



Boreal forests (dark green in map above) span northern North America (and similar forests occur across Eurasia). In North America, upland boreal forest canopies are generally dominated by mixtures of aspen, jack pine (or lodgepole pine in the west), spruces, and balsam fir. They are fire-driven systems; fires occur frequently during hot dry summers. Cool climates slow decay, and debris builds up on forest floors. Conifer wood and needles are resinous and burn well. Even forest structure can promote fire; note persistent dead branches in red spruce forest at left; these can act as ‘fire ladders’ increasing the chance of fires climbing into the forest canopy (‘crowning’) and spreading. Fires can cover vast areas and largely eliminate tree cover.



In ecological terms, fire is seen as a *disturbance*; while appearing destructive, all of the species native to this system have *adaptations* allowing them to persist in the face of fire. Ecologically, it's most informative to think of fires (and disturbances in general) as changing environment and resource regime. While some resources are likely to be lost or reduced (for example, nitrogen in organic forms is lost to the atmosphere as biomass is burned), some important resources are likely to become *more* available. LIGHT – typically the most limiting resource in closed forests, is immediately abundant. Following fire, *water* can be more available to plants because mature trees are not extracting it from the soil and 'transpiring' it as vapor. Some mineral nutrients (Ca, P, K, Ca), previously tied up in wood, as ash is deposited on forest floor, become available for plant growth. Soils are typically warmer, fostering plant growth.



Immediately following fire, burned areas typically experience lush growth of species not evident at all in the pre-fire forest. These are typically species intolerant of shade (poor competitors for light). They include some annual or short-lived species whose seeds are dispersed widely and abundantly and *colonize* following fire; fireweed – *Epilobium* sp, at left – is such a species. Others, like blueberries (*Vaccinium* sp, right), germinate from buried seed that may remain viable in the soil for years or decades (constituting what's known as a 'soil seed bank'; germination can be triggered by both increased soil temperature and by increased concentrations of water or mineral nutrients. These species typically grow rapidly, flower and fruit and fade away within a few years as trees re-establish a canopy and light competition dominates the forest understory.



Tree species also show diverse adaptations allowing them to recolonize burned areas. Jack pine (*Pinus banksiana*) has cones that remain closed on the tree for many years; the seeds included in the cones can remain viable for years, constituting a kind of aerial seed bank. When fires heat the cones, the resins sealing them closed melt, the cone scales separate, and seeds are shed on the recently burned forest floor.

The jack pine stand in lower right photo was burned about a decade prior to the photo. Jack pine was dominant prior to the fire, and a solid stand of jack pine seedlings has established since the fire. In a few more years, the understory will be fully shaded again.



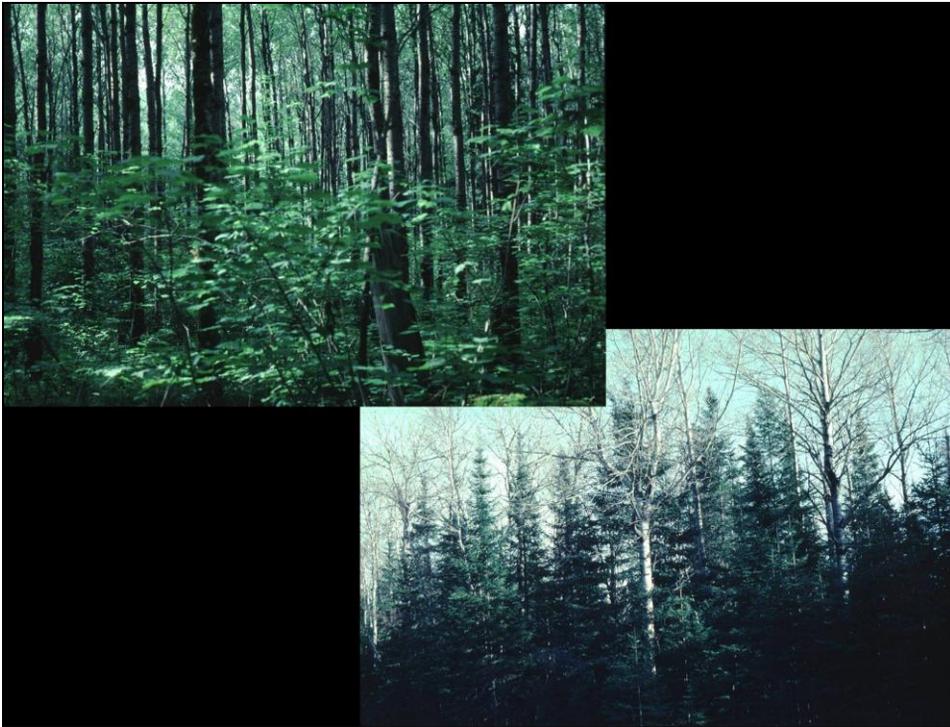
But jack pine can't tolerate low light levels. As the pine stand becomes closed, no further jack pine seedlings can persist. The canopy here is a post-fire cohort of jack pine – all about the same age. Such *even-aged* stands are typical immediately after large disturbances like fire. The young trees in the understory are spruce (*Picea* spp) and balsam fir (*Abies balsamea*); these species are *shade-tolerant* – capable of surviving long periods in very low light. They also cast heavier shade than jack pine.

Eventually, as jack pine canopy trees die (they typically live little more than a century), they'll be replaced by these shade-tolerant species. At lower right, scattered dead and dying jack pine trees (with more irregular canopy shape) are still present in a stand increasingly dominated by spruce (balsam fir is more typically shorter, and a 'subcanopy' species).



Aspens (*Populus* sp) do not have persistent seed-banks; their light, wind-borne seeds are short-lived. They can establish in a burned area if seeds happen to be available. However, they also re-establish dominance in burned aspen forests because their root systems are not killed by fire and generate dense stands of *root-sprouts*. (Many sprouts may originate from a single root system, constituting, in effect, a clonal patch. These may expand over several fire cycles, so that a single genetic individual can spread over acres).

As they grow, aspen sprout cohorts compete for light and most succumb. This is sometimes referred to as the 'self-thinning' stage of stand develop.



Like jack pine, aspens are not at all tolerant of low light. Seedlings and sprouts do not survive under shade, so more mature aspen stands show no regeneration.

Again after a century or so, aspen trees begin to die of old age, and are replaced by shade-tolerant species (here, again, spruce).



