4 · Disturbance, stand development, and successional trajectories

Introduction
What are the major changes in stand structure over time (stand development) and what changes in composition over time (succession) accompany developmental changes? How do these changes occur in major forest types of the Lake States forests? These are the major questions examined in this chapter. Many studies on stand dynamics in the Great Lakes forests—studies which used methods described in Chapter 3—are synthesized here. The chapter starts with basic schemes for development and succession. Then I proceed to case studies of five major forest types that illustrate the types of variations on the basic schemes of development and succession that occur among forests.

Basic stand development sequence
Four basic stages of development that stands go through after stand-replacing disturbance were described by Oliver (1981). I present these stages in a form modified to fit the context of cold-temperate hardwood–boreal transition zone forests of the Lake States (Figure 4.1).

![Diagram: Stand development sequence]

Figure 4.1. Four basic stages of stand development.

Complications of this basic scheme of four stages that occur in different forest types will be described in detail later on this chapter. Stages of development are important to keep in mind when thinking about disturbance regimes throughout the rest of the book because it is disturbance regimes that determine the proportion of stands in each stage of development. For example, with short-rotation logging, all stands across the landscape will be in the initiation and stem-exclusion stages of development with no chance to go on to the old multi-aged stage.

Stage 1. Initiation. This stage follows major disturbance, such as stand-leveling wind, crown fire or clear-cut logging.

- The open space is filled in with individuals that arrive by seed (e.g. paper birch and aspen after fire), stump sprouts (e.g. oak forest after fire), roots sprouts (e.g. aspen after clear cutting), or advance regeneration (e.g. sugar maple or other shade-tolerant species after a tornado).
- The individuals are part of an age group called a cohort.
- This stage lasts from the time of stand-replacing disturbance until the new cohort forms a continuous canopy and trees begin competing with each other for light and canopy space.

Stage 2. Stem exclusion. During this stage, the canopy is dense enough to prevent new saplings from growing into the canopy—there is no space available for new canopy trees.

- The canopy continues to have only one dominant cohort, with a unimodal dbh distribution. The canopy upper surface is relatively smooth.
- Competition among trees is intense and density-dependent self-thinning is the major cause of mortality.
- Crowns are small enough so that when one tree dies, the other trees are able to fill the vacated space in the canopy by expanding their branches horizontally. This situation continues for 100–150 years in northern hardwoods and red or white pine stands, but may last only 20 to 40 years in some aspen and jack pine stands.

Stage 3. Demographic transition. At this point, a stand undergoes demographic transition from one cohort of trees in the canopy to more than one cohort. There may be a wave of high mortality as many trees reach senescence at the same time.

- The crowns of the trees are now large enough so that when one dies the surrounding trees cannot fill the gap. As a result, a new cohort of trees

has space to enter the canopy. The dbh distribution has the remnants of an old unimodal peak in larger size classes and a new peak in the small size classes. This can be called a 'compound dbh distribution'.

• If the stand was originally composed of a pioneer species such as paper birch, shade-tolerant trees such as sugar maple, hemlock, beech or spruce and fir may begin entering the canopy.

• There are more gaps in the canopy and more light on the forest floor than during the stem-exclusion stage. Mid-tolerant trees such as basswood, green ash, yellow birch and white pine may be able to enter the canopy through some of the larger canopy gaps.

• Mortality undergoes a transition from mostly density-dependent self-thinning to mostly density-independent mechanisms such as senescence and blowdown due to weakened wood caused by heartrot or disease. Dense clusters of young trees in large gaps still undergo self-thinning (i.e. the whole stand development sequence may repeat itself at the neighborhood spatial scale within gaps).

• The stand begins to take on 'old growth' characteristics, with large rotten logs on the forest floor, many sizes of trees, and an uneven canopy surface.

• This stage lasts from the time the first trees younger than the disturbance cohort are able to grow into the canopy until the disturbance cohort no longer has a significant presence in the stand.

Stage 4. Multi-aged. At this point demographic transition to uneven-aged status is complete, and the forest has many age classes and size classes of trees in the canopy. There may be few or no remnants left from the original cohort. Mortality is continuous at a relatively low level, caused by death of single trees or small groups of trees.

• The dbh distribution is characterized by many small trees, with a steep decline in number of trees until the middle size classes, where the decline becomes more shallow or levels off, followed by another sharp decline in the largest size classes. The dbh distribution results from a high rate of mortality for small trees (which are undergoing self-thinning in gaps), low mortality for middle-aged trees, and high mortality for large, senescent trees.

• Changes in species composition, development of old growth characteristics, and density-independent mortality with some self-thinning in gaps described for the reinitiation stage continues.

• This stage will last until another stand-replacing disturbance occurs.

Many readers will undoubtedly notice that I have changed the last two stages from Oliver's scheme (Oliver 1981, Oliver and Larson 1996). What I call 'demographic transition' was referred to as 'understory reinitiation' by Oliver. I made this change because in the Great Lakes Region, this stage has a lot of variability among forest types. Some forests have an understory layer of tree seedlings in all stages of development. However, those seedlings rarely have any chance at all of growing into the mid-story and then capturing a gap as long as the stand is in the stem-exclusion stage. Therefore, the understory is not really reinitiated at a given point in time. What I call the 'multi-aged' stage of development was referred to as 'old growth' by Oliver. The problem with 'old growth' is that it has become a political term that has many different definitions used by managers in different countries and in different states throughout the United States. Environmentalists have tagged any forests with large trees, or old trees (especially older than people's maximum lifespan), as 'old growth'. This includes stands of long-lived species such as oak, maple, and white pine in the Great Lakes Region that are 120-150 years old but still in the stem-exclusion or demographic-transition stages of development. Therefore, to avoid confusion with these many political definitions of old growth, I have introduced the term 'multi-aged' forest. This term is also a good descriptor of the forests in question, since we are always talking about forests that have undergone transition from even-aged to uneven-aged. Multi-aged says exactly what it means with no ambiguity.

