IDEA AND PERSPECTIVE

Testing the assumptions of chronosequences in succession

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Abstract

Many introductory ecology textbooks illustrate succession, at least in part, by using certain classic studies (e.g. sand dunes, ponds/bogs, glacial till, and old fields) that substituted space for time (chronosequence) in determining the sequences of the succession. Despite past criticisms of this method, there is continued, often uncritical, use of chronosequences in current research on topics besides succession, including temporal changes in biodiversity, productivity, nutrient cycling, etc. To show the problem with chronosequence-based studies in general, we review evidence from studies that used non-chronosequence methods (such as long-term study of permanent plots, palynology, and stand reconstruction) to test the space-for-time substitution in four classic succession studies. In several cases, the tests have used the same locations and, in one case, the same plots as those in the original studies. We show that empirical evidence invalidates the chronosequence-based sequences inferred in these classic studies.

Keywords

Chronosequence, dune succession, glacial till succession, hydrarch succession, old-field succession, vegetation change, vegetation dynamics.

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INTRODUCTION

Succession is one of the oldest concepts in ecology (Johnson 1979; Pickett *et al.* 1992). Many introductory ecology textbooks (e.g. Odum 1953; Oosting 1956; McNaughton & Wolf 1973; Ricklefs 1990; Krebs 2001; Stiling 2002; Rose & Mueller 2006; Keddy 2007) have used certain early (classic) examples of vegetation succession: coastal sand dunes, ponds/bogs/small lakes, till substrate following glacial retreat, and agricultural fields following abandonment. All of these classic studies used the space-for-time substitution (chronosequence) method to study the succession.

In this paper, we review these classic examples of chronosequence-based succession and the studies that have tested the chronosequence assumptions and inferences. These classic examples are: Cowles (1899) study of sand dune succession, Dachnowski's (1912, 1926a) study of hydrarch succession, Cooper's (1923a,b, 1931, 1939) and Crocker & Major's (1955) studies of succession on till substrate following glacial retreat, and Billings' (1938) and Oosting's (1942) studies of old-field succession. In several cases, the tests of these chronosequence-based successions have used the same locations and, in one case, the same plots as those in the original studies. The results of these tests show that, regardless of how we may choose to define succession, there is sufficient empirical evidence to reject continued use in textbooks of these particular chronosequence-based examples of succession.

At one time or another, many of us have used chronosequences in our studies, often reluctantly because there seemed to be no other method that offers the convenience of using contemporary spatial patterns to infer long-term vegetation change. Many important contemporary ecological studies rest, at least in part, on chronosequence methodology, for example, studies of biodiversity (Addison *et al.* 2003), nutrient cycling (Vitousek *et al.* 1995), productivity and carbon flux (Law *et al.* 2003; Litvak *et al.* 2003), natural and anthropogenic disturbances (DeLuca *et al.* 2002), restoration (Aide *et al.* 2000), and global change (Choi & Wang 2004; Grunzweig *et al.* 2004). Because of such widespread continued use of chronosequences, it is essential to address the fundamental problems that may arise from such use; we do so by using the classic chronosequence-based textbook examples of succession.

DEFINITION AND ASSUMPTIONS OF CHRONOSEQUENCES

Because of the length of time required to actually observe the successional vegetation changes in a single site, studies of succession used the method of substituting space for time, generally referred to in ecology as a chronosequence (for the purpose of this paper, we will use 'space-for-time substitution' as equivalent to chronosequence). This method infers a time sequence of development from a series of plots differing in age since some initial condition, i.e. time since the site became available for occupation or colonization or the time since last disturbance. It makes the critical assumption that each site in the sequence differs only in age and that each site has traced the same history in both its abiotic and biotic components. If these assumptions are correct, then each site will have repeated the successional sequence of every other older site up to its present age. This is the same assumption made in static life tables that allows the age distribution of a population taken at one point in time to represent the survivorship curve (Johnson *et al.* 1994).

There have been previous critiques of the chronosequence method in ecology that pointed out its inherent problems and limitations (e.g. Collins & Adams 1983; Pickett 1988) and suggested the need to validate or justify the critical assumptions that abiotic and biotic conditions have remained constant over the time span of the successional change under study and that all sites have tracked the same history. Unfortunately, the justification generally provided in chronosequence-based succession studies involves, at best, an indication that all sites share a similar substrate or topographic position (e.g. Billings 1938). Many ecologists and foresters have continued to use the chronosequence method to study succession [e.g. 249 references (2000–2007) obtained on Web of Science using the search terms 'chronosequence AND succession', a majority without testing the chronosequence assumptions].

TESTING THE ASSUMPTIONS OF CHRONOSEQUENCES

Dune succession

Although preceded by earlier studies of vegetation succession on coastal dunes (e.g. Beck-Mannagetta 1890; Warming 1895), the classic study of dune succession widely cited in English-language (especially American) textbooks is that by Cowles (1899), who examined plant communities on sand dunes along the southern shore of Lake Michigan. As the post-glacial lake receded over time, it resulted in the formation of a sequence of sand dunes representing former beach ridges. From the vegetation found growing on the sequence of dunes that varied in age, Cowles (1899, 1901), and subsequently Whitford (1901), inferred a sequence of vegetation development that is repeated in numerous ecology textbooks (e.g. McNaughton & Wolf 1973; Ricklefs 1990; Krebs 2001; Smith & Smith 2001). The vegetation sequence for dune succession generally presented in textbooks (e.g. Fig. 1) tends to show a simple linear successional sequence of annuals, sand-binding dune grasses, cottonwoods, pines, and oak, despite the fact that Cowles (1899) had emphasized that only perennial dune grasses, shrubs, and trees such as cottonwoods were dune-forming plants (with cottonwoods germinating 'in protected depressions on the upper beach', p. 182) and had described different successional pathways for different dune locations (e.g. windward vs. lee slopes). Although Cowles (1899) and Clements (1916) appeared to recognize a more complex succession on dunes than that illustrated in Fig. 1, they had a firm belief in the predictable directional replacement of species to a climax driven by habitat modification by plants; i.e. the seral plants modify the light and edaphic conditions of the dunes, leading to a more mesophytic environment that culminates in the mesophytic climax forest characteristic of the lake region.

