FOREST VEGETATION AND SOIL SUCCESSION
The natural process of change

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Summary

Forest communities are complex systems comprised of populations of organisms representing every kingdom of life – plants, animals, fungi, protists, and monists – living and growing together on the land. They are part of a larger group of communities that constitute the regional ecosystem, or landscape. Forest communities are developmentally related to the surrounding communities in ways that can be characterized through chronosequence studies. Chronosequences from southeast Alaska and subarctic Canada are described and interpreted as indicating that, while early successional processes facilitate forest growth and productivity, later successional processes tend to slow and inhibit forest growth and regeneration. In many places forests are seen to have transitioned into peat bogs over the course of several thousand years. This is thought to reflect the true climax nature of bog ecosystems.

Forest to bog transitions are linked to two main developmental processes: podzolization and paludification. Podzolization affects many northern forests and involves the translocation of iron, aluminium, clays and organic compounds in response to vegetation, especially mosses, acidifying and leaching the soils. This is often followed by paludification, which occurs as peat-forming mosses, such as *Sphagnum* species, become established and expand.

From the perspective of succession, forests are seen to flourish under early successional conditions, conditions that are enhanced by periodic or regular disturbances. However, where disturbances are eliminated, forests begin to show decline as a consequence of natural successional changes. This work points to the potential for managing forest ecosystems through the maintenance of disturbance regimes and the remediation of acidification tendencies in the vegetation and soils.

Introduction

All living things undergo cycles of change – life cycles if you will – involving periods of growth, expansion, and maturation followed by periods of deterioration, contraction, and death. If at some point along this cycle the seeds for the next generation are sown, and these seeds regenerate, then that system will reform, grow, evolve, mature, collapse, and die again. And so on. We see these cyclic processes occurring in cells, organisms, and ecosystems alike. After nearly four billion years, it can be said with some certainty that these inherent cycles in nature, be they phenological cycles, life cycles, or successional cycles, constitute successful strategies for the maintenance of life on Earth.

Ecosystems and succession

Take an assortment of plants, including trees, shrubs, forbs, grasses, ferns, and mosses; a collection of animals, including mammals, birds, snakes, snails, insects, and worms; various fungi, including toadstools, lichens, bracket fungi, mycorrhizae, leaf rusts, yeasts, and slime molds; lots of protists, including paramecium, rotifers, phytoplankton, diatoms, and amoebas; and a whole lot of monists, including cyanobacteria, nitrifiers, denitrifiers, methanogens, and viruses; place them together in a watershed, water regularly, allow for a few thousands years of soil development, and Nature willing, you will have grown yourself an ecosystem. Ecosystems are massive living, breathing forms with distinctive shapes, colors and textures that feed and grow in fairly predictable ways. Like the cells of an organism, trillions of individual organisms work in concert to modify their environment and self-organize into communities and landscapes (and seascapes) which undergo developmental successions of birth, growth, maturation, senescence and death. The set of characteristic stages in ecosystem succession that occur over years, decades, centuries, and millennia is referred to as a sere.

Ecosystems are complex systems that exhibit various degrees of self-organization and self-regulation (Klinger 2004). They possess patterns and behaviours that are fractal, or self-similar, in appearance. From an earth system perspective they are the organs of Gaia (Lovelock 1995). Ecosystems are key to the regulation of oxygen, temperature, ocean salinity and just about everything else that is needed to sustain life. Inhalations and exhalations of forest ecosystems are vital in the planetary respiratory system and the exchange of atmospheric carbon dioxide.

From time to time ecosystems are perturbed by forces like fires, floods, landslides, hurricanes, volcanoes and glaciers. These are the destructive negative feedbacks built into the life cycles of ecosystems. But, no matter how severe the disturbance, a new ecosystem will eventually be born.

There are three major kinds of developmental seres in terrestrial ecosystems: xeroseres, successions occurring on well-drained sites; mesoseres, successions occurring on poorly-drained sites; and hydroseres, successions occurring in freshwater ponds and lakes. Seres can be identified through chronosequences, natural experiments where phenomena such as retreating glaciers or volcanic cycles have created a series of surfaces of increasing age. Seres can also be characterized by simply observing the major changes in vegetation and soils at any given site over many years and decades.

The first sere I ever studied was in the Front Range of Colorado, where several historic flood events created a set of river terraces bearing a chronosequence of plant communities (Figure 1). The sere began with a meadow of annual grasses and forbs, followed by a dense thicket of willows, followed by stands of aspen and pine, and ended in what I believed was a climax forest dominated by 200+-year-old Douglas firs. Because these communities were found on well-drained soils, this succession would be considered a xerosere. Over the years, I have observed that similar versions of this sere are pervasive over much of the Colorado Front Range. While the species are not always the same, the growth forms at each of the stages show remarkable similarity from place to place.

