

Implications of Modern Successional Theory for Habitat Typing: A Review

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ABSTRACT. The habitat type classification system (HTCS) is widely used in the western United States and has recently been applied in the Lake States. This classification system is based on three premises, two of which are embodied in the Clementsian theory of succession. These premises are (1) the climatic or potential climax is the same for all sites that have similar growing environments within a region, (2) the climax stage of succession reflects the inherent productivity of a site better than any other stage, and (3) after disturbance, the understory stabilizes more quickly than, and independent of, the overstory. The current understanding of succession, disturbance, and interactions between overstory and understory was reviewed and showed that the three premises on which HTCSs are based cannot be accepted *a priori* as widely applicable. In particular, it was concluded that (1) most sites will never support a climax stage (*sensu* Clements); (2) disturbances, past land use, and stochastic events can lead to multiple pathways on a single "type" of site; and (3) the overstory often exerts a significant effect on the understory. Thus, a land classification system that relies solely or heavily on vegetation, such as the HTCS, should be based on a new theoretical foundation and incorporate the known variation and stochasticity of vegetation dynamics. This means a new standard and additional analyses must be incorporated during the development of HTCS's so that the systems are more accurate, widely applicable and as useful as possible. *FOR. SCI.* 42(1):67-75.

Additional Key Words: Disturbance, stochastic events, overstory and understory interactions.

Forest managers must have a land classification system in order to manage efficiently. In the United States, foresters have traditionally used cover type and site index as the criteria to classify specific land units (Carmean 1975, Clutter et al. 1983, Smith 1986). These two parameters are readily understood by all foresters, are easy to determine, and provide information needed to manage the current stand. However, both parameters are limited in their long-term usefulness; in addition, site index cannot usually be applied in uneven-age stands, is often applicable to only one species, and sometimes site index cannot be determined because of composition, stocking levels, or past insect and pathogen damage (Carmean 1975, Clutter et al. 1983).

Since the late 1960s, alternative means of classifying forestland have been developed and adopted in different parts of the country; these include multifactor hierarchical classification systems, ecological land types, and habitat types. The most widely applied of these methods in the West is habitat type (Smith 1986, Wellner 1989); this system is also

used in parts of the Lake States. The habitat type classification system (HTCS) was developed in the Intermountain region by Daubenmire and Daubenmire (1968). Habitat typing is preferred over cover typing and site index because (1) it represents an ecologically based system; (2) the site class can be determined regardless of overstory composition, tree size, and density; and (3) the site quality evaluation is permanent (Daubenmire and Daubenmire 1968, Daubenmire 1976, Kotar 1988). Thus, this system of site classification was a distinct improvement over the traditional method, in part because it has a broader ecological basis (Arno and Pfister 1977, Kotar 1988).

During the 1970s and early 1980s, HTCSs were produced for almost all of the public forestlands in the western United States (Wellner 1989). These HTCSs covered the elevational gradient from ponderosa pine to subalpine fir forests, and ranged from Arizona (Hanks et al. 1983) to Idaho (Steele et al. 1981). In 1983, the first HTCS in the eastern United States was developed for the upper peninsula of Michigan and

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northeastern Wisconsin (Coffman et al. 1983). The only other HTCS east of the Mississippi was developed for northern Wisconsin 5 yr later (Kotar et al. 1988).

All HTCSs are based on these premises:

1. The vegetation—association of Daubenmire and Daubenmire (1968)—reflects the “algebraic sum of all environmental factors” that affect plant growth (Daubenmire 1976).
2. The climax or potential-climax stage of succession reflects the inherent productivity of a site better than any other stage (Daubenmire 1976).
3. (a) The understory vegetation stabilizes more quickly after disturbance than the midstory or overstory (Daubenmire and Daubenmire 1968, Pfister and Arno 1980, Kotar 1986, Pfister 1989) and thus, (b) it is not necessary to have the climax or potential climax overstory in place in order to identify the habitat type (Pfister 1989).
4. The climatic climax (Daubenmire and Daubenmire 1968) or potential climax (Steele et al. 1981, Kotar et al. 1988, Pfister 1989) is the same for all sites that have similar growing environments within a region.