Stand development can also be placed on a continuous scale. For example, in sugar maple forests of Upper Michigan, modal stand diameter, proportion of total crown area in large trees (>46 cm dbh), and ratio of mature (26-45.9 cm dbh) to large trees are useful measures for quantifying stage of stand development (Lorimer and Frelich 1998). Figure 4.2 shows the dbh distribution for six stands ranging from young even-aged to nearly balanced all-aged. Stands with <45% of the crown area in large trees have unimodal diameter distributions, and as the ratio of large to mature trees exceeds 1.5, the form of the diameter distribution changes from unimodal to multi-modal, irregular, or descending monotonic, and the ratio of large to mature trees also increases throughout this sequence (Figure 4.2). Thus, these scaling factors allow the placement of stands on a developmental continuum that continues further than a chronosequence of stand ages. This can be an advantage because stand age becomes difficult or impossible to determine at or beyond the demographic transition stage of development.
Succession, fluctuation, and stand development

Another aspect of stand development to keep in mind is its relationship to changes in species composition, commonly referred to as succession or fluctuation. I use the common definition of succession: a directional change in species composition over time, where one species or group of species replaces another. Changes in composition of lesser magnitude than replacement are termed 'fluctuation', where the relative proportion of two or more species shifts over time. Fluctuations may be major (e.g. the ratio of maple to hemlock shifts from 25:75 to 75:25) or minor (e.g. the ratio of maple to hemlock shifts from 40:60 to 60:40).

What about the relationship between changes in composition and stand development: do they necessarily parallel one another? As shown in the five case studies below, sometimes stand development is accompanied by succession, but often it is not. There is often the incorrect assumption by many that stand-replacing disturbance always initiates a new successional sequence. Severe disturbance always initiates a new stand development sequence, which has sometimes in the past been called 'physiognomic succession' to differentiate it from the classical notion of succession that refers strictly to changes in species composition over time.

Before we launch into case studies that spell out the relationships between species composition change and stand development, it is necessary to have an understanding of what is meant by 'a directional change in composition over time', as was stated in the definition of succession above. The four stages of stand development described above are definitely directional, but what about successional development? Predicting the direction of succession in forests has been a major focus of ecological research as long as the science of ecology has existed (e.g. Gleason 1927, Clements 1936, Watt 1947, Curtis 1959, Drury and Nisbet 1973, Horn 1974, West et al. 1981, Peet 1992, Frelch and Reich 1995b). I have detected five major models of successional direction in the literature (Figure 4.3).

Cyclic model

Succession starts with composition state A, then proceeds to state B, C, etc., eventually returning to state A. Cyclic succession was first proposed by Watt (1947) and has been one of the major models employed by
**Divergent model**

One community (state A) diverges into two or more states (B, C, etc.), over time. The divergence involves feedback switches that magnify initial minor differences, and, once the differences are large, allow their perpetuation (Wilson and Agnew 1992). An example of this process could be a post-fire aspen stand that could easily succeed to pine, oak and maple on three adjacent sites. These differences in trajectory could be caused by soil differences that favor different species or by differences in seed availability.

**Parallel model**

Communities in states A and B each undergo stand-replacing disturbance, and each returns to the same state shortly after the disturbance. This is what some would call no succession, or is used to describe return to original condition after a short period of transient dynamics. Parallel succession can occur in the North American boreal forest, where species such as jack pine or black spruce can dominate adjacent stands. When stand-replacing fires occur in such areas the species in the pre-fire stand are the only seed source, and the post-fire stand maintains the same tree composition (Dix and Swan 1971, Heinselman 1981a,b, Johnson 1992).

**Individualistic model**

Also called multiple pathways of succession (Cattelino et al. 1979), individualistic succession occurs when stochastic variables, such as timing of major seed crops of the important tree species, droughts, disturbances, and other factors interact to produce multiple pathways of succession at different times at the same location. This model emphasizes continuous change and there may not be a stable endpoint. For example, a gap in the forest canopy formed in one decade could be filled by paper birch merely because paper birch had a good seed year and other species did not. If the paper birch later die of old age during a drought they may be replaced by a species with drought-tolerant seedlings, such as white cedar, if that species happens to be nearby.

**Predicting successional direction**

There are several difficulties with trying to predict successional direction in a real-world forest. The first of these is obvious in theory but often
invisible in the field. Namely, disturbance regimes are often complex, with several different types of disturbances. The result is what I call a ‘successional system’, with many developmental and successional stages related to each other in a web that may include segments of any or all of the five directional models of succession. An investigator who does not manage to isolate individual segments of the whole system for study will likely end in confusion, since their data will show elements of more than one directional model, which may wash each other out. In my opinion this is why there are so many studies done where large numbers of field plots and variables such as soil type, disturbance type, and stand age, are put into multi-variate ‘black boxes’, such as multiple regression, ANOVA, factor analysis, ordination, or canonical correlation, and end up with significant results that only explain 5% of the variation. It is nice to know that there is a significant trend in the data, but one also needs to explain differences among plots to have true predictive ability.

Other factors that may obscure our ability to predict direction of succession in forests include lack of spatial context, lack of consideration of spatial scale, and inadequate knowledge of successional mechanisms. Reviews of succession (Drury and Nisbet 1973, Facelli and Pickett 1990) suggest that the spatial context in which succession occurs is not adequately taken into account in many studies. Neighborhood effects, such as seed rain, shading, and nutrient feedbacks to the soil through litterfall, all play a role in determining how succession proceeds underneath the canopy of every tree. The successional direction for an entire stand (1–10 ha scale) is the sum of all these neighborhood trends, and a number of recent studies attempt to integrate these spatial effects into successional studies (e.g. Lippe et al. 1985, Hubbell and Foster 1986, Smith and Huston 1989, Freligh et al. 1993, Freligh and Reich 1995b). Research on forest succession often concentrates on processes that occur at a single spatial scale. For example, a large number of papers have been published that examine individual tree gaps (e.g. Runkle 1982) or that examine stands (e.g. Grigal and Ommann 1975) or that analyze landscapes (e.g. Payette et al. 1989, Dansereau and Bergeron 1993). An example of the data-interpretation difficulties this may create occurs for fir–spruce–birch forest reported by Buell and Niering (1957). This forest may be a uniformly mixed forest, with individual trees of different species next to each other (the result of convergent succession), or a series of small mono-dominant stands (the result of divergent succession). However, since no spatial data are presented, this is impossible to ascertain.