There is ample empirical evidence against this classic textbook dune successional sequence; see review by
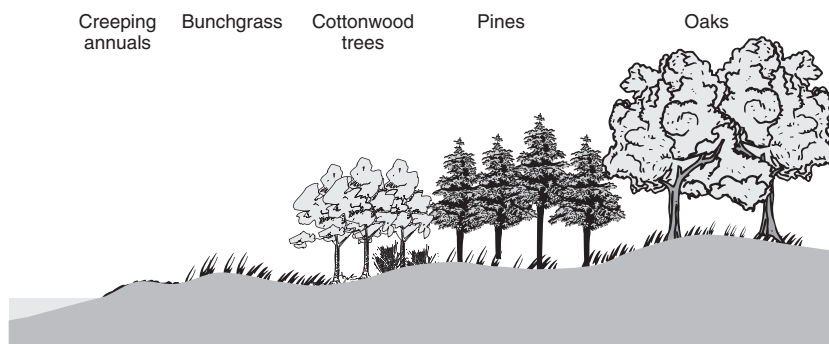

Creeping annuals   Bunchgrass   Cottonwood trees   Pines   Oaks

Figure 1 Widely used textbook example of sand dune succession. Reproduced from McNaughton, *General Ecology*, 1E. ©1973 Brooks/Cole, a part of Cengage Learning, Inc., with permission. http://www.cengage.com/permissions.

Miyanishi & Johnson (2007). The first addresses the role of annuals such as *Cakile edentula* in dune succession. This species is found primarily on sandy areas of the beach that are kept bare in the fall and early spring by high waves (Payne & Maun 1981). Despite the contention in McNaughton & Wolf (1973) that the dune grasses replace the annuals in this succession, *Cakile* is not a dune pioneer and is not replaced by *Ammophila*. The seeds of *Cakile* are dispersed onto the beach driftline by high waves in fall and winter (Payne & Maun 1981). However, their habitat is also regularly swept bare by these same high waves. Thus, the habitats of the annual *Cakile* and perennial *Ammophila* are segregated by the seasonal wave disturbance, and it is the disturbance regime, not the time factor, that determines where these two species grow.

The second line of evidence against this dune successional sequence concerns the cottonwoods (*Populus*), shown in Fig. 1 dominating the second dune ridge behind the *Ammophila*-dominated foredunes. The inference from this diagram and stated explicitly in some texts is that this second ridge had once been dominated by *Ammophila* and was subsequently invaded by cottonwoods (McNaughton & Wolf 1973; Krebs 2001). However, not only Cowles (1899) but numerous other studies (Fuller 1912; Downing 1922; Weaver & Clements 1929; Olson 1958; Poulson 1999) have reported that the cottonwoods establish only on moist germination beds such as depressions on the beach, low pannes, swales, or recently in-filled runnels, all with surfaces close to the water table. This species does not successfully colonize dunes previously established by *Ammophila*. However, once established, the cottonwood seedlings are tolerant of subsequent sand deposition by virtue of their rapid vertical growth and adventitious roots (Fuller 1912; Poulson 1999). Once again, it is not facilitation by *Ammophila* that explains the occurrence of cottonwoods on the second dune ridge but the particular historical sequence of a moist germination bed close to the water table followed by subsequent sand deposition after the seedlings had become well-established.

The third argument against the classic dune successional sequence was made by Olson (1958) who did a much more extensive study of the same Lake Michigan dunes studied by Cowles. Olson had the advantage of being able to date the dunes; his study showed that dunes of equal ages had a wide range of vegetation cover types, and he concluded that the vegetation found on any particular dune location depended on topographic location and disturbance history. Olson's study showed that tree species, such as *Tilia americana* and other hardwood trees, could be found on young dunes, particularly on steep lee slopes and in protected pockets. He also argued against eventual replacement of black oak-dominated communities by beech-maple forest on the oldest dunes (not shown in Fig. 1 but predicted as the eventual climatic climax in this succession by Cowles (1901) and Clements (1916)), citing carbonate leaching of the older dune soils to produce acidic conditions that are not tolerated by beech or sugar maple.

Finally, the argument of facilitated dune succession leading to the directional progressive change from dune grasses to mesophytic forest was based on hypothesized changes to the light conditions and sandy soil brought about by each successive dominant species (Cowles 1899). In particular, it was hypothesized that the plants changed soil properties (such as field capacity, pH, and base saturation) in a way that facilitated successful establishment by the next seral dominants. However, these purported changes to the soil were themselves based on chronosequence studies (e.g. Salisbury 1925; Morrison 1973). Subsequent studies by Baldwin & Maun (1983) and Poulson (1999) failed to find significant differences in many of these soil properties (e.g. humus content, CEC, depth of A-horizon) between dunes of varying age with different vegetation cover. Furthermore, through experimental seeding and seedling transplant studies, Lichter (2000) was able to show that so-called 'later' successional species, such as *Juniperus communis*, *Pinus strobus*, and *Quercus rubra*, could successfully establish on young dunes with minimal soil development, further supporting Olson's (1958) earlier study. Thus, Lichter as well as Chadwick & Dalke (1965) concluded that soil development was not a significant factor explaining species distributions on dunes.

