N. 1975. Sprouting response in *Prunus serotina* Erhr.: Multivariate analysis of site, forest structure and growth rate relationships. Amer. Midl. Naturalist 94: 72–87.

——— **& G. Cottam.** 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in southern Wisconsin oak forests. Ecol. Monogr. 41: 153–177.

Barnes, B. V., D. R. Zak, S. R. Denton & S. H. Spurr. 1998. Forest ecology. 4th ed. John Wiley & Sons, New York.

Bellingham, P. J. & A. D. Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89: 409–416.

Bond, W. J. & J. J. Midgley. 2001. Ecology of sprouting in woody plants: The persistence niche. Trends Ecol. Evol. 16: 45–51.

Borchert, R. 1976. The concept of juvenility in woody plants. Acta Hort. 56: 21–36.

Bosela, M. J. & F. W. Ewers. 1997. The mode of origin of root buds and root sprouts in the clonal tree *Sassafras albidum* (Lauraceae). Amer. J. Bot. 84: 1466–1481.

Brown, C. L., R. G. McAlpine & P. P. Kormanik. 1967. Apical dominance and form in woody plants: A reappraisal. Amer. J. Bot. 54: 153–162.

Brown, J. H. 1960. The role of fire in altering the species composition of forests in Rhode Island. Ecology 41: 310–316.

Burns, R. M. & B. H. Honkala (eds.). 1990. Silvics of North America. 2 vols. U.S. Forest Serv. Handb. 654.

Burrows, G. E. 1990. Anatomical aspects of root bud development in hop pine (*Araucaria cunninghamii*). Austral. J. Bot. 38: 73–78.

Butts, D. & J. T. Buchholz. 1940. Cotyledon numbers in conifers. Illinois State Acad. Sci. Trans. 1940: 58–62.

Canadell, J. & P. H. Zedler. 1994. Underground structures of woody plants in Mediterranean ecosystems of Australia, California, and Chile. Pp. 177–210 *in* M. T. Kalin Arroya, P. H. Zedler & M. D. Fox (eds.), Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia. Springer-Verlag, New York.

Carr, D. J., R. Jahnke & S. G. M. Carr. 1984. Initiation, development, and anatomy of lignotubers in some species of *Eucalyptus*. Austral. J. Bot. 32: 415–437.

Christensen, N. L. 1985. Shrubland fire regimens and the evolutionary consequences. Pp. 86–100 *in* S. T. A. Pickett & P. S. White (eds.), The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Church, T. W. & R. M. Godman. 1966. The formation and development of dormant buds in sugar maple. Forest Sci. 12: 301–306.

Cook, J. E. & T. L. Sharik. 1998. Oak regeneration in the southern Appalachians: Potential, problems, and possible solutions. Southern J. Appl. Forest. 22: 11–18.

Cooper-Ellis, S., D. R. Foster, G. Carlton & A. Lezberg. 1999. Forest response to catastrophic wind: Results from an experimental hurricane. Ecology 80: 2683–2696.

Crow, T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—A review. Forest Sci. 34: 19–40.

———. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia 91: 192–200.

Curtis, J. D. 1946. Preliminary observations on northern white cedar in Maine. Ecology 27: 23–36.

DeByle, N. V. 1964. Detection of functional intraclonal aspen root connections by tracers and excavation. Forest Sci. 10: 386–396.

De Kroon, H. & J. van Groenendael (eds.). 1997. The ecology and evolution of clonal plants Backhuys Publ., Leiden.

Del Tredici, P. 1992. Natural regeneration of *Ginkgo biloba* from downward growing cotyledonary buds (basal chichi). Amer. J. Bot. 79: 522–530.

———. 1995. Shoots from roots: A horticultural review. Arnoldia 55(3): 11–19.

———. 1998a. Aging, rejuvenation, and propagation in trees. Comb. Proc. Int. Pl. Propogag. Soc. 48 637–642.

———. 1998b. Lignotubers in *Sequoia sempervirens:* Development and ecological significance. Madroño 45: 255–260.

———, **H. Ling & G. Yang.** 1992. The *Ginkgos* of Tian Mu Shan. Conservation Biol. 6: 202–209.

Diller, O. D. & E. D. Marshall. 1937. The relation of stump height to the sprouting of *Ostrya virginiana* in northern Indiana. J. Forest. 35: 1116–1119.

Everham, E. M., III & N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. (Lancaster) 62: 113–185.