The foundation of habitat typing is thus based on (1) successional theory, (2) the role of disturbance in community organization and composition, and (3) the use of indicator plants. The objective of this article is to examine implications that the current understanding of succession and disturbance has for habitat typing. This examination is warranted because (1) the premises listed above involve several key ecological processes about which much information has accumulated over the past 20 yr, and (2) the topics of disturbance and succession have been areas of active theoretical and mechanistic research during the last 15-20 yr. As described below, disturbance and succession are intimately linked processes and concepts, and thus one cannot be discussed without considering the other. The theoretical basis and practical applications of indicator plants are not reviewed here because this topic has been addressed by Daubenmire (1976), Spurr and Barnes (1980), La Roi et al. (1988), Archambault et al. (1989), and others.

Evolution of Successional Theory: 1960–1992

Clementsian Theory Dominates Pre-1960

The first fully described successional sere in the United States was for the sand dune region around Lake Michigan (Cowles 1899). Shortly after the turn of the century a comprehensive theory of succession was proposed by Frederic Clements (Clements 1916). His theory dominated thinking on succession for at least 40 yr, and is clearly one of the most important ecological theories of the century (McCormick 1968, Drury and Nisbet 1973, Connell and Slatyer 1977, MacMahon 1980, McIntosh 1985, Kingsland 1991). Some contemporaries disagreed with Clements and published alternative explanations for, or views on, temporal changes in

vegetation (Cooper 1926, Gleason 1926, Tansley 1935). The most influential and widely cited is Gleason (MacMahon 1980, McIntosh 1985, Kingsland 1991). Thus, during the early 1900s two theories of succession vied for dominance: the predictable, unidirectional, community-oriented theory of Clements (1916, 1928) and the individual species-based, environmentally random theory of Gleason (1926). One point of agreement between Clements and Gleason was disturbance; they regarded it as an uncommon-to-rare phenomenon, largely extrinsic to the community, and thus not integral to the successional process. Clements' theory is centered around the mechanisms of “reaction” and competition, and stated that succession almost invariably led to the regional or climatic climax (Clements 1916, 1928, 1936). Reaction was defined as the influence of plants on the environment and is the mechanism that dictated that the stages of succession occur in only one order and that it be unidirectional. The dominance of Clements' “classic” theory is clearly indicated by the content of many ecology texts (e.g., Odum 1959, Margalef 1968) and in E. Odum's classic ecosystem paper (1969).

Clements' theory is important for reasons other than its dominance. His thorough description included mechanisms and process that are integral to virtually all vegetation dynamics (Pickett et al. 1987), and a subset of these processes is the foundation for most subsequent theories of succession. The only significant, widely accepted refinement of Clements' theory that occurred before 1960 was a shift from a single climatic climax to the polyclimax viewpoint (Tansley 1935, Whittaker 1953). However, two additional theories of plant dynamics were presented before 1960. Watt (1947) showed that vegetation change in several communities was best understood at the patch level. At this scale, the temporal changes in composition are cyclic, and the patches form a mosaic which constitutes the community. Egler (1954) proposed the Initial Floristics Model of succession which stated that all species that will be a part of the sere are present very early in the sequence. This differs significantly from Clements' theory by essentially discounting the importance of reaction and attaching more significance to chance events that contribute to the propagules that are present for colonization in any given year. These alternative ideas, beginning with Gleason, paved the way for the development of a “Modern Theory” of succession.

Challenge to the Clementsian Theory

In 1968 a review and examination of “traditional successional concepts” was published in an obscure outlet (McCormick 1968). This author pointed out several *possible* weaknesses in the Clementsian-based theory of succession; those not noted in previous works included (1) the reaction process had not been proven to be as universal and important as Clements claimed, (2) competition between plants had rarely been clearly demonstrated and thus may not be as important as indicated by Clements, (3) allelopathic effect had not been factored in (Clements can not be faulted on this point), and (4) several of the mechanisms that drive succession can operate simultaneously.

Five years later Drury and Nisbet (1973) explicitly challenged the Clementsian theory. They presented examples from a variety of ecosystems and regions which were inconsistent with, or contrary to, the classic theory. They argued that the autecological or physiological level was the appropriate scale to explain succession, not the community level as proclaimed by Clements (1928) and Odum (1969). Though no new theory was proposed, they suggested that any new theories of succession should incorporate the effects of evolution. The importance of this paper was the compilation of evidence which strongly questioned the generality and applicability of Clements' theory.