Interestingly, a careful reading of Cowles' (1899) original observations (not viewed through the lens of succession) suggests the actual processes and mechanisms determining species composition of the dunes. He noted that '[p]erhaps no topographic form is more unstable than a dune' and 'on the whole the *physical forces of the present* [italics ours] shape the floras as we find them' (p. 96). In fact, the dynamic nature of sand dunes has been extensively studied by coastal geomorphologists, who have been concerned with the availability of sand or sand budgets (e.g. Bowen & Inman 1966; Davidson-Arnott 1988; Loope & Arbogast 2000; Bauer & Davidson-Arnott 2002), and aeolian geomorphologists interested in the transport of sand by wind (e.g. Hesp 1988, 1996, 2002; Namikas & Sherman 1998; van Dijk *et al.* 1999; Arens *et al.* 2001; Arbogast *et al.* 2002; Hesp & Martínez 2007). Even established dunes are subject to sand transport when a sand supply upwind becomes available for transport, resulting in buried forests and soil profiles (Cowles 1901; Wolfe 1932; Ranwell 1958; Anderton & Loope 1995; Loope & Arbogast 2000). Thus, much of the current literature recognizes sand burial (and erosion) as the most important factor influencing the distribution of coastal dune vegetation, particularly on the foredunes (e.g. van der Valk 1974; Zhang & Maun 1990; Martínez & Moreno-Casasola 1996; Kent *et al.* 2001; Maun 2004).

Recently, Miyanishi & Johnson (2007) proposed as an approach to studying the vegetation on coastal dunes the coupling of an understanding of sand budgets and aeolian sand transport in the formation and development of dunes (see references in previous paragraph) with the large literature available on species' tolerances for sand deposition and erosion (e.g. Maun & Lapierre 1984, 1986; Harris & Davy 1987; Sykes & Wilson 1990; Maun 1996, 2004). Such an approach would provide a more useful framework for explaining the distribution of plant species on dunes, particularly the foredunes (Moreno-Casasola 1986; Tyndall *et al.* 1986; Hayden *et al.* 1995; Maun & Perumal 1999; Dech & Maun 2005). On stabilized dunes further inland, other disturbances such as fire, grazing, insect outbreaks, logging, etc. play a more dominant role in influencing vegetation than sand movement.

Hydrarch succession

The classic hydrosere or hydrarch succession for small water bodies, such as bogs, ponds, and small lakes, described in textbooks (e.g. Ricklefs 1990; Roberts *et al.* 1993) is based on the zonation of vegetation observed around these water bodies. The spatial zones of plant cover occurring outward from the open water were used to infer the temporal stages in the conversion (succession) of open water to a mesic

forest characteristic of the climatic region (Dachnowski 1912; Clements 1916; Gates 1926; Tansley 1939). According to Weaver & Clements (1929, p. 65):

> the area once covered by deep water becomes transformed into a forest, a phenomenon clearly conceivable when one follows the actual processes of development. … This whole developmental process in action may be found about lake margins where each stage is shown as a definite zone.

The figure often used to illustrate this conversion process (Fig. 2) was first presented by Dachnowski (1912, 1926a). The seral stages for this succession in freshwater systems were typically given as: submerged plants, floating plants, reed swamp, sedge meadow, woodland, and climax forest (Weaver & Clements 1929), although some differences were recognized in the stages between the succession of bogs and that of ponds and lakes. Tansley (1939) described similar stages in British systems: water plants (hydrophytes), reeds and bulrushes, marsh and fen plants, shrubs and trees, and finally the climax forest.

Although Clements' (1916) explanation for succession relied primarily (or solely) on habitat changes brought about by the plants themselves [i.e. Tansley's (1935) autogenic succession], Tansley's (1939) explanation for hydrarch succession involved both autogenic and allogenic processes:
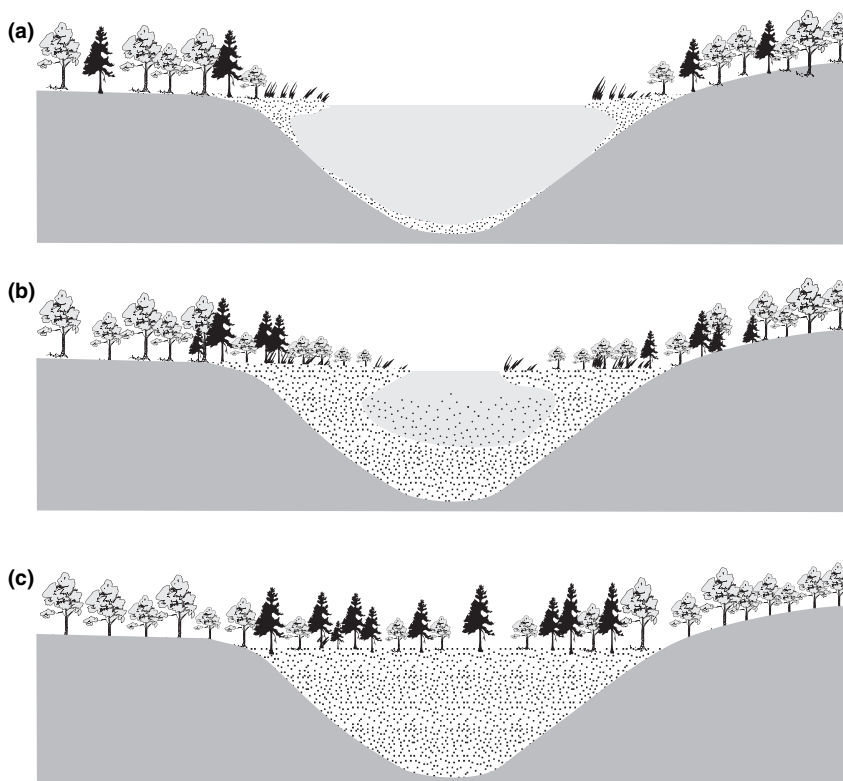

Figure 2 Textbook example of hydrarch succession based on vegetation zonation around a small freshwater body and showing conversion of open water to forest. From Dachnowski (1926a).

the infilling of the basin and raising of the submerged soil surface was presumed to occur through a combination of accumulation of partially decomposed organic matter from the plants growing on, in, and around the water body and deposition of sediments from overland flow.