Case studies of forest development and succession

Case study 1: The birch–white pine, hemlock–hardwood successional system

The persistence and widespread success of white pine in presettlement forests of eastern North America, and its dependence on fire, is a paradox because white pine does not have adaptations to fire possessed by the classic fire-adapted species. Although white pine responds favorably to exposed mineral soil seedbeds and high sunlight after fires, it does not have serotinous cones like jack pine and black spruce, the ability to sprout vegetatively after fire like aspen and birch, or widespread and abundant seeds nearly every year like aspen and birch. White pine does possess the compensating life-history characteristics of long lifespan, ability of mature individuals to survive surface fire, moderate tolerance to shade, and the ability to grow in poor environments, such as riverbanks and rock outcrops, giving it a permanent refuge (at least it was permanent before humans removed these refuges) from disturbance and competition by shade-tolerant species (Figure 4.4).

Stand development after severe fire

There is a delicate balance between the abundance of white pine and fire: too much fire and the system shifts to mostly paper birch; too little fire and white pine succeds to sugar maple–hemlock forest. Thus white pine has the curse of mid-successional species in that it can't get along with fire and can't get along without it. Severe natural fires ignited by lightning occur in the range of white pine during spring, or late summer/autumn, after 2–3 months of drought at the sub-continental scale (Haines and Sando 1969, Heinselman 1973, Cwynar 1977). White pine is most abundant in areas where the rotation period, or mean interval between severe fires, is 150 to 300 years (Freligh 1992). If the fire cycle becomes more than 300 years for any reason, then hardwoods invade and change the fuel type in such a way that fires become much less common. Windthrow and other treefall gaps then become the dominant disturbance type. Forests within the range of white pine experience treefall mortality of 10% or more every 70 years on average, and they experience stand-leveling windthrow at intervals of 1000 to 2000 years (Lorimer 1977, Canham and Loucks 1984, Whitney 1986, Freligh and Lorimer 1991a). Windthrow is generally not favorable for white pine establishment, although a few white pine generally occur in post-blowdown stands. Only one instance of heavy recruitment of white pine after windthrow is mentioned by the literature (Hough and
Table 4.1. Period of peak seedling recruitment for white pine (starting the year after fire, and ending at the number of years indicated)

<table>
<thead>
<tr>
<th>Peak recruitment (yr)</th>
<th>Associated species( ^a )</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Red maple, gray birch, white ash, cherry</td>
<td>Pennsylvania, USA</td>
<td>Hough and Forbes 1943</td>
</tr>
<tr>
<td>20</td>
<td>Hemlock, paper birch</td>
<td>New Hampshire, USA</td>
<td>Henry and Swan 1974</td>
</tr>
<tr>
<td>20</td>
<td>Pin oak, bur oak, jack pine</td>
<td>Wisconsin, USA</td>
<td>Frelich 1992</td>
</tr>
<tr>
<td>25</td>
<td>Aspen, paper birch, red maple</td>
<td>Minnesota, USA</td>
<td>Frelich 1992</td>
</tr>
<tr>
<td>25–30</td>
<td>Aspen, red pine</td>
<td>Ontario, Canada</td>
<td>Cwynar 1977</td>
</tr>
<tr>
<td>25–35</td>
<td>Paper birch, red maple, hemlock</td>
<td>New Hampshire, USA</td>
<td>Foster 1988a</td>
</tr>
<tr>
<td>20–40</td>
<td>Chestnut, red maple, red and white oak</td>
<td>Pennsylvania, USA</td>
<td>Hough and Forbes 1943</td>
</tr>
<tr>
<td>40</td>
<td>Paper birch, aspen</td>
<td>Quebec, Canada</td>
<td>Maisurrow 1935</td>
</tr>
</tbody>
</table>

Note:
\( ^a \) Species recruited at the same time.

Forbes 1943), although many instances of heavy recruitment after fire are documented.

White pine has abundant seed crops every 3–5 years and very slow growth during the first 5–10 years after germination. In addition, after severe crown fire only a few surviving white pine remain in most forest stands. Therefore, seedling establishment by white pine in post-fire stands usually takes place over 20–40 years under a faster growing or earlier established canopy of aspen, birch, red maple or oak (Table 4.1). Some white pine seedlings may be present right away in the stand initiation phase of development if restocking by other species is slow (Figure 4.5). The shade cast by aspen or oaks is not as dense as that in hemlock-hardwood stands, so that growth of the mid-tolerant white pine seedlings is good — usually 0.3–0.6 m per year. Near the end of the stem exclusion phase of development (which varies from 40 to 80 years of age), many of the white pine are tall enough to take positions in the upper canopy as the birch begin to die (Figure 4.5).

During the demographic-transition stage white pines enter the canopy
A pattern of cyclic succession

A repeating sequence of severe crown fires with intervening low to moderate-severity surface fires can lead to long-term dominance by white pine in one stand for several thousand years (Davis et al. 1994, 1998, Figure 4.6). There would be pulses of species such as paper birch after each major fire, so that some succession would occur from time to time. When old multi-aged white pine stands are maintained by surface fires, periods of several centuries with little succession are also possible. Other cycles may also occur in which the birch/white pine forest alternates with

![Diagram](image_url)

**Figure 4.6.** Cyclic succession in the birch, white-pine, sugar maple successional system. Diameter distributions at various ages after stand-killing fire are indicated by solid lines, long dashed lines and dash-dotted lines for white pine, paper birch, and sugar maple, respectively. After Frellich (1992).

at different times, as gaps caused by the death of mature birch appear. In addition, other white pine may have been in the canopy from the early stand initiation phase, and others are suppressed under larger white pines. These processes lead to differential growth rates and the development of a hierarchy with rapidly growing canopy-emergent white pine and slower growing trees in intermediate and overtopped crown classes. The diameter distribution becomes bimodal (Figure 4.5).