Pickett (1976) expanded on the evolutionary aspect of succession and produced the first theory of succession based on the evolution of strategies that are best suited to the environmental conditions along a successional continuum. The ultimate basis for the different strategies was the degree of recombination; species that dominate after disturbance have the least amount of recombination, whereas late successional dominants have the greatest degree. Pickett also made several other claims that are consistent with the "modern" view of succession; he noted that disturbance is common and integral to the process, that predation may exert a significant influence, and that biotic pressures such as grazing are also often important.

Alternative Theories

In the late 1970s, three alternative models of succession were proposed (Connell and Slatyer 1977). Each model incorporated varying levels of importance in (1) the timing of species establishment, (2) competition for space and resources, and (3) autecological characteristics such as longevity and shade tolerance. Their approach differed from the classic theory in that they assumed there was not a climax stage, and that no steady state was necessarily reached. Contrary to Clements, they recognized disturbance as a pervasive and frequent force, and assumed species from all stages of succession may colonize after a disturbance.

The Facilitation Model (Connell and Slatyer 1977) retains the classic successional component of one species (or group) preparing the way for another. It deviates from Clements (1928), Odum (1969) and Margalef (1968) in that it does not invoke a high level of community organization with internal, positive feedback mechanisms. The second model, Tolerance, states that species change is determined by life history characteristics such as growth rate, ease of dispersal and the ability to capture and use resources. Simply put, competition and resource use efficiency will dictate which species dominate. Inhibition was the name given the third model because the initial cohort (group) effectively prevents all other species from becoming established for as long as they remain on the site. Compositional change only occurs when the initial cohort dies or is eliminated by an insect, pathogen, or localized disturbance. This model deviates the most from the Clementsian theory because succession may be arrested, it may go in any direction, and the initial stage is competitively superior. Connell and Slatyer (1977) concluded that the Facilitation Model seemed to fit primary succession, very

little evidence was found to support the Tolerance Model, and the Inhibition Model had the most empirical support. With the exception of Egler (1954), Connell and Slatyer were the first to propose a set of possible models, and to point out that primary and secondary succession may incorporate fundamentally different mechanisms.

Grime (1977) added another facet to the developing "modern" theory of succession. A ramification of his theory on plant strategies was that plants with the 'Ruderal' strategy will dominate early succession and that 'Stress Tolerant' species will dominate late in succession. This is primarily an extension of the point made by Pickett (1976). However, his theory indicated that site quality would exert a substantial effect on the successional trajectory. Species with the 'Competitive' strategy would increase in importance, in the intermediate stages of succession, as the productivity of the site increased. Thus, Grime's hypothesis contrasted with the classic theory in that any species with the appropriate strategy is likely to be present early or late in a successional sere, and that site quality interacts with the sere which occurs.

A successional theory for fire adapted ecosystems, the Vital Attribute Theory (Cattalino et al. 1979, Noble 1981), was proposed in the late 1970s. This theory is best viewed as a refinement of the Gleason Hypothesis, as expanded by the suggestions of Drury and Nisbet (1973), because a limited set of life history characteristics is used to predict succession chronology. This theory was for one kind of ecosystem only, but was also more specific than any previous theory in stating which characteristics determine succession. Their contribution to the development of succession theory was the direct incorporation of disturbance regime into the model and the explicit demonstration of multiple pathways for a single site-type (but see Olson 1958).

In the 1980s, two of the major components of the Clementsian theory were brought into question and two new successional theories were proposed. One article demonstrated that for a particular site, no species or species group exists that is capable of forming a climax (McCune and Cottam 1985). The other important contribution was that *dissimilar* forests may develop on similar sites (McCune and Allen 1985). The former article reinforced the importance of disturbance regime, including disease, to succession and provided another piece of evidence contrary to the classic concept of climax. The work by McCune and Allen (1985) in Montana provided the strongest evidence to date of the dominant role that chance and/or stand history can exert on vegetational development. This work showed that succession can have multiple endpoints and can be stochastic, both major deviations from the classic theory of succession.