In general, studies of hydrarch succession in both Europe and America have been based on the chronosequence method (e.g. Transeau 1903; Pearsall 1920; Walker 1940; Dansereau & Segadas-Vianna 1952). The first non-chronosequence-based study of hydrarch succession that appears in the literature was that of Heinselman (1963) who used evidence from stratigraphy, topography, and vegetation to reconstruct the history of Myrtle Lake in Minnesota (Fig. 3). Rather than the water-filled depression filling in and the open water converting to a forest as initially hypothesized by Dachnowski (1912), the result was bog expansion, paludification of surrounding areas, rising water tables, and maintenance of the open water, albeit at a higher elevation.

Walker (1970) noted that 'Current ecological theory … maintains the view that mire zonation recapitulates hydrosere history.' To test the hydrarch succession inferred from chronosequence studies, he used pollen analyses of cores from small and large inland basins in Britain. Based on his results, Walker commented: 'The most impressive feature of these data is the variety of transitions which have been recorded' and 'It is impossible to select a "preferred" sequence' (p. 123). He concluded that,

> the range of vegetation types in a single locality at any one time does not necessarily reflect the sequence which has led to the current pattern at that site, nor does it alone predict the future of the vegetation there even if allogenic influences can be excluded (p. 137).

As previously shown by Heinselman (1963), Walker also recognized the critical significance of the entry of *Sphagnum* that generally resulted in a persistent bog stage. In fact, because of the widespread and apparently persistent nature of *Sphagnum* bogs in the boreal zone, a number of studies (Katz 1926; Van Breemen 1995; Klinger 1996) have even proposed it as the climax community!
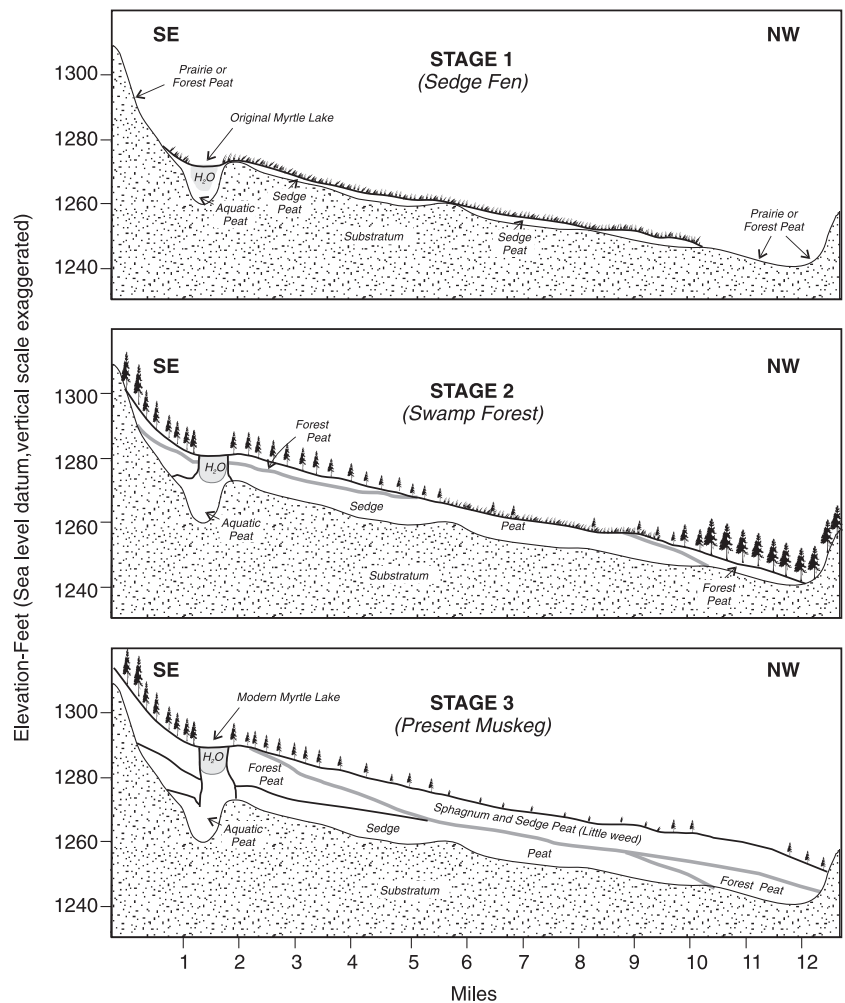

Figure 3 Reconstruction of vegetation changes at Myrtle Lake, Minnesota. Reproduced from Heinselman (1963), with permission from the Ecological Society of America.

Another paleoecological test by Jackson *et al.* (1988) investigated a chronosequence of dune ponds at Miller Woods in Michigan, which showed a sequence of plant communities from submersed and floating macrophytes in the youngest ponds to emergent plants (*Typha angustifolia*) as the dominants in the oldest ponds. They used pollen analysis to test whether the observed spatial pattern represented the temporal pattern of vegetation change within the oldest 3000-year-old pond as originally proposed by Shelford (1911); see also Shelford (1963, p. 51). What Jackson *et al.* (1988) found was that the *Typha* stands in the oldest ponds had developed only in the last 150 years in response to local human disturbance. They concluded that '[m]odern vegetational differences along the chronosequence reflect differential effects of disturbance rather than autogenic hydrarch succession' (p. 928).

Finally, a long-term study of a small kettle-hole bog in Michigan by Schwintzer (1978) showed that the vegetation changed repeatedly between a *Chamaedaphne* association and bog forest. From the coincidence of the vegetation shifts with recorded changes in climate and water levels, Schwintzer concluded that allogenic (weather-related) changes in bog water levels were the major forcing function in the observed vegetation changes.