The dynamics of changes in community composition and structure following disturbance are called **SUCCESSION**; this term was first used in this context by Henry D. Thoreau about 150 years ago, and successional processes have been a central study in community ecology for generations. There has been much debate about how *predictable and deterministic* succession is. For now, recognize that several factors are likely to be important in shaping the course of succession: 1) the nature of the disturbance and how it affects resource availability, 2) the availability of colonists (seeds, dispersing individuals, etc) that can live in the new environment, 3) how the first colonists *change* the environment by altering resource availability, and 4) how these changes and arrival of new species shape the competitive balance among species. In general, over 'successional time' (time since initiation of successional sequence), competition both within and between species tends to become more intense, and, in forest ecosystems, light typically becomes limiting. Communities of other organisms (animals, fungi, etc.) also undergo predictable successional dynamics, but these are mostly driven by changes in the nature of the plant community.



Other species can have other modes of coping with fire. Red pine (*Pinus resinosa*) is distributed in southern portions of the boreal forest and somewhat southward. It is typical of drier sites where it establishes a fairly open canopy, often with an understory of low shrubs, grasses, and herbs. Red pine needles accumulate in thick, persistent layers. These conditions favor frequent fire, but, because red pine bark is highly fire resistant, and frequent fires keep a tall understory from developing (to carry fire to the pine crowns), mature trees generally survive fires. However, fires occasionally burn through the bark at the base of trees, leaving scars that can be used to date fires – upper left.



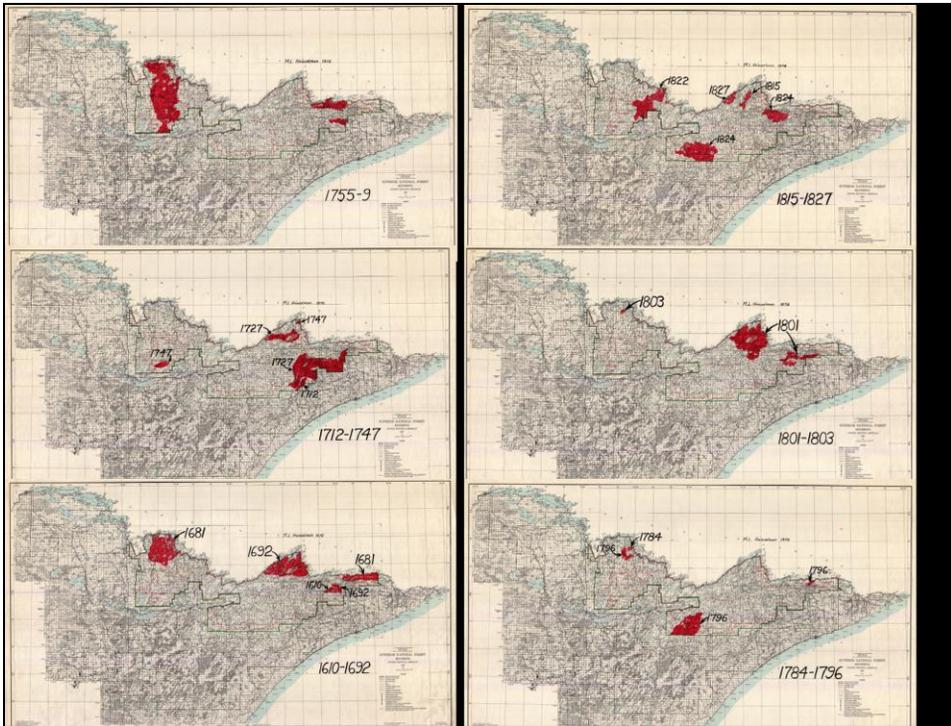
Red pine scars can often be precisely dated. This section of a burned stump shows a series of fire scars; these can be recognized by interruptions in the ring sequence by a charred layer (where the growing/live outer layers of the trunk were killed), followed by progressive 'healing' from the edge of the scar as new wood is formed and each ring progressively expands over the damaged area. This is particularly apparent in relation to the 1764 fire scar on the section at lower left. This tree died over 100 years before the stump section was collected (red pine wood is extremely resistant to rot), however, it was possible to 'cross-date' fire sequences with scars found on more recent and living trees so that precise dates could be assigned to each fire scar and to the tree's initial 'birth'. (The art and science of reconstructing growth sequences and environmental information from tree rings is called 'dendrochronology'.)



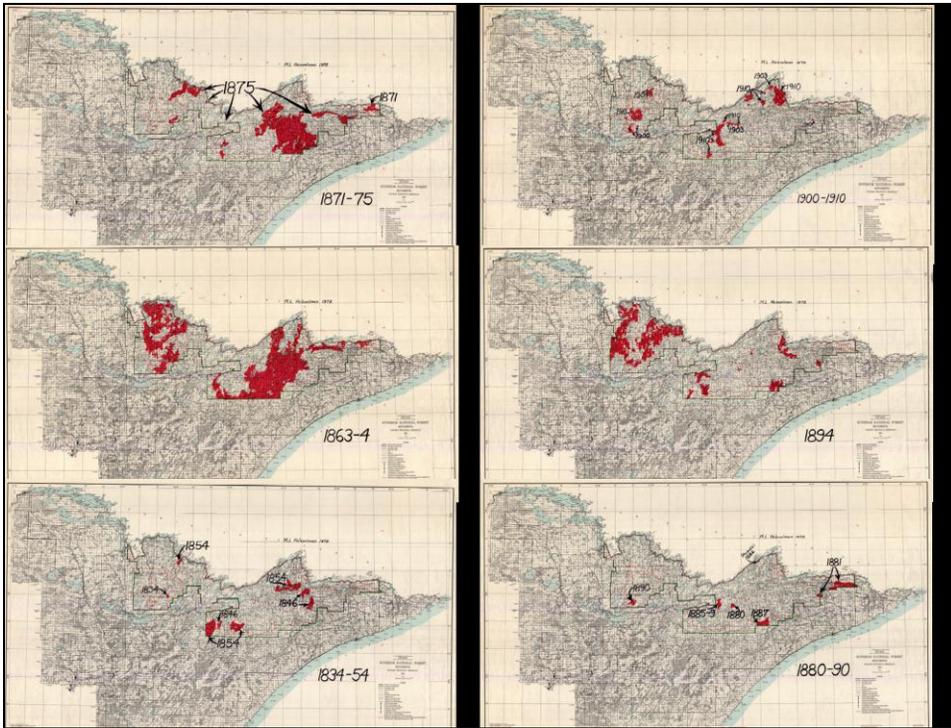
Fire boundaries are often sharply visible on the landscape, recognizable by contrasting age, size, and composition of stands. Forests in the foreground are young (note the fine texture of the canopy indicating small trees) and aspen dominated...