Two types of low-severity disturbance facilitate the transition from demographic transition to old multi-aged phases of development, which generally occurs between 100 and 200 years of age. White pine is very susceptible to high winds and the larger the tree, the more susceptible it is (Stoekeler and Arbogast 1955, Foster 1988b). Therefore, trees in the canopy emergent position are often toppled by wind and other white pines from a lower position are released into the canopy. A second disturbance may be surface fires at intervals of 20–40 years (Frisell 1973). If shade-tolerant hardwoods are invading the understory they may be killed by surface fires. Also, a few of the large white pine may be killed by surface fires, opening gaps for recruitment of new white pine seedlings and saplings. The gaps caused by wind and surface fire cause a stand to become increasingly multi-aged, with a multi-modal diameter distribution. White pine stands may be maintained in the old multi-aged stage for one to several centuries until another severe crown fire occurs (Heinselman 1981b).
Table 4.2. Chance of an individual stand surviving one or more rotation periods under a constant probability of fire with stand age

<table>
<thead>
<tr>
<th>Number of rotation periods</th>
<th>Stands surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>36.8</td>
</tr>
<tr>
<td>2</td>
<td>13.5</td>
</tr>
<tr>
<td>3</td>
<td>5.0</td>
</tr>
<tr>
<td>4</td>
<td>1.8</td>
</tr>
</tbody>
</table>

hemlock–hardwood forest (Figure 4.6). A necessary condition for succession from white pine to hemlock–hardwood is several centuries without severe crown fire and infrequent surface fire. Two major factors can cause or accelerate such successional events. First, fire may miss a stand by chance. Under natural conditions disturbances that occur at random with respect to stand age may skip individual stands for one or more consecutive rotations (Van Wagner 1978). For example, if the natural rotation period for crown fire in white pine forest is 200 years, then 14% of all stands may survive two rotation periods (400 years) and a few stands may even survive three or four rotation periods (Table 4.2). This would be enough time for succession to northern hardwoods. Successive windstorms would selectively remove the much taller canopy–emergent pines and release understory shade–tolerant species such as hemlock and sugar maple — a process known as disturbance–mediated accelerated succession (Abrams and Nowacki 1992). The second factor promoting the switch to hemlock–hardwood forest is species composition–fuel feedbacks. If a white pine stand is missed by fire for 2–4 centuries, and species like hemlock and sugar maple become a major component of the forest, then the fuels become more difficult to burn, and the rotation period for fires is lengthened. This is consistent with the relative lack of recent burns and abundance of recent windfalls recorded by the nineteenth century land surveyors in northern Wisconsin and Upper Michigan (Bourdo 1956, Canham and Loucks 1984), and with observations that northern hardwood forests are fairly resistant to burning (Stearns 1949, Curtis 1959, Miller 1978, Bornmann and Likens 1979). Other factors can also contribute to the paper birch/white pine to hemlock–hardwood successional trend: (1) a coincident change to cooler and wetter climate (Davis et al. 1992, 1994, Clark et al. 1996); (2) fine–textured soils that favor rapid growth of hemlock and hardwoods; and (3) the presence of topographical firebreaks.

Succession from hemlock–hardwood forest back to paper birch/white pine requires a severe fire (Figure 4.6). However, hemlock–hardwood stands have moist foliage and relatively low canopy bulk density, and they cannot carry a crown fire. Therefore this successional event will be rare and be facilitated by windfall–fire interactions. Although severe fires are not common in hemlock–hardwood forests (Frelch and Lorimer 1991a), slash from a stand–leveling windfall event can be quite extensive and provide the necessary fuel for severe fires (Stearns 1949, Whitney 1986, Foster 1988a, Lorimer 1977). The post–fire successional sequence commonly included paper birch and white pine. Drought is a necessary factor for windfalls to burn. At any one time on a natural landscape there are areas of recent windfall. However, they are much more likely to burn if a drought occurs. A coincident change to a warmer/drier climate, sandy soil, and lack of topographical firebreaks will aid this successional sequence and allow the return of the birch/white pine forest.

Succession, stand development and wind in the hemlock–hardwood forest

These forests have a tendency to undergo divergent succession, segregating into hemlock–dominated and sugar maple–dominated stands (Davis et al. 1994; see Chapter 6, ‘Sylvania case study’, for more detail). Once these hemlock or sugar maple–dominated stands are established, however, many centuries can go by without any succession within stands (Davis et al. 1998). The previously described double whammy of windfall followed by fire, causing the birch–white pine–hemlock–hardwood cycle, does not occur very often. Instead, most of the dynamic action is in constantly changing stand structure (Figure 4.7).

These forests experience many single treefall gaps, a moderately large number of disturbances that kill 5–40% of the trees, and very few stand–leveling wind events. The medium disturbances have a greater cumulative impact on the forest than either single tree gaps or stand–leveling wind (see Chapter 6, ‘Wind regimes and landscape structure’). As a result, there are few even–aged stands, and few all–aged stands, but many very complex multi–aged stands. Therefore the basic stand development scheme needs some refinement to take into account many different types of multi–aged stands. There does not seem to be a straight–line sequence of stand development, but rather a ‘web of development’, with many interlinked types of stands and developmental pathways. Frelch and Lorimer (1991b) identified eight different structural types, all of which work equally well for hemlock and sugar maple stands, and can be viewed as variations on the central theme of the four basic stand development stages (Box 4.1, Figure 4.8).
Pole stand (early stem exclusion):
Young even-aged stand that develops from growth in a sapling stand. A substantial majority of the canopy area is occupied by saplings, poles, and mature trees (trees 26.0–45.9 cm dbh), with aggregate crown area of poles greater than that of saplings or mature trees.

Mature stand (late stem exclusion):
Middle-aged, even-aged stands resulting from growth of a pole stand. A substantial majority of the canopy area is occupied by poles, mature trees, and large trees (>46.0 cm dbh), with aggregate crown area of mature trees greater than that of poles or large trees.