As with the dune succession example, later ecologists appeared to ignore qualifications in the early chronosequence-based studies; for example, Dachnowski (1926b) recognized that peat profiles 'show that the historical sequence of vegetation does not necessarily correspond with the horizontal zonation and succession of plant associations at the surface' (p. 134). Also, Pearsall (1920, p. 196) had noted: 'Actual observation shows that the types of succession are very numerous' (i.e. the successional sequences are much more complex than that given in textbooks). Pearsall inferred different sequences, based on siltation rates as well as substratum, and also recognized some 'apparently reversible' changes dependent on the rate and type of siltation. Despite this early recognition of problems with the classical hydrarch succession as well as the clear subsequent tests of the hypothesized succession, the early diagram by Dachnowski (1912) indicating the succession of open water to terrestrial mesic forest has remained the legacy in textbooks.

On the other hand, the dynamic nature of wetlands has been well studied by hydrologists who have recognized that water levels fluctuate over time (e.g. Winter 1989; Woo & Rowsell 1993; Winter & Rosenberry 1995; LaBaugh *et al.* 1998; Johnson *et al.* 2004) and are controlled by the balance between water inputs and outputs that are, in turn, controlled by hydrological processes, such as precipitation, evapotranspiration, groundwater exchange, and surface water inputs and outputs (see Hayashi & van der Kamp 2007). Water levels in wetlands show interannual and interdecadal oscillations related to climatic variability (Winter & Rosenberry 1998; van der Valk 2005). Also, disturbances or changes in landuse in the catchment can result in dramatic changes in hydrological processes and, hence, water levels (van der Kamp *et al.* 1999, 2003).

For the past 30 years, van der Valk *et al.* have conducted studies in the vegetation dynamics of prairie wetlands (e.g. van der Valk & Davis 1976, 1978; van der Valk & Welling 1988; van der Valk 1994; Seabloom *et al.* 2001; Seabloom & van der Valk 2003). Their studies have shown that wetland plant species have various life-history strategies (e.g. lifespan, seed longevity, dispersal, vegetative reproduction) that can explain their establishment, persistence, or extinction under varying water level regimes. In 1981, van der Valk proposed a qualitative model to explain and predict changes in wetland species distributions in response to changing water-level regimes in wetlands; more recently, he reviewed the current understanding of post-disturbance coenocline development in prairie wetlands (van der Valk 2007). Thus, it is clear that the vegetation of wetlands can be better understood through an understanding of the dynamic nature of wetlands with their fluctuations in water levels and the responses of plant species to these changes.

Glacial till succession

Cooper's (1923a,b, 1926, 1931, 1939) studies at Glacier Bay, Alaska, provided the textbook example of primary succession on glacial till following ice retreat (e.g. Ricklefs 1990; Begon *et al.* 1996; Krebs 2001; Smith & Smith 2001; Molles 2002; Stiling 2002; Rose & Mueller 2006). As described in these texts, the succession begins with the pioneer

> mosses and a few shallow-rooted herbaceous species, notably *Dryas*. Next, several kinds of willow (*Salix*) appear, prostrate species at first, but later shrubby types. Soon alder (*Alnus crispus*) enters the succession and after *c.* 50 years produces thickets up to 10 m tall with a scattering of cottonwood. The alder is invaded by sitka spruce (*Picea sitchensis*), forming a dense mixed forest which continues to develop as western hemlock (*Tsuga heterophylla*) and mountain hemlock (*T. mertensiana*) become established.
>
> (Begon *et al.* 1996)

Again, this primary successional sequence is based on the vegetation found on sites that were deglaciated at different times and thus were inferred to represent different ages or stages of vegetation development.

Similar to the dune succession example, the explanation for this vegetation development was based on Clements' facilitation hypothesis. This explanation was bolstered by the much-cited study by Crocker & Major (1955), in which the soil properties of pH, carbon content, and nitrogen

content were measured at sites of different ages. Their study showed that the youngest sites had high pH but low carbon and nitrogen levels, whereas the older sites with alder had lower pH but higher carbon and nitrogen. Although this study was also based on a chronosequence, it was accepted as strong evidence, if not confirmation, for the facilitation explanation; i.e. that the late successional spruce and hemlock can only establish after soil modification (particularly nitrogen fixation) by the alders (Colinvaux 1993; Begon *et al.* 1996; Keddy 2007).

However, in order to test this hypothesized sequence of vegetation development on glacial till, we must look to empirical evidence from studies using methods *other* than chronosequence. Both Chapin *et al.* (1994) and Fastie (1995) studied succession at Glacier Bay, using some of the same sites that Cooper had established but different methods. Chapin *et al.* (1994) investigated spruce germination, seedling survivorship, and seedling growth in the first 2 years following planting in soils collected from the various aged sites as well as following seed planting in the actual sites. Their study showed that germination and seedling survivorship of spruce was not significantly better in the alder sites than in the pioneer sites. In general, the presence of alders inhibited rather than facilitated seedling establishment and growth of spruce. Chapin *et al.*'s results refute Colinvaux's (1986, 1993) assertion that 'it is undeniable that primary succession on glacial till at Glacier Bay is driven by habitat modification, at least in its early stages' (p. 422). In fact, as Chapin *et al.* (1994) state: 'the major facilitative effect of alder may occur after spruce emerges above the alder canopy' (p. 170).