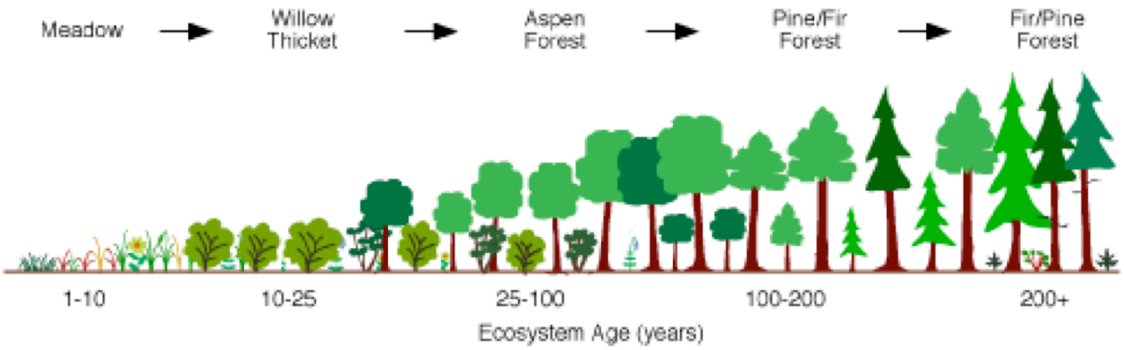

Figure 1. A generalized successional sequence of vegetation communities described from a river terrace chronosequence in the Colorado Front Range.

Climax theory

Successional theory, which has been developed mainly from a vegetation perspective, is a central topic of debate among ecologists, divided, generally, between two viewpoints. The long-standing organismic viewpoint is that succession represents a developmental, ontogenic process in ecosystems resulting in the formation of structurally and compositionally stable (climax) communities (Clements 1916; Margalef 1963; Odum 1971). From this perspective, climax ecosystems are equivalent to the developmental stage of maturity or adulthood in an organism. This view holds that succession toward a hypothetical climax community, usually old-growth forest, is a deterministic process of vegetation change in the sense that if one knows the initial environmental and biological conditions the successional sequence can be predicted.

Conversely, the individualistic viewpoint considers succession to be an indeterministic process of change in response to forces in the physical environment and to the various life history traits of the individuals involved (Gleason 1926). This view questions the existence of climax communities in light of work showing that old-growth forests do not exhibit structural or compositional stability (Jones 1945; Raup 1963). Also, early succession in many places has been shown to progress along several different pathways due primarily to the influence of exogenous forces and is therefore not readily predictable (Connell & Slatyer 1977).

This paper takes the view that, despite the sometimes unpredictable nature of youthful ecosystems, succession is a deterministic process that follows the rules of self-organization and self-regulation (Kauffman 1993). Thus, in the absence of disturbance, successional pathways tend to converge onto a narrow range of mature, late successional communities, and, that in the absence of large-scale physical disturbance, terrestrial and freshwater vegetation successions converge onto climax communities exhibiting structural and composition stability of the order of thousands of years.

Disturbance is considered here to be any environmental phenomenon resulting in the sudden (< 1 yr) decline or death of a majority of the individuals of one or more dominant species in a community. Examples of disturbances are grazing, fires, landslides, hurricanes, floods, extreme droughts and volcanic eruptions.

Interestingly, a lineage of ecologists studying peatlands have repeatedly suggested that terrestrial successions, rather than ending in climax forests, continue on and culminate in climax peat bogs and mires. Successions leading to climax peatlands have been described in Siberia (Katz 1926), southeast Alaska (Zach 1950), northern Alaska (Viereck 1966), British Isles (Walker 1970), and various locations in the tropics (Flenley 1978).

The notion of a peat bog being a climax community is supported by the observation that vast areas of old-growth undisturbed forest in Alaska, Canada, Scandinavia, Russia and elsewhere are slowly being converted to peatlands (Neishtadt 1977). Peatlands are landscapes of assorted plant communities growing on peat-rich soils. Peatland communities come in various types: bogs, fens, muskegs, swamps, marshes, mires, and moors. Peatlands often form by paludification, the collapse and death of old-growth forest trees and their eventual replacement by more acid-loving species dominated by dwarf trees, ericaceous shrubs, sedges, and peat-forming mosses, especially *Sphagnum* species. Peatlands, themselves, go through a series of developmental stages which appear to converge, over time, into ombrotrophic peat bogs. Ombrotrophic refers to the condition of peat bogs that have grown so thick that the surface vegetation is decoupled from the underlying mineral soil and groundwater such that all the moisture and nutrients are derived from the atmosphere.

Chronosequence studies

Southeast Alaska

Chronosequences are fortuitous natural experiments that allow us to substitute space for time. Places in nature can be identified where sites that are adjacent to each other in space are also proximal in their origin. That is, each site has originated just prior to an adjacent site. Receding glaciers, shifting rivers, isostatic rebound, and tectonic uplift are processes that typically produce chronosequences.

Southeast Alaska is home to a number of well-documented chronosequences. Glacier Bay is a newly emerging landscape where glaciers have receded over 60 miles in the past few hundred years. Here the land reveals its story plainly in footsteps down the valley, much like the pages of a book. At glacier's edge the new land looks barren, but the soils are, in fact, already teaming with bacteria, algae, and many other cryptic life forms. A bit further down the valley pioneer plants such as dwarf fireweeds and mountain avens dot the land. Keep walking and grasses and dwarf willows will appear, followed by alders that form dense thickets and fix nitrogen in the soils. Further on, cottonwood trees start to emerge from the alders, and soon a cottonwood forest appears. Continuing down the slope we run into an occasional young spruce tree, then many young spruces. By the time we've reached the tall, old-growth spruce forest at the end of the valley, we will have walked the equivalent of 250 years of ecosystem growth and development.