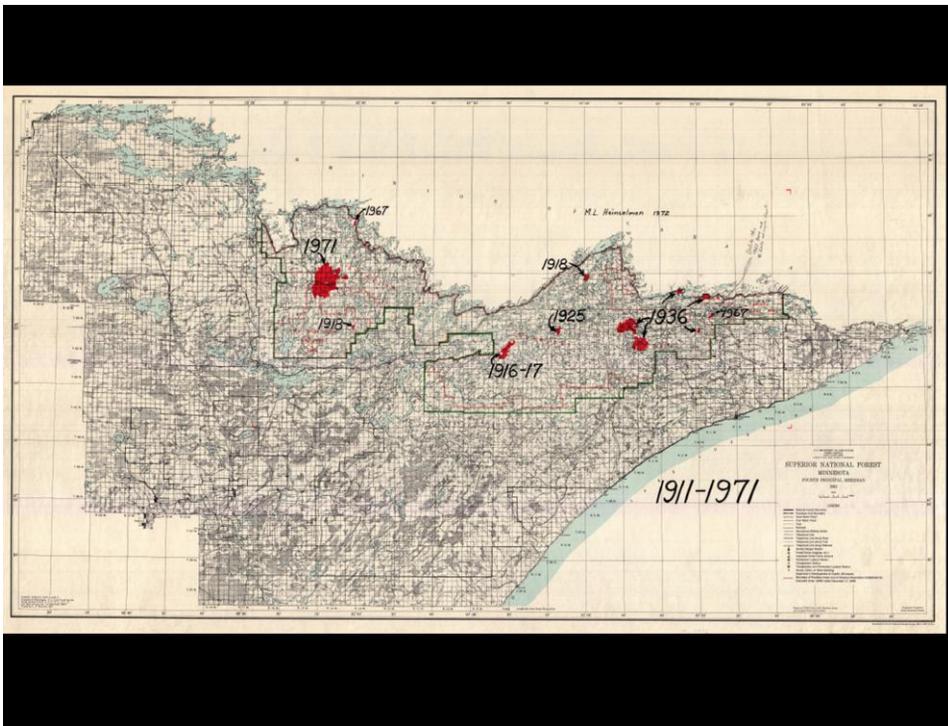
The Boundary Waters Canoe Area of northern Minnesota, at the southern edge of the boreal forests, includes about a million acres of never-logged forests. Many lakes and wetlands provide fire-breaks, tending to define the edges of burns. Fire histories can be reconstructed by aging trees like jack pine and aspen (which almost always originate following a fire), and dating fire scars on other species of trees.



Miron (Bud) Heinselman, a research with the Forest Service and the University of Minnesota, spent years intensively mapping fire history for the BWCA. Since fires rarely kill all trees in the areas they burn, he could often detect several fires for a given area. However, as fires burn over previously burned and regenerated areas, older fires eventually become undetectable. The oldest fire Heinselman could date (from fire scars on red pines) was in 1610 (east edge of lower left map); that fire may have been much more extensive, since surrounding areas have burned several times subsequently. Generally, both fire extent and intervals between large fires vary substantially.



Note the extremely extensive fires of 1863-64; these years are known from historical records to have been unusually hot and dry.

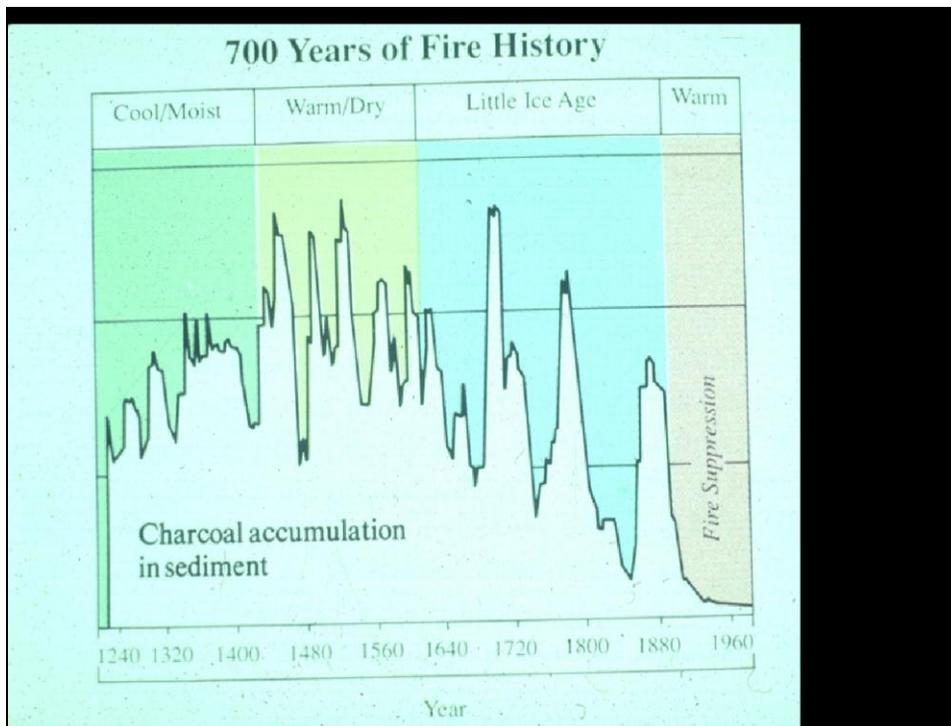


Since 1900, fires have been actively suppressed by forest managers, and none have been extensive. OVERALL (prior to 1900), Heinselman estimates that a given site was likely to have burned, on average, about every 120 years.