Subsequently, Fastie's (1995) use of dendrochronological methods enabled testing of the hypothesis that the alder thickets found in the intermediate-aged sites are a necessary stage in the development of the spruce or spruce-hemlock forest. Spruce trees that establish either concurrent with or after the establishment of an alder thicket show in their growth rings a period of suppression with growth release after they have topped the alder canopy. Such growth ring patterns were found in the intermediate-aged sites. How-

ever, in the three oldest sites covered by spruce-hemlock forest, the trees did not show these signs of suppression and release. Furthermore, stand reconstructions for all of the sites showed that the recruitment of spruce in the younger sites was substantially slower than in the three oldest sites. The conclusion here is that there were no alder thickets in the three oldest sites at the time the spruce trees established, and therefore spruce recruitment and growth was not inhibited by the presence of an alder thicket. On the other hand, the younger sites were occupied by alders when spruce began recruiting. Fastie attributed the difference in recruitment patterns between the three oldest sites and all of the younger sites to the proximity of the former group to refugial spruce forests. At the time of ice retreat from each site, the three oldest sites were only 1.2–4.0 km from old growth refugia with spruce, while the younger sites were 7.5–34.0 km from spruce refugia and 23 to 27 km from the nearest stands with 10 cone-bearing spruce per hectare. Thus, with a nearby abundant seed source, the newly exposed till on the oldest sites was rapidly colonized by spruce. However, on the younger sites, species with better dispersal ability (e.g. small seeds) such as willows, alders, and cottonwoods were able to recruit before spruce.

The conclusion we can draw here is that there is no particular sequence of species dominants *required* in the development of plant cover on glacial till. As Chapin *et al.* (1994) concluded: 'The order in which species colonize at Glacier Bay correlates closely with dispersability' (p. 169). The initial colonizers are determined primarily by the availability of propagules, and the rate of recruitment and growth by later-arriving species is generally inhibited, at least initially, by the presence of the earlier occupiers.

Old-field succession

Our final example gleaned from textbooks (e.g. Goudie 1989; Ricklefs 1990; Krebs 2001; Smith & Smith 2001; Molles 2002) is the secondary succession on abandoned agricultural fields (Fig. 4). This example is based on a study by Oosting (1942) who examined former agricultural fields
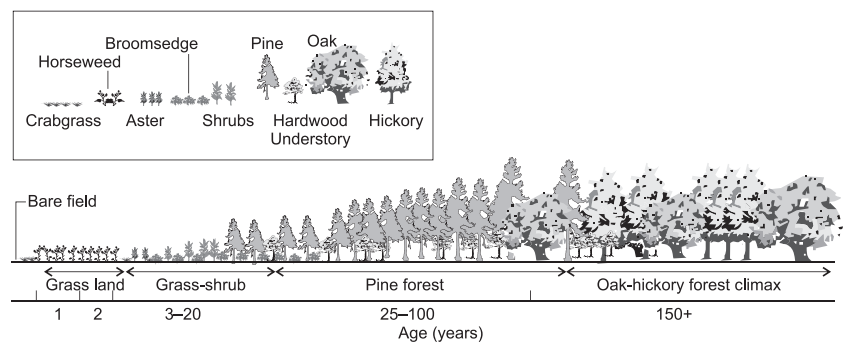

Figure 4 Textbook example of oldfield succession on the North Carolina Piedmont. Reproduced from Goudie (1989), with permission from Wiley-Blackwell.

on the Piedmont of North Carolina that varied in time since abandonment: 1 to 3-year-old abandoned fields and 11 to 75-year-old pine stands (based on tree ages, not time since abandonment). According to Oosting (1942, p. 7): 'Succession following abandonment of upland fields is represented by distinct communities which follow each other rapidly in the early stages.' These early communities were dominated by *Leptilon canadense* and *Digitaria sanguinalis* (first year), *Aster ericoides* and *Ambrosia artemisiifolia* (second year), and *Andropogon* spp. (third year). From his chronosequence, Oosting also inferred that pines replace *Andropogon*, forming closed stands in 10–15 years, and are subsequently replaced by the climax oak-hickory (*Quercus-Carya*) forest by 70–80 years. As Buell *et al.* (1971, p. 67) stated:

> The reasonable assumption is made that succession within a local area on a uniform substratum follows a generally predictable course and that any one field, within limits, represents a stage through which all others will pass or have passed.

Subsequently, old-field succession was described more generally in textbooks as follows:

> bare fields are quickly covered by a variety of annual plants. Within a few years, most of the annuals are replaced by herbaceous perennials and shrubs. The shrubs are followed by pines, which eventually crowd out the earlier successional species; pine forests are in turn invaded and then replaced by a variety of hardwood species that constitute the last stage of the successional sequence.
>
> (Ricklefs 1990, p. 678)

The usual explanation for this succession is again that it is driven by the modification of the light environment (i.e. creation of increasingly shady conditions) and soil properties (increase in organic matter and soil profile development) by each preceding community (Goudie 1989).

However, although this textbook explanation implies that the species are invading the fields in a relay when conditions for their establishment are appropriate, McQuilkin (1940), Oosting (1942), and Keever (1950) had all noted that the dominants of later successional stages such as pines were commonly already present in fields 1 year after abandonment in North Carolina. Similarly, on the Piedmont of New Jersey, '[t]he dominants of older fields are all present in newly-abandoned fields' (Bard 1952, p. 208). Furthermore, Coile (1940) did not find soil characteristics to be related causally to the invasion of pine into abandoned farmland. Thus, in their review of the evidence on old-field succession, Drury & Nisbet (1973, p. 345–346) concluded: 'No evidence indicated that development of a [soil] profile is associated with the replacement of the vegetation type responsible by another one.' Rather, the observed change in dominance in the first few years following abandonment was best explained by differential growth rates among species and likely some suppression by faster-growing species (Egler's (1954) initial floristics composition model).

The colonization by plant species into abandoned fields is, however, dependent on the availability of propagules. As Keever (1950) noted, both the time of year and the species found in neighbouring fields at the time of last cultivation affect what seeds are available for germination as well as the conditions for seedling establishment. Thus, '[o]ne field from which sweet potatoes were harvested in late fall was dominated by ragweed the following year and another such field was dominated by horseweed' (p. 247). Others have also noted the importance of nearby seed sources in determining species presence in abandoned fields (Beckwith 1954; Buell *et al.* 1971). Not surprisingly, the first woody dominants to appear in abandoned fields in the central basin of Tennessee were found to be species of *Ulmus* and *Celtis*, not pines, as no pines are native to this area (Quarterman 1957).