Farmer, R. E. 1962. Aspen root sucker formation and apical dominance. Forest Sci. 8: 403–410.

Fontanier, E. J. & H. Jonkers. 1976. Juvenility and maturity of plants as influenced by their ontogenetical and physiological aging. Acta Hort. 56: 37–44.

Gilbert, E. F. 1966. Structure and development of sumac clones. Amer. Midl. Naturalist 75: 432–445.

Groff, P. A. & D. R. Kaplan. 1988. The relation of root systems to shoot systems in vascular plants. Bot. Rev. (Lancaster) 54: 387–422.

Hallé, F. 1999. Ecology of reiteration in tropical trees. Pp. 93–107 *in* M. H. Kurmann & A. R. Hemsley (eds.), The evolution of plant architecture. Roy. Bot. Gard., Kew, London.

———, **R. A. A. Oldeman & P. B. Tomlinson.** 1978. Tropical trees and forests. Springer-Verlag, New York.

Hara, M. 1987. Analysis of seedling banks of a climax beech forest: Ecological importance of seedling sprouts. Vegetatio 71: 67–74.

Harcombe, P. A. & P. L. Marks. 1983. Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). Oecologia 57: 49–54.

Harper, J. L. 1977. Population biology of plants. Academic Press, London.

Henry, J. D. & J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material—An approach to the study of forest succession in southwest New Hampshire. Ecology 55: 772–783.

Hibbs, D. E. & B. C. Fischer. 1979. Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). Bull. Torrey Bot. Club 106: 222–227.

Hough, A. F. 1937. A study of natural tree reproduction in the beech-birch-maple-hemlock type. J. Forest. 35: 376–378.

James, S. 1984. Lignotubers and burls—Their structure, function, and ecological significance in Mediterranean ecosystems. Bot. Rev. (Lancaster) 50: 225–266.

Jenik, J. 1994. Clonal growth in woody plants: A review. Folia Geobot. Phytotax. 29: 291–306.

Johnson, P. S. 1975. Growth and structural development of red oak sprout clumps. Forest Sci. 21: 413–418.

———. 1978. Predicting oak stump sprouting and sprout development in the Missouri Ozarks. U.S. Forest Serv. Res. Pap. NC–149.

Jones, R. H. & D. J. Raynal. 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). Amer. J. Bot. 73: 1723–1731.

Kajimoto, T. 1992. Dynamics and dry matter production of below ground woody organs of *Pinus pumila* trees growing on the Kiso mountain range in central Japan. Ecol. Research 7: 333–339.

Kays, J. S. & C. D. Canham. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. Forest Sci. 37: 524–539.

Keeley, J. E. & P. H. Zedler. 1998. Evolution of life histories in *Pinus.* Pp. 219–249 *in* D. M. Richardson (ed.), Ecology and biogeography of *Pinus.* Cambridge Univ. Press, Cambridge.

Kemperman, J. A. & B. V. Barnes. 1976. Clone size in American aspens. Canad. J. Bot. 54: 2603–2607.

Koop, H. 1987. Vegetative reproduction of trees in some European natural forests. Vegetatio 72: 103–110.

Kormanik, P. P. & C. L. Brown. 1967. Root buds and the development of root suckers in sweetgum. Forest Sci. 13: 338–345.

Kozlowski, T. T. 1971. Growth and development of trees. Academic Press, New York.

Kruger, E. L. & P. B. Reich. 1993a. Coppicing alters ecophysiology of *Quercus rubra* saplings in Wisconsin forest opening. Physiol. Pl. (Copenhagen) 89: 741–750.

——— & ———. 1993b. Coppicing affects growth, root:shoot relations and ecophysiology of potted *Quercus rubra* seedlings. Physiol. Pl. (Copenhagen) 89: 751–760.

Larson, D. W., U. Matthes & P. E. Kelley. 2000. Cliff ecology: Pattern and process in cliff ecosystems. Cambridge Univ. Press, Cambridge.

Leffelman, L. J. & R. C. Hawley. 1925. Studies of Connecticut hardwoods: The treatment of advance growth arising as a result of thinnings and shelterwood cuttings. Yale Univ. School Forest. Bull. 15.

Liming, F. G. & J. P. Johnson. 1944. Reproduction in oak-hickory forest stands of the Missouri Ozarks. J. Forest. 42: 175–180.

Little, S. 1937. Relationships between vigor or resprouting and intensity of cutting in coppice stands. J. Forest. 36: 1216–1223.

