FORESTRY FACTS

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Forest Succession

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Succession is the natural replacement of plant or animal species, or species associations, in an area over time. When we discuss forest succession, we are usually talking about replacement of tree species or tree associations.

Each stage of succession creates the conditions for the next stage. Temporary plant communities are replaced by more stable communities until a sort of equilibrium is reached between the plants and the environment. The following sequence is usually observed if sufficient time passes and no disturbance occurs:

Plant Community	Description
Grass-forb:	Forbs, grasses and shrubs dominate the site. Seedlings may be present.
Shrub-seedling:	Trees tend to share and then begin to dominate the site. The intolerant species (see Forestry Fact No. 79, Tolerance of Tree Species) grow rapidly and dominate over tolerant species.
Sapling-pole:	Trees eventually overtop and out-compete the forbs and shrubs. The intolerant trees continue rapid height growth while the tolerant trees occupy their respective niche.
Young:	Growth is still rapid. Tree-to-tree competition may be severe resulting in competition caused mortality. Any intolerant individuals that drop behind may die and their growing space may be occupied by tolerant trees.
Mature:	Competition caused mortality continues. Both intolerant and tolerant trees may share the main canopy. In mixed conifer stands there may be a distinct layering of intolerants and tolerants.
Climax:	A relatively stable plant community which has a dominant plant population suited to the environment. Tolerant species dominate the site and the climax species will reproduce successfully under their own shade. These species will maintain the community under the current climatic conditions. Intolerant trees cannot reproduce.

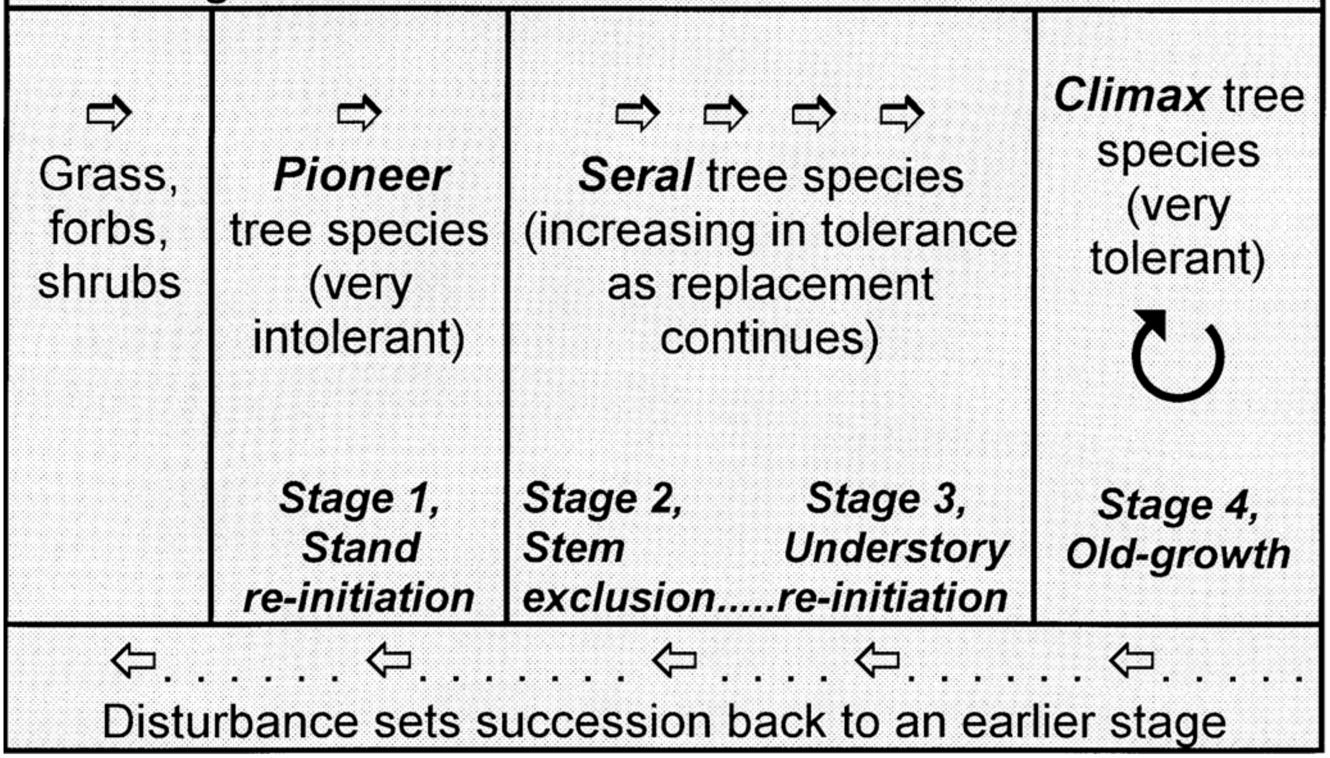
Disturbance

The rate of natural succession is affected whenever a disturbance such as fire, a windstorm, pests or management activities occurs on the site. The more severe the disturbance, or the more often disturbances occur, the slower will be the natural process of succession.