Because of the relatively fast rate of vegetation development on newly bared sites with soils (e.g. following farm abandonment) as opposed to that on soil-less substrate (e.g. sand dunes or glacial till), it has been possible to test old-field successional sequences inferred from chronosequence studies through long-term monitoring of permanent plots. For example, in prairie regions such as Kansas and Oklahoma, Booth (1941) had described the chronosequence-based successional stages for abandoned fields as: 'weed, annual grass, perennial bunch grass, fully-developed prairie' with an oak-hickory woodland or savanna eventually replacing the grasses on more mesic sites in the absence of human disturbance. However, Collins & Adams (1983, p. 187), using 32 years of permanent plot data, concluded that

> development from pioneer weeds to prairie on uncultivated sites does not require four stages in an orderly sequence, nor has such a sequence ever been conclusively demonstrated to occur on one site.

Similarly, Bard's (1952) chronosequence-based study of old-field succession on the New Jersey Piedmont has been tested through the establishment in 1958 (Buell *et al.* 1971) and continued studies (e.g. Pickett 1982, 1983; Myster & Pickett 1990) of permanent plots in 10 old fields at the Hutcheson Memorial Forest. These studies have not supported Bard's (1952) inferred successional sequence, either in the early stages [e.g. Pickett (1983) reported an absence of Bard's *Andropogon* stage] or later stages [e.g. Pickett (1982) found multiple peaks of abundance and long periods of presence of Bard's early successional herbaceous species]. The variation observed in vegetation change among the old fields could be explained by the variation

in factors such as year of abandonment (interannual climatic variation), season of abandonment and adjacent vegetation (seed availability), last crop planted (irrigation, herbicide, and nutrient treatments), etc. (Myster & Pickett 1990). Buell *et al.* (1971, p. 73) concluded:

> When one examines the data from different areas it does not appear that there is a uniform pattern for tree invasion of old fields throughout the deciduous forest region, and hence little basis for generalization.

DISCUSSION AND CONCLUSIONS

These classic chronosequence studies persist in textbooks and teaching perhaps because they present a simple, linear, pedagogical device that gives order to the confusing array of vegetation observed on the landscape and allows the past to be understood by the present vegetation patterns; i.e. they appear to allow one to 'walk back in time'. As a result, much of our understanding of vegetation change and the management advice proffered have been based on chronosequence studies. Furthermore, many of us have a vested interest in the validity of chronosequences because we have used it, often unquestioningly, in our research on vegetation change. However, as shown in the previous sections, the inferences from chronosequences for all four of the textbook examples of succession have been found to be incorrect due to the fact that the key assumption of this method (that all sites used to represent various stages of development have traced the same history) was invalid.

Rode (1961) cautioned that any inferences from using a space-for-time substitution must be validated from data using other methods. When other methods (e.g. long-term study, stratigraphy, palynology, stand reconstruction) were used to investigate these classic studies of succession, they showed clearly that the inferred sequences did not represent the actual temporal changes that had occurred in any given site. Therefore, there seems little justification for the continued use of these examples in textbooks to illustrate the concept of succession, except perhaps in a historical context. If used in this way, it should also be pointed out that these inferred sequences have been refuted by subsequent studies.

This also raises the issue of the continued use of the space-for-time substitution in contemporary research without strong validation of the critical assumption and corroborating evidence through the use of other methods of study. In many of the published studies that have used the chronosequence method to study vegetation change, authors have not adequately justified its use through tests of its assumptions. Some simply assume that the spatial sequence they observe represents a temporal sequence: 'It is often possible to work out the probable successional relations of an area by a careful study of the zonal communities within that area' (Walker 1940, p. 95). Or their justification lies in other studies reporting similar sequences; as one editor of a prominent ecology journal commented: 'All these chronosequences cannot be wrong.' But repeated use of the same faulty method does not strengthen the inferred conclusions. In those studies that do attempt to justify the use of chronosequence method, the justification is based on the study sites having similar mineral substrate or topography. However, although these may be *necessary* conditions, they are not *sufficient* because they still fail to justify the more critical assumption that all sites have traced the same history. Without this assumption, the series of sites cannot be inferred to represent necessary stages of some successional sequence or vegetation/ecosystem development. As indicated in this and previous reviews (e.g. Drury & Nisbet 1973) of the literature, the evidence from actual tests of this assumption indicates that this assumption is generally not met, not only in the cases of the four examples discussed here but also in numerous other situations where chronosequences have been used to infer temporal changes. For example, Roozen & Westhoff (1985) analysed temporal changes (1953–1980) in salt-marsh vegetation from permanent plots along an altitudinal transect and found that the spatial zonation of the salt-marsh vegetation could not be related to temporal changes observed in any zone along the transect. Chazdon *et al.* (2007) studied stand dynamics within permanent plots in two Neotropical forests and showed that chronosequence-based trends had little to do with age since abandonment. They concluded that plots followed idiosyncratic pathways of species accumulations, likely driven by edaphic factors, land-use history, and landscape matrix. Zobel & Kont (1992) found that species composition of alvar communities along a coastal zone transect characterized by land uplift was determined by the ecological conditions rather than the age of any particular site. When site conditions were similar, differences between communities of different-age sites were negligible. Finally, Hotchkiss *et al.* (2000) clearly showed how past climate changes would have caused the rates of soil and ecosystem development to differ significantly along a chronosequence of sites in Hawaii.