The two most recent successional theories are the Resource-Ratio Hypothesis (Tilman 1985) and the Life History/Competition Model (Huston and Smith 1987). Tilman's (1985) hypothesis is different and more specific because he proposed that successional change is driven by the ratio of two resources (amounts actually available) and the ability of various species to acquire these two necessary resources. The resources that make up the ratio are usually light and a below-ground resource. The hypothesis is based on the premises that

resource levels change through time, that the most limiting resource often varies among sites within a region, and that species are adapted to a specific ratio of limiting resources. Thus, the changes in composition that occur within a sere are driven by the acquisition and use of the two most limiting resources; as they change, so does the composition. One recent experimental test of Tilman's hypothesis found that competitive abilities of old-field grasses did not fit the hierarchy predicted (Tilman and Wedin 1991).

The Life History Model (Huston and Smith 1987) is also an extension of Gleason's "Individualistic" Hypothesis; that is, species-by-species replacement can explain most community-level successional patterns. The model relies on competition as the driving force of succession and uses a wide array of species attributes to predict the composition at a given point in time. Thus, this model is similar to the Vital Attribute Model but its applicability is not restricted to frequently disturbed systems. Furthermore, this model clearly demonstrated the potential impact of specific site conditions on the sere, building on the suggestion by Grime (1977). For example, beginning with the same compositional mixture, a moisture-limited site produced a different pathway than one on which nitrogen was the most limiting resource. Unlike Tilman's hypothesis, the Life History Model does not assume that an equilibrium is usually reached, and it recognizes that a substantial level of stochasticity exists, especially in the colonization phase.

In 1987, a thorough review of Connell and Slatyer's (1977) models was published (Pickett et al. 1987). They concluded that these models were too simplistic to explain a complete sere and that two or more of the proposed mechanisms usually operate at the same time. Several studies of particular ecosystems have demonstrated that this is indeed the case (e.g., Walker and Chapin 1987, DeSteven 1991). They also contributed significantly to the development of a new theory by pointing out that model, pathway, and mechanism are not synonymous and must be defined clearly and considered separately.

Two other facets of the modern view of succession have emerged within the past 15–20 yr, but it is difficult to ascribe these to any one or group of authors. A recent book on succession theory and prediction listed two "major conceptual trends" since the mid-1970s: (1) a shift toward a more mechanistic (as opposed to holistic) explanation of succession (which is obvious if one looks at the theories reviewed above), and (2) the rejection of the equilibrium paradigm, which was exemplified by Clements (1928, 1936) and Odum (1969), and a move toward a nonequilibrium paradigm (Glenn-Lewin et al. 1992). This latter trend was explicitly proposed and demonstrated early in the mid-1970s by Horn (1975) who modeled secondary succession as a stochastic process.

Applicability of Modern Successional "Theory" to Habitat Typing

The Modern Successional "Theory"

The extensive work on succession during the last 2 decades suggests that the concept has been, and is, in a continu-

ing state of definition (see, e.g., Pickett et al. 1987, Bonan and Shugart 1989, Gleason and Tilman 1990, Rydin and Borgegard 1991, Tilman and Wedin 1991). However, one fact is clear: the theories of the early and mid-1900s are no longer ascribed to in their original form. Despite the lack of complete agreement, several components are consistent among most (sometimes all) modern theories. The points of commonality may be viewed as the core of our current understanding of succession. Those components include:

1. Disturbance is frequent enough in most terrestrial ecosystems to exert a significant influence on vegetation dynamics within a time frame that is relevant to resource management (Stearns 1949, Loucks 1970, Heinselman 1973, White 1979, Spurr and Barnes 1980, Oliver 1981, Runkle 1981, Sprugel and Bormann 1981, Whitney and Johnson 1984, Pickett and White 1985, Whitney 1986, Peet 1988, Bonan and Shugart 1989, Agee 1991); thus (a) many systems never reach a stable sere or potential climax (Harcombe and Marks 1978, Sprugel and Bormann 1981, McCune and Cottam 1985, Whitney 1986, Huston and Smith 1987); (b) multiple pathways are common (Olson 1958, Cattellino et al. 1979, Scheiner and Teeri 1981, Abrams et al. 1985, Halpern 1988, Kotar et al. 1988, Bonan and Shugart 1989, Keane et al. 1990); (c) retrogression is a plausible pathway (Cattellino et al. 1979, Abrams et al. 1985), as is accelerated movement toward a late successional stage (Whitney and Johnson 1984, Abrams and Scott 1989, Veblen et al. 1991) and (d) succession may be arrested for a period of time (Niering and Goodwin 1974, Whitney and Johnson 1984, Abrams et al. 1985).
2. Random influences play a significant role (Gleason 1926, Eglar 1954, Abrams et al. 1985, McCune and Allen 1985, Huston and Smith 1987, Sharik et al. 1989).
3. At least some life history attributes must be used to explain succession (Roberts and Richardson 1985, Tilman 1985, Pickett et al. 1987, Huston and Smith 1987, Halpern 1989).
4. Different mechanisms may drive succession on closely related sites and/or at different times within a sere (Connell and Slatyer 1977, Roberts and Richardson 1985, Tilman 1985, Host et al. 1987, Huston and Smith 1987, Leak 1987, Pickett et al. 1987, Keane et al. 1990).