——— **& F. Mergen.** 1966. External and internal changes associated with basal-crook formation in pitch and shortleaf pines. Forest Sci. 12: 268–275.

Loehle, C. 2000. Strategy space and the disturbance spectrum: A life history model for tree species coexistence. Amer. Naturalist 156: 14–33.

Luken, J. O. 1990. Gradual and episodic changes in the structure of *Rhus typhina* clones. Bull. Torrey Bot. Club 117: 221–225.

MacDonald, J. E. & G. R. Powell. 1983. Relationship between stump sprouting and parent-tree diameter in sugar maple in the first year following clear-cutting. Canad. J. Forest Res. 13: 390–394.

Marr, J. W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. Ecology 58: 1159–1164.

Matoon, F. E. 1909. The origin and early development of chestnut sprouts. Forest. Quart. 7: 34–47.

McIntyre, A. C. 1936. Sprout groups and their relations to the oak forests of Pennsylvania. J. Forest. 34: 1054–1058.

Merz, R. W. & S. G. Boyce. 1956. Age of oak "seedlings." J. Forest. 54: 774–775.

Mesleard, F. & J. Lepart. 1989. Continuous basal sprouting from a lignotuber: *Arbutus unedo* L. and *Erica arborea* L., as woody Mediterranean examples. Oecologia 80: 127–131.

Mitton, J. B. & M. C. Grant. 1996. Genetic variation and the natural history of quaking aspen. BioScience 46(1): 25–31.

Molinas, M. L. & D. Verdaguer. 1993. Lignotuber ontogeny in the cork-oak (*Quercus suber*; Fagaceae), II. Germination and young seedling. Amer. J. Bot. 80: 182–191.

Muller, C. H. 1951. The significance of vegetative reproduction in *Quercus*. Madroño 11: 129–137.

Ng, F. S. P. 1999. The development of the tree trunk in relation to apical dominance and other shoot organizational concepts. J. Trop. Forest Sci. 11: 270–285.

O'Dea, M. E., J. C. Zasada & J. C. Tappeiner. 1995. Vine maple clone growth and reproduction in managed and unmanaged coastal Oregon Douglas-fir forests. Ecol. App. 5: 63–73.

Ohkubo, T. 1992. Structure and dynamics of Japanese beech (*Fagus japonica* Maxim.) stools and sprouts in the regeneration of the natural forests. Vegetatio 101: 65–80.

———**, T. Tanimoto & R. Peters.** 1996. Response of Japanese beech (*Fagus japonica* Maxim.) sprouts to canopy gaps. Vegetatio 124: 1–8.

Paillet, F. L. 1984. Growth-form and ecology of American chestnut sprout clones in northeastern Massachusetts. Bull. Torrey Bot. Club 111: 316–328.

———. 1988. Character and distribution of American chestnut sprouts in southern New England woodlands. Bull. Torrey Bot. Club 115: 32–44.

Pate, J. S., R. H. Froend, B. J. Bowen, A. Hansen & J. Kuo. 1990. Seedling growth and storage characteristics of seeder and resprouter species of mediterranean-type ecosystems of S.W. Australia. Ann. Bot. (London) 65: 585–601.

Perala, D. A. 1974. Growth and survival of northern hardwood sprouts after burning. U.S. Forest Serv. Res. Note NC–176.

Peterken, G. F. 1996. Natural woodland. Cambridge Univ. Press, Cambridge.

Peterson, C. J. & R. H. Jones. 1997. Clonality in woody plants: A review and comparison with clonal herbs. Pp. 263–289 *in* H. de Kroon & J. van Groenendael (eds.), The ecology and evolution of clonal plants. Backhuys Publ., Leiden.

——— **& S. T. A. Pickett.** 1995. Forest reorganization: A case study in an old-growth forest catastrophic blowdown. Ecology 76: 763–774.

Powell, D. S. & E. H. Tryon. 1979. Sprouting ability of advance growth in undisturbed hardwood stands. Canad. J. Forest Res. 9: 116–120.

Putz, F. E. & R. R. Sharitz. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, U.S.A. Canad. J. Forest Res. 21: 1765–1770.

Rackham, O. 1986. The history of the countryside. J. M. Dent, London.

Reinartz, J. A. & J. W. Popp. 1987. Structure of clones of northern prickly ash (*Xanthoxylum americanum*). Amer. J. Bot. 74: 415–428.