In order to provide some perspective on the use of chronosequences in ecology, we might consider the history of geomorphology, a discipline that arose concurrently with ecology. Contemporaneous with the Clements vs. Gleason views on plant communities in ecology were the Davis vs. Gilbert views on landforms in geomorphology (see Drury & Nisbet 1971). In both debates, the issue was between a 'big picture' view of fitting together individual segments of the landscape into a developmental ('genetic') scheme and an approach of understanding the mechanisms operating within each segment. By the latter half of the 20th century,

geomorphologists had abandoned most of Davis' developmental framework and their focus had shifted from landform descriptions to the study of geomorphic transport processes. At the same time, the focus in ecology had been gradually shifting away from the description of vegetation patterns (actual or idealized) to the study of processes involved in plant–environment (e.g. moisture-nutrient gradients), plant–plant (e.g. competition), and plant–animal (e.g. predation) interactions, as well as to the studies of dispersal, species migrations, population dynamics, and other ecological processes that play a role in vegetation dynamics. Thus most of contemporary ecological research is focussed on understanding the mechanisms producing the observed patterns, rather than on attempting to fit the pattern into some hypothesized or idealized developmental framework.

It is clear that the chronosequence method is not generally useful in the study of vegetation dynamics, as the assumption of stability (biotic and abiotic constancy) over the time span of any successional sequence is highly unlikely. Since the time of the early studies by Cowles, Shelford, Dachnowski, etc., our understanding of moderate-to long-term climatic changes (e.g. atmospheric teleconnections such as the El Niño-Southern Oscillation, Pacific Decadal Oscillation, and North Atlantic Oscillation) and of natural disturbances (such as fires, windstorms, and floods), as well as the relationships between these two, has grown substantially.

In conclusion, we think it is time to recognize the overwhelming empirical evidence invalidating these classic chronosequence-based examples of succession and to stop using them in ecology textbooks and course curricula. It is also time to require ecological studies using chronosequences to provide *strong* tests of its critical assumptions rather than ignoring them or simply paying lip-service to them.

REFERENCES

Addison, J.A., Trofymow, J.A. & Marshall, V.G. (2003). Abundance, species diversity, and community structure of *Collembola* in successional coastal temperate forests on Vancouver Island, Canada. *Appl. Soil Ecol.*, 24, 233–246.

Aide, T.M., Zimerman, J.K., Pascarella, J.B., Rivera, L.W. & Humfredo, M.-V. (2000). Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restor. Ecol.*, 8, 328–338.

Anderton, J.B. & Loope, W.L. (1995). Buried soils in a perched dunefield as indicators of late Holocene lake-level change in the Lake Superior Basin. *Quatern. Res.*, 44, 190–199.

Arbogast, A.F., Hansen, E.C. & Van Oort, M.D. (2002). Reconstructing the geomorphic evolution of large coastal dunes along the southeastern shore of Lake Michigan. *Geomorphology*, 46, 241–255.

Arens, S.M., Baas, A.C.W., Van Boxel, J.H. & Kalkman, C. (2001). Influence of reed stem density on foredune development. *Earth Surf. Proc. Land.*, 26, 1161–1176.

Baldwin, K.A. & Maun, M.A. (1983). Microenvironment of Lake Huron sand dunes. *Can. J. Bot.*, 61, 241–255.

Bard, G.E. (1952). Secondary succession on the Piedmont of New Jersey. *Ecol. Monogr.*, 22, 195–215.

Bauer, B.O. & Davidson-Arnott, R.G.D. (2002). A general framework for modeling sediment supply to coastal dunes including wind angle, beach geometry, and fetch effects. *Geomorphology*, 49, 89–108.

Beck-Mannagetta, G. (1890). *Flora von Nieder-Österreich. C.* Gerold, Vienna.

Beckwith, S.L. (1954). Ecological succession on abandoned farm lands and its relation to wildlife management. *Ecol. Monogr.*, 24, 331–347.

Begon, M., Harper, J.L. & Townsend, C.R. (1996). *Ecology: Individuals, Populations and Communities*, 3rd edn. Blackwell Sciences, Oxford, UK.

Billings, W.D. (1938). The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr.*, 8, 437–500.

Booth, W.E. (1941). Revegetation of abandoned fields in Kansas and Oklahoma. *Am. J. Bot.*, 28, 415–422.

Bowen, A.J. & Inman, D.L. (1966). *Budget of Littoral Sediments in the Vicinity of Point Arguello, California. U.S. Army Corps of Engineers Tech. Memo. No. 19.* Coastal Engineering Research Center, Washington, DC.

Buell, M.F., Buell, H.F., Small, J.A. & Siccama, T.G. (1971). Invasion of trees in secondary succession on the New Jersey Piedmont. *Bull. Torrey Bot. Club*, 98, 67–74.

Chadwick, H.W. & Dalke, P.D. (1965). Plant succession on dune sands in Fremont County, Idaho. *Ecology*, 46, 765–780.

Chapin, F.S., Walker, L.R., Fastie, C.L. & Sharman, L.C. (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.*, 64, 149–175.

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martinez-Ramos, M., Bongers, F. & Finegan, B. (2007). Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. Lond. B*, 362, 273–289.

Choi, Y.H. & Wang, Y. (2004). Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Global Biogeochem. Cycles*, 18, Art. No. GB4016. doi.1029/2004GB 002261.

Clements, F.E. (1916). *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institute of Washington, Washington, DC.

Coile, T.S. (1940). Soil changes associated with loblolly pine succession on abandoned agricultural land of the Piedmont Plateau. *Duke Univ. Sch. Forest. Bull.*, 5, 1–85.

Colinvaux, P. (1986). *Ecology*. John Wiley & Sons, New York, NY.

Colinvaux, P. (1993). *Ecology 2*. John Wiley & Sons, Inc., New York, NY.

Collins, S.L. & Adams, D.E. (1983). Succession in grasslands: Thirty-two years of change in a central Oklahoma tallgrass prairie. *Vegetatio*, 51, 181–190.

Cooper, W.S. (1923a). The recent ecological history of Glacier Bay, Alaska: Permanent quadrats at Glacier Bay: An initial report upon a long-period study. *Ecology*, 4, 355–365.

Cooper, W.S. (1923b). The recent ecological history of Glacier Bay, Alