Plant Community Succession – The Time Dimension of Management

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Succession is probably one of the most commonly misunderstood and misapplied concepts of ecology. In its purest form, succession is a process by which orderly change in biotic communities over time culminates in a predictable and stable end point called the ***"climax".*** Because the set of stages leading to stability is called the ***"sere"***, the relative position of communities in the series is often referred to as "**seral stages**" when naming them; early-seral, mid-seral, late-seral, or climax. It is generally acknowledged that even climax communities will vary over time with weather cycles, animal population cycles, and other natural events. This is often referred to as their being in a "dynamic equilibrium" in which variation happens without the community ever losing its fundamental structure and composition. For example, a climax sagebrush steppe community (Fig. 1) may have less total plant cover and proportionally less grass cover at the end of a 30-year drought cycle, but will still be undeniably recognizable as a sagebrush steppe community. Stability in climax communities often comes from their ability to buffer variations in environmental conditions and their rapid recovery after stresses are removed (their resilience). Perennial grasslands, for example, tend to accumulate soil organic matter that increases soil moisture storage and facilitates water infiltration, thus making climax grasslands less sensitive to seasonal and yearly differences in precipitation than earlier successional stages that have yet to accumulate organic matter.

Figure 1. Sage brush - grass steppe, Eastern Oregon USA.

As with most branches of Science, plant community ecology has advanced incrementally over time. This process has been described as "standing upon the shoulders of giants" because of the reverence with which later generations now look back upon the insightfulness of these founding fathers. Much of what we currently know about plant community development and the broad-scale distribution of communities across landscapes was already recognized over 100 years ago. Perceptive observers of vegetation in the 1890's could broadly predict the general nature of plant communities that could eventually dominate a type of ecozone. They could, for instance, separate what could eventually become a sagebrush steppe from a nearby area that would be a mixed semi-arid conifer forest. C. Hart Merriam published his description of vegetation "life Zones" changing with elevation in 1890. We still recognize and use these zones today [see http://www.radford.edu/~swoodwar/CLASSES/GEOG235/lifezone/merriam.html]. Early ecologists could not, however, reliably predict the actual plant composition of the climax stand, and when (or if) it would occur. This is pretty much where we still are today. Frederic C.

Clements probably had more influence on the North American view of plant community ecology than any other person. His view of plant communities as a discrete organism in which individual plants serve the whole structure much as the individual cells of plants form the plant is the predominant metaphor for ecosytems today. His description in the 1916 book *Plant succession – an analysis of the development of vegetation* that “each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development.” and that succession is a “definite process, comparable in its chief features with the life history of an individual plant” is also the one that prevails today. We organize communities in a sequence from infancy (early-seral), through juvenile (mid-seral), young adult (late-seral) and mature (climax). We accept that, just as with a person, plant communities must eventually age and die to be replaced with younger stages that will eventually mature to maintain dominance of the climax vegetation type. We often hear about the need to rejuvenate “old decadent” stands of forest trees by removing aged trees so that a new generation may grow in their place. This process can also be seen in climax “old growth” conifer forests in which insect attack, blow-down, or other events open up patches in the forest that then proceed through succession to reproduce that same type of vegetation. Ancient old growth forests are often a mosaic of individual stands of varying ages. Climax is stable at the landscape, but not the individual stand scale. So, it is illogical to think of preserving an individual old growth forest stand. It is interesting to note here that both functionally and legally, the term ‘old growth” is defined by stand structure rather than tree age. What it actually represents is a judgment that the stand has the structure and functions of a climax stand for that particular site. It may occur at very young ages for productive sites and at very old ages for unproductive sites within the range of a particular plant community.

Figure 2. Sheep graze conifer forest to alter secondary succession during the perennial grass stage of succession in a regenerating timber stand 6 years after harvesting.