Each of these components, except number three, have the potential to produce a sere that is inconsistent with the classic view of succession as formulated by Clements (1928) and amended by Whittaker (1953). Furthermore, components 1, 2, and 4 have a direct bearing on the theoretical basis of HTCSs because it includes many components of Clements' theory. Consequently, it is worthwhile to examine the relationship between these components and the concept/use of habitat typing.

Lack of a Potential Climax or Stable Sere

The fact that many sites will never support the "climax" (*sensu* Clements) is obviously not compatible with Premise 4 (Introduction). By itself, failure to meet this foundational

premise would not weaken the basis of habitat typing (Pfister 1989). However, a degree of stability in secondary succession is essential (Pfister 1989). If this is not present, the question arises: "Do habitat types clearly and consistently reflect inherently different site potentials?" [Premise 2]. For those sites that do not reach a potential climax or stable, late-successional stage, the HTCS must be reevaluated using another association (successional stage) to best reflect the site. However, it is not clear which should be used. As Daubenmire (1976, p. 119) stated: "Seral species are responding as much to the temporary increase in radiant energy . . . , or to the temporary reduction in root competition, . . . as to the intrinsic climatic and edaphic factors" Thus, it would be more difficult to know and determine which association is a clear indicator of the inherent productivity of the site.

Given the likelihood of multiple pathways (Olson 1958, Cattelino et al. 1979, Abrams et al. 1985, Kotar et al. 1988, Bonan and Shugart 1989, Keane 1989, Keane et al. 1990), there are often five or six associations that can occupy a particular type of site at the same point in the successional sere (e.g., Kotar et al. 1988). If this is true for later successional stages, which the data suggest occurs relatively often, then the selection and evaluation of possible "site quality indicator associations" (Kotar 1988, Archambault et al. 1989) becomes more problematic. This difficulty is likely to be compounded because: (1) on sites of intermediate quality a group of overstory species can occur on two to four different HTs (e.g., Pfister et al. 1977, Kotar et al. 1988); (2) retrogression is possible on some sites, especially where moderate to high intensity disturbance occurs at a short interval relative to the time it would take the late successional association to form; and (3) succession can be arrested, at least long enough to affect resource management planning (Niering and Godwin 1974, Abrams et al. 1985). Thus, it may be extremely difficult to determine which association, if any, accurately reflects the potential of the site. That is, Premises 1 and 2 are brought into question. Under these conditions, the *species* occupying the site would be the primary determinant of productivity, and the habitat type designation would not provide any additional information.

Stochastic and Disturbance Effects

The frequency of disturbance, the possibility of multiple successional pathways and random influences bring into question another important tenet of HTCS—the role of the overstory and its relationship to the understory [Premise 3]. These three influences can result in an overstory that varies continuously on a given site and can produce two totally different overstories on two sites of the same inherent potential. Thus, as Daubenmire and Daubenmire (1968, p. 52) claimed, the understory must develop completely independent of the overstory composition and dynamics. But does this occur? This assumption dictates that the composition of the overstory exert no, or little, direct influence on the understory. Furthermore, overstory composition must not affect forest floor/soil characteristics significantly and thereby indirectly determine understory composition, abundance or dynamics.

