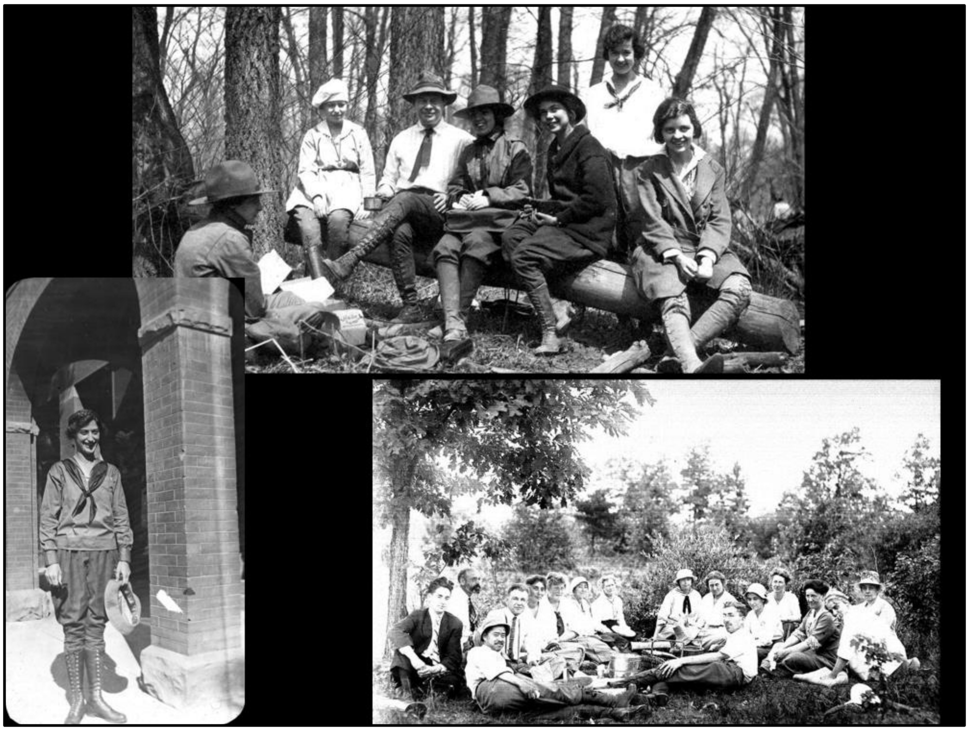
Examples of *ecological succession* so far concern how communities develop following *disturbance* of a pre-existing community; in these instances, the sequence of succession may be much influenced by the nature of the pre-disturbance community (in the form of seed-banks, organic matter accumulations, etc.). Ecologists often distinguish between (re)development of communities following disturbance and development of ecological communities on new substrates where conditions are not shaped by a pre-existing community. The former process is called *secondary succession* (e.g., dynamics following a forest fire or blowdown); the latter is *primary succession* (the initial development of ecological systems where none existed previously). Unstabilized dunes of pure sand can be a substrate for *primary succession*.



Historical interlude: Primary succession on dunes was first studied by Henry C. Cowles (middle, upper photo) at the University Chicago in the years around 1900. Many photos of his botany classes are archived at the Library of Congress 'American Memory' website. They're interesting for the field costumes. Also note the high proportion of women in the botany classes; at this time, botany was considered an appropriate field of study for women; conversely, it was sometimes regarded as *in*appropriate for men…

In large dune fields along the south and west shores of L. Michigan, Cowles recognized that dunes closest to the lake were youngest and dunes progressively further from the lake were older. He reasoned that the vegetation along such a series of dunes might represent different stages along a sequence of vegetation development (assuming that the different dunes have developed under relatively similar circumstances). This approach to studying long-term dynamics – comparing current samples from different places that are presumed to be at different stages of a similar process – is a common approach now, and is referred to as a *space-for-time substitution* (or, sometimes, a *chronosequence* study).

The youngest dunes are a stressful place for plant growth. They're not very fertile (quartz sand contains little in the way of mineral nutrients), sand does not hold water well (because the soil pores are relatively large), and the substrate is extremely unstable. The sand is continuously shifting in the wind, and roots of plants might be exposed, or the plants smothered. Most types of plants can't survive this. Some have special adaptations that allow them to cope. *Ammophila breviligulata* or beach grass (found also along the east coast), for example, is able to send out new roots along the stem as it gets buried, and to spread by sending out horizontal underground stems (or rhizomes). As beach grass spreads across the dune, its roots tend to bind the loose sand and gradually stabilize it.

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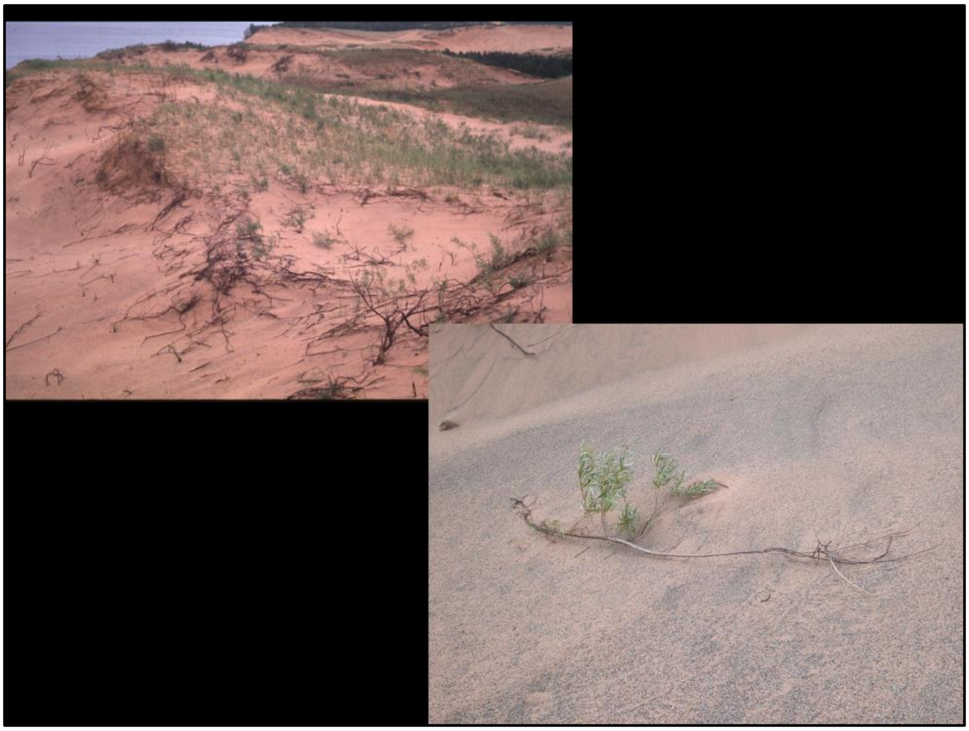
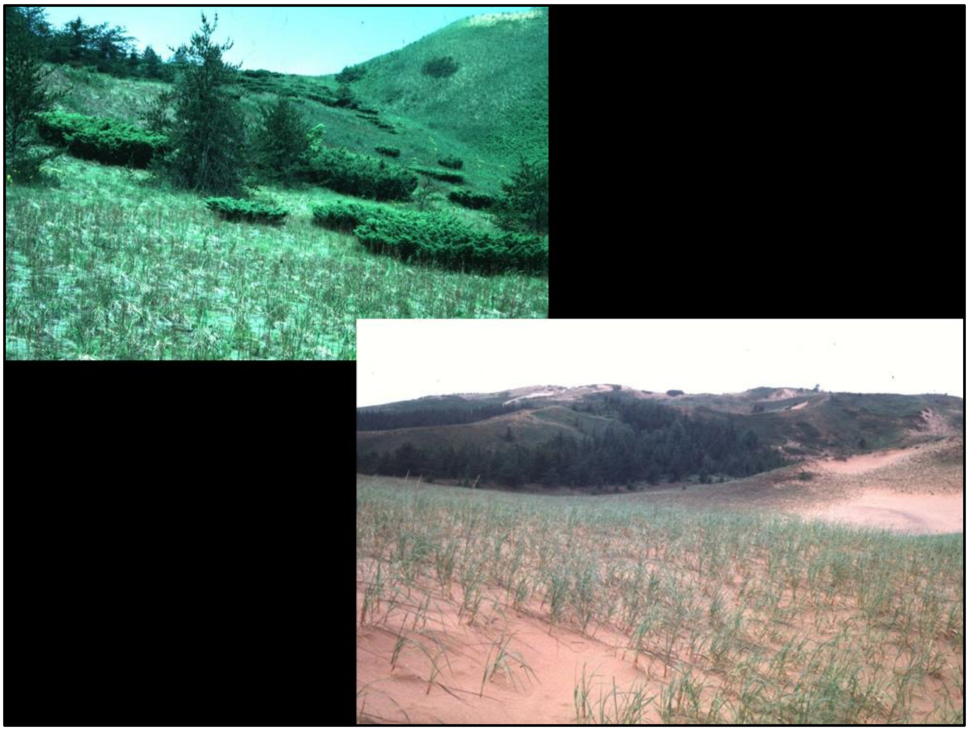
Other plants can do similar things; wild strawberry (top) can also spread with aboveground *stolons*. As the sand is stabilized, woody plants can become established. Willows are one of the earliest types of woody plants that can colonize the dunes; they, too, are able to root along buried stems and survive some burying. Note that accumulation of a mound of wind-blown sand around the willow shrub at lower right.