Multi-aged break-up stand (demographic transition):
Typically an old, first-generation stand after canopy-leveling windstorm that has more mature and large trees than a mature forest, but does not yet have a broadly uneven-aged structure. These stands result from growth and development in mature stands.

Multi-aged pole stand (a subdivision of the multi-aged stage):
A stand with size structure similar to that of a pole stand, but not originating from a sapling stand. Unlike a pole stand, widely scattered age classes are present. Multi-aged pole stands result when a moderately severe windstorm reduces the stature of any of the other multi-aged stand types or a steady-state stand, by removing most of the large and mature trees and leaving behind mostly pole-sized trees. A windstorm that creates multi-aged pole stands does not quite reduce stand stature enough to place the stand in the sapling stage.

Multi-aged mature stand (a subdivision of the multi-aged stage):
A stand with structure similar to that of a mature stand, but not originating from a pole stand. Unlike a mature stand, widely scattered age classes are present. Multi-aged mature stands result when a moderately severe windstorm reduces the stature of old multi-aged stands or steady-state stands, by removing large trees while leaving mature trees intact. This stage can also result from continued growth in a multi-aged pole stand.

Old multi-aged stand (a subdivision of the multi-aged stage):
A stand that has gone more than 250 years since the last canopy-leveling disturbance and has a canopy dominated by mature and large trees. Usually at least 50% of the canopy area is occupied by large trees. Generally, several to many widely scattered age classes are present that are unequal in area occupied. Old multi-aged stands result from growth of multi-aged break-up, multi-aged pole, or multi-aged mature stands, or from partial canopy removal in a steady-state stand.

Steady-state stand (a subdivision of multi-aged stand, also sometimes called balanced all-aged stand):
A stand that has gone more than 250 years since the last major disturbance and has experienced continuous formation of small scattered treefall gaps over the last 250 years, so that the area of new gap formation has been relatively constant over time.
Figure 4.8. Eight stages of stand development in hemlock-hardwood forest. See Box 4.1 for definitions.

Case study 2: The southern-boreal jack pine-aspen, spruce-fir-birch-cedar successional system

Basic development sequence
These jack pine, aspen and black spruce dominated boreal forests are as similar to those of central Canada as one can find in the lower 48 states. Within the primary forest remnants of the Boundary Waters Canoe Area Wilderness (BWCAW), the natural processes of disturbance and forest development still occur. These forests on nutrient-poor shallow soil over granitic bedrock originate after severe crown fires (Figure 4.9). Under the pre-European natural disturbance regime, severe crown fires had a rotation period of approximately 50–70 years (Van Wagner 1978, Heinselman 1981b).

Sometimes fires occur in young stands (<10 years old), an age at which the conifers do not produce much seed, and aspen comes to dominate the post-fire stand (Heinselman 1973). Otherwise, if fires occur when jack pine and black spruce are old enough to produce abundant seed, then those species dominate the post-fire stand. Jack pine has serotinous cones that remain closed until scorched, and after a crown fire, seeds rain down by the millions on every hectare. Black spruce has semi-serotinous cones; a few open every year, but the majority are stored in the canopy and open after fire. Surveys of seedling densities after fire indicate that densities of 100,000 to 300,000 seedlings per hectare are common 2–3 years after fires (Heinselman 1981b). This initiation phase of development lasts less than a decade, by which time a very thick young forest closes the canopy. After that, stem exclusion begins and continues until
approximately age 100 (Frelich and Reich 1995b). Demographic transition occurs between age 100 and 150 as large gaps form when small groups of jack pine die. Balsam fir, white cedar and paper birch invade these gaps, and black spruce also increases its importance within stands during those years. Finally, when the original jack pine have nearly all died, after age 150, stands become a mixture of the ‘climax species group’ of black spruce, balsam fir, paper birch and white cedar, a more complex group than the hypothetical spruce–fir often mentioned in the literature (Frelich and Reich 1995b, Figure 4.10).

All directions of succession occur in this forest
Can parallel, convergent, divergent, cyclic and individualistic succession all occur at the same time in one forest? Yes, but it all depends on how you look at the system. Let’s examine the system at several spatial scales and also compare stands of many different ages at one point in time and the same stands at several points in time. Frelich and Reich (1995a) accomplished this suite of analyses by mapping all trees within some stands, reconstructing stand history since the last fire, and examining the spatial structure and composition of stands of widely varying ages (origins from 1801 to 1976) on aerial photographs of the same forest taken in 1934, 1961 and 1991. Air photo interpretation proceeded by classifying forest blocks of 1 ha, 4 ha, or 16 ha in size on all three air photos into one of the following four spatial structures (Figure 4.11):

1. Solid Matrix (MAS). Block is nearly completely dominated by one species (makes up >90% of tree cover).
2. Matrix with Inclusions (MAI). One mono-specific patch comprises at least 50% of the area.
3. Mosaic (MOS). The block has mono-specific patches (>0.25 ha in
area) of two or more species. No one patch comprises 50% or more of the tree cover; however, one species may occupy more than one patch, and may comprise more than 50% of cover.

4. Mixture (MIX). The block has more than one species, but patches >0.25 ha comprise <10% of the area. Thus, the species form a diffuse mixture.

The above classification leads to a simple quantification of forest texture. Results reveal that young stands are predominantly matrices of jack pine, sometimes with inclusions of aspen at 1 ha, 4 ha and 16 ha spatial scales (Figure 4.12). Mosaics of jack pine and aspen also occur in some young stands, especially at the 16-ha scale. Mixtures of species are rare among young stands. In contrast, mature forests in the stem exclusion stage show that black spruce that were initially present in the understory make their way into the canopy, so that some forest blocks at 1 ha, 4 ha, and 16 ha spatial scales move from the matrix with inclusion to the mosaic or mixture spatial structure. Old and very old forests are mixtures of black spruce, balsam fir, paper birch, and white cedar at all spatial scales (Figures 4.10, 4.12).

