

## Tree uprooting: review of impacts on forest ecology

Randall J. Schaetzl<sup>1</sup>, Scott F. Burns<sup>2</sup>, Donald L. Johnson<sup>3</sup> & Thomas W. Small<sup>4</sup>

<sup>1</sup>*Department of Geography, Michigan State University, East Lansing, MI 48824-1115, USA;* <sup>2</sup>*Department of Petroleum Engineering and Geosciences, Louisiana Tech University, Ruston, LA 71272, USA;*

<sup>3</sup>*Department of Geography, University of Illinois, Urbana, IL 61801-3671, USA;* <sup>4</sup>*Department of Geography, Frostburg State University, Frostburg, MD 21532-1099, USA*

Accepted 27.12.1988

**Keywords:** Forest disturbance, Gap-phase replacement, Mosaic structure, Pit/mound microtopography, Seedling establishment, Species richness

### Abstract

This paper reviews the ecological effects of tree uprooting. In many forests, disturbance by uprooting is the primary means of maintaining species richness and diversity. Treefall may be due to exogenous factors or it may be endogenously created, although the former predominate. The canopy gap formed by downed trees is often vital to community vegetation dynamics and successional pathways, by providing high light niches (gaps) for pioneer species, by encouraging release of suppressed, shade-tolerant saplings, and through recruitment of new individuals. Nutrient cycling may be affected by uprooting as subsoil materials are brought to the surface, via additions of woody debris to the forest floor, through exposure of bare mineral soil, and by changes in throughfall chemistry. The influence of the resultant pit/mound microtopography on understory herb distribution is largely due to microclimatic and microtopographic variation. Tree seedling distribution, however, is related to microtopography primarily through differences in soil morphology, nutrition, and moisture content of mound and pit sites.

### Introduction

This paper focusses the effects of tree uprooting on forest growth, succession, structure, and composition, as well as faunal activities. Uprooting must be distinguished from other forms of treefall that involve only bole break or snap, in that it disrupts and mixes soil in the process (Schaetzl *et al.* 1989). Therefore, it is both a vegetational and a pedological disturbance agent (McIntosh 1961). Disturbance such as branch breakage or defoliation by strong winds, and natural senescence followed by bole break ('broken tree gaps') are not examined in detail herein because up-

rooting generally has not occurred. Rather, we focus on processes and products of uprooting (many of which may also occur during bole break). Because uprooting leads to canopy gap formation, gap phase replacement is also examined.

Herein we provide a topically focussed addition to other reviews on forest disturbance (Watt 1947; Bray 1956; Pickett & White 1985). Other papers either focussed on forest disturbance in general (White 1979) or gap phase dynamics (Runkle 1982, 1985b), exhibited a distinct regional focus (Bormann & Likens 1979a), or centered on regeneration following disturbance

(Grubb 1977). The above works do not address the effects of uprooting *sensu stricto* on forest ecology. Nor do they discuss the effects of pit/mound topography on germination and establishment. This paper, in conjunction with a related review (Schaetzel *et al.* 1989), focusses on the uprooting process and relates it to other factors in the forest ecosystem.

### Disturbance in forest ecosystems

Many primeval forests are no longer viewed as slowly evolving communities, undergoing auto-genic successional processes and endogenous (internally-created) disturbance, ultimately resulting in climax (Clements 1936; Cline & Spurr 1942; Daubenmire 1968), or steady state stands (Whittaker 1975; Bormann & Likens 1979a). Rather, most forests are thought to be in a constant state of flux from the dynamic action of wind, fire, and other disturbances (Dix & Swan 1971; Frissell 1973; Henry & Swan 1974; Sprugel 1976; White 1979; Lorimer 1980; Hytteborn *et al.* 1987). Current theory emphasizes the role of allo-genic succession, whereby new individuals are recruited into the community shortly after disturbance, rather than the steady recruitment of more tolerant species (Raup 1957, 1964; Drury & Nisbet 1973; Henry & Swan 1974; Oliver & Stephens 1977; Harcombe & Marks 1978). Nonetheless, neither view is mutually exclusive; both types of processes interact in most stands (White 1979). Loucks (1970) viewed community dynamics as a type of 'stationary process' with 'random perturbations' (disturbances) imposed on the system at recurring intervals. Webb (1958) observed that, in many areas of the wet tropics disturbances occur at greater frequency than the life span of most trees, effectively preventing the attainment of any type of 'climax' forest. Lorimer (1980) pointed out that all-aged climax stands can only develop when disturbance recurrence intervals are longer than the life span of the dominant trees (see also Brokaw 1985; Runkle 1985b; Bongers *et al.* 1988).

Natural disturbances range on a continuum

from 100% exogenous to 100% endogenous in type (White & Pickett 1985). Exogenous disturbances result from forces external to the community (Webb *et al.* 1972; Reiners & Lang 1979; Bormann & Likens 1979a; White 1979). Wind, ice storms, drought, lightning, avalanches, and fires are only a few types of exogenous disturbance (see also Lorimer 1980 and White & Pickett 1985). These types of disturbance are often large-scale, catastrophic events resulting in all-aged forest stands or stands composed of several well-defined age cohorts (Goodlett 1954; Wyatt-Smith 1954; Lorimer 1980; Whitney 1986). In many instances, however, only small areas may be affected (White 1979).

Endogenous or internal disturbance is often equated with small-scale treefall of perhaps one or a few individuals (Bormann & Likens 1979a). Isolated fall of this type usually involves dead trees, taller trees, or those weakened by fire or insect attack (Cline & Spurr 1942; Dunn *et al.* 1983; Harcombe & Marks 1983). Foster & Reiners (1983) defined 'dead tree gaps' as those formed when trees died while standing; a prime example would be the death of *Castanea dentata* trees by the chestnut blight (Woods & Shanks 1959; see also Harcombe & Marks 1983). Whereas such treefall is often deemed endogenous (Reiners & Lang 1979), White (1979) noted that for treefall to be truly endogenous, senescence must be independent of environment – a situation that may be relatively uncommon (see, however, Foster 1977; Strong 1977).

### Uprooting as a type of disturbance

Uprooting is a major disturbance factor in most natural (unmanaged) forests (Cooper 1913; Sernander 1936; Stearns 1949; Webb 1958; Wright 1974; Pritchett 1979). Schaetzel *et al.* (1989) reviewed the pedologic, biotic, and topographic factors that promote or inhibit uprooting. White (1979) summarized several studies that had determined incidence of windstorm damage in different environments, and concluded that in many areas, disturbance by wind was more common than

periods of tranquility. Nichols (1935) noted that windfall is a common and widespread process in the boreal forest, whereas in deciduous forests it is less frequent and usually confined to single, scattered trees. On the other hand, windfall is considered a major disturbance factor in Japanese beech forests (Nakashizuka 1987). Foster & Reiners (1983) found that 24% of the total land area in a subalpine forest was composed of canopy gaps (see also Runkle 1982, 1985).

In many regions catastrophic blowdown is often accompanied by fire (Cline & Spurr 1942; Stearns 1949; Frissell 1973; Lorimer 1977; Whitney 1986) or mass movements (Veblen & Ashton 1978), resulting in further disturbance. Broad, even-aged stands of *Pinus strobus* in the northeastern United States are thought to have been the result of catastrophic blowdown that, in most instances, was followed by fire (Goodlett 1954; Bormann & Likens 1979a). In areas of low fire frequency, windthrow takes on even greater ecologic importance as a primary disturbance agent (Wardle 1970; Putz 1983; Hytteborn & Packham 1985; Jane 1986; Hytteborn *et al.* 1987; Leemans & Prentice 1987). Other work (Sprugel 1976; Iwaki & Totsuka 1959) has documented that senescence, followed by bole break and establishment of new cohorts, is a natural process in some alpine fir forests.

Forest disturbance by uprooting occurs on a continuum from widespread, catastrophic blowdown to isolated, uprooted trees (Runkle 1985b; White *et al.* 1985). Catastrophic events such as volcanic eruptions, hurricanes, tornadoes, and downbursts can level broad expanses of forest (Jones 1945; Stoeckeler & Arbogast 1955; Oliver & Stephens 1977; Pickett 1980; Dunn *et al.* 1983; Schaetzl *et al.* 1989). In many areas in the Rocky Mountains, for example, stands of *Pinus contorta* replace *Picea-Abies* forest after massive blowdowns. Repeated, large scale windstorms in northeastern Australia have led to the development of 'cyclone scrub' forests with low canopies, abundant lianas, and a few scattered emergents (Webb 1958; see also Richards 1955). Stands of *Nothofagus* usually require catastrophic disturbance for regeneration (Veblen 1985; Jane

1986). The smallest canopy gaps may be only as large as a single treefall and thus in comparison to large gaps, they (1) form more frequently, (2) have greater density in many forests, and (3) close more quickly (Monk 1961; Barden 1981; Foster & Reiners 1983, 1986).

### Recovery from disturbance

Marks (1974) summarized two general responses of forests to disturbance: (1) reorganization of vegetation established prior to the disturbance, and (2) establishment of new individuals. Examples of the former include (1) expansion of branches of existing trees into the canopy gap, (2) production of epicormic branches by undamaged trees, (3) vegetative reproduction (stump sprouts and root suckers) by damaged individuals, and (4) release of advanced reproduction (Runkle 1982). The second major type of disturbance involves direct seeding into the disturbed area or germination of dormant seeds already present. Marks' (1974) summary provides the basis for discussion in this section.

Treefall promotes stand heterogeneity and species richness by recruitment of intolerant species into the canopy gap (Watt 1947; Bray 1956; Loucks 1970; Henry & Swan 1974; Fox 1977; Oliver & Stephens 1977; Veblen & Ashton 1978; Hibbs 1979; White 1979; Pickett 1980; Naka 1982; Putz 1983). Whereas much of this work has been performed in mid-latitude forests, Strong (1977) argues that frequent treefalls are even more important in maintaining species diversity in tropical forests. His conclusion is based on the assumption that understorey (tree) species richness is greater in tropical forests, and thus recruitment into the canopy is often accomplished with new species; in temperate forests, in-migration of new species into the canopy gap is less common. Putz *et al.* (1983) discussed how both the size, frequency, and type (uprooted, snapped, or died while standing) of disturbance can affect species composition and regeneration.

Gap-phase replacement after uprooting occurs by stimulating growth in the high-light region of a

canopy gap (Grubb 1977). Monk (1961) summarized three components typically involved in gap closure: (1) shade-tolerant species, present in a suppressed state before the gap was formed, (2) shade-intolerant species, present in the understorey before gap formation, and (3) opportunistic species with wind-transported seeds. Swaine & Whitmore (1988) accept only two categories and prefer the terms pioneers (shade-intolerant) and non-pioneers (shade-tolerant). Gap-phase replacement is often the only way that many intolerant tree species can reach the canopy. For example, in the wet tropics almost half of the tree species rely on canopy gaps for successful regeneration (Hartshorn 1980).

Forests undergoing gap-phase replacement often have a mosaic-like structure containing patches of shade-tolerant, shade-intolerant and mid-successional species (Jones 1945; Watt 1947; Bray 1956; Horn 1975; Richards & Williamson 1975; Williamson 1975; Bormann & Likens 1979a; Hytteborn *et al.* 1987), although evidence to the contrary has been reported (Henry & Swan 1974; Oliver & Stephens 1977). Sernander (1936) referred to this type of physiognomy as 'storm-gap structure'.

Community response to gap formation is related to gap size (Minckler & Woerheide 1965; White 1979; Lorimer 1980; Runkle 1982; Hibbs 1982; Brokaw 1985a; White *et al.* 1985). Indeed, the variability in gap sizes acts in great part to enhance or maintain overall community diversity (Denslow 1980; Runkle 1984). In large gaps, high light intensities at the forest floor promote establishment of intolerant species (Skeen 1976; Oliver & Stephens 1977; Hibbs 1982; Runkle 1982; Dunn *et al.* 1983; Brokaw 1985a). Spurr (1956) noted that replacement following widespread blowdown depended not only on the type and presence of advance growth, but on whether the downed timber was removed by logging. Root sprouting may also be common, depending on the species present before the disturbance (Marks 1974). Many gaps of large and intermediate size continue to expand as trees die or fall at the periphery, further underscoring the dynamics of the process (Hartshorn 1980; Runkle 1984; Foster & Reiners 1986).

Disturbance on an intermediate scale often results in the mosaic structure indicative of gap-phase replacement (Bray 1956; Strong 1977; Foster & Reiners 1983, 1986; Brokaw 1985a). Richards & Williamson (1975) noted that in gaps of intermediate size, several individuals of a species with a narrow crown may eventually fill in the gap, leading to a mosaic pattern of even-aged trees. If, however, a wide-crowned species invades the gap, only one or two individuals may survive and patchiness may not be as evident. Bray (1956) stressed the importance of seedling and sapling growth rates to the determination of which species eventually fills in the gap. Gaps of intermediate size had greater densities of pioneer species than smaller gaps in a tropical forest, due in part to higher light levels and decreased rotor competition from standing trees (Brokaw 1985a). Depending on pioneer species invasion and growth, however, intermediate size gaps may experience considerable recruitment of suppressed, shade-tolerant saplings (Watt 1925; Sernander 1936; Webb 1958; Runkle 1981, 1982; Hibbs 1982; Brokaw 1985a; White *et al.* 1985). Gaps fill in somewhat by crown expansion (Dunn *et al.* 1983; Runkle 1982), although Trimble & Tyron (1966) caution that rates of crown expansion may be a less important factor in reducing light available to the forest floor than has been assumed.

Small gaps may be the most common type of canopy disturbance. For example, White *et al.* (1985) found that 78% of all canopy gaps in a *Picea-Abies* forest were formed by the fall of a single tree. The recovery pattern within small gaps is often unpredictable (Barden 1979), depending on site, size, disturbance frequency, and pre-disturbance canopy composition (Lorimer 1980; Runkle 1981, 1984). Many such gaps are filled in by growth of suppressed, shade-tolerant saplings (Brewer & Merritt 1978), or produce only increased lateral growth of canopy trees (Marks 1974; Oliver & Stephens 1977; Hibbs 1982). Sapling densities may even be greater in small gaps than in larger gaps, presumably because the negative aspects (numerous fallen boles and branches) in the latter outweigh the advantages of increased light (Runkle 1982, 1984). Localized

types of canopy disturbance and replacement are commonly caused by the standing death of a tree, accompanied by fall at a later time (Woods & Shanks 1959; Spurr & Barnes 1980; Harcombe & Marks 1983; Putz *et al.* 1983), referred to as 'dead tree gaps' (Foster & Reiners 1986). Hytteborn *et al.* (1987) distinguished between group regeneration patterns (large gaps) and 'tree for tree' replacement, typical of small canopy gaps.

Many gaps quickly fill in vegetatively with sprouts from tree species such as *Acer rubrum*, *Alnus*, *Betula*, *Fagus*, *Hippophae*, *Laurelia*, *Populus*, *Salix*, *Rhododendron*, *Tilia*, and *Ulmus* (Curtis 1959; Monk 1961; Marks 1974; Runkle 1982; Veblen 1985), and from vegetatively reproducing shrubs (Hytteborn *et al.* 1987). Suckers have the advantage of established root systems of the parent tree and can quickly fill in the gap, even where light intensities are too low for seedling establishment (Koop 1987). On certain soil types, many if not all the uprooted trees may root or trunk sprout *en masse*, leading to dense stands of reiterative stems (Grasveld & Imming 1987).

Disturbance is an important 'resource release' factor (Dunn *et al.* 1983; Mladenoff 1987). The gap provides for a temporary reduction in resource utilization, and increased input of other resources (Marks 1974). Although increased light quantity and improved spectral properties appear to be the most important aspects of resource release (Minckler *et al.* 1973; March & Skeen 1976; Chazdon & Fletcher 1984; Vitousek & Denslow 1986), other factors that favor establishment and growth are changes in moisture, heat, and nutrition (Cook & Lyons 1983). Higher soil moisture levels beneath canopy gaps (Minckler *et al.* 1973) are primarily due to reduced canopy interception losses and lower rates of root uptake (Douglass 1967). Soils beneath gaps in an old-growth *Acer-Tsuga* forest had higher pH values, phosphorus and nitrogen content, and nitrification rates than did adjacent forest plots (Mladenoff 1987), although calcium and potassium levels were lower. Changes in throughfall chemistry may also affect growth beneath canopy gaps (Marks 1974).

The successful colonization (by seeds) of a disturbed site is a function of (1) a relatively good

seed year, (2) migration of seeds into the site, (3) appropriate timing of seed arrival and the disturbance event, and (4) favorable microclimatic conditions within the disturbed area (Marks 1974; Canham & Marks 1985). For true 'pioneer' species, the above set of conditions is achieved in most large and intermediate-sized gaps, (see Cook & Lyons 1983 for a discussion). 'Fugitive' species (Hutchinson 1951) with highly dispersible seeds, such as *Betula* and *Populus*, are more likely to germinate in the centers of large gaps than are species like *Fagus* or *Quercus*, which have larger seeds and may be restricted to peripheral regions (Watt 1925; Marks 1974; Grubb 1977). Other components of colonization include a complicated set of conditions that trigger germination of buried seeds (Cook & Lyons 1983). Marks (1974) suggested that buried *Prunus pennsylvanica* (and perhaps *Rubus* spp.) seeds often germinate in response to a disturbance, but could not isolate a specific environmental component that triggers germination. Increased heat alone may promote germination (Vazquez-Yanes & Orozco-Segovia 1982). Webb (1958) speculated that the increased light beneath gaps may be enough to trigger germination of *Acacia* seeds that otherwise would have remained dormant.

Seedling establishment and recruitment within gaps may be spatially variable (Canham & Marks 1985). Environmental factors such as light, moisture, substrate, and physical disturbance by the falling crown all change systematically across the gap. Many treethrow gaps have distinct zones of bare soil where root/soil masses have been uprooted, regions of decaying wood beneath the bole and crown, and relatively undisturbed, high light areas, all of which create a diversity of germination niches (Anderson & Swift 1983; Cook & Lyons 1983; Putz 1983; Vitousek & Denslow 1986). Fallen tree crowns can dramatically affect suppressed saplings (White *et al.* 1985). In most cases the effect is to physically damage the understorey plants, although this may be offset by increased survivorship for those not injured (Lorimer 1980). Richards & Williamson (1975) reported that mechanical damage by the treefall, coupled with dense vine growth within the

decumbent crown, led to a near absence of one understorey palm species in sections of a gap.

Suppressed saplings that respond to the additional resources in gaps and exhibit increased growth rates are said to be 'released' (White *et al.* 1985; Foster & Reiners 1986). Henry & Swan (1974) defined one criterion for release: an increase of 2.5 times in tree ring widths for at least 4 consecutive years. Release may also take place in neighboring canopy and sub-canopy trees as their branches expand laterally into the gap (Lorimer 1980; Hibbs 1982; Naka 1982; Runkle 1982; Foster & Reiners 1986). Evidence of release is often used to date the formation of the gap (Raup 1941; Henry & Swan 1974; Oliver & Stephens 1977; Barden 1979, 1981; Lorimer 1980; Runkle 1982).

Canopy gaps can also lead to accelerated growth and increased richness in understorey vegetation (Thompson 1980). Monk (1961) reported increased vine and shrub growth beneath gaps, as well as higher densities of dogwood (*Cornus florida*). *Phytolacca americana*, which normally attains heights of several cm beneath dense canopies and never flowers there, grows to nearly two meters and flowers profusely beneath gaps (Monk 1961). Hytteborn *et al.* (1987) noted decreased numbers of bryophytes below gaps (especially large gaps) because of lower humidities and increased desiccation.

### Effects of pit/mound topography on forest ecology

An important implication of uprooting is the exposure of bare, mineral substrate and the possible formation of treethrow pits and mounds (Falinski 1978). This type of soil disturbance (floralturbation; see Johnson *et al.* 1987) can promote increased regeneration because the bare mineral soil provides for additional diversity of germination microsites (Sernander 1936; Hutnik 1952; Cook 1971; Thompson 1980; Beatty 1984; Brokaw 1985b; Beatty & Stone 1986; see also Harper *et al.* 1965). Canopy gaps created by uprooting often have more pioneer species than those

created by bole snap, due simply to the unearthing of mineral soil (Putz *et al.* 1963). Dunn *et al.* (1983) attributed increases in *Betula allegheniensis* seedlings in gaps to their light, wind-blown seeds and to the abundance of exposed mineral soil (see also Hutnik 1952; Bray 1956; Bormann *et al.* 1970; Forcier 1975; Grubb 1977). Hytteborn *et al.* (1987) noted that *Vaccinium* spp. invade gaps via vegetative reproduction, but reproduce primarily by seeds if mineral soil is exposed.

Recently-formed uprooting mounds are favorable germination sites because of lack of competition (both above and below ground), thin litter cover, high porosity and aeration, low bulk density, high summertime soil temperatures, and the incorporation of fresh organic materials (Lutz 1940; Thompson 1980; Burrows 1977). Many mounds contain viable seeds, unearthed during uprooting (Oosting & Humphreys 1940; Thompson 1980; Cook & Lyons 1983). Goder (1961) suggested that mound soils may have higher nutrient concentrations due to in-mixing of subsoil materials. Lutz (1940) found no statistically significant differences, for several nutrient types, between undisturbed soils and those disturbed by uprooting. Vitousek & Denslow (1986) observed lower N, P, and carbon, and higher N mineralization rates and pH in uprooted soils ('root-throw zone' of canopy gaps) than in soils below an undisturbed canopy. Beatty (1984) reported that mound soils were lower in nutrient content, CEC, and organic matter than were soils in treethrow pits. In contrast to recently-uprooted soils, old uprooting mounds may be unfavorable sites for germination because of thick litter layers; in some regions, leachate from the litter cover on older mounds may actually inhibit germination (Putz 1983).

In forests with pit/mound microtopography, it is common to find many trees growing on mounds (Henry & Swan 1974). Collins & Pickett (1982) demonstrated statistically that more trees grew on mounds, and fewer in pits, than would be expected in a random distribution. Lyford & MacLean (1966) observed that, although less total surface area was occupied by mounds than by level areas, 60.4% of all trees in their study

area were located on mounds and only 37.6% were on level areas; the remainder were in pits. Goodlett (1954; Denny & Goodlett 1956) found that, in northern Pennsylvania, trees were most common on the sides, not tops, of mounds and that virtually no trees were growing in pits (see also Lutz 1940; Hutnik 1952; and Dixon & Place (1952). Goder (1961) observed that 83.6 to 100% of seed-bearing hemlock trees occurred on mounds, and suggested that this was due in part to high rates of seedling survival there. Zeide (1981) used *Betula lutea* trees growing on mounds to date the uprooting event because the species quickly colonizes mounds and can endure exposure of its root system as the mound erodes. In some regions, the moist and cool poleward-facing mound slopes are more favorable for germination than undisturbed sites or other mound exposures (Lutz 1940). Koop (1987) provided several examples of vegetative reproduction, wherein decumbent tree trunks had formed adventitious roots after they had fallen across a former treethrow mound.

The normally low rates of establishment in pits is usually ascribed to wet conditions with occasional standing water (and ice), and thick litter accumulations (Hutnik 1952; Goodlett 1954; Hart *et al.* 1962; Lyford & MacLean 1966; Stone 1975; Beatty 1984). Falinski (1978) discussed a type of hydric successional sequence for treethrow pits. Seedlings in pits often must endure repeated frost heave (Stone 1975), dense mycelial mats of saprophytic fungi (Goder 1961), soil compaction and lack of aeration (Cook 1971), such that a complete absence of trees from pits is not uncommon (Denny & Goodlett 1956; Zeide 1981; Collins & Pickett 1982).

In contrast, some plants preferentially grow in pit microsites (Rozmakhov *et al.* 1963). On mounds, large seeds of species such as *Fagus* and *Acer* are easily visible to rodents and birds, or cannot easily lodge in the soil. Other seeds may later be concealed by litter in pits and germinate (Hutnik 1952). Henry & Swan (1974) found that 34% of *Acer rubrum* trees in a New Hampshire forest grew in depressions that comprised only 9% of the surface. In excessively-drained or lithic

soils, pits may be favored for seedling germination and survival because of increased moisture levels (Cook 1971). Finally, Lyford & MacLean (1966) discussed means by which knowledge of favored microsites for tree germination could be used in forest site preparation.

Pit/mound microtopography has a pronounced impact on the distribution of non-woody vegetation as well as trees (Collins *et al.* 1985). In a study of such relationships, Beatty (1984) found that understory herbs often have patchy distributions, closely related to microtopography. Struik & Curtis (1962) found a significant positive association between treethrow mounds and the herb *Hepatica acutiloba*. Thompson (1980) studied the patterns of understory herbs on fallen logs and in treethrow pits, and found that they colonized these sites primarily via vegetative reproduction or animal seed dispersion mechanisms or animals. Monk (1961) ascribed increased moss cover beneath canopy gaps to exposed mineral soil and abundant supplies of decaying wood. Because of the shallow rooting of many understory herbs, their increased growth beneath gaps may be due more to increased throughfall precipitation than to high light intensities (Anderson *et al.* 1969).

Tree uprooting adds woody residues to the forest floor which, in some environments, may persist for a century or more (McFee & Stone 1966). Many plants preferentially establish on rotting tree trunks (Cook 1971; Spurr & Barnes 1980; Thompson 1980; Bratton 1976; Handel 1976, 1978; Putz 1983; Maser & Trappe 1984; Hytteborn *et al.* 1987). Trees that often utilize decumbent trunks as seedbeds include *Picea abies* (Sernander 1936; Hytteborn *et al.* 1987) *Tsuga canadensis*, *Betula lutea* (Curtis 1959; Bormann *et al.* 1970; Forcier 1975), and *Picea sitchensis* (Franklyn & Dyrness 1969). White *et al.* (1985) recorded seedling densities on fallen logs that were 30 times greater than in gaps or beneath the closed canopy. Considering that many trees are already dead prior to fall (Falinski 1978; Cremeans & Kalisz 1988), tree trunks may provide sites for seedling establishment very shortly after fall. Goder (1961) evaluated several substrates typically found on decaying logs for

their potential as *Tsuga* germination and seedling establishment sites. In descending order, he concluded that the most favored sites were: moss mats, moist exposed wood, and bark without moss cover (see also McFee & Stone 1966). Sernander (1936) devised a 'necrotisation scale' of one to six for decumbent trunks, with six being most decayed. He found that *Picea* seedlings were most common on trunks in stages five and six.

### Effects of uprooting on fauna

Although little work has been done on the effects of uprooting on fauna, several studies are summarized here. Olszewski (1968) found that rodent travel routes were significantly affected by decumbent boles. The dominant species (*Apodemus flavicollis*) routinely travelled on tops of the boles, whereas the more subdued *Clethrionomys glareolus* was generally restricted to routes beneath – less convenient for communication but providing faster and improved shelter. In Belgium, mice and moles preferentially burrow and seek shelter in the more porous, drier soils of treethrow mounds, eventually leading to further faunal pedoturbation as foxes later tear apart the mounds in search of the rodents (R. Langohr, pers. comm. 1987). Talbot (1934) noted that many ant nests are located within or near fallen logs; Troedsson & Lyford (1973) observed high numbers of ant nests in treethrow mounds. Logs and uprooting pits are preferred sites of bird and mammal defecation, further underscoring the impact of treefall on seed dispersal (Thompson 1980). Webster (1963) found little change in bird populations before and after a tornado had cleared a canopy gap of approximately 3 ha<sup>2</sup>, but speculated that noticeable changes would be more evident in future years.

### Acknowledgements

We thank S.G. Shetron and J.R. Harman for comments on an early draft of this paper, and four reviewers, whose insight improved the paper's quality.

### References

- Anderson, J.M. & Swift, M.J. 1983. Decomposition in tropical forests. In: Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (eds), *The tropical forest*. pp. 287–309. Blackwell Scientific Publications, Oxford.
- Anderson, R.C., Loucks, O.L. & Swain, A.M. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology* 50: 255–263.
- Barden, L.S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. *Oecologia* 44: 141–142.
- Barden, L.S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. *Oikos* 37: 205–209.
- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65: 1406–1419.
- Beatty, S.W. & Stone, E.L. 1986. The variety of soil microsites created by tree falls. *Can. J. For. Res.* 16: 539–548.
- Bongers, F., Popma, J., Meave del Castillo, J. & Carabias, J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55–80.
- Bormann, F.H. & Likens, G.E. 1979a. Catastrophic disturbance and the steady state in northern hardwood forests. *Amer. Sci.* 67: 660–669.
- Bormann, F.H. & Likens, G.E. 1979b. Pattern and process in a forested ecosystem. Springer-Verlag, New York.
- Bormann, F.H., Siccama, T.G., Likens, G.E. & Whittaker, R.H. 1970. The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. *Ecol. Mon.* 40: 373–388.
- Bratton, S.P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. *Am. Nat.* 110: 679–693.
- Bray, J.R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology* 37: 598–600.
- Brewer, R. & Merritt, P.G. 1978. Wind throw and tree replacement in a climax beech-maple forest. *Oikos* 30: 149–152.
- Brokaw, N.V.L. 1985a. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- Brokaw, N.V.L. 1985b. Treefalls, regrowth, and community structure in tropical forests. In: Pickett, S.T.A. & White, P.S. (eds), *The ecology of natural disturbance and patch dynamics*, pp. 53–69. Academic Press, New York.
- Burrows, C.J. 1977. Forest vegetation. In: Burrows, C.J. (ed.), *Cass: history and science in the Cass District, Canterbury, New Zealand*, pp. 233–257. Dept. of Botany, Univ. of Canterbury.
- Canham, C.D. & Marks, P.L. 1985. The response of woody plants to disturbance: Patterns of establishment and growth. In: Pickett, S.T.A. & White, P.S. (eds), *The ecology of natural disturbance and patch dynamics*, pp. 197–216. Academic Press, New York.



- Chazdon, R.L. & Fletcher, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *J. Ecol.* 72: 553–564.
- Clements, F.E. 1936. Nature and structure of the climax. *J. Ecol.* 24: 252–284.
- Cline, A.C. & Spurr, S.H. 1942. The virgin upland forest of central New England. *Harvard For. Bull.* 21.
- Collins, B.S. & Pickett, S.T.A. 1982. Vegetation composition and relation to environment in an Allegheny hardwoods forest. *Am. Midl. Nat.* 108: 117–123.
- Collins, B.S., Dunne, K.P. & Pickett, S.T.A. 1985. Responses of forest herbs to canopy gaps. In: Pickett, S.T.A. & White, P.S. (eds), *The ecology of natural disturbance and patch dynamics*, pp. 217–234. Academic Press, New York.
- Cook, B.D. 1971. Tree-age distributions in a northern hardwood forest. M.Sc. Thesis, McGill Univ., Montreal.
- Cook, R.E. & Lyons, E.E. 1983. The biology of *Viola fimbriatula* in a natural disturbance. *Ecology* 64: 654–660.
- Cooper, W.S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. I. *Bot. Gaz.* 55: 1–44.
- Cremeans, D.W. & Kalisz, P.J. 1988. Distribution and characteristics of windthrow microtopography on the Cumberland Plateau of Kentucky. *Soil Sci. Soc. Am. J.* 52: 816–821.
- Curtis, J.T. 1959. *The vegetation of Wisconsin*. Univ. of Wisconsin Press, Madison.
- Daubenmire, R. 1968. *Plant communities: A textbook of plant synecology*. Harper and Row, New York.
- Denny, C.S. & Goodlett, J.C. 1956. Microrelief resulting from fallen trees. In: *Surficial geology and geomorphology of Potter County, Pennsylvania*. USGS Prof. Paper 288: 59–66.
- Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18–21.
- Dix, R.L. & Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. *Can. J. Bot.* 49: 657–676.
- Dixon, A.C. & Place, I.C.M. 1952. Influence of microtopography on the survival of spruce and fir reproduction. *Silvic. Leaflet 68*, Forestry Branch, Can. Dept. of Resources and Development.
- Douglas, J.E. 1967. Effects of species and arrangement of forests on evapotranspiration. In: Sopper, W.E. & Lull, H.W. (eds), *Proceedings of the International Symposium on Forest Hydrology*, pp. 451–461. Pergamon, New York.
- Drury, W.H. & Nisbet, I.C.T. 1973. Succession. *J. Arnold Arbor.* 54: 331–368.
- Dunn, C.P., Guntenspergen, G.R. & Dorney, J.R. 1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. *Can. J. Bot.* 61: 211–217.
- Faliński, J.B. 1978. Uprooted trees, their distribution and influence on the primeval forest biotope. *Vegetatio* 38: 175–183.
- Forcier, L.K. 1975. Reproductive strategies and the co-occurrence of climax tree species. *Science* 189: 808–809.
- Foster, J.R. & Reiners, W.A. 1983. Vegetation patterns in a virgin subalpine forest at Crawford Notch, White Mountains, New Hampshire. *Bull. Torrey Bot. Club* 110: 141–153.
- Foster, J.R. & Reiners, W.A. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio* 68: 109–114.
- Foster, R.B. 1977. *Tachigalia versicolor* is a suicidal neotropical tree. *Nature* 268: 624–626.
- Fox, J.F. 1977. Alternation and coexistence of tree species. *Am. Nat.* 111: 69–89.
- Franklyn, J.F. & Dyrness, C.T. 1969. *Vegetation of Oregon and Washington* USDA For. Serv. Res. Paper PNW-80.
- Frissell Jr, S.S. 1973. The importance of fire as a natural ecologic factor in Itasca State Park, Minnesota. *Quat. Res.* 3: 397–407.
- Godet, H.A. 1961. Hemlock reproduction and survival on its border in Wisconsin. *Trans. Wisc. Acad. Sci. Arts Lett.* 50: 175–182.
- Goodlett, J.C. 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. *Harvard For. Bull.* 25: 1–93.
- Grasveld, P. & Imming, J. 1987. *Natuurlijke ontwikkelingen op Drentse stormvlaktes*. Rept. Res. Inst. Nature Mgmt., Leersum.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* 52: 107–145.
- Handel, S.N. 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae), a new North American Myrmecochore. *Am. J. Bot.* 63: 1071–1079.
- Handel, S.N. 1978. The competitive relationship of three woodland sedges and its bearing on the evolution of ant-dispersal of *Carex pedunculata*. *Evolution* 32: 151–163.
- Harcombe, P.A. & Marks, P.L. 1978. Tree diameter distributions and replacement processes in southeast Texas forests. *For. Sci.* 24: 153–166.
- Harcombe, P.A. & Marks, P.L. 1983. Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). *Oecologia* 57: 49–54.
- Harper, J.L., Williams, J.T., & Sagar, G.R. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *J. Ecol.* 53: 273–286.
- Hart, G., Leonard, R.E. & Pierce, R.S. 1962. Leaf fall, humus depth, and soil frost in a northern hardwood forest. *USDA For. Serv. Res. Note NE-131*.
- Hartshorn, G.S. 1980. Neotropical forest dynamics. *Biotropica* 12 (Suppl.): 23–30.
- Henry, J.D. & Swan, J.M.A. 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. 1979. The age structure of a striped maple population. *Can. J. For. Res.* 9: 504–508.
- Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. *Can. J. For. Res.* 12: 522–527.
- Horn, H.S. 1975. Forest succession. *Sci. Am.* 232(5): 90–98.

- Hutchinson, G.E. 1951. Copepodology for the ornithologist. *Ecology* 32: 571–577.
- Hutnik, R.J. 1952. Reproduction on windfalls in a northern hardwood stand. *J. For.* 50: 693–694.
- Hytteborn, H. & Packham, J.R. 1985. Left to nature: Forest structure and regeneration in Fiby Urskog, Central Sweden. *Arboricult. J.* 9: 1–11.
- Hytteborn, H., Packham, J.R. & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of northern Sweden. *Vegetatio* 72: 3–19.
- Iwaki, H. & Totsuka, T. 1959. Ecological and physiological studies on the vegetation of Mt. Shimagare. II. On the crescent-shaped 'dead trees strips' in the Yatsugatake and the Chichibu Mountains. *Bot. Mag.* 72: 255–260.
- Jane, G.T. 1986. Wind damage as an ecological process in mountain beech forests of Canterbury, New Zealand. *N.Z.J. Ecol.* 9: 25–39.
- Johnson, D.L., Watson-Stegner, D., Johnson, D.N. & Schaetzl, R.J. 1987. Proisotropic and proanisotropic processes of pedoturbation. *Soil Sci.* 143: 278–292.
- Jones, E.W. 1945. The structure and reproduction of the virgin forest in the North Temperate Zone. *New Phytol.* 44: 130–148.
- Koop, H. 1987. Vegetative reproduction of trees in some European natural forests. *Vegetatio* 72: 103–110.
- Leemans, R. & Prentice, I.C. 1987. Description and simulation of tree-layer composition and size distribution in a primaeval *Picea-Pinus* forest. *Vegetatio* 69: 147–156.
- Lorimer, C.G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* 58: 139–148.
- Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61: 1169–1184.
- Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. *Am. Zool.* 10: 17–25.
- Lutz, H.J. 1940. Disturbance of forest soil resulting from the uprooting of trees. *Yale School of For. Bull.* 45.
- Lyford, W.H. & MacLean, D.W. 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard For. Paper* 15.
- March, W.J. & Skeen, J.N. 1976. Global radiation beneath the canopy and in a clearing of a suburban hardwood forest. *Agric. Metr.* 16: 321–327.
- Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Mon.* 44: 73–88.
- Maser, C. & Trappe, J.M. 1984. The seen and unseen world of the fallen tree. *USDA For. Service, Gen. Tech. Rept. PNW-164.*
- McFee, W.W. & Stone, E.L. 1966. The persistence of decaying wood in the humus layers of northern forests. *Soil Sci. Soc. Am. Proc.* 30: 513–516.
- McIntosh, R.P. 1961. Windfall in forest ecology. *Ecology* 42: 834.
- Minckler, L.S. & Woerheide, J.D. 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. *J. For.* 63: 103–107.
- Minckler, L.S., Woerheide, J.D. & Schlesinger, R.S. 1973. Light, soil moisture, and tree reproduction in hardwood forest openings. *USDA Forest Serv. Res. Paper NC-89.*
- Mladenoff, D.J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* 68: 1171–1180.
- Monk, C.D. 1961. The vegetation of the William L. Hutcheson Memorial Forest, New Jersey. *Bull. Torrey Bot. Club* 88: 156–166.
- Naka, K. 1982. Community dynamics of evergreen broadleaf forests in southwestern Japan. I. Wind damaged trees and canopy gaps in an evergreen oak forest. *Bot. Mag.* 95: 385–399.
- Nakashizuka, T. 1987. Regeneration dynamics of beach forests in Japan. *Vegetatio* 65: 169–175.
- Nichols, G.E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. *Ecology* 16: 403–422.
- Oliver, C.D. & Stephens, E.P. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology* 58: 562–572.
- Olszewski, J.L. 1968. Role of uprooted trees in the movements of rodents in forests. *Oikos* 19: 99–104.
- Oosting, H.J. & Humphreys, M.E. 1940. Buried viable seeds in a successional series of old field and forest soils. *Bull. Torrey Bot. Club.* 67: 253–273.
- Pickett, S.T.A. 1980. Non-equilibrium existence of plants. *Bull. Torrey Bot. Club* 107: 238–248.
- Pickett, S.T.A. & White, P.S. (eds) *The ecology of natural disturbance and patch dynamics.* Academic Press, New York.
- Pritchett, W.L. 1979. *Properties and management of forest soils.* Wiley, New York.
- Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64: 1069–1074.
- Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., & Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011–1020.
- Raup, H.M. 1941. An old forest in Stonington, Connecticut. *Rhodora* 43: 67–71.
- Raup, H.M. 1957. Vegetational adjustment to the instability of site. *Proc. Papers Union Conserv. Nature Nat. Resour.* 36–48.
- Raup, H.M. 1964. Some problems in ecological theory and their relation to conservation. *J. Ecol.* 52: 19–28.
- Reiners, W.A. & Lang, G.E. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. *Ecology* 60: 403–417.
- Richards, P.W. 1955. The secondary succession in the tropical rain forest. *Sci. Progr.* 43: 45–57.
- Richards, P. & Williamson, G.B. 1975. Treefalls and patterns

- of understory species in a wet lowland tropical forest. *Ecology* 56: 1226–1229.
- Rozmakhov, I.G., Serova, P.P. & Yurkina, S.I. 1963. Effect of forests on microcomplexity of soils. *Sov. Soil Sci.* 1131–1136.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041–1051.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of North America. *Ecology* 63: 1533–1556.
- Runkle, J.R. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarctic Ecol.* 7: 157–164.
- Runkle, J.R. 1985a. Comparison of methods for determining fraction of land area in treefall gaps. *Forest Sci.* 31: 15–19.
- Runkle, J.R. 1985b. Disturbance regimes in temperate forests. In: Pickett, S.T.A. & White, P.S. (eds), *The ecology of natural disturbance and patch dynamics*, pp. 17–33. Academic Press, New York.
- Schaetzl, R.J., Johnson, D.L., Burns, S.F. & Small, T.W. 1989. Tree uprooting: review of terminology, process, and environmental implications. *Can. J. For. Res.* 18.
- Sernander, R. 1936. Granskär och Fiby Urskog. En studie över strömluckornas och marbuskarnas betydelse i den svenska granskogens regeneration. *Acta Phytogeog. Suec.* 8: 1–232.
- Skeen, J.N. 1976. Regeneration and survival of woody species in a naturally-created forest opening. *Bull. Torrey Bot. Club* 103: 259–265.
- Sprugel, D.G. 1976. Dynamic structure of wave-generated *Abies balsamea* forests in the north-eastern United States. *J. Ecol.* 64: 889–911.
- Spurr, S.H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* 37: 443–451.
- Spurr, S.H. & Barnes, B.V. 1980. *Forest ecology*. 3rd ed. Wiley, New York.
- Stearns, F.W. 1949. Ninety years of change in a northern hardwood forest in Wisconsin. *Ecology* 30: 350–58.
- Stoeckeler, J.H. & Arbogast Jr, C. 1955. Forest management lessons from a 1949 windstorm in northern Wisconsin and upper Michigan. *USDA For. Serv. Exp. St. Pap.* LS-34.
- Stone, E.L. 1975. Windthrow influences on spatial heterogeneity in a forest soil. *Eidgen. Anstalt Forstl. Versuch Swes. Mitt.* 51: 77–87.
- Strong, D.R. 1977. Epiphyte loads, tree falls, and perennial forest disruption: A mechanism for maintaining higher tree species richness in the tropics without animals. *J. Biogeog.* 4: 215–218.
- Struik, G.J. & Curtis, J.T. 1962. Herb distribution in an *Acer saccharu* forest. *Am. Midl. Nat.* 68: 285–296.
- Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.
- Talbot, M. 1934. Distribution of ant species in the Chicago region with reference to ecological factors and physiological tolerances. *Ecology* 15: 416–439.
- Thompson, J.N. 1980. Treefalls and colonization patterns of temperate forest herbs. *Am. Midl. Nat.* 104: 176–184.
- Trimble Jr, G.R. & Tryon, E.H. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. *J. For.* 64: 104–108.
- Troedsson, T. & Lyford, W.H. 1973. Biological disturbance and small-scale spatial variation in a forested soil near Garpenburg, Sweden. *Stud. For. Suecica* 109.
- Vazquez-Yanes, C. & Orozco-Segovia, A. 1982. Seed germination of a tropical rain forest pioneer tree *Heliconia donnell-smithii* in response to diurnal fluctuations of temperature. *Physiologia Plantarum* 56: 295–298.
- Veblen, T.T. 1985. Stand dynamics in Chilean *Nothofagus* forests. In: Pickett, S.T.A. & White, P.S. (eds), *The ecology of natural disturbance and patch dynamics*, pp. 35–51. Academic Press, New York.
- Veblen, T.T. & Ashton, D.H. 1978. Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio* 36: 149–167.
- Vitousek, P.M. & Denslow, J.S. 1986. Nitrogen and phosphorous availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.* 74: 1167–1178.
- Wardle, J. 1970. The ecology of *Nothofagus solandri*: IV. Growth and general discussion of parts I to IV. *New Z. J. Bot.* 4: 609–646.
- Watt, A.S. 1925. On the ecology of British beechwoods with special reference to their regeneration. Part II. The development and structure of beech communities on the Sussex Downs. *J. Ecol.* 35: 1–22.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1–22.
- Webb, L.J. 1958. Cyclones as an ecological factor in tropical lowland rainforest, North Queensland. *Aust. J. Bot.* 6: 220–228.
- Webb, L.J., Tracey, J.G. & Williams, W.T. 1972. Regeneration and pattern in the subtropical rainforest. *J. Ecol.* 60: 675–695.
- Webster, J.D. 1963. Tornado-disturbed beech-maple forest. *Audubon Field Notes* 17: 496–497.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45: 229–299.
- White, P.S., MacKenzie, M.D. & Busing, R.T. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Can. J. For. Res.* 15: 233–240.
- White, P.S. & Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: An introduction. In: Pickett, S.T.A. & White, P.S. (eds), *The ecology of natural disturbance and patch dynamics*, pp. 3–13. Academic Press, New York.
- Whitney, G.G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. *Ecology* 67: 1548–1559.
- Whittaker, R.H. 1975. *Communities and ecosystems*. 2nd ed., MacMillan, N.Y.
- Williamson, G.B. 1975. Pattern and seral composition in an

- old-growth beech-maple forest. *Ecology* 56: 727–731.
- Woods, F.W. & Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smokey Mountains National Park. *Ecology* 40: 349–361.
- Wright, H.E. 1974. Landscape development, forest fires, and wilderness management. *Science* 186: 487–495.
- Wyatt-Smith, J. 1954. Storm forest in Kelantan. *Malay. For.* 17: 5–11.
- Zeide, B. 1981. Method of mound dating. *For. Sci.* 27: 39–41.