Beyond Glacier Bay are older landscapes with chronosequences showing details of the later stages of landscape succession. The marine terraces and volcanic slopes of nearby Mount Edgecumbe indicate that the tall spruce forests are soon replaced by tall hemlock forests, which in turn are replaced by the short-statured, open canopy forests of cypresses, hemlocks and/or pines. These tend to give way to dwarf forests, then to bog forests, and finally to ombrotorphic *Sphagnum* peat bogs. The entire succession of vegetation from barren lands to bogs in southeast Alaska, which takes place over several thousand years, is summarized in Figure 2. This figure also shows the acidification of soils during succession with a pronounced lowering of the soil pH (increase in acidity) in the conifer forest stages.

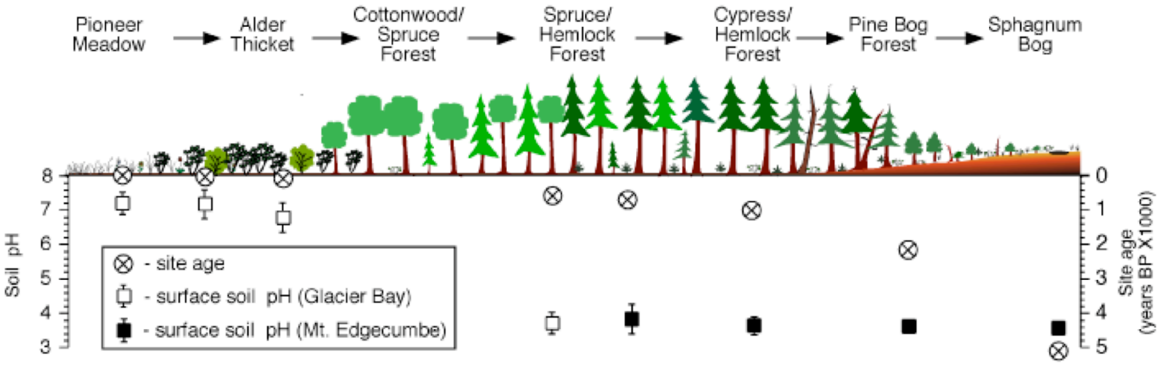

Figure 2. Summary of successional changes in vegetation and soils in southeast Alaska based on chronosequence studies from Glacier Bay (Chapin et al. 1994) and Mt. Edgecumbe (Klinger 1988).

The peat bogs in the region are extremely old. On Mt. Edgecumbe the radiocarbon ages of basal peats range from around 5000 to over 8000 years BP. Analyses of the age and structure of the peat stratigraphy, as well as paleoecological surveys of plant and insect remains, provide unambiguous evidence that the peat bog communities in southeast Alaska are relatively stable, climax ecosystems over periods of many thousands of years (Klinger et al. 1990).

Hudson Bay lowland

During the last ice age a huge mass of ice, the Laurentide ice sheet, blanketed most of Canada. At this time the weight of the ice on the land was so great that it depressed the Earth's crust to below sea level in places. With the end of the ice age and the melting of the ice sheet, the crust has now rebounded and new lands have gradually emerged out of the sea. This process is called isostatic rebound and in places like the Hudson Bay lowland, it has given rise to a distinct series of former beaches appearing as ridge and swale communities that ring the shores of the bay.

The beach ridge and swale chronosequence described from the Hudson Bay lowland has been found to be more than 5500 years old (Klinger et al. 1994). Hidden in this chronosequence are actually two chronosequences, each with an exceptional record of developmental pathways in the vegetation and soils. One, the xerosere, follows the ridge tops, and the other, the mesosere, follows the swales.

The ridge succession (Figure 3) begins in meadows of grasses and forbs, which give way to thickets of willows. Aspen forests soon replace the willows. White spruce forests then replace the aspen forests. The arrival of the black spruce at around 1000 years marks a strong shift to very acidic, peaty soils leading to the eventual demise of the spruce forests. Next come the bog forests of stunted black spruces and ericaceous shrubs growing in thick beds of *Sphagnum* mosses. In time, the trees disappear and the ridges become buried beneath thick blankets of *Sphagnum* bogs.

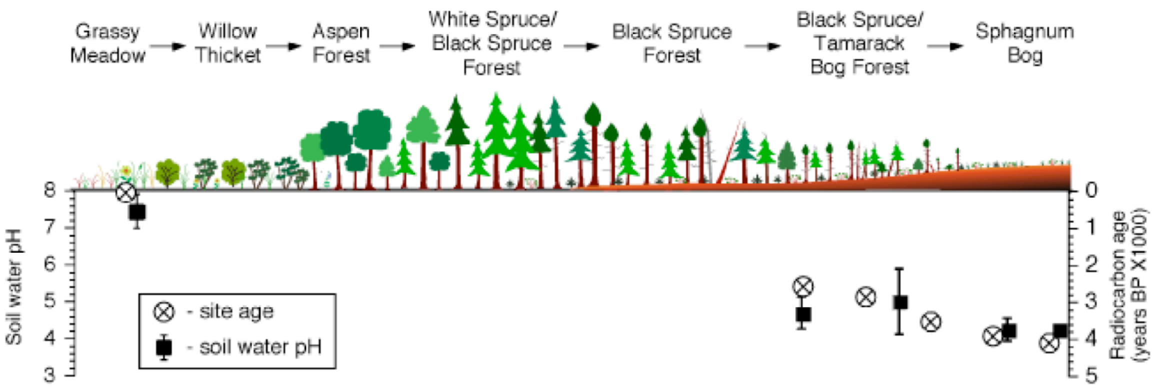

Figure 3. Summary of successional changes in a xerosere from the Hudson Bay lowland based on chronosequence studies by Klinger et al. (1994) and Klinger & Short (1996).

The swale succession (Figure 4) begins in salt marshes, which soon become freshwater marshes. These give way to willows and then to minerotrophic tamarack fens on peaty soils. Tamarack fens are colonized by black spruce, which eventually coalesce into bog forests. In the end, the bog forests become overgrown by *Sphagnum* mosses and ombrotrophic peat bogs are formed.

Through the course of both these successions the soil water pH becomes more acidic, ranging from 7.7 in the youngest marshes to 3.9 in the oldest bogs. This drop of three to four pH units during succession amounts to a 1000 to 10,000-fold increase in hydrogen cation concentration. Succession is a case where aging and acidification seem to go hand-in-hand.

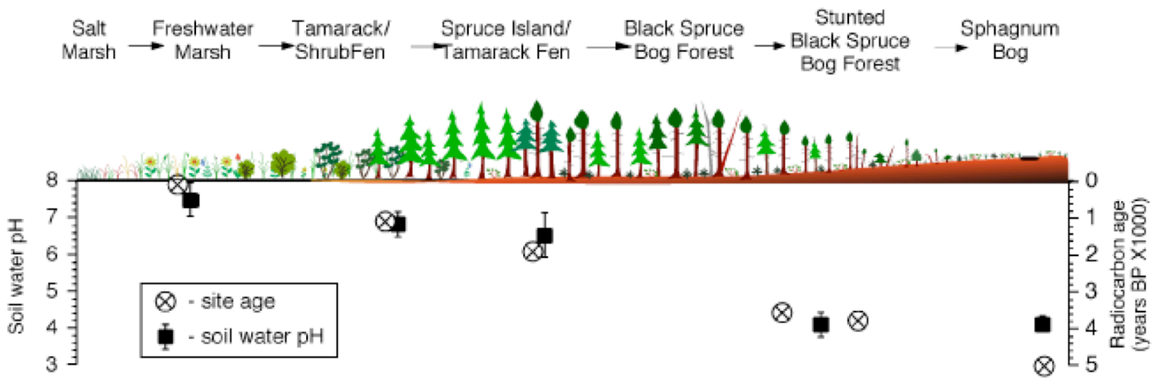

Figure 4. Summary of successional changes in a mesosere from the Hudson Bay lowland based on chronosequence studies by Klinger et al. (1994) and Klinger & Short (1996).

Despite differences in initial conditions and species composition, both sets of successional pathways converge onto *Sphagnum*-dominated bog ecosystems, a conclusion backed by pollen and macrofossil studies (Klinger & Short 1996). These climax peat bogs are well-suited to maintain their character and moisture content for many thousands of years into the future. In fact, it will probably take another Laurentide-size glacier to remove all the peat that has accumulated in the lowland.

Subarctic Québec

In subarctic Québec the retreating Laurentide ice sheet exposed numerous depressions and kettle holes that now hold the many freshwater lakes and ponds that dot the land. Gradual infilling from the margins over the years has created chronosequences of vegetation change in these freshwater ecosystems (hydroseres).

As shown below, floating herbaceous vegetation colonise lakes in the Schefferville region of northern Québec (Figure 5). These floating mats thicken and eventually become grounded mats of mosses and sedges. Where *Sphagnum* mosses proliferate, the peat depth grows to well above the water table and bog vegetation develops.

This classic model of bog succession, also termed terrestrialization, has long been thought to culminate in climax upland forest. Thus, once established the *Sphagnum* bogs were said to thicken further so that the surface would rise and become dry enough for the surrounding forests to invade and thrive, eventually reaching the regional climax forest stage.

But that is not the case here, for what appears to be one continuous successional sequence is actually two separate chronosequences that meet in the middle, at the *Sphagnum* bog stage. One is the terrestrialization chronosequence from open water to *Sphagnum* bog described above, and the other is a paludification chronosequence from spruce forest to *Sphagnum* bog. This is described in Figure 5, which shows forests growing on relatively young, mineral-rich soils, with little or no peat cover. Age and structure data on the trees, soils, and peats from two different sites near Schefferville indicate that spruce forest is not invading *Sphagnum* bog, it is the bog that is invading the forest (Klinger 1996a).