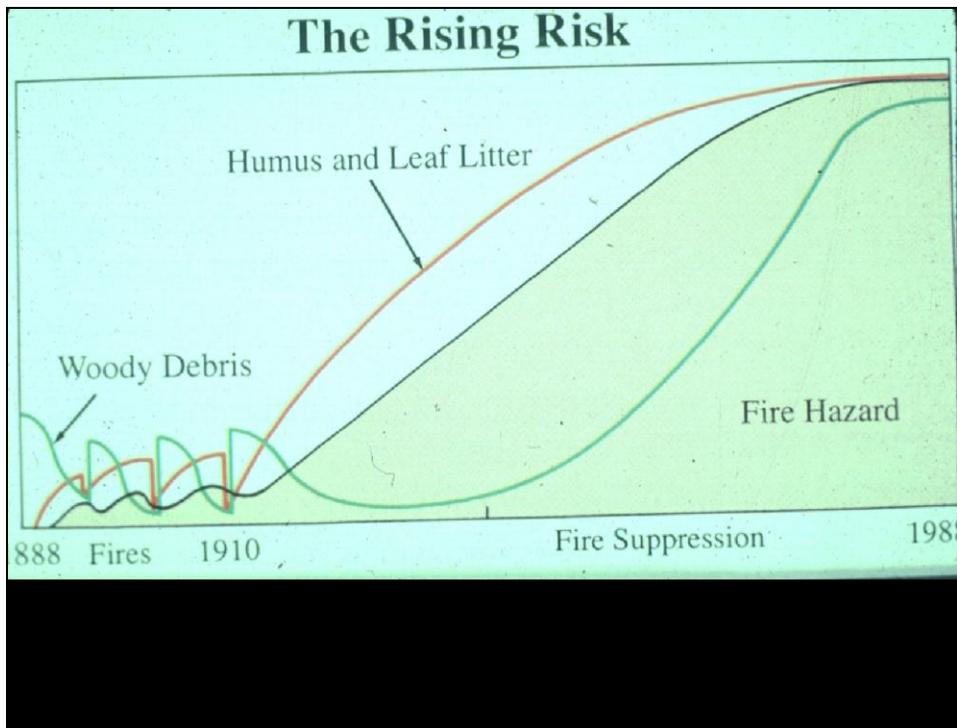
Heinselman's work offered a new perspective on community and landscape pattern. Previously, ecologists tended to focus on particular sites or stands and ask whether communities were stable, unstable, changing predictably, etc. Heinselman made it obvious that, while individual *stands* in the boreal region are rarely stable or 'equilibrial' (while spruce-fir forests might, in principle, be relatively stable, since these species can reproduce in their own shade, stands are rarely fire-free long enough to reach this stage), it is possible to look at the *whole landscape*, at a scale where many different fire histories are incorporated, and see a sort of stability at that scale. While different '*patches*' are constantly changing (since there was likely a fire less than 150 years ago), a landscape including many patches might include patches of all ages and types so that, while they're all changing, at any given time there'll be some proportion of patches at all successional stages. This is sometimes referred to as the 'shifting mosaic' model of landscape dynamics. If disturbance occurs at a roughly constant rate and scale, after a time, the shifting mosaic can be 'dynamically stable'.



However, some sites, on downwind sides of large lakes or on islands, burn much less frequently, while other areas burned more frequently.



Charcoal accumulates in lake sediments just like pollen and can be used to reconstruct approximate fire frequency and intensity for areas around lakes. Here is a diagram of charcoal abundance for a lake near the BWCA. It suggests that Heinselman's maps, because they cover a relatively cool, moist period called the 'Little Ice Age', may not represent fire cycles for other conditions. During the Little Ice Age, fires around this lake tended to be relatively well-separated – but to show dramatic peaks (perhaps corresponding to dry periods when accumulated fuel loads would burn all at once. In the previous drier, warmer period, the 'background' frequency of fires was higher.



Fire frequencies are a function of how fuel builds up, increasing fire hazard, and likelihood of ignition. If fires are suppressed, fires can become both more likely and, once ignited, far more intense.



Boreal forests are typically harvested through clear-cutting. In some respects, clear-cutting resembles fire as a disturbance; in other respects it is different. However, a more 'selective' mode of cutting, or cutting in small patches, would be even more unlike natural fire disturbances. Forest management is, increasingly, designed to mimic natural disturbance dynamics that have produced 'desirable' forest compositions.



Fire is important in many ecosystems. Here, longleaf pine forests of the southeastern U.S. are savanna-like. They're maintained by very frequent fires (they burn almost every year) maintaining an open, grassy understory, while pines more than 2-3 m tall survive the rapid passage of relatively cool ground fires (their bark is fire-resistant). Understory plants rapidly resprout from roots or rhizomes that survive fire (lower left: grass resprouting). The pines can spend many years as very short seedlings with little above-ground growth (upper right); in this 'grass stage' of growth, fires may singe the needles, but won't kill the stem tip that remains at ground level. Meanwhile, seedlings develop a large taproot, storing accumulated reserves. At some point, these reserves are mobilized to permit very rapid upward growth and within 2-3 years (lower right, a seedling after the first year of this growth), the seedling can reach heights of >2 m and, with luck, be tall enough to escape being killed by fire.



Pitch pine (*Pinus rigida*) may lose living foliage to fires in the Pine Barrens of New Jersey, but dormant buds buried beneath the bark can subsequently sprout to produce new twigs (called 'epicormic shoots') and foliage (lower right). Several oak species also live in these 'barrens' communities. Fires kill above-ground portions of the oaks, but massive root masses (called 'root stools' – left) give rise to new sprouts following fire. Fires can be quite frequent, so oak-shoots may rarely get to be more than a few years old, but the root structures may be decades or centuries old.



Other types of disturbance create forest openings at different scales in time and space, liberating resources from competition in different patterns. Beaver activity creates canopy openings both by felling of trees and by flooding (note dead trees above).

Older beaver ponds (lower right) gradually fill with sediments, terrestrial vegetation re-establishing once beavers cease to maintain the pond. Photo above shows two beaver ponds in different stages of succession. While the scales are different, different species are involved, and the nature of the interactions among species are different, this pattern can be compared to the 'shifting mosaic' of successional patches in the BWCA forests. Not all parts of the landscape are subject to beaver disturbance, of course, so this patchwork or mosaic applies only to portions, but most waterways hosted beaver populations in the past.



Upland forests of northeastern North America – the ‘northern hardwood’ forests from the Great Lakes to New England -- probably experienced disturbance regimes at multiple spatial and temporal scales. Mortality of scattered individual canopy trees due to blow-down, disease, or insect attack is constant. The small canopy gaps created by such mortality increase light availability somewhat, but probably don’t make much difference with respect to other resources. They are generally inadequate for ‘shade-intolerant’ species to establish with any frequency. Instead, they are typically filled, in older forests, by ‘release’ (rapid growth) of pre-existing seedlings and saplings of shade-tolerant species that have been ‘suppressed’ by low light levels in the understory. Highly tolerant species like hemlock and beech can persist as very slow-growing suppressed seedlings for decades (foresters refer to these suppressed individuals as ‘advance regeneration’). Less tolerant species would not survive. This cycle is often referred to as ‘gap-phase dynamics’, and it can lead to long-term persistence of shade-tolerant species replacing themselves – but it can also be thought of as a ‘shifting mosaic’ successional landscape, where the ‘patches’ are the size of individual trees (or perhaps two or three trees), and the ‘return time’ for disturbance is simply the tree life-time. Single-tree ‘gap-phase’ dynamics are probably insufficient to maintain coexistence of any but the most shade-tolerant species over the long term.

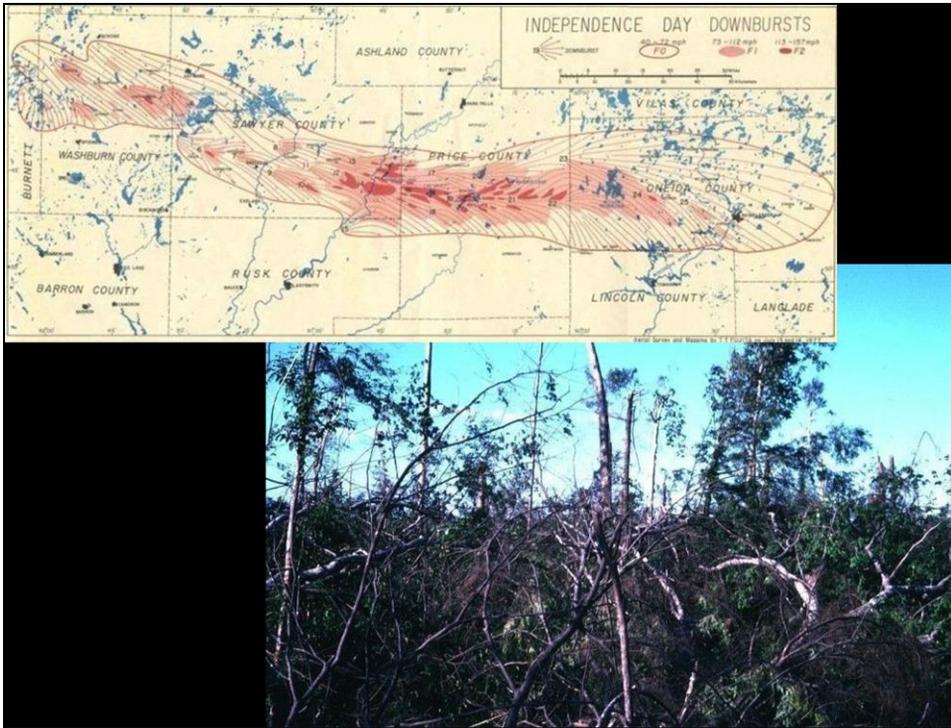


But these forests also experience more extensive wind-disturbance. The left photo is a tornado track in upstate New York: the blow-down is about 40 m across and perhaps 100 m long. Upper right photo is a blowdown created by an intense local thunderstorm in northern Michigan (aerial view below); this storm produced 'clumped' mortality, with patches of a few to dozens of trees blowing down together, producing gaps about 30 m across. These disturbances increase light availability dramatically; they probably also influence availability of soil moisture (because large trees are not extracting and transpiring large quantities of moisture) and mineral nutrients (as dead wood and roots decay, soil is heated increasing rates of decay and chemical transformations).

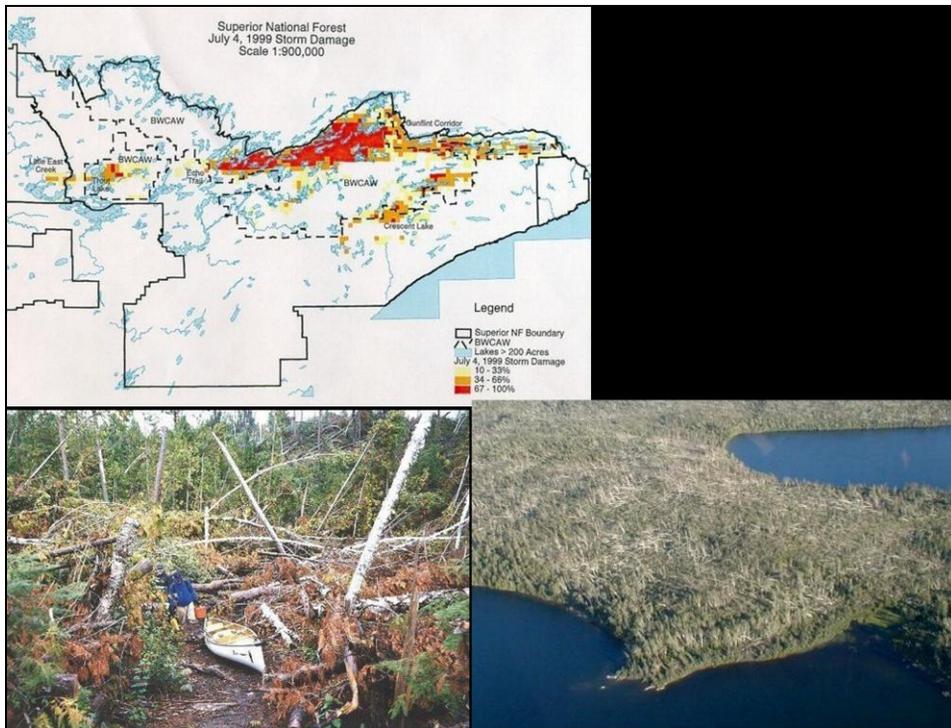


These larger blow-downs release large patches of suppressed seedlings of tolerant species (like sugar maple, upper right), but elevated light levels (and, probably, longer periods before canopy is re-established) also make establishment of less tolerant species more likely. Tip-up mounds and decaying stumps can also provide special ‘microsite’ conditions – little competition, protection from competition, etc. -- that can be exploited by specialized species. Some of these species germinate from long-dormant seeds in the soil ‘seed bank’ (for example, some cherries and elderberry – lower left, and blackberries). Yellow birch is also a specialist “mound germinator” (upper left), and its persistence in mature forests may depend substantially on this type of disturbance.

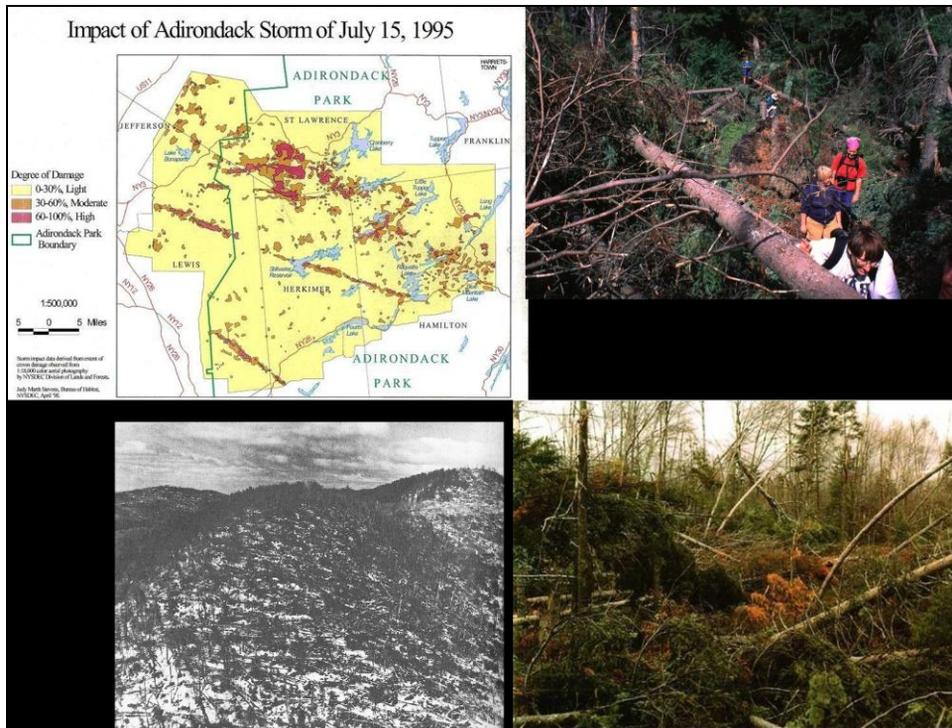
Again, landscapes subject to this sort of process may be considered a mosaic of patches in various stages of ‘recovery’ from disturbance – a shifting mosaic with patches on the scale of a few 10s of m across. But what is the ‘return time’? How often is disturbance likely to return to a particular spot? Hard to guess from direct observation, as the return time is certainly many decades to some centuries – and such events don’t leave readily ‘date-able’ signatures like fire-scars and distinct cohorts of fire-responding species.