Like Clements, most modern ecologists have observed that primary vegetation succession (stating from bare rock or mineral sand/ash) tends to proceed from simple, small stature plants such as lichens and mosses, through annual grasses and forbs, to perennial grasses and forbs, to shrubs, then to trees. The progression generally goes from small, less demanding, to larger, more resource demanding vegetation. Site potential features such as climate, topography, and soil parent material along with the availability of colonizing plants and animals all affect the rate of succession and how far along the sequence a particular site will get before resource scarcity limits further development. Arid sites may stop at a perennial grass climax while more mesic sites nearby reach a grass shrub climax dominated by bitterbrush or even form an open canopied conifer forest. Primary succession tends to be fairly orderly and predictable. Unfortunately, primary succession is very uncommon. Reaction following disturbance, called secondary succession, is much more common, and much more complex. Although ecologists disagree upon their relative importance, most recognize that there are two basic processes that drive succession: **Relay floristics**, and **Initial floristics**. In relay floristics, each vegetation stage modifies the environment through soil formation, microclimate modification, and other effects to make it more suitable for plant growth. This increases stability by reducing the immediate effects of short-term environmental fluxuations in temperature and moisture, but potentially provides conditions for competitors from the next stage to enter and eventually dominate the community. Thus each seral stage prepares the environment for the next one. This is the main process operating during the early stages of primary succession. Because the range of plants that can potentially grow under very harsh conditions is small, early primary succession is fairly similar wherever it occurs around the world. Late primary succession and all secondary succession occur where soil, microclimate, and other site features have already been changed by previous plant occupation. There are often a wide range of plants that could grow if they can reach the site and can compete with existing occupants. Since established plants often have a competitive advantage over seedlings, the first arrivals can hinder or even exclude other plants. Timing of arrival on site affects plant success and the nature of the subsequent succession. Seeds, bulbs, rhizomes, or other plant reproductive parts may be present at the time of disturbance, or may arrive at varying times after disturbance, depending upon the proximity of mother plants and the availability of wind, water, animal, or other modes of travel. All this makes the initial floristic composition of stands extremely variable between different sites and even between disturbance events on the same site. When one considers the chance effect of variability in climate (temperature and moisture) both before, during, and immediately after disturbance on surviving resident vegetation and on the success of plants establishing after their arrival, it is easy to understand why species composition during secondary succession is difficult to predict. Secondary succession heavily reflects initial floristics, although relay floristics also operates.

Figure 3. Douglas-fir trees and grass/subclover Silvopasture in Western Oregon, USA.

Relay floristics operates at both large and small scales. Subclover is an early seral nitrogen fixing forb that is often seeded in western Oregon pastures and agroforests to provide N for perennial ryegrass that is a nitrogen loving, later seral grass. Initially, perennial ryegrass does not grow well until the subclover increases soil nitrogen sufficiently to stimulate grass growth. This can take several years. Then, perennial ryegrass out-competes the subclover and dominates the pasture for several years until it runs short of nitrogen and subclover reasserts itself. This cycle of clover and grass years may repeat itself over and over. In general, it is difficult to maintain plants from different successional stages together in a stand. The heavy grazing necessary to maintain subclover by controlling competition from grass is detrimental to perennial ryegrass. Overgrazed pastures have lots of clover but little grass, while undergrazed pastures have grass but little clover. It is challenging to get the right timing and amount of grazing to suite both plants. Natural stands of plants containing a mix of species from different seral stages tend to occur during transition from one stage to another. They are by their nature unstable. Our fabricated mixed-stage pasture and agroforest stands are also inherently unstable, and, therefore, difficult to maintain. Agroforest silvopastures (Fig. 3), for example, seek to maintain both the perennial grassland and forest stages of a normal forest succession together for an unnaturally long period. Considerable management effort must be applied to favor tree growth during the early, predominately grassland phase, and then later to maintain grassland under the expanding tree canopy of the predominately forest phase.

Initial floristics theory tells us the obvious; that what you have on site today is the best indication of what you will have on site tomorrow. If you want to see what will come into a newly opened up forest stand following tree harvest, look at what is on site now and what mother plants are within reach of the cut area. Also, if you want to make sure that a favored plant prospers after disturbance, seed it, plant seedlings, leave mother plants, or in some way help it to increase its presence on site immediately after fire, plowing, over use by herbivores, drought, or other disturbances. Again, this is pretty obvious. We plant corn after plowing corn fields because we want corn plants to dominate the resulting stand of vegetation. If we didn't do this, weeds, unharvested corn, and whatever other plants could reach the field would be the vegetation next year. We plant seeds or young nursery plants, or leave mother "seed trees" of desired species following tree harvesting in order to ensure that desired trees quickly occupy and spaces created.