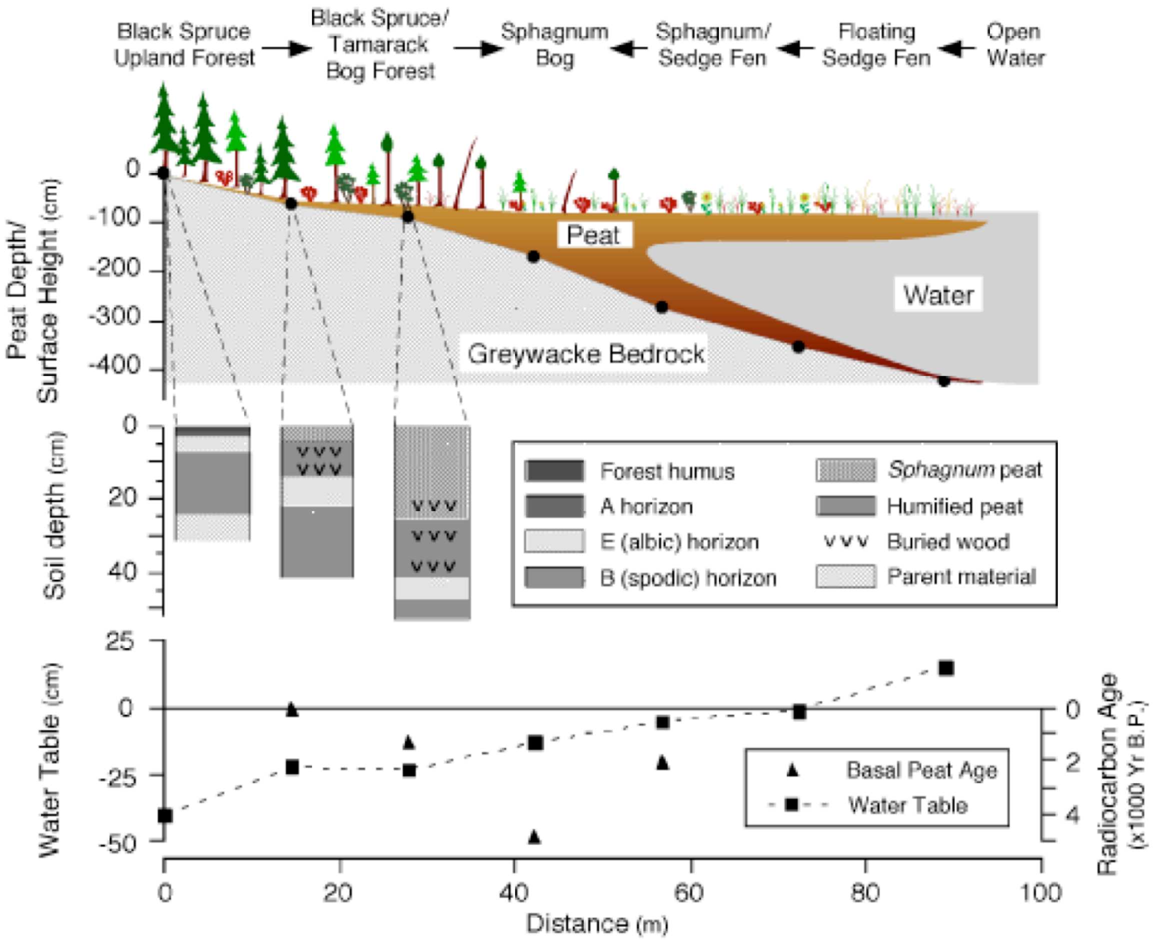

Figure 5. Summary of successional changes in vegetation and soils along a lake margin based on a chronosequence study by Klinger (1996a). Note that both a xerosere and a hydrosere are represented at this site.

Thus, while the nearby water bodies are undergoing terrestrialization, the spruce forests are undergoing podzolization and paludification as the bog vegetation expands upslope from lake margins. A summary diagram of the proposed genesis of this kind of landscape is presented in Figure 6.