Given the variation in overstory composition that *can* occur, and the large number of factors that can affect understory composition, there is sufficient evidence to question the assumptions stated in the paragraph above. As potential overstory richness increases, and as the likelihood of occupancy by species with different leaf phenologies increases, the more likely it is that the overstory will play a role in determining the understory. Therefore, the assertion by Daubenmire and Daubenmire (1968) [above] should not be accepted without testing because the strength of these interactions and influences vary from place to place. The mechanisms and influences which can contribute include:

1. allelopathy (e.g., Jameson 1968, McCormick 1968, Rice and Pancholy 1972, Gabriel 1975, Horsely 1977, Tubbs 1977);
2. varying competitive abilities of co-occurring species (e.g., Lorimer 1983, Elliott and White 1987);
3. different overstories can result in *significantly* different forest floor and upper soil stratum characteristics in less than 75 yr (Broadfoot 1951, Ovington 1954, 1956, 1958a, 1958b, Alban 1969, Anderson et al. 1969, Rolfe and Boggess 1973, Messenger 1975, Carmean et al. 1976, Rogers 1978); and
4. regeneration and growth of understory species (herbaceous and woody) are affected by
 - (a) litter type (deciduous vs. conifer) (Rogers 1978, Collins 1990, Williams et al. 1990);
 - (b) litter depth (Beatty 1984, Collins and Good 1987, Collins 1990);
 - (c) soil moisture (Anderson et al. 1969, Hett and Loucks 1971, Beatty 1984, Horn 1985, Collins and Good 1987);
 - (d) soil nutrient levels (Rogers 1978, Beatty 1984);
 - (e) herbaceous composition (Maguire and Formann 1983, Elliott and White 1987);
 - (f) light quantity and quality (Spurr and Barnes 1980, Collins and Good 1987, Messier and Bellefleur 1988, Wayne and Bazzaz 1993); and
 - (g) type of disturbance (Abrams et al. 1985, Veblen et al. 1991, Duffy and Meier 1992).

Thus, the overstory could determine the understory composition to a significant degree via mechanisms such as allelopathy and competition. In addition, each association of overstory and understory within a habitat type can lead to a unique, or at least substantially different, set of understory environmental conditions. These sets of conditions will sometimes lead to significantly different sets of understory species on the same site type, which casts doubt on the generality of Premise 3a. Therefore, in mixed species forests it should not be assumed that overstory composition has no appreciable effect on understory development. These effects are more likely in eastern North America, and in the parts of the West where aspen (*Populus* spp.) can be part of the sere. However, it should not be ruled out in other parts of the West (Jameson

1968, Alban 1969, Elliott and White 1987, Agee 1991, Veblen et al. 1991).

The disturbance-free period needed for a habitat type to be identified from the understory is 40-60 yr in the East and 60-80 yr in the West. Superimposed on top of this requirement is the 200-500 yr (West) period necessary for a late succession, stable association to form (Pfister 1989). Nonetheless, the 40-80 yr period may not be sufficient for the understory to stabilize and allow clear, positive identification of the habitat type. Two examples, one from the Southeast and one from Alaska, show why this can be true. Successional changes in these two regions were described using a chronosequence of stands. In the oak-pine (*Quercus-Pinus*) forests of the Southeast, the understory changed rapidly for the first 40-50 yr, stabilized for approximately 100 yr, then exhibited a substantial shift in composition between ages 150 and 200 (Nicholson and Monk 1974). A similar temporal pattern occurred in the understory of spruce-hemlock (*Picea-Tsuga*) forests of southeast Alaska, with the reestablishment of a shrub-herb understory at 140-160 yr (Alaback 1982). Thus mature or old-growth communities that had been free of moderate-to-intense disturbance for more than 100 yr would sometimes be necessary to identify the understory component (but see Metzger and Schultz 1984) of the potential climax community. In the Lake States and Intermountain regions, very few old-growth stands exist (Barnes 1989, Bogliano 1989) and thus second growth stands were used to work out the HTCS's (Kotar et al. 1988, Pfister 1989). Therefore, it is probable that the composition of the potential climax has not been accurately identified for some habitat types.