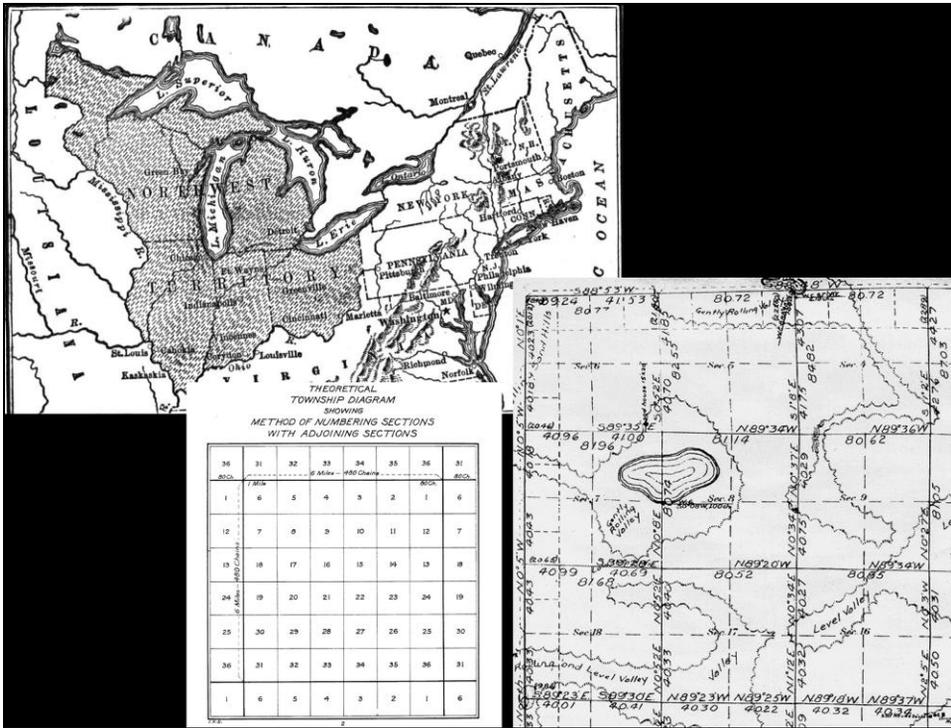
As weather records and observations improved, researchers came to recognize that severe local blow-downs were often part of larger, regional events. This map shows the path of a severe storm in northern WI in 1977. Over an area about 120 miles long and 25 miles wide, local winds reached velocities of up to 150 mph, comparable to a moderate tornado (but these were clearly not tornadic). The arrows show directions of damage-causing winds (identified by direction of tree-fall and of debris fans from structures).



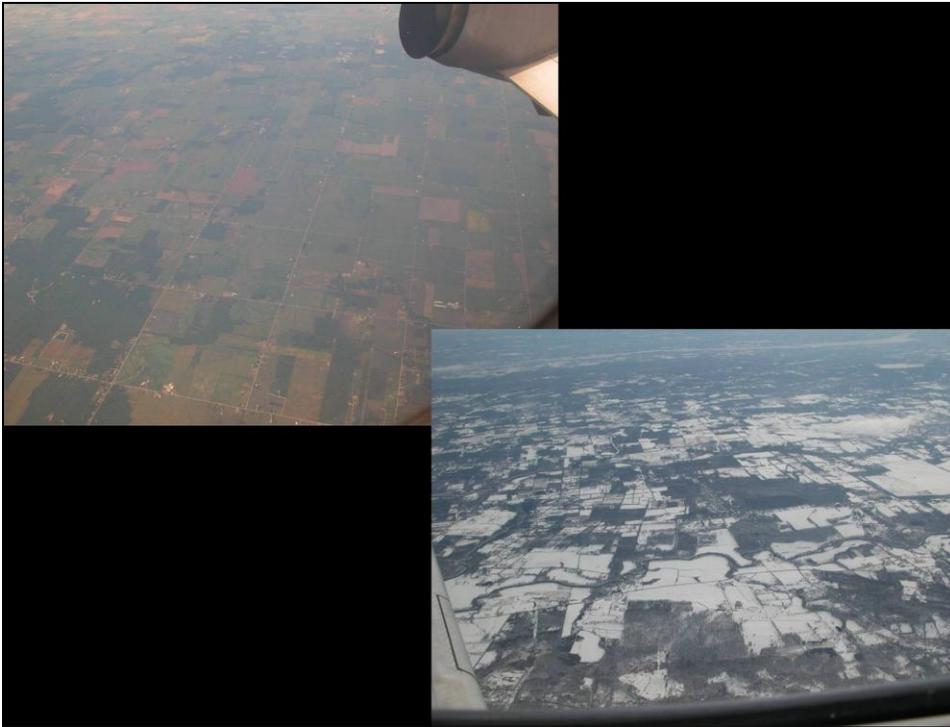
Modern understanding of climate/weather systems, along with more sophisticated technologies for monitoring storms over large areas (satellite, radar), have allowed meteorologists to recognize similar, distinctive phenomena where wind disturbance can be much more extensive and severe than the assumed 'typical' gap-phase pattern of mortality of individual trees or small patches. 'Derechos' or 'supercell' thunderstorms can generate very high winds (>150 km/hr) over large areas (although their tracks tend to be composed of many smaller, intense patches due to high wind events called 'downbursts'.) You can look up these terms at wikipedia for more information. This 1999 derecho in the Boundary Waters destroyed > 2/3 of canopy trees in areas totaling thousands of ha – larger than all but the worst fire events reconstructed by Heinselman.