Following a major disturbance, **pioneer species**, such as aspen or jack pine, will become established in open areas under full sunlight. Eventually, in the absence of further disturbance, these pioneer species will be replaced by **seral species** that will occupy the site through a series of successional stages, leading ultimately to a plant community comprised of **climax** species.

Forest successional stages are closely tied to the tolerance of various tree species (see Forestry Fact No. 79, Tolerance of Tree Species, for more information). For example, very tolerant species such as sugar maple, beech and hemlock are climax species on many sites in Wisconsin where they are capable of normal growth. However, sugar maple does not typically grow on dry, sandy soils

Figure 1. ***The Process of Forest Succession***



and therefore cannot replace jack or red pine on such sites.

Other Stand Changes

In addition to the well-studied changes in species composition during succession, there are other changes, in the structure and function of the stand, that are also taking place. Although the changes are subtle and continuous, ecologists have developed relatively simple stand development classification systems to classify forests according to their stage of succession. Figure 1 illustrates the four basic stages of stand development recognized for even-aged forests, and shows how they relate to the typical forest plant communities.

Stand re-initiation denotes the beginning of succession. Woody and foliage biomass steadily increase during this stage. Another important characteristic of this stage is that resources that influence tree growth (e.g. light, water and nutrients) are abundant relative to the other stages of stand development.

The second stage, **stem exclusion**, marks the onset of intense inter- and intraspecies competition for limiting resources, resulting in mortality or self-thinning. Foliage mass reaches a maximum near the onset of this second stage - this is noteworthy because foliage is the tissue that carries on photosynthesis and is the primary tissue regulating the growth of the forests. Foliage mass remains relatively stable or decreases by 10-30% in the older stages of stand development and this decline may be responsible for decreased forest growth in older forests (see the next section).

The third stage, **understory re-initiation**, is characterized by renewed growth of the understory in response to gaps in the canopy caused by tree mortality.

The fourth stage is referred to as **old-growth**; managed forests seldom reach this stage because the growth of these forests is often 10-70% less than young forests in the stand re-initiation or stem exclusion stages.

Succession and Nutrition

Foresters and ecologists have long-known that the growth of forests decreases as they age; however, the causes for the age-related decline have remained a mystery until recently. What is emerging is an interesting story that suggests the decline in forest growth, and other age-related functional changes, are because of the changes in stand structure.

Most notable is the dramatic changes in the nutrient cycles of forests during succession because of the changes in litter quality. Except for forests growing in heavily polluted areas, forests derive the bulk of their annual requirement of nutrients from minerals released from decomposing leaves, branches, stems and roots.

During the early stages of succession a high proportion of the litter is comprised of leaf tissue which, compared to branches and stems, is more easily decomposed by decomposers because of its greater nutrient concentration. In the later stages of succession however, the annual production of tissue falling to the forest floor is comprised of more woody tissue (e.g. branches and stems resulting from the self-thinning stage). Woody tissue decomposes slower than foliage by a factor of 10 to 100, resulting in nutrients being sequestered (locked up) for decades in the branches, twigs and stems.

Numerous studies have shown that nitrogen may limit growth in mature conifer forests while several recent studies suggest that calcium and potassium may limit growth of mature northern hardwood forests. The steady decline in nutrient availability during succession adversely affects leaf photosynthetic rates and causes trees to grow more fine roots and less foliage and stem wood.

A second possible cause for the decline in tree growth during succession is related to greater constraints of transporting water to the top of the tree and end of the long branches in mature trees. Just as it is more difficult to suck water through a long versus short straw, trees have a more difficult time providing water to the very tops of the canopy of mature trees. To compensate for the inefficient plumbing, large trees have a more conservative water balance. If water transport up the stem cannot keep pace with water loss from the canopy (this process is called transpiration) the tree suffers irreparable water stress. Therefore, to avoid permanent damage mature trees restrict the opening of the pores on leaves (stomata) where carbon dioxide is absorbed into the leaf for photosynthesis, and water is lost from the leaf to the atmosphere.

In summary, it seems likely that nutrient and water transport constraints may be responsible for the decline in tree growth during succession and both of the constraints are directly or indirectly related to changes in the structure of the forest during succession.

Impact on Forest Management

Understanding forest succession is very important when we make forest management prescriptions. On some sites it is often easier to work with the natural progression and maintain one of the late successional stages than it is to maintain an early stage.

When harvests are prescribed, heavier cuts cause, in general, greater disturbance to the natural succession process than do light selection cuts. Therefore, if you are hoping to regenerate certain species naturally following a harvest, it is important to know what successional stage these species typically occupy; and, what type of harvest will generate the desired conditions for stand establishment.

What can woodland owners do to minimize the decline in forest growth in aging stands? The most obvious solution is to reduce the rotation length of the forest. Another option might be to fertilize the forest to prevent a nutrient limitation; however, this approach is not inexpensive and in many cases would not be cost-effective. Finally, landowners can minimize the reduction in growth by managing forests such as northern hardwoods (sugar maple, yellow birch, basswood and hemlock) on an uneven-aged basis. Uneven-aged management, while not appropriate for all species, does maintain a balance of healthy, vigorous trees and a smaller number of mature trees.