This process is not irreversible; severe storms (or foot or vehicular traffic) can disrupt the root systems and cause ‘blow-outs’ where the sand becomes loose and mobile again. In the lower image, an exposed willow root is producing a leafy sprout in a blow-out.



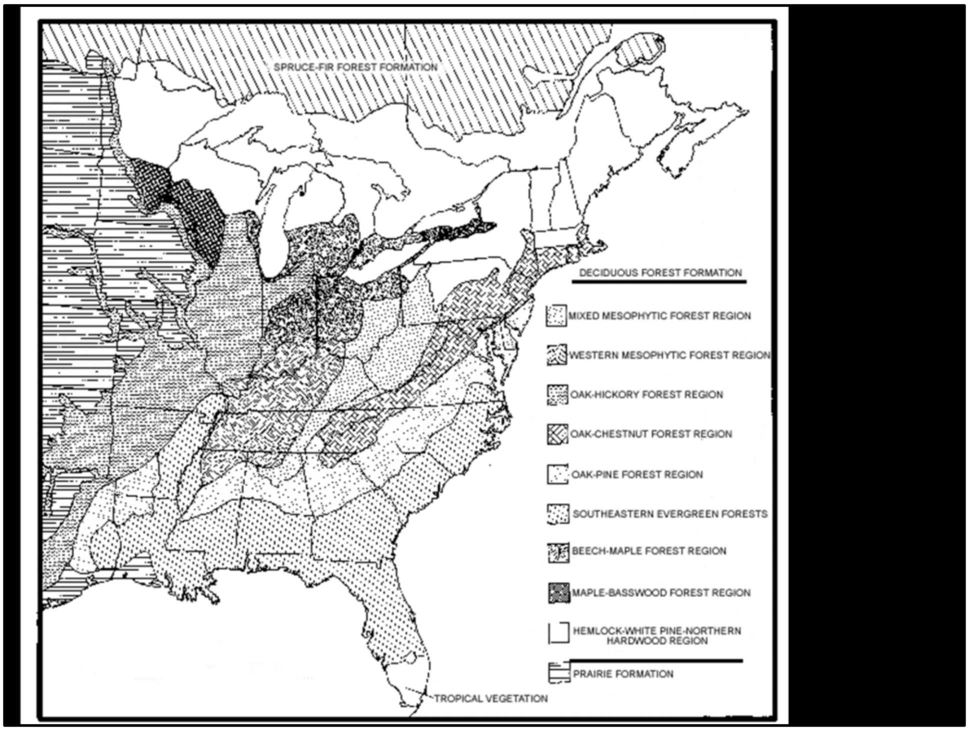
But, generally, earlier colonists *change the environment* – adding organic matter and nutrients to the soil, binding it in place with root networks, etc. -- in such a way to make it more amenable to other species. Older, stabilized dunes are colonized by additional species of woody plants, including trees; as these grow and spread, they shade out the early successional grasses and willows. The alteration of environment by earlier colonists so as to favor other species is sometimes called *facilitation*.

The forest in the background occupies one of the older dunes, and is dominated by beech and maple – shade-tolerant species. Cowles was one of the first people to recognize the potential for *plants in early succession to alter habitat conditions in such a way as to make the establishment of later-successional species possible* when those species might have been entirely unable to survive on the site initially. This is very different from most secondary successional dynamics; there is no reason why spruce and fir *can't* grow on a newly burned site, for example; they just, typically, don't get there and grow as quickly as jack pine and aspen. But beech and maple trees would be entirely unable to survive on a new sand dune. The process of habitat alteration that permits (and is essential for) establishment of later-successional species (superior competitors) is called *facilitation*. It can be important in primary successions.