Analysis of transitions of the same forest block over time (between 1934 and 1991, or between 1961 and 1991) confirm that young stands move from solid matrices and matrices with inclusions to mosaics and mixtures over time. Stands that started out as mosaics in 1934 change to mixtures by 1991, and finally, all observed transitions in very old stands result in the continuation of the mixture spatial texture. Of those 1-ha blocks of forest that start out as solid matrices in 1934, some stay in the same category until 1991, while others change to matrices with inclusions or to mixtures. These varying pathways depend on the erratic distribution of canopy-gap formation, which may miss some 1-ha blocks for decades, hit others lightly creating a few small openings that become inclusions, or create many openings resulting in a mixture. Thus, all blocks that are solid matrices will eventually make their way to the mixture category, but the timing will vary depending on the fine-scale spatial and temporal distribution of canopy mortality. Also, bigger blocks of forest undergo transition from matrix to mosaic to mixture slightly faster than smaller blocks. This is expected because as canopy openings cause transition of bigger blocks to mosaics and mixtures, there could be 1-ha blocks embedded within a large block that by chance escape canopy disturbance and temporarily remain a solid matrix (Figure 4.12).

Spatial patterns in an example of very old forest where all trees were

Figure 4.12. Spatial structure by stand age and spatial scale in the near-boreal forest. Percentage of blocks (1, 4, and 16 hectares in size) that are solid matrices (MAS), matrices with inclusions (MAI), mosaics (MOS), or mixtures (MIX) are shown for young (0–10 year old), mature (41–100 year old), old (101–150 year old), and very old (>150 years). From Frelich and Reich (1995a).
mapped are complex, with multiple and single-tree patches of each of the four climax species, along with a few remnants of the original pine cohort (Figure 4.13). Average patch size is small (35 m²), but 20–40% of area is in the largest patches (ranging approximately from 1000 to 2300 m²). Surprisingly, there is no contagion within species between mature trees and seedlings in gaps, or between standing dead trees that recently died and saplings in gaps (Figure 4.14). In fact, the four species black spruce, balsam fir, paper birch and white cedar are apparently replacing each other on a patch-by-patch basis within the stands (Table 4.3). The patches are renewed by small-scale disturbance events, including senescence of old birch, summer thunderstorm winds, and heavy wet snow accompanied by strong winds that commonly take down small groups of white cedar and black spruce. Spruce budworm is also common in these older stands, and despite its name, infests mostly balsam fir. Most fir trees do not live beyond 40 years for this reason, even though the species is capable of living 200 years. There are virtually always young fir in the forest understory that are not killed by budworm, and when they mature they are infested themselves (Heinselman 1981a).
Table 4.3. Transition probabilities of from species-to-species on two plots

<table>
<thead>
<tr>
<th>Transition from (n)</th>
<th>Black spruce</th>
<th>Balsam fir</th>
<th>Paper birch</th>
<th>White cedar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thenceen Island (192 year old stand)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jack/red pine (77)</td>
<td>0.286</td>
<td>0.195</td>
<td>0.325</td>
<td>0.195</td>
</tr>
<tr>
<td>Black spruce (43)</td>
<td>0.326</td>
<td>0.209</td>
<td>0.349</td>
<td>0.116</td>
</tr>
<tr>
<td>Balsam fir (49)</td>
<td>0.286</td>
<td>0.327</td>
<td>0.224</td>
<td>0.163</td>
</tr>
<tr>
<td>Paper birch (11)</td>
<td>0.181</td>
<td>0.545</td>
<td>0.273</td>
<td>0.0</td>
</tr>
<tr>
<td>White cedar (12)</td>
<td>0.083</td>
<td>0.0</td>
<td>0.167</td>
<td>0.750</td>
</tr>
<tr>
<td>All (192)</td>
<td>0.276</td>
<td>0.240</td>
<td>0.292</td>
<td>0.193</td>
</tr>
<tr>
<td>Fishehook Island (127 year old stand)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jack pine (20)</td>
<td>0.600</td>
<td>0.050</td>
<td>0.300</td>
<td>0.050</td>
</tr>
<tr>
<td>Black spruce (44)</td>
<td>0.610</td>
<td>0.023</td>
<td>0.364</td>
<td>0.0</td>
</tr>
<tr>
<td>Paper birch (1)</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0*</td>
<td>0.0</td>
</tr>
<tr>
<td>All (65)</td>
<td>0.600</td>
<td>0.031</td>
<td>0.354</td>
<td>0.015</td>
</tr>
</tbody>
</table>

Transition frequency

<table>
<thead>
<tr>
<th>Transition from (n)</th>
<th>Black spruce</th>
<th>Balsam fir</th>
<th>Paper birch</th>
<th>White cedar</th>
</tr>
</thead>
<tbody>
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<td>0.015</td>
</tr>
</tbody>
</table>

Note:
* Note sample of 1.
Source: After Frellich and Reich (1995b).

Now, in light of the evidence just presented, we return to the question at the beginning of this section: can all directions of succession occur in one forest at the same time? The following paragraphs summarize the empirical evidence.

Parallel succession clearly occurs when stands that still have substantial numbers of jack pine or aspen burn (Heinselman 1973, 1981a,b, Frellich and Reich 1995b, and Figure 4.10). Based on the landscape-level analysis of the BWCAW by Heinselman (1973), parallel succession in tree-species composition occurred at all spatial scales from individual tree to landscape.

Divergent succession is occurring at fine-grained spatial scales, such as the individual tree scale and the 0.25 ha scale (Figure 4.13). Whether reconstructing history of one stand via increment core analysis or following stands over time on sequential air photos, all young stands eventually progress to mosaics or mixtures that can be viewed as very small stands of individual species.

Convergent succession is occurring in the very same stands experiencing divergent succession, at the exact same time, at spatial scales of 1 hectare or more (Figure 4.12). The mixture or mosaic of black spruce, balsam fir, paper birch, and white cedar looks pretty much the same on one hectare as on another.

Cyclic succession occurs when old stands burn, because a substantial proportion of late-successional species invades the jack pine or aspen, before burning and returning to those early successional species (Figure 4.10). The fact that some species such as balsam fir and white cedar do not invade many stands for 100 years or more after fire, and are removed at the time of fire, indicates that cyclic succession occurs.

Succession is individualistic in these forests, because the timing of transition from a matrix of jack pine to a mixture of spruce, fir, birch and cedar depends on the timing of death of the jack pine, which in turn depends on the random nature of windthrow that creates openings in the canopy. The timing of invasion by late-successional species also depends on the distance from surviving seed sources after severe fires, which varies tremendously throughout the BWCAW. A third factor leading to individualistic succession is the random timing of severe crown fires. If a stand burns when young, parallel succession is sure to occur. If it burns when old, cyclic succession occurs. If it burns when very old, and there is no jack pine left, a different as yet unobserved trajectory will occur.

Near-boreal forest summary

A scientist studying these forests with some sort of philosophical agenda as to which models of succession are most elegant or theoretically attractive could get the data to fit any successional model they wanted by adjusting the temporal and spatial scale of analysis. Conversely, the confused scientist who doesn't understand the scale-dependent nature of this forest is likely to remain confused after analyzing the data. I recommend multi-scale, multi-temporal analyses of succession because it appears that the true picture of succession can only be arrived at in that way.

One implication of the study of stand response to disturbance in the near-boreal forest is that stable oscillation between successional states is unlikely. Ludwig et al. (1997) describe a boreal forest where preferential browsing of aspen and birch in young stands and poor reproduction of aspen under its own canopy lead to succession to fir, which in turn increases the density of fir foliage in the canopy until budworm has an ideal breeding environment, and an outbreak occurs which kills much of the canopy. Then fire occurs and the system goes back to the aspen-birch stage. However, when disturbance severity and timing is the main driver of forest change — such as in the near-boreal case study —
such stable-limit cycles are unlikely because there is no reason that disturbances of similar severity should return on a regular basis. Forest-fire intensity, or the rate at which heat energy is released per unit time, is very dependent on degree of dryness of fuels and the weather at the time of the fire in boreal forests (Johnson 1992). Fire intensity has a large influence on whether a fire will stay on the ground or enter the crowns within a closed-canopy conifer forest, and this in turn determines whether the canopy trees are killed. Thus, fire severity is extremely variable from one event to the next — literally as variable as day-to-day weather. Windstorms have a similar variability in degree of blowdown caused, depending on wind speed and condition of stands hit by the wind (Freligh and Lorimer 1991a). Budworm damage to balsam fir in the near-boreal forest depends on stand composition at the stand and landscape levels (Bergeron et al. 1995), thus leading to a wide range of tree mortality among stands. In addition, with an equal chance of burning across stands of all ages, the timing of natural disturbances in the near-boreal forest is very erratic for a given stand. The chance of stand-killing fire does not increase with age, so that the cycle does not necessarily have to go back to the early-successional stage within a certain time frame. Paleoeccological analyses of Swain (1973) and Bergeron et al. (1998) confirm that climate change, by regulating the disturbance regime, has governed the balance between the early-successional group jack pine—aspen, and the late-successional species group white cedar—spruce—fir—birk over the last several millennia in the near-boreal forests of Minnesota and southern Quebec. The spatial structure of the forest at several scales also influences the chances of a regularly oscillating system. If a near-boreal forest is to switch back and forth from jack pine to cedar as the disturbance regime changes, the seed source for species in each forest type must always be present. However, cedar and fir are often removed from stands by severe fires (Freligh and Reich 1995a), and the placement of refuges from fire and size of fire cause large variation in the amount of time it takes for cedar and fir to reinvade after fire, from decades to centuries. Because of this and climate changes, the forest is not likely to cycle through the jack pine and cedar phases on any regular basis.

Case study 3: The near-boreal birch—spruce—fir successional system

This variant of near-boreal forest occurs on sites with better quality soils that are relatively deep and fine textured compared with the jack pine forest (Ohmann and Ream 1971). These are dense forests of mixed aspen, birch, balsam fir, white spruce, and red maple. Good soils favor paper birch and aspen immediately after fire, rather than the conifers. Therefore, these forests were undergoing constant succession in response to fire. Fires remove fir and spruce, replacing them with birch and aspen that dominate the initiation and stem-exclusion developmental phases. During the demographic-transition phase of development (age 50–80 years), balsam fir, white or black spruce and red maple invade from intact forest surrounding the burnt areas, attaining dominance by 80–100 years after fire, and remaining as a multi-aged stand until removed by the next fire. The fir and spruce were often high in density, and able to propagate crown fire as well as jack pine forest. But because they were on less drought-prone soils, they did not burn as often. Average intervals between stand-killing fires were about 100 years (Heinselman 1981a). Successional direction can be both parallel (young aspen stands return quickly to aspen when burned) or cyclic (older stands succeed to fir and then return to aspen when burned).

Case study 4: The near-boreal birch—white and red pine, spruce—fir successional system

Near the borders of lakes, on peninsulas, and on islands within the BWCAW, the severity of fires was often lower than on the contiguous uplands dominated by jack pine, aspen and black spruce. The lake edges are often so rocky that fuel for fires was not contiguous, the humidity was higher, the vegetation in some cases could tap into the water table and remain wet even during droughts, and finally, in some areas, a concentration of large lakes served as fire breaks that interfered with the free movement of crown fires across the landscape. In such areas, crown fires occurred much less often (150–200 years average interval) than in the jack pine forest, and many fires dropped to the ground to become surface fires. Such a disturbance regime, with infrequent crown fires and frequent surface fires, favors the development of red and white pine forests (Heinselman 1973, Freligh and Reich 1995b). Red and white pine can only survive fire as mature adults, meaning that they can only survive surface fire, during which the peak temperature inside the bark does not get high enough to kill living cells, and the foliage is not killed. Saplings are usually killed by fire, since their bark is too thin to provide that much insulation, and the tree can be girdled by fire. Individual mature trees that survive the fire are the source of seed.
If there is a major crown fire, most of the large pines are killed. Paper birch invades rapidly, grows much faster than any pine seedlings present, and dominates for all of the initiation and stem-exclusion developmental phases. The few large pines that survived after crown fire, as well as pines outside the burned area, provide the seed source for a gradual reinvansion of the stand underneath the young birch canopy. This wave of reinvasion by white pine typically takes 1–4 decades (Frelich 1992). As the stand reaches the demographic transition phase of development, white pine break through the birch and begin to dominate the canopy by age 100. At this age, the stands reach a triple-point for potential future development and succession. The stand could have another crown fire and go back to the birch-dominated reinitiation phase. The second possibility is that no fire will occur, leading to succession to shade-tolerant species, mainly black spruce, balsam fir and white cedar (Heinselman 1973, 1981b, Frelich and Reich 1995a). Windstorms hasten succession to spruce and fir because the much taller pines are susceptible to blowdown. The third potential pathway for development of the 100-year-old birch forest with pine breaking through the canopy, is that one or more surface fires will occur. Although the mean age at time of stand-killing fire is 150–200 years, some stands go for 400–600 years without stand-killing fires (Heinselman 1973). White and red pine can be maintained for 600 years or more, as long as surface fires occur regularly. Minor surface fires remove shrubs, invading late-successional tree species, and thick duff, allowing for establishment of new cohorts of young pines. If surface fires continue to occur, the stands become multi-aged, usually with 2–4 main age groups (Frisell 1973, Heinselman 1973, Frelich 1992).