The importance of initial conditions on subsequent processes is the basis for Chaos theory. Since natural succession is inherently chaotic, the best we can do in managing vegetation is to realize that our predictions of future vegetation structure and stability are best guesses. The farther into the future we project our guess, the less accurate it probably will be. We must have some sense of future implications for us to act today. Successional trends observed in local vegetation can provide useful references, but chaos suggests that every thing we do is at best a hypothesis. No two areas or two years are the same. We should be constantly examining our expectations and comparing them to field observations to see if our vision is actually happening. This is part of the "art" of natural resource management. Again, the obvious applies. If you are having good results, keep doing that. If things aren't working, it is time to try something else.

The two most commonly held misperceptions about succession are that it is smooth, and that it is symmetric. By **smooth**, I mean that it grinds along inexorably headed the same way, a little each year. In fact, succession is often a very messy process that occurs in jerks with long periods of little change in between. It may actually go backwards awhile before resuming its forward progress. I lived in west Texas for 4 years and never saw a single mesquite tree seedling. This was a bit of a surprise because mesquite invasion is a major range problem. Mesquite grows well in west Texas, but is a subtropical plant that needs adequate moisture and low plant competition for its seedlings to establish. This is not a common event in semi-arid Texas except right after a drought. Once established, mesquite is a very tolerant and long-lived plant that is difficult to kill (Fig. 4). It is often the uncommon events such as droughts, freezes, disease/insect attacks, or unusually rainy years that alter competition and provide the necessary push for reproduction and vegetation change. The cohorts of similarly-aged plants that are often observed in desert communities reflect this reliance on infrequent climatic events or disturbances for reproduction. This means that you have to have a proper time frame to interpret succession. The lack of current reproduction on site may not mean that the stand is not

Figure 4. Mesquite trees sprouting after fire in West Texas.

reproducing itself. Apparent stability may be just that, apparent. Vegetation is just waiting for a triggering event in order to move on to the next successional stage.

By **symmetric,** I mean that succession going forward follows the same path as going backward. Clements called externally driven movement away from climax "retrogression". Retrogression is often thought of as a more or less temporary diversion from succession and that the normal progression towards climax can resume its former course once the factors causing retrogression are removed. This is the logic behind the idea of reversing the rangeland retrogression caused by overgrazing in the pre-World War 2 era by simple removing livestock today, or by restoring salmon runs by removing dams so that things can go back to pre-dam conditions. In no other parts of our life experiences is such "going back' possible. As the old saying goes "you can never go home again". This is because things have moved on. They have changed in your absence. The same is true of biological processes. If we make a raison by drying a grape, we do not really expect to restore the grape to its former state by soaking it in water? It is illogical to think that succession is unique in that it is reversible and that time alone will restore things to the way they were. Because initial conditions are never the same twice, no two successions will follow exactly the same route and have exactly the same outcome. When we overgraze or build a dam, the ecosystem seeks a new equilibrium incorporating this new factor. When overgrazing ceases or the dam is removed, the system again seeks a new equilibrium. If the new initial state contains persistent effects such as soil loss, loss of original species, down cutting of stream channels, or presence of particularly competitive plants or animals from off site, succession may be slow to proceed or may be diverted to a new path with a different climax community. This is the basis for state-and- transition models that allow for succession to by irrevocably switched from one pathway to another by fundamental changes in initial conditions. These models are really a modernization of Sir Arthur Tansley's polyclimax theories published in the1920's and 1930's. He recognized, as we still do, that plant succession may follow different pathways depending upon the influences acting on vegetation. Fire, grazing, hydrologic events such as gulley cutting, soil erosion, or soil deposition and other strong persistent influences such as arrival of new plants or animals all drive succession towards unique outcomes that may be stable as long as the new driving factors remain effective.

Forest, range, perennial pasture, and agroforest system are typically more subject to successional pressures than are agronomic field cropping systems in which vegetation is harvested and renewed each year. In general, the longer that the production system is in place, the more attention must be given to understanding and manipulating the successional processes. This usually begins with manipulating initial floristics if the land is planted with the desired vegetation, then quickly shifts to participating in relay floristics as competition between plants is managed by fertilization and grazing/harvesting of understory plants or by pruning/thinning of overstory plants. We seek to avoid crossing successional thresholds leading to undesired outcomes by controlling soil erosion, excluding invasive species, or by maintaining current controlling factors such as fire or grazing. As managers, we know that change is a normal part of stand development over time. We anticipate it and manipulate it as the time dimension of land management.