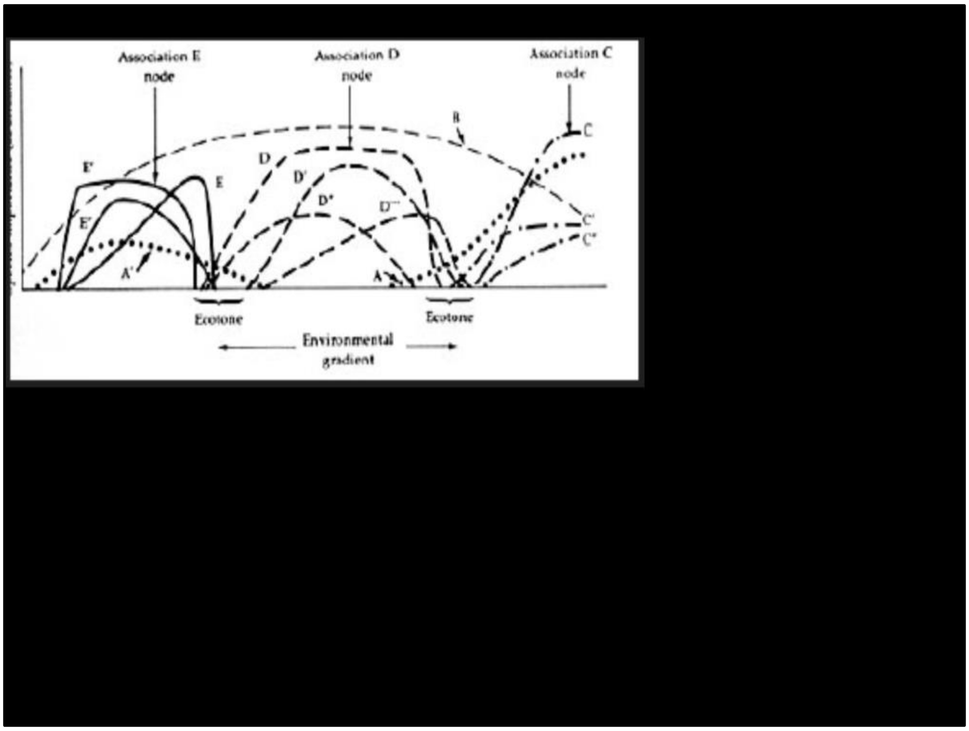
" The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies... Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity its development."

MORE HISTORY:

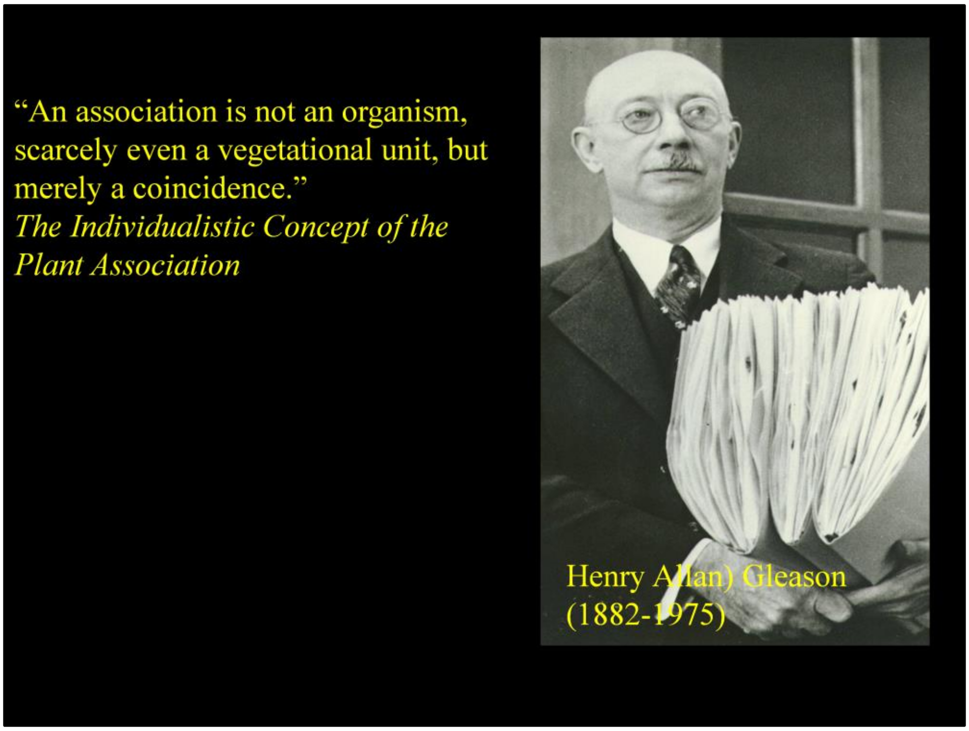
Cowles' ideas about succession suggested that the sequence of community change during succession is a) predictable, and b) leads eventually to a stable, 'climax' community. These ideas were developed and codified by Frederick Clements in the early 1900s. Clements argued that ecological communities were highly integrated entities, analogous to organisms; in his model, succession was parallel to the development of an organism from infancy to adulthood. This model emphasizes the notion of 'facilitation' by early-successional communities as parallel to early stages of development of an individual organism 'preparing' for later stages.



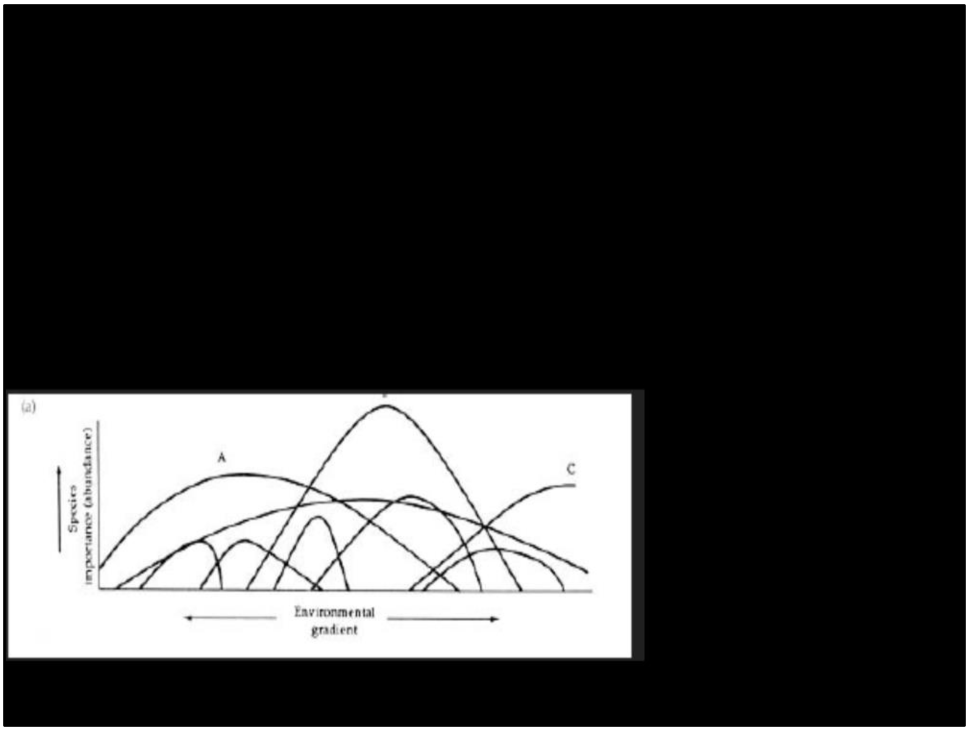
This model of communities as highly integrated entities also led to the perception of communities as coming in particular, distinct ‘types’ (just as organisms come in particular, distinct species). In keeping with this thinking, many maps of communities or ecosystem-types show distinct boundaries. (This map is from an important book by ecologist E. Lucy Braun on the deciduous forests of eastern North America.)



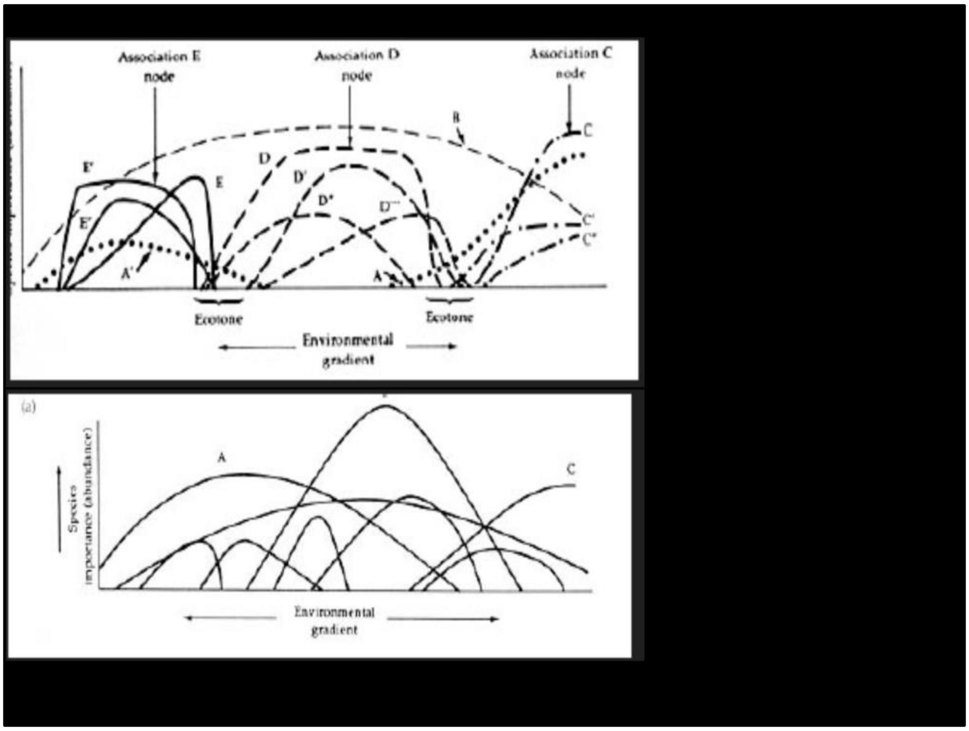
This notion of communities as **discrete** systems with **deterministic** developmental pathways is sometimes called the 'pseduo-organismic' hypothesis, and it is generally associated with Frederic Clements. In this model, for example, if you traveled along an environmental gradient (say the slope of a mountain), you would encounter long stretches where communities would be relatively constant, with narrow zones of transition from one community to the next. Such transition zones were called 'ecotones'.



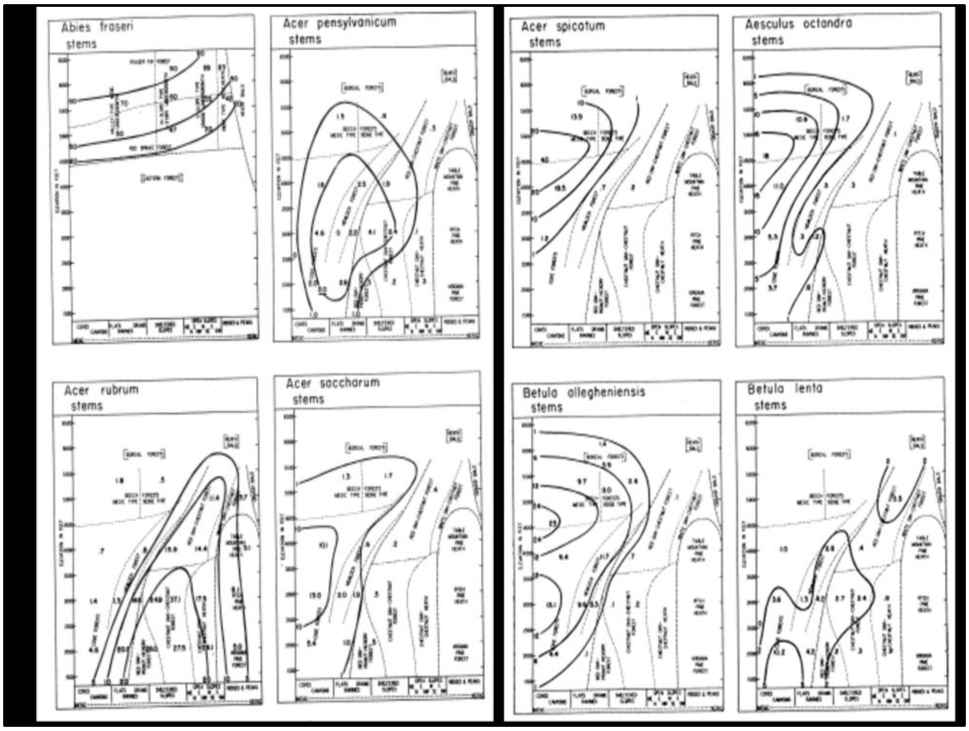
Some ecologists questioned Clementsian thinking, doubting whether real communities and ecosystems were so tightly organized and predictable. Henry Gleason was one of the most important of these skeptics. He argued that environments varied so complexly and historical influences have been so strong that species assemblages are much less integrated and predictable, and that transitions should tend to be gradual. His *individualistic hypothesis* of community assembly argued that each individual species would be distributed according to its unique environmental tolerances and the chances of dispersal. This would mean, he argued, that each successional pathway might vary uniquely from others, and community composition should vary continuously with environment.



So, if you traveled the same environmental gradient considered earlier, you would witness a gradual and continuous turn-over of species and a *community continuum*. This is sometimes called the ‘continuum concept’ of community organization.



Clements' 'pseudo-organismic' concept illustrated at top – predictable associations with ecotones – Gleason's continuum concept at bottom – no sharp boundaries, no recognizably distinct 'associations.



These conflicting ideas remained little tested for many years until, in the late 1950s, several ecologists began to generate large data-sets from vegetation sampling across landscapes. Robert H. Whittaker collected data from habitats across the diverse landscape of the Smoky Mts. He mapped distributions of individual tree species against elevation (vertical axis here) and a moisture axis related to steepness and direction of slope (horizontal axis here). Think of the solid curves on these graphs as analogous to contour lines on a topographic map. The ‘high points’ or peaks represent habitats of maximum abundance. Whittaker found that species distributions did not fall into coherent groups; rather, each species’ distribution was unique – much as predicted by Gleason’s individualistic hypothesis.

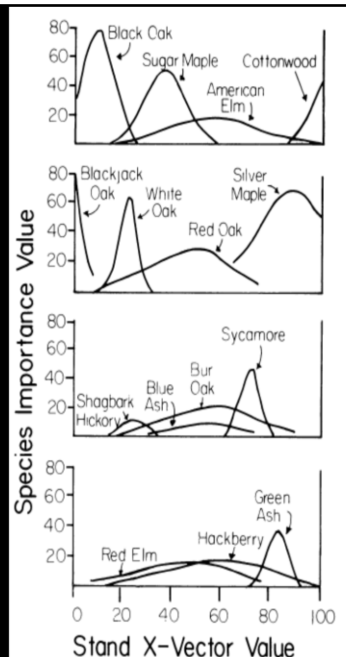
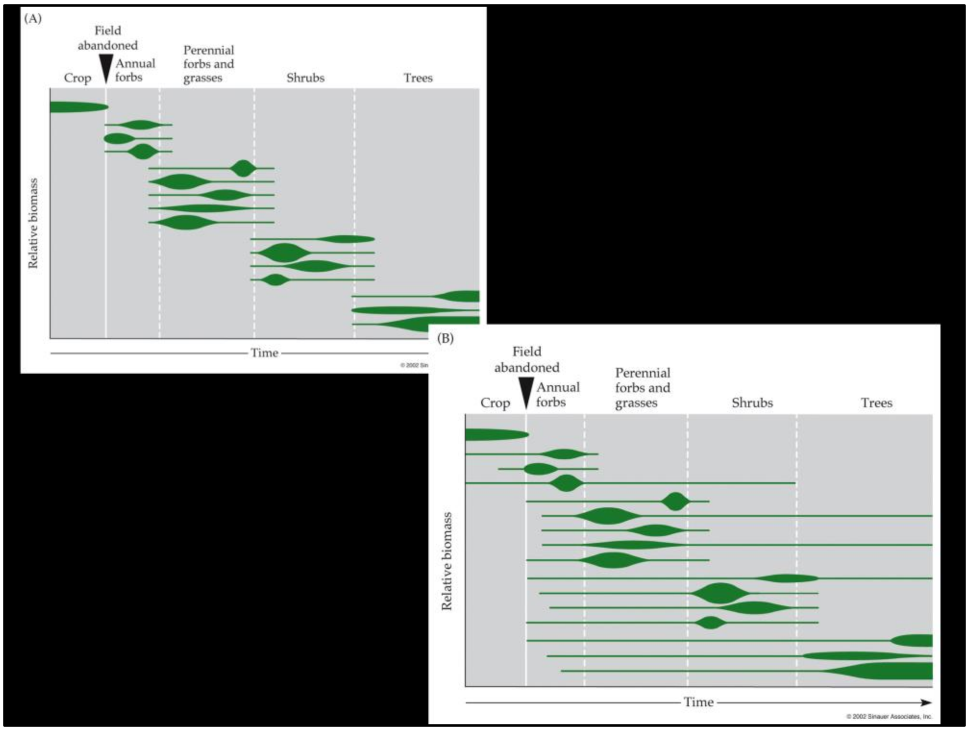


Fig. 1. Gaussian curves ($P < 0.05$) for fifteen tree species populations along a moisture gradient in central Illinois.

Similar studies by John Curtis at the University of Wisconsin showed species distributed individualistically along moisture gradients. These studies and others ultimately led to general acceptance that communities were more ‘individualistic’ and varied in a continuous way along gradients – i.e., Gleason’s model. (Fortunately, Gleason lived long enough – into his 90s (see slide with his photo) – to see his ideas vindicated.



Similar debates concerned how communities changed over *time* in succession – did distinct communities predictably give way to one another? Or did species arrive, thrive, and fade away due to competition according to individual tolerances and when they arrived?

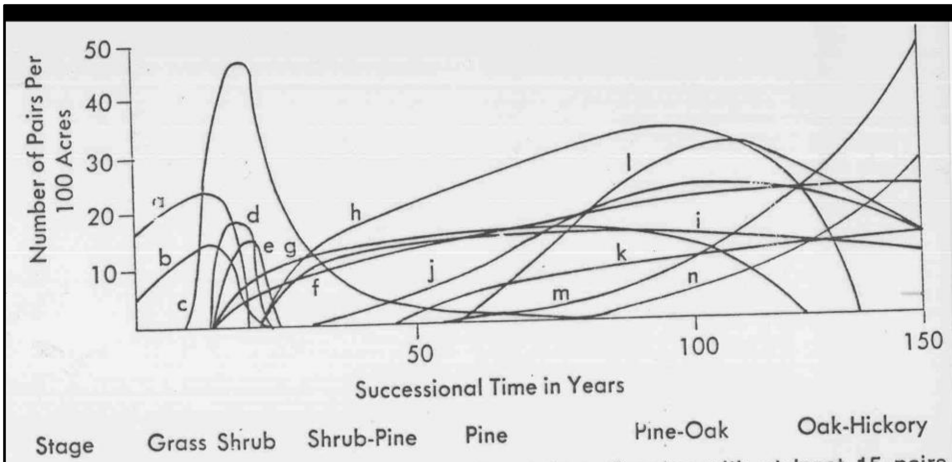
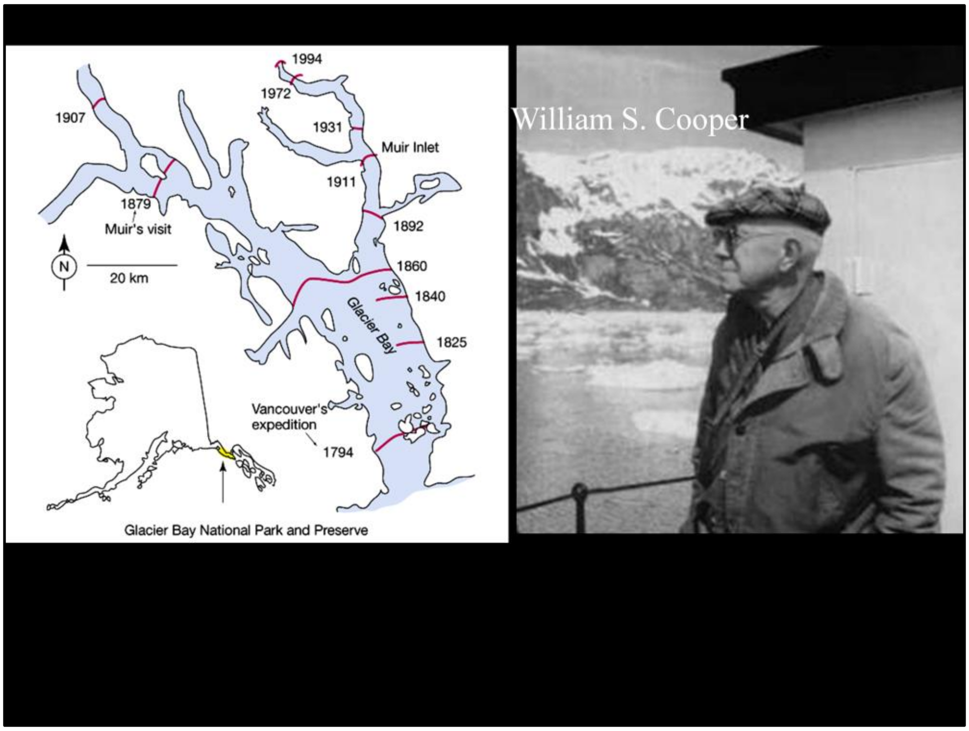


Figure 4.13. Bird populations in successional time. Species with at least 15 pairs per 100 acres (40 ha) are shown for an old field-to-forest succession in the Piedmont region of Georgia: (a) grasshopper sparrow, (b) meadowlark, (c) field sparrow, (d) yellowthroat, (e) chat, (f) cardinal, (g) towhee, (h) pine warbler, (i) summer tanager, (j) Carolina wren, (k) tufted titmouse, (l) hooded warbler, (m) red-eyed vireo, and (n) wood thrush. [Johnston and Odum, 1956, Table 1; and Ricklefs, 1973, Fig. 39.7.]

Here is a diagram of bird species presence across communities of different age (in succession following agricultural abandonment in North Carolina). The pattern is *mostly* 'Gleasonian' – i.e., species abundances changing individualistically and gradually. A rapid turnover at about 20 years corresponds to the establishment of woody canopy – from 'bird perspective' a sharp change in environment…

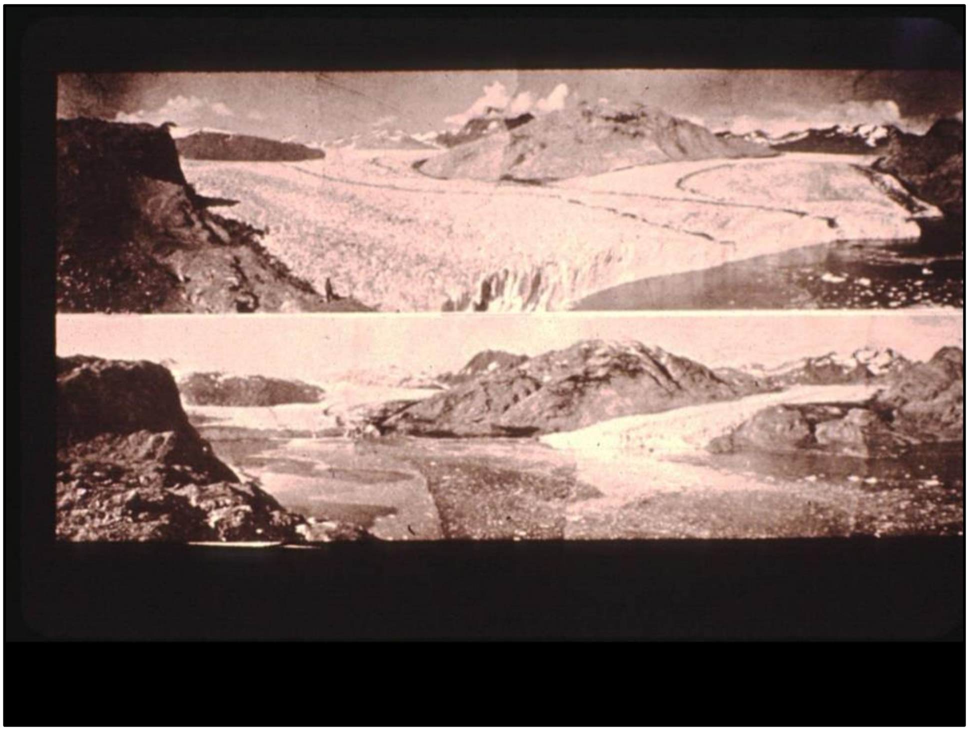
‘Classical’ succession-to-climax theory has generally held that, following *any* kind of disturbance, communities will eventually return to the climatically determined ‘climax’ state. Gleasonian individualistic ideas do not necessarily predict this. In some cases, ecologists have documented cases where, following disturbance, community succession seems *not* to lead back to the prior community. Here, forests logged about 125 years previously have failed to regrow as forests at all (typically, tree cover is re-established after 20-30 in this area in northern Michigan). A different community of grasses, ferns, small shrubs, and lichens seems quite stable. There are various hypotheses for why this should occur, but such examples challenge traditional ideas of succession.

Here, a Vermont old-field, after about 60 years, has not regrown to forest, but is dominated by shrubby dogwoods, asters, and goldenrod. Some of these species may chemically suppress tree regeneration (this is called *allelopathy*).



Finally, a couple of additional classic stories of primary succession to end the section on community succession.

William S. Cooper (University of Minnesota) studied succession following glacial retreat at Glacier Bay in Alaska. Glacier Bay was completely filled with ice until about 1800. Subsequent recession exposed fresh ‘glacial till’ substrate. Observations over the years allowed Cooper to assign dates for particular areas and ages to the communities liviing there.



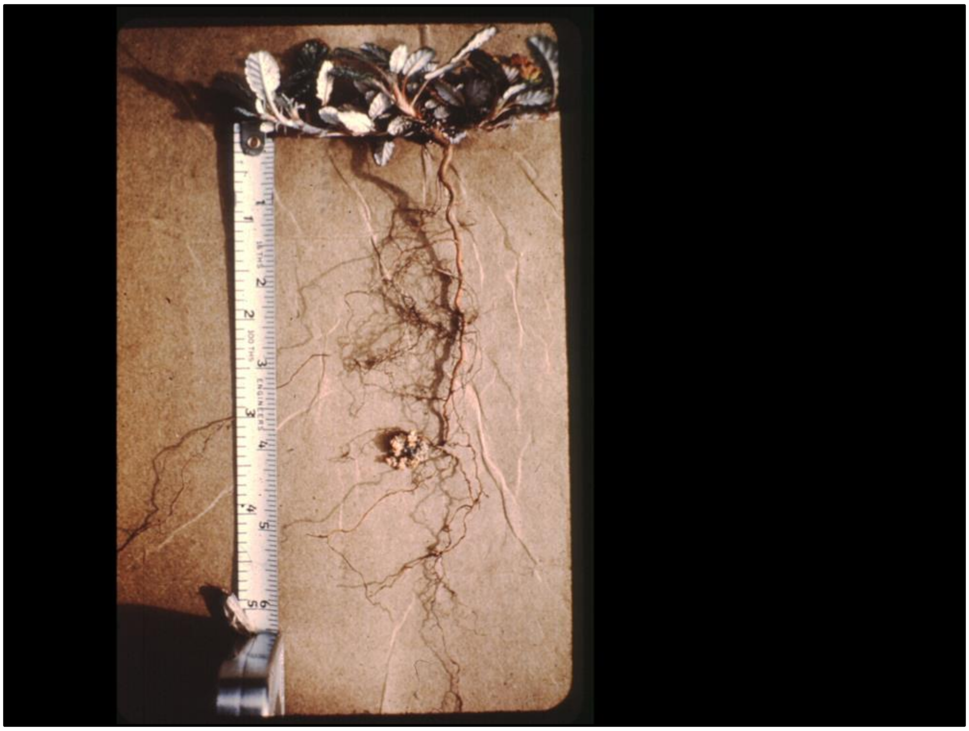
An example of glacial recession (these and subsequent slides are copied from Cooper's photos, so some are rather faded…)

Fresh glacial till is extremely poor in nitrogen

Here is an early-successional fireweed, extremely stunted by lack of N

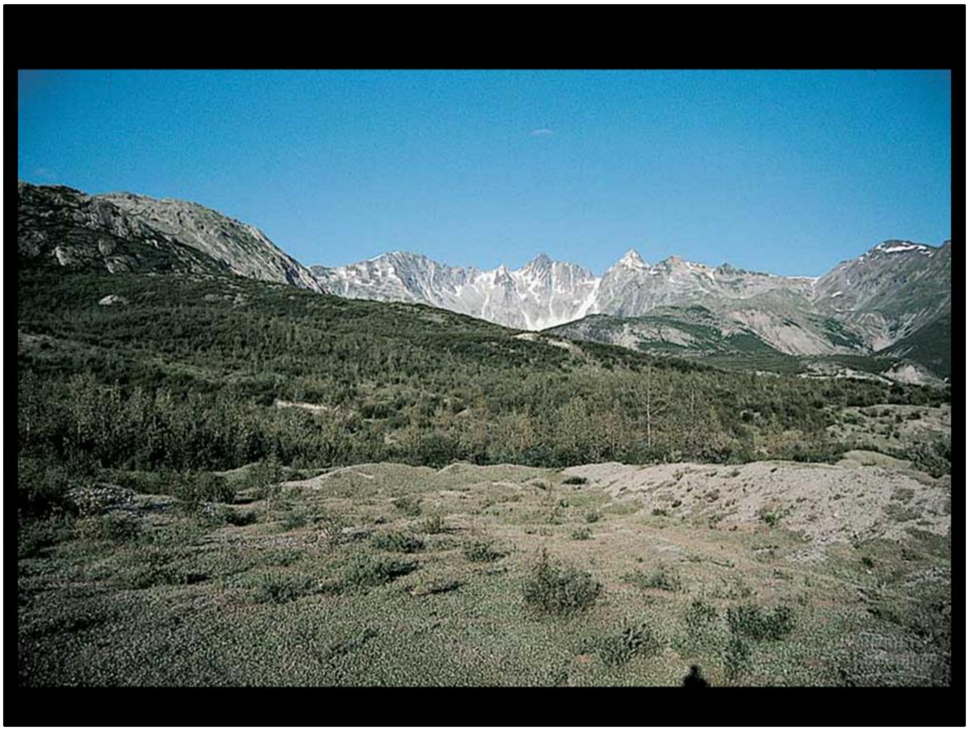
In this situation, nitrogen-fixing species are strongly favored. Here, a lupine (nitrogen-fixer) is thriving on the new till surface without much competition; a fireweed growing next to it (pink) is much larger than other fireweeds not benefiting from the lupine's presence.

Bird droppings (here, concentrated due to raptors' habit of perching on high points like this rock) can also provide nutrients.



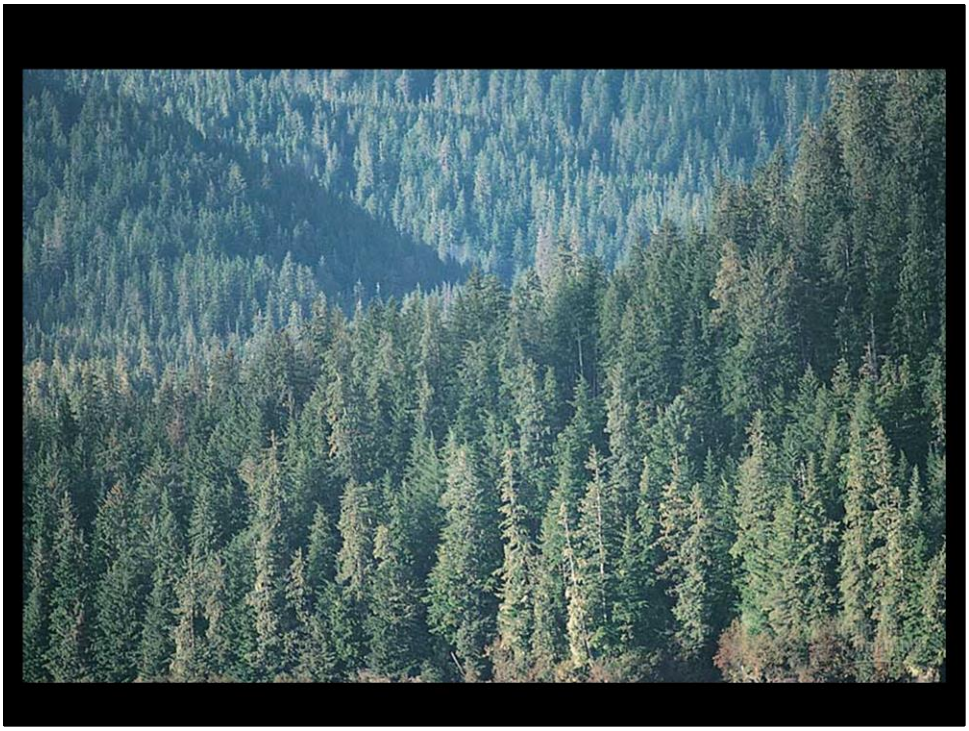
Not all N-fixers are legumes; this plant – called *Dryas* – is N-fixing but in another family. You can see the nodules on the roots where the N-fixing bacteria reside.

After 20-30 years, the till is covered by nitrogen-fixinig species of several families (the pinkish white is *Dryas* in bloom), including the small trees – alders – shown here. As alder cover spreads, most of the other early successional plants are displace due to light competiton. I.e., *light has become limiting.*



Younger surface in the foreground with lupines and ‘*Dryas*’ (another nitrogen fixer); alders in the middle distance; and, in the background, shade-tolerant spruces replacing the alders

Eventually, western hemlocks, the most shade-tolerant species in the region, come to dominate (after perhaps 300-500 years).



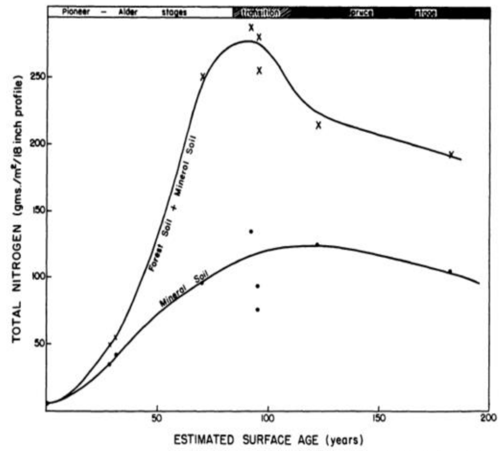


Fig. 14. Differences in the total nitrogen content of soils on surfaces of varying ages.

Soil Development in Relation to Vegetation and Surface Age at Glacier Bay, Alaska

Robert L. Crocker; Jack Major

The Journal of Ecology, Vol. 43, No. 2. (Jul., 1955), pp. 427-448.

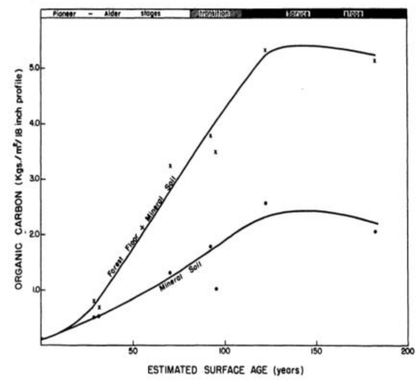
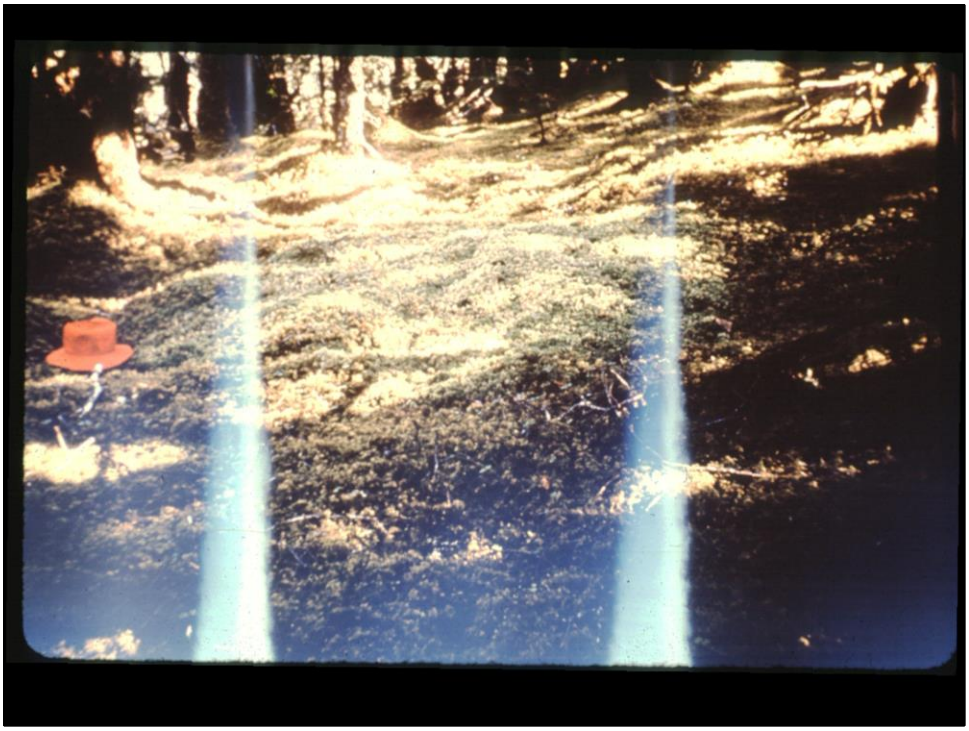
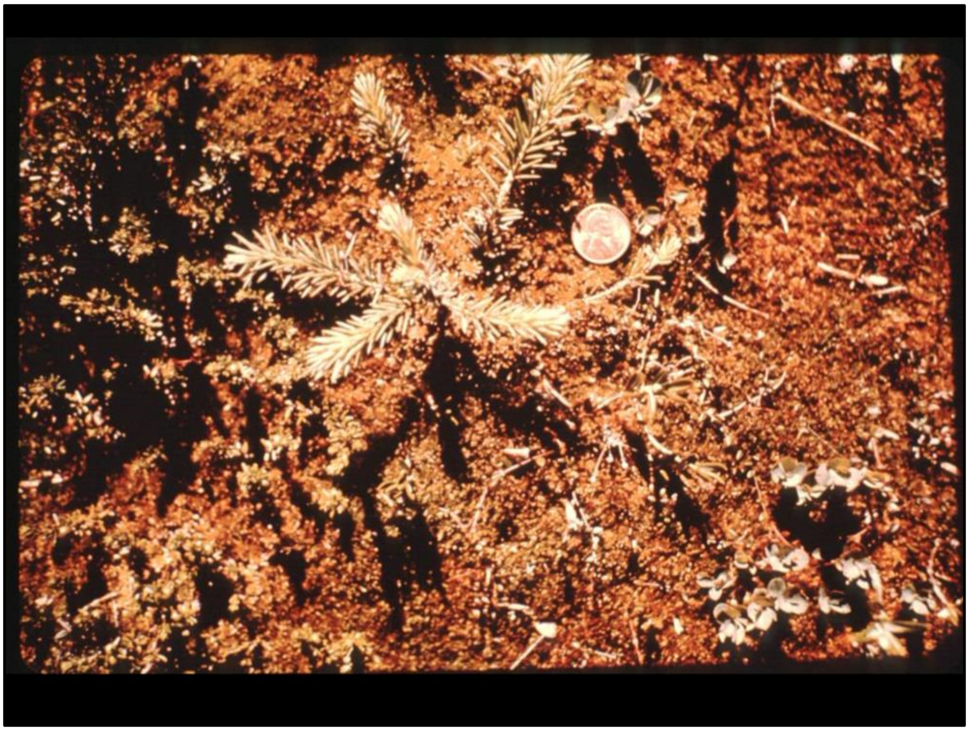


Fig. 12. Organic carbon accumulation within the mineral soil and forest floor.

Over the course of succession, nitrogen concentrations in the soil increase as nitrogen-fixing activity adds N-rich organic matter to the soil. After spruce and hemlock displace the alder, however, N-concentrations tend to go back down again.



In this cool, moist climate, *Sphagnum* mosses (related to those we saw in the bog) tend to develop in the shade of spruce and hemlock forests. These mosses are biological sponges; they retain water. Consequently, water tables tend to rise. This photo shows a mat of *Sphagnum* growing in a hollow in the forest.



As water tables rise, seedlings of spruce and hemlock are overgrown and drowned. Tree regeneration begins to fail.

Even mature trees become unhealthy and die as their roots are continuously flooded.

And forests are replaced by open bogs – a process called *paludification*

Where decay of the organic peat is acclerated (here, by a plant called skunk cabbage that generates heat), small pockets of open water can form in what was once upland forest.

Once established, bogs can spread laterally. Here, the spreading of bog into forest is apparent in the line of dead trees at the edge of the bog

Eventually small patches of open water can develop (they are called ‘flarks’). This whole process seems to run contrary to classical successional theory that regarded the forest of shade-tolerant hemlock as the climax. Some traditionalists attempted to ‘explain’ this process as ‘reverse succession’, and described the bog as a ‘disclimax’ (if you name a problem it’s no longer a problem).

Volcanic eruptions provide a dramatic opportunity to study succession. Mt. St. Helens in the Cascades of Washington state has been particularly well studied since a major eruption in 1980. In a large area below the main eruption site, deposits of volcanic material many meters thick initiates a primary succession.

Ash surfaces left by the eruption are also N-poor, so often favor nitrogen-fixers. Otherwise the course of succession is largely determined by dispersal rates.

Again, N-fixers play an important role. Occasionally, remnant logs were deposited on or near the surface of the ash flows; these can also provide a localized source of nutrients as they decay.

Some areas suffered near-complete destruction of pre-existing forests, but did not experience deep ash deposits; these areas undergo secondary succession influenced by dormant seeds, existing deposits of organic material in the soil, resprouting roots, etc.

Some areas just out of the blast zone were not much disturbed; these can serve as seed sources for rapid recolonization.

In even more moderately affected areas, trees were killed by the blast, but not blown down.

Soils in forests throughout the region show layers of ash deposits from past eruptions. These serve as an important input of some nutrients. This stand was not killed by the eruption, but received several cm of fertilizing ash.

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