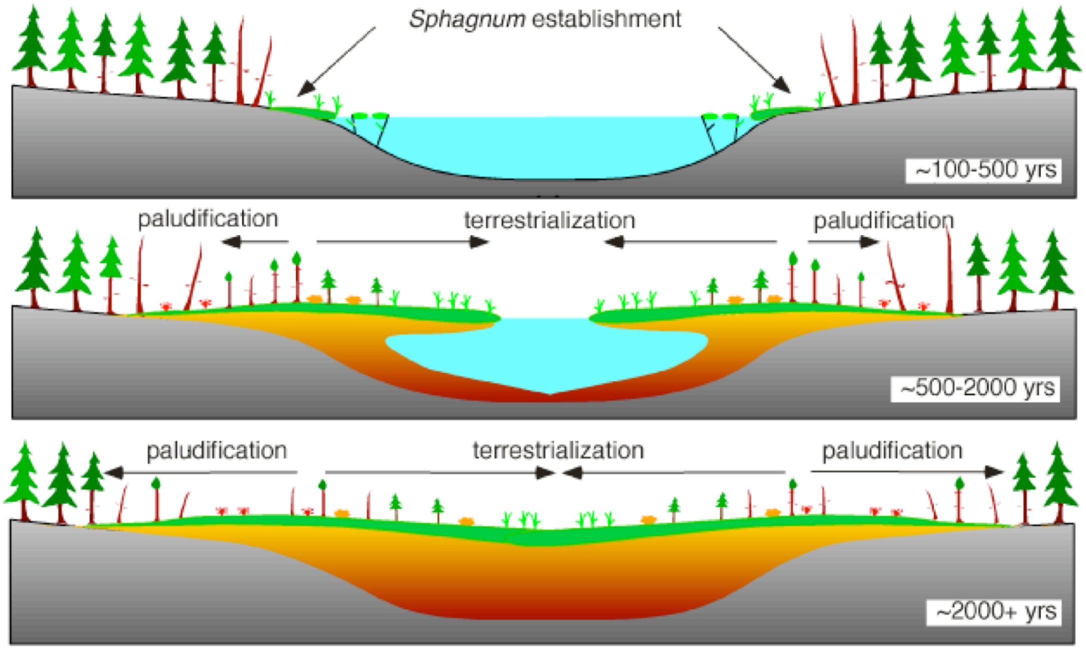

Figure 6. Hypothesized developmental stages of peat bog formation in freshwater lakes and ponds in subarctic Canada. Redrawn from Klinger (1996a).

The succession of old-growth forest to peat bog is no small feat. Entire forests collapse and die, only to be repopulated by other forest species that in turn collapse and die. This is happening all over Alaska and Canada, as well as in Britain where there has been much interpretive work on forest to bog transitions (Dimbleby 1962; Chapman 1964; Smith & Taylor 1969; Tallis 1975; Bennett 1984). Most of these studies agree that these transitions are accomplished via two pedological processes, podzolization and paludification.

Podzolization

Podzolization is a characteristic soil-forming process in northern coniferous forests (Jenny 1980). It is defined by the degree of translocation of iron, aluminium, clays, and humic acids from the A horizon to the B horizon. Podzols are typically formed under conifers, heaths, peat mosses and other types of vegetation that tend to acidify the surface soils (Miles 1985).

Soils that have undergone intense podzolization are called spodosols. Spodosols are comprised of a dark organic-rich A horizon, above a strongly-leached ash-colored E horizon, over a yellowish/reddish illuvial B horizon. A characteristic of spodic B horizons is the presence of localized concentrations of iron. In the late stages of podzolization these iron-rich bands condense to form placic horizons, or ironpans, rock-hard soil layers that block roots and impede drainage. A profile of a young spodosol in southeast Alaska is shown in Figure 7.

The high degree of chemical alteration during podzolization is demonstrated in a study by Heilman and Gass (1974), who examined the characteristics of seven spodosols in southeast Alaska. They found that all seven spodosols exhibited similar chemical properties in the upper horizons despite large differences in parent materials. Parent substrates included a range of igneous, metamorphic, and sedimentary rock types.

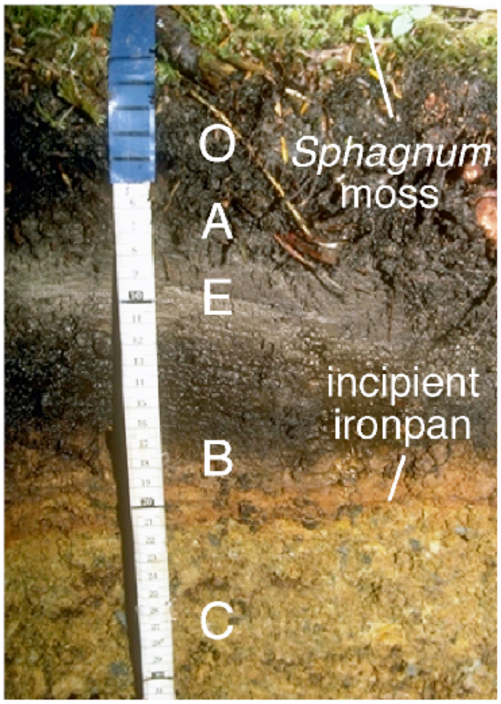

Figure 7. Example of a young volcanic soil in southeast Alaska that has been strongly podzolized. Soil is classified as a Typic Haplohumod.

Podzolized soils are acidic with low levels of exchangeable bases and high levels of exchangeable iron and aluminium. Such conditions of poor soil fertility, where nutrient cations are deficient and heavy metals approach toxic concentrations, are associated with the general decline of forest vegetation (Klinger 1996b).

Paludification

Paludification is the term given to the conversion of well-drained forests to saturated peat bogs through the swamping of the soils. Miles (1985, p.576) defines paludification as: "the failure of trees to regenerate because of prolific growth of *Sphagnum* mosses". Most peat bogs evidently form via paludification, as is indicated by intact stumps and other remains of forest vegetation typically preserved at the base of bogs (Katz 1926; Smith & Taylor 1969; Chapman 1964; Tallis 1975; Bennett 1984).

Whereas podzolization describes the genesis of spodosols during mid succession, paludification describes the late successional replacement of spodosols by histosols. Impeded drainage caused by ironpan formation in spodosols may help initiate paludification; however, once peat formation has commenced, water flow is mostly impeded by the peat itself.