In the rocky lands and sandy lands, white and red pine form stands in areas where fire has less than average presence than the surrounding landscape, due to protection from fire by the landscape and topographical setting. These pines cannot perpetuate themselves without surface fire, and they cannot get along with frequent crown fire either. The fire regime and topographic setting has to be just right, which is why red and white pine occupied a relatively small proportion of Minnesota's forest landscape (about 13%) even in presettlement times (Frelich 1995). The timing of crown fires and surface fires determined whether these forests underwent succession from paper birch to white and red pine, and then on to more shade-tolerant species, or whether they remained multi-aged pine stands for several centuries, or whether they reverted to the jack pine or aspen forest type.

Case study 5: Peatland black spruce
Black spruce has a tendency to occupy wetland sites with sphagnum peat, low pH and low nutrient supply (Heinselman 1963, 1970). Wetland areas that are cut off from ground-water flow get most of their water from rainfall and are the most acidic. These are the raised peatlands that hold onto rain water like a sponge, occupying most of the 'Big bog' just to the west of the BWCAW. Other areas with slowly moving ground water have minerals which neutralize the acid produced by sphagnum mosses, leading to dominance by tamarack or cedar.

These lowland conifer forests did support canopy-killing fires, but only half as often as uplands, so that the average interval between fires was about 150–200 years (Heinselman 1981a). Burning usually did not cause much change in tree composition. The main change that occurs in upland areas after fire is invasion of paper birch and aspen, but these two species do not grow well on peatlands. Succession from one conifer to another on peatlands is determined more by long-term changes (over centuries and millennia) in the thickness of peat, changes in drainage patterns, and climate change than by fires (Heinselman 1963).

Because fires were relatively infrequent in the peatlands, many stands reached old ages. Generally, the stem-exclusion phase lasted until age 150–200 years (Heinselman 1963, Groot and Horton 1994). Stands over 200 years old go through demographic transition and eventually become multi-aged. The developmental changes in this case are not accompanied by any successional change.

Summary: general trends of succession and time lines of stand development
Here I present a quick guide to succession (Box 4.2) in the five forest types discussed earlier in the chapter along with idealized time lines of succession as I believe it would proceed under the historic natural disturbance regime (Figure 4.15). These two features can provide the reader with a condensed tabular and visual summary of the chapter.

**BOX 4.2. GUIDELINES FOR SUCCESSIONAL CHANGE**

THE BIRCH–WHITE PINE, HEMLOCK–HARDWOOD SUCCESSIONAL SYSTEM

- Windfall–severe slash fire combination converts hemlock–hardwood to birch. This type of event has a frequency under natural conditions in the Lake States of once every 100–2000 years.
- Birch succeeds to white pine over a 100–200 year period. Surface fire maintains white pine and lack of fire allows succession back to hemlock–hardwood.
- Hemlock–hardwood forest can sustain light surface fires and windthrow (if the slash does not burn) with no change in successional status.
- The dynamics of the hemlock–hardwood forest are dominated by a web of structural changes as the forest responds to repeated low to moderate-severity treefall disturbance.

**The Jack Pine–Aspen, Spruce–Fir–Birch–Cedar Successional System**
- Severe crown fire at intervals of 20–120 years allows perpetuation of jack pine and aspen.
- Two severe crown fires within a short time remove jack pine and give dominance to aspen.
- Chance lack of fire for more than 200 years allows succession to spruce–fir–birch and cedar.
- Multi-aged spruce–fir–birch–cedar forests can be maintained by windthrow and gap dynamics until the next fire. They may succeed to aspen and black spruce if burned.

**The Birch, Spruce–Fir Successional System**
- Severe fire with mean rotation of 100 years results in removal of spruce and fir and replacement by birch.
- Chance lack of fire for more than 100 years allows succession to fir and spruce.
- Fir and spruce can be maintained by windthrow and budworm.

**The Birch–White and Red Pine, Spruce–Fir Successional System**
- Severe fire with mean rotation of 150–300 years results in removal of pine and/or spruce and fir, and their replacement by birch.
- Surface fires with mean rotation of 20–40 years can maintain multi-aged pine.
- Chance lack of all types of fire for >200 years (shorter time if wind helps to prematurely remove pines) allows spruce and fir to replace pine.
- Spruce and fir can be maintained by wind and budworm gap dynamics.

**Peatland Black Spruce**
- Severe fire results in self-replacement by black spruce.
- Windthrow results in self-replacement by black spruce.
- Succession (if it occurs at all) depends on peatland development and change in drainage patterns.

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Figure 4.15. Idealized time lines of succession for five forest types under the historic disturbance regime in the Lake States. Large triangles, small triangles, and dots indicate the occurrence of stand-replacing fire, light surface fire, and stand-leveling wind, respectively. BA, paper birch and aspen; SF, spruce–fir; SFBC, spruce–fir–birch–cedar; RmRo, red maple and red oak; R-WP, red and white pine.