Differential response to disturbances, year-to-year effects of weather, past land use, insect outbreaks, and disease epidemics often introduce an element of stochasticity and unpredictability into succession. For example, temporal differences in rates of eastern white pine (*Pinus strobus*) establishment, on similar sites, have been found in the Lake States (Sharik et al. 1989). Different types and intensities of disturbance have led to substantially dissimilar understories in several ecosystems (e.g., Scheiner and Teeri 1981, Abrams et al. 1985, Halpern 1989). This occurs because different intensities (size, degree of litter consumption) and alternative disturbances produce differences in the forest floor environment (Swank and Vose 1988, Poulson and Platt 1989, Phillips and Shure 1990, Covington and Sackett 1990, Keane et al. 1990). In the northern Appalachian mountains, disturbance and land use were the most important influences on the abundance of *Quercus* spp. advance regeneration (Carvel and Tryon 1961, Bowersox and Ward 1972). Random climatic events such as exceptionally dry or moist periods can determine if or how much regeneration occurs in the Southwest (Schubert 1974) and Lake States (Hett and Loucks 1971). All of these impacts can contribute to the lack of a stable stage by maintaining varying, early successional associations. This creates a situation in which Premise 1 does not apply because the climatic climax or potential climax (Premise 4) is never reached. The result would be that the inherent site potential (Premise 3) would not be reflected well by HTs. A

less intractable outcome could be that the stochastic influences extend the time needed for a stable understory to form.

Conclusions

This review has shown that our understanding and view of succession has evolved significantly since 1960. Recent theories have amended and built on what was described and proposed in the early 1900s by Clements, Gleason, and others. However, no single theory has become widely accepted (Pickett et al. 1987) and the "unfinished successional revolution" (Johnson 1979) continues.

Nonetheless, the current consensus solidly supports two important conclusions: (1) a large number of factors can influence succession (Pickett et al. 1987) and (2) succession can be quite variable between similar sites. Given this, and the assessments presented above, a reanalysis of some of the assumptions underlying habitat types is warranted. This does not mean that existing HTCSs are invalid. For example, under specific disturbance regimes, succession follows a sequence that is exactly as predicted by the Clementsian model (Cattalino et al. 1979, Bonan and Shugart 1989). However, this is the exception not the rule. A relatively large number of influences can weaken or undermine the four premises of habitat types, and the frequency with which they apply mandates that the assumptions behind a HTCS be examined and, wherever possible, tested.

It is during the HTCS development phase that the influences explained here should be tested and incorporated as necessary. For some areas and topics, for example successional pathways in the northern Rocky Mountains, most of the data exist (Cattalino et al. 1979, McCune and Allen 1985, Keane 1989, Keane et al. 1990). On the other hand, more hypothesis testing is needed for most of the influences outlined above. The appropriate tests include:

1. Does understory composition and/or species abundance vary among "early mature," mature and "late mature" stages? That is, are "late mature" communities essential to identify the potential climax?
2. Is understory development affected by overstory composition?
3. Do different disturbance types or intensities result in contrasting pathways? If so, do they converge? When?
4. Is the Initial Floristic Composition affected significantly by (a) spatial variation in the seed bank, (b) the composition of the surrounding vegetation, (c) yearly weather patterns, and/or (d) biotic influences? If so, does this variation lead to multiple endpoints, the lack of a stable stage, or alter the time it takes for a stable stage to form?

An HTCS which tests these possible effects, and incorporates them as warranted, will have evaluated the full range of factors which can influence succession. An HTCS developed within this framework will be more sound theoretically and should differentiate among similar habitat types more clearly and consistently (see, e.g., Figure 6 in Arno and Pfister 1977).

This will minimize problems in application of the system (Archambault et al. 1989) and provide more specific ecological information about each habitat type. An example would be all possible pathways and associations which can and do occur within each habitat type (e.g., Keane 1989).

An HTCS developed within a modern theoretical framework will not be infallible; random influences and undetectable impacts from past land use will still create associations that do not fit a recognized type. And it is possible that the rate and direction of species turnover ("a" above), coupled with local effects ("d"), will make it impossible to delineate part of the HT continuum in certain regions. It is important that we remain open to this possible limitation of a classification system which is based solely on vegetation. In regions where an HTCS can be successfully developed, there will probably still be overlap between similar HTs in a few ecological characteristics and rates. However, a more up-to-date theoretical foundation will provide the user with a system that can be applied more widely and used for a greater variety of purposes.

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