The water table soon becomes perched, meaning it is held near the surface by the mosses and peat, unconnected hydrologically to the groundwater table. As the peat thickens, the soils eventually become histosols, a class of organic soils (eg, bog soils) characterized by nearly pure accumulations of undecayed or partially decayed organic matter. It is not uncommon to find albic (E), spodic (B), and thick iron layers (eg, bog iron) preserved beneath histosols.

Discussion

Processes of soil development during succession are critically linked to major structural and compositional changes that occur in the transformation of forest to bog. Here, soil scientists get credit for pointing out the key role of the vegetation in the podzolization and paludification of soils during forest to bog transitions (eg, Ugolini & Mann 1979; Jenny 1980; Miles 1985).

To better see the relationship of podzolization and paludification processes in vegetation succession let us return to southeast Alaska, where the gradual upslope stabilization of unconsolidated volcanic ash deposits on Mt. Edgecumbe had produced a chronosequence of vegetation communities and soil types. These vegetation and soil types, as previously reported (Klinger 1996b), are summarized in Figure 8.

In the overall succession of soil orders, using the Soil Survey Staff (1975) taxonomy, entisols and inceptisols give way to spodosols and histosols. This points to the significance of podzolization (spodosol genesis) and paludification (histosol genesis) in the development of this landscape. Other studies of soil chronosequences in southeast Alaska have reported similar results and concluded that the peatlands here are ‘biopedological’ in origin (Ugolini & Mann 1979).

In my own work I’ve found that where podzolization is intense, the forests are likely to be in poor health. I find, too, that where forests are already paludified they are likely to be in a severe state of decline. There is little doubt that, with the advance of bog vegetation, trees are dying and failing to fully regenerate. Understanding the mechanisms by which bog vegetation accomplishes this has been a scientific obsession of mine for decades.

First, let me share some observations on mosses and lichens. Mosses and lichens may be small organisms, but ecologically they are highly influential, both aiding and abetting the health of a forest, depending upon their abundance. Where moss and lichen cover is light, trees and forests appear to do just fine. But time and again I’ve found that where moss and lichen cover is heavy the trees are suffering.

The damaging effects of mosses on tree roots has been documented and discussed in several previous studies (Klinger 1990; Cornish 1999; Klinger 2005). In light of these findings it is clear to see how mosses may facilitate the succession of forest to peatland. Besides being linked to fine root mortality, mosses are also linked to reductions in the radial growth of trees. Glancing back to the slopes of Mt. Edgecumbe (Figure 9) we see that, coincident with increases in *Sphagnum* moss cover, there are highly significant (~ 50%) reductions in the (standardized) radial growth of nearby trees (n=250). These growth reductions are presumably related to acidification (by *Sphagnum* mosses) having negative effects on soil fertility and tree root health, thus influencing radial growth rates. In a separate study in the montane fir/pine forests of Colorado that investigated total moss biomass and (standardized) radial growth, similar reductions (25 to 40%) were reported in the highest (vs. lowest) moss biomass sites (Cornish 1999). These studies suggest that major reductions in tree growth may be occurring as mosses reach high abundances in unburned and undisturbed forests.