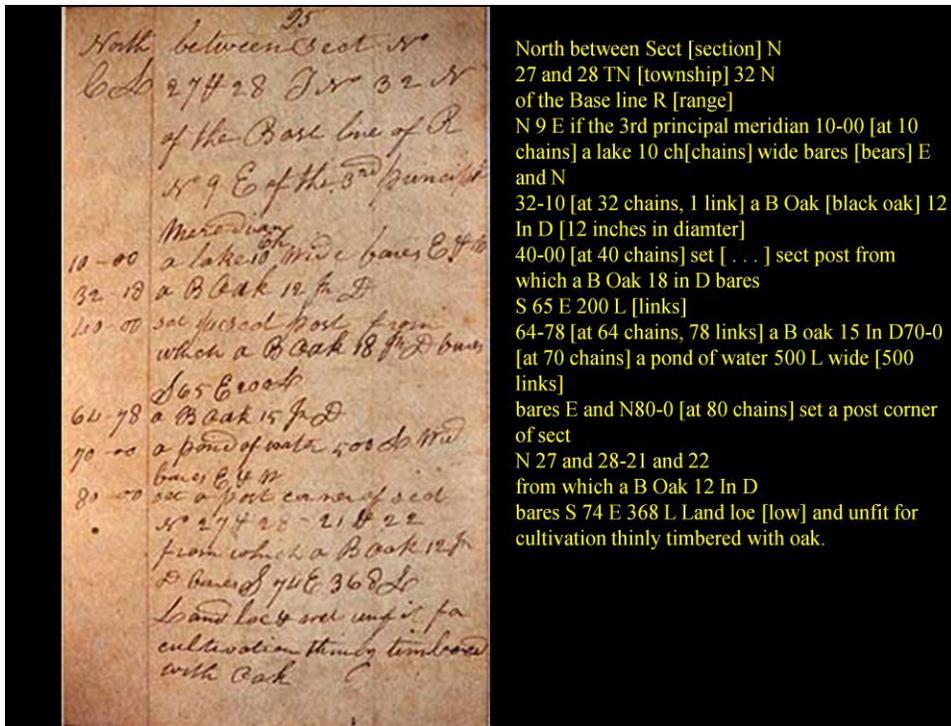
A similar event in the Adirondack Mts. of NY in 1995. The long narrow strips are probably associated tornados. Derechos typically occur in mid-summer, and they may be as frequent as one or two every year somewhere in the eastern U.S. BUT JUST HOW OFTEN might such massive wind disturbances occur at any given location? What is the 'return time'? What is the likely successional time-frame between disturbances?



Charles Canham and Orie Loucks assessed frequency of large blow-downs for Wisconsin northern hardwood forests using historical research. The Northwest Ordinance of 1787 called for surveying unallocated lands of the old Northwest Territory in Townships 6 miles square; townships were, in turn, subdivided into 36 Sections of 1 square mile. Surveyors were required to describe land along the lines bordering these sections, documenting and marking ‘bearing trees’ or ‘witness trees’ every half-mile (these would be used to help mark the boundaries of land granted to homesteaders), describing land quality – *and noting blow-downs, fires, and clearings* that the survey line passed through.



(Geographical aside: Under the Northwest Ordinance, roads were laid out on a square-mile grid along section lines, and land was typically granted in 160-acre (0.5x0.5 mile) 'quarter-sections'. This is quite visible from the air for most of the settled portions of the U.S. from Ohio westward (upper left). In a few areas in the southwestern U.S. and in Louisiana, where EuroAmerican (Spanish or French) settlement had already occurred, pre-existing land grants applied and the Northwest Ordinance system was not used. In earlier-settled lands of the original colonies (upstate NY at lower right), land was subdivided in a much more happenchance and irregular way.



This is a page from one of the surveyors' notebooks with 'translation'. Charles Canham analyzed these notebooks, noting surveyors' descriptions of blow-downs and other disturbances. These included length of clearings along survey lines, so these data allowed mapping and assessing sizes of a sample of larger disturbances. The researchers also mapped current blow-downs from aerial photographs.

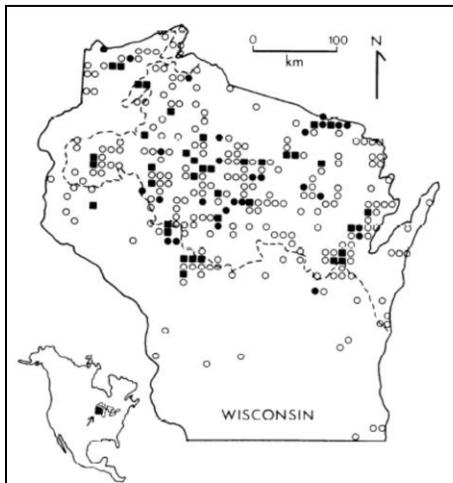


FIG. 1. The distribution of blowdowns in presettlement Wisconsin (circa 1834-1873). The dashed line is the southern and western limit of the mesic, hemlock-northern hardwood forest in the state, taken from the map "Presettlement Vegetation of Wisconsin" (Wisconsin Geological and Natural History Survey 1965) based on work by the University of Wisconsin Plant Ecology Laboratory. The symbols represent the total area of blowdowns in 9328-ha townships: ○ = 1-324 ha; ● = 325-649 ha; ■ = >649 ha.

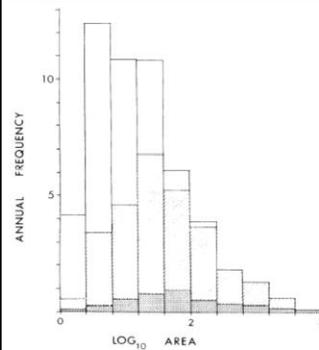


FIG. 2. Annual frequencies of presettlement blowdowns and contemporary tornadoes (1953-1977) by logarithmic size-classes (size measured in hectares) within the 6 560 000-ha region occupied by the presettlement hemlock-hardwood forests of northern Wisconsin. The stippled portions of bars are contemporary tornadoes. Blowdowns actually recorded by surveyors are shown with hatching, while the estimated regional totals for smaller size-classes are indicated by the open portions of the bars.

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#### CATASTROPHIC WINDTHROW IN THE PRESETTLEMENT FORESTS OF WISCONSIN<sup>1</sup>

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Fig. 1 shows the estimated total area of blowdowns in each township as estimated from surveyors' description and data. The dashed line is the approximate southwestern boundary of northern hardwood forests similar to those of interior New England. Fig. 2 shows their estimate of *annual frequency* for the entire study area of blowdowns of various sizes. The hatched portions of bars are blowdowns actually recorded by surveyors. The unshaded portions are their estimates of numbers that were not recorded because they did not fall on a survey line (this is a function of the size of the blowdown relative to the 1-mile distance between survey lines. The size axis is logarithmic. Thus, they estimate that about six blowdowns of just under 100 ha (log 2) occurred annually somewhere in northern Wisconsin, along with perhaps two or three of > 1000 ha (log 3). They estimated 'return time' – estimate interval between events for a particular site -- for *catastrophic* blowdowns (nearly all trees killed) to be roughly 1200 years (about ten times the return time for fire in the Boundary Waters).

## LANDSCAPE AND REGIONAL IMPACTS OF HURRICANES IN NEW ENGLAND

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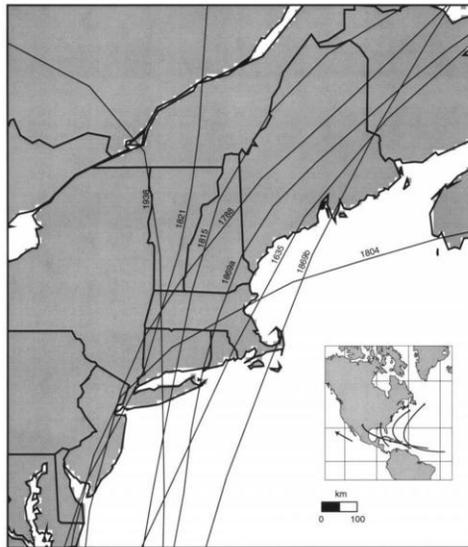


FIG. 1. Tracks of eight hurricanes that caused F3 damage on the Fujita scale (see Table 1) in the study region during the historical period (1620–1997). Inset: common hurricane paths in the North Atlantic (adapted from Dunn and Miller 1964).

In New England, particularly near the coast, hurricanes are relatively frequent and constitute the most common major disturbance. Researchers at Harvard Forest have, through extensive historical research, reconstructed the paths of major hurricanes for the last several centuries.

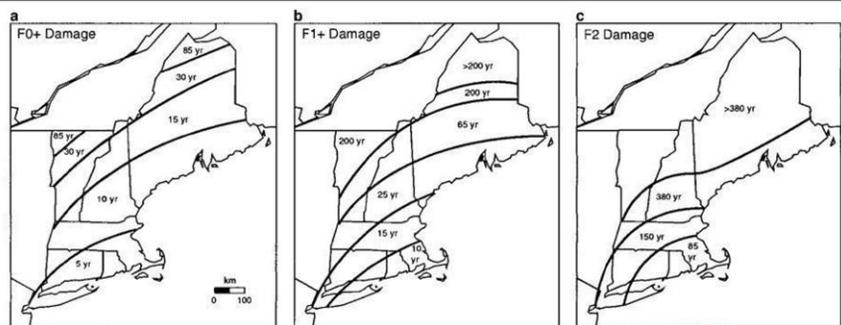
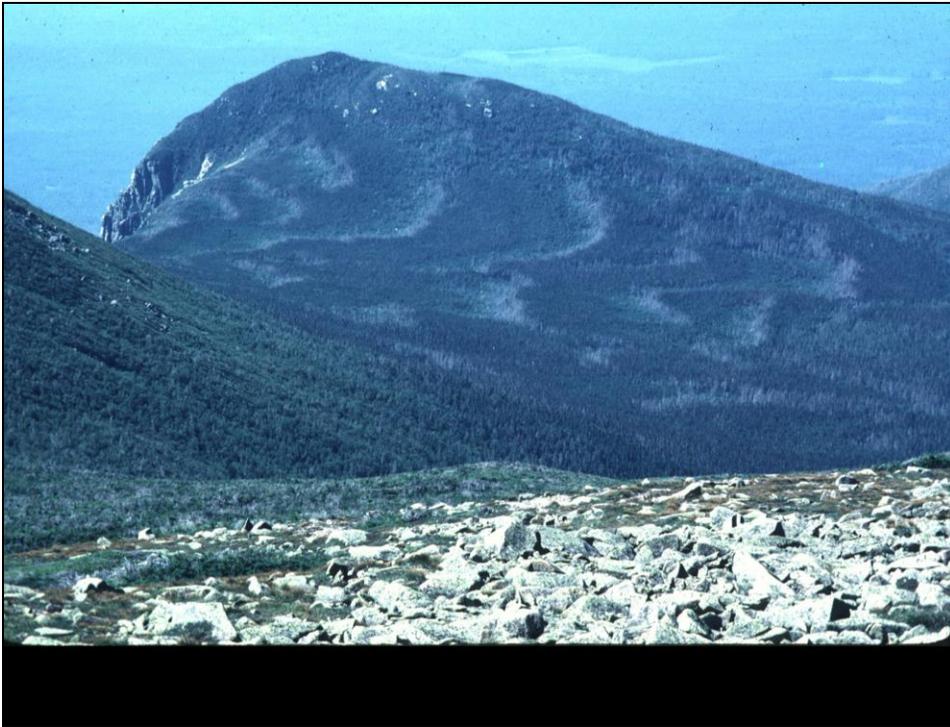


FIG. 8. Smoothed regional gradients in reconstructed hurricane damage, using best-fit values for the radius of maximum winds: mean return intervals for (a) F0+ damage (1871–1997), (b) F1+ damage (1800–1997), and (c) F2 damage (1620–1997).

These reconstructions allowed modeling of hurricane risk; these maps show rough ‘return times’ for hurricanes of progressively more severe nature. “F2 damage” is the most severe, with large areas losing the majority of canopy trees.



There are many other regional patterns of disturbance and successional response. At high elevations in some of the northern Appalachians, forests are almost exclusively dominated by balsam fir. In these *monotypic* forests, mortality is often due to exposure to high winds and icing damage in the winter. When a gap occurs in an aging stand of fir, trees on the downwind side of the gap become more exposed and vulnerable to mortality, and a 'wave' of mortality moves outward and downwind, eventually becoming a linear band of dying trees progressing across the landscape. Fir trees regenerate massively immediately following a wave of mortality, establishing an even-aged stand in which most trees become vulnerable to mortality at about the same time/age, setting the stage for the next 'fir wave'. The waves in this forest (on Mt. Katahdin in Maine) are around 250 m apart and perhaps 60-70 years apart.



Successional dynamics were studied on boulders in the intertidal zone near Santa Barbara, CA. Severe storms roll boulders over exposing new 'substrate', which is then colonized by certain types of algae that are good at dispersal and rapid growth (e.g., 'sea lettuce' – the bright green algae above). Over time, other species settle and overgrow the first colonists, gradually shading and displacing them (e.g., *Gigartina* brown algae on the right-hand boulder above). Given sufficient time without disturbance, mussels settle on the rocks and crowd out all algae – until a storm rolls the boulder over again.