Ross, M. S., T. L. Sharik & D. W. Smith. 1986. Oak regeneration after clear felling in southwest Virginia. Forest Sci. 32: 157–169.

Roth, E. R. & G. H. Hepting. 1943. Origin and development of oak stump sprouts as affecting their likelihood to decay. J. Forest. 41: 27–36.

——— **&** ———. 1969. Prediction of butt rot in newly regenerated sprout oak stands. J. Forest. 67: 756–760.

Runkle, J. R. 1985. Disturbance regimens in temperate forests. Pp. 17–33 *in* S. T. A. Pickett & P. S. White (eds.), The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Sakai, A. & S. Sakai. 1998. A test for the resource remobilization hypothesis: Tree sprouting using carbohydrates from above-ground parts. Ann. Bot. (London) 82: 213–216.

———**, T. Ohsawa & M. Ohsawa.** 1995. Adaptive significance of sprouting of *Euptelea polyandra*, a deciduous tree growing on steep slopes with shallow soil. J. Pl. Res. 108: 377–386.

———**, S. Sakai & F. Akiyama.** 1997. Do sprouting tree species on erosion-prone sites carry large reserves of resources? Ann. Bot. (London) 79: 625–630.

Sander, I. L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. J. Forest. 69: 809–811.

Schier, G. A. 1983. Vegetative regeneration of Gamble oak and chokecherry from excised rhizomes. Forest Sci. 29: 499–502.

Sealy, J. R. 1949. The swollen stem-base in *Arbutus unedo*. Kew Bull. 4: 241–251.

Smith, D. M., B. C. Larson, M. J. Kelty & P. M. S. Ashton. 1997. The practice of silviculture: Applied forest ecology. 9th ed. John Wiley & Sons, New York.

Solomon, D. S. & B. M. Blum. 1967. Stump sprouting of four northern hardwoods. U.S. Forest Serv. Res. Pap. NE–59.

Sonoyama, N., N. Watanabe, O. Watanabe, S. Niwa & Y. Kubota. 1997. Ecological significance of sprouting traits of cool-temperate tree species in a northern mixed forest. Jap. J. Ecol. 47: 21–29 (in Japanese).

Stone, E. L. & S. M. Cornwell. 1968. Basal bud burls in *Betula populifolia*. Forest Sci. 14: 64–65.

——— **& M. H. Stone.** 1954. Root collar sprouts in pine. J. Forest. 52: 487–491.

Sutton, R. F. & R. W. Tinus. 1983. Root and root system terminology. Forest Sci. Monogr. 24.

Swan, F. R. 1970. Post-fire response of four plant communities in south-central New York state. Ecology 51: 1074–1082.

Tiedemann, A. R., W. P. Clary & R. J. Barbour. 1987. Underground systems of Gambel oak (*Quercus gambelii*) in central Utah. Amer. J. Bot. 74: 1065–1071.

Timell, T. T. 1986. Compression wood in gymnosperms. Springer-Verlag, New York.

Van Groenendael, J. M., L. Klimes, J. Klimesova & R. J. J. Hendriks. 1997. Comparative ecology of clonal plants. Pp. 191–209 *in* J. Silvertown, M. Franco & J. L. Harper (eds.), Plant life histories. Cambridge Univ. Press, Cambridge.

Ward, W. W. 1966. Oak-hardwood reproduction in central Pennsylvania. J. Forest. 64: 744–749.

Wendel, G. W. 1975. Stump sprout growth and quality of several Appalachian hardwood species after clearcutting. U.S. Forest Serv. Res. Pap. NE–329.

White, P. S. & S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pp. 3–13 *in* S. T. A. Pickett & P. S. White (eds.) The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Whitney, G. G. 1994. From coastal wilderness to fruited plain. Cambridge Univ. Press, Cambridge.

Wilson, B. F. 1968. Red maple stump sprouts: Development the first year. Harvard Forest Pap. 18.

Wong, K. M. 1994. A note on root sucker production in the conifer *Dacrydium xanthandrum* (Podocarpaceae) on Mount Kinabalu, Sabah. Sandakania 4: 87–89.

Zahner, R. & N. V. DeByle. 1965. Effect of pruning the parent root on growth of aspen suckers. Ecology 46: 373–375.

Zimmermann, M. H. & C. L. Brown. 1974. Trees: Structure and function. Springer-Verlag, New York.

Zon, R. 1904. Chestnut in southern Maryland. U.S.D.A. Bur. Forest. Bull. 53.