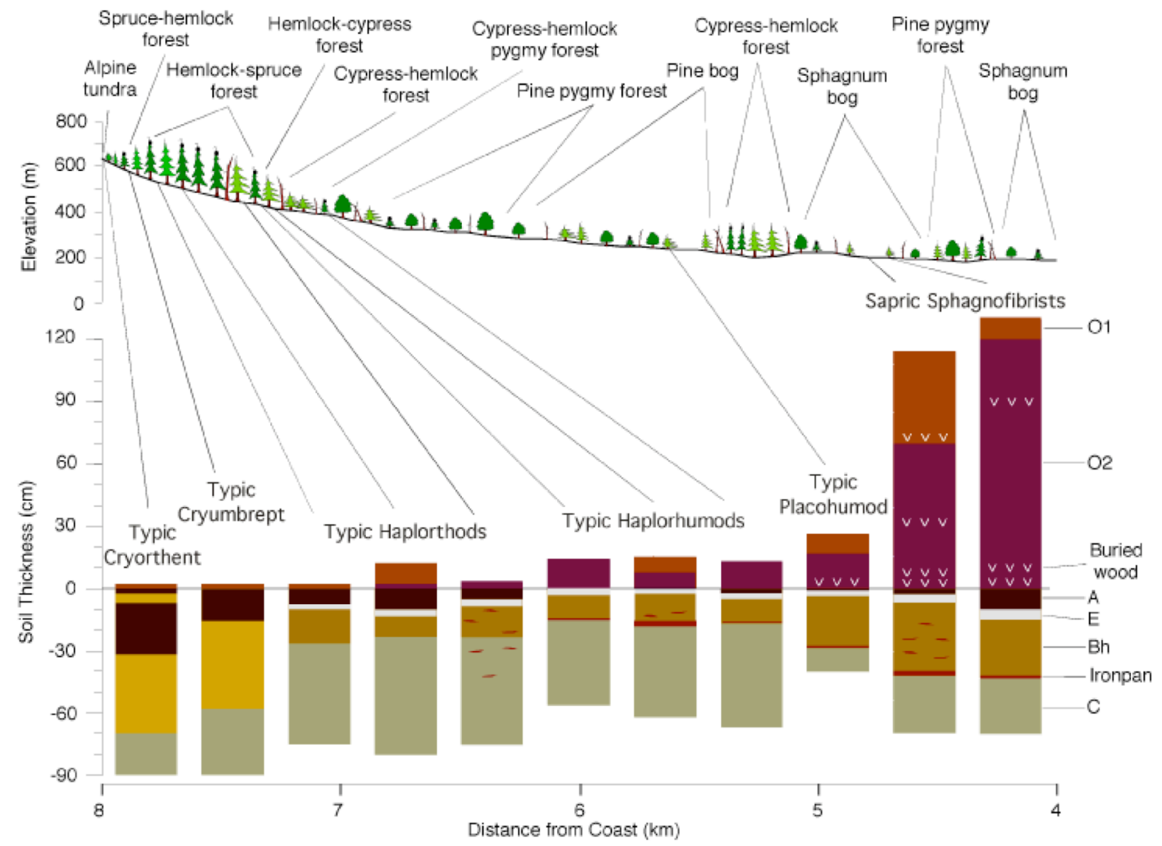

Figure 8. Vegetation and soil structural changes observed along the Mt. Edgecumbe chronosequence in southeast Alaska. Youngest sites are to the left, oldest sites are to the right. Redrawn from Klinger (1996b).

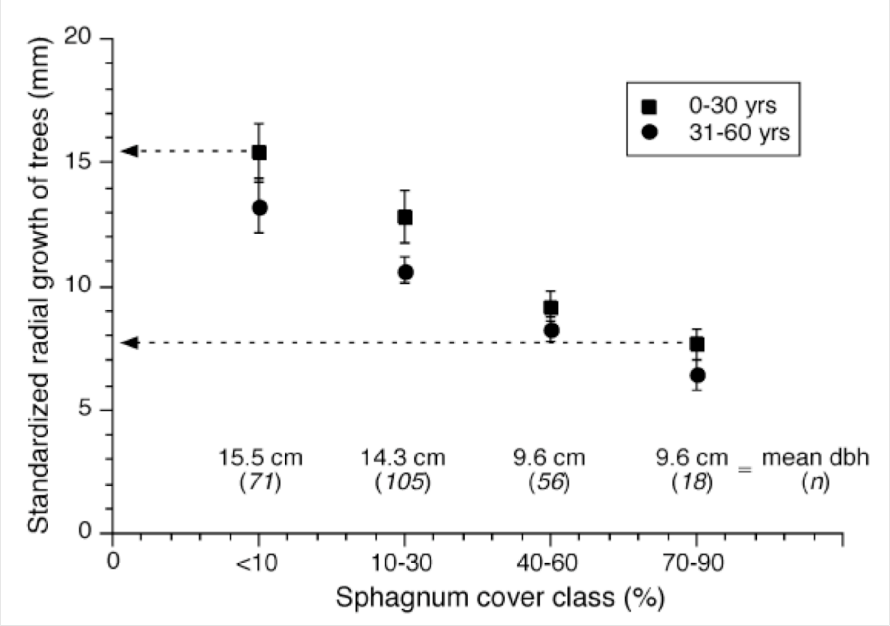

Figure 9. Standardized radial growth of trees on Mt. Edgecumbe in southeast Alaska measured under conditions of varying Sphagnum cover. Redrawn from Klinger (1990).

Conversely, studies indicate that lands that regularly experience disturbances such as grazing or fires are not as susceptible to acidification, podzolization, and paludification (Miles 1985). Disturbances help to rejuvenate plants and soils through the release of bound up resources. Fires and grazing are known to help neutralize acidity in the soils. This is all consistent with the model of ecosystem development described above.

Conclusion

In the attempt to frame the succession of forests and soils in a whole ecosystem context I have presented information on a theory of succession that draws from the conclusions of both ecologists and soil scientists. This theory views the vegetation and soils as inseparable parts of a developing ecosystem. The concept of a mature, climax ecosystem is extended to include peat bogs as climax ecosystems. Chronosequence studies from Alaska, Canada and elsewhere are presented as evidence for the climax status of peat bogs.

Regarding forest to peatland transitions, scientists have identified two key soil processes, podzolization and paludification. Podzolization begins in the conifer forest stage of succession and is initiated by the acidification from vegetation, especially mosses. Iron, aluminum and other important substances are leached from the upper soil horizons and deposited in the lower horizons. In the late stages of podzolization, ironpans form and alter the drainage patterns of the soils. Paludification closely follows podzolization, and is initiated by the establishment and growth of peat-forming mosses such as *Sphagnum*.

Once the swamping effects of paludification take hold in a forest there is little, short of a massive disturbance (eg. glaciation), which can reverse it.

The importance of this work to foresters and tree care professionals is in the recognition that most northern forests are susceptible to podzolization and paludification processes, and that these can result in damaging effects on trees and soils. Miles (1985, p.580) wisely concludes in his overview of succession and soils in Britain: “Tending the soil does not necessarily imply direct technological intervention; soil can be tended indirectly by managing the vegetation.” Being able to identify the early stages of acidification and podzolization and, in response, managing the vegetation properly may be the key to helping keep many of our forests in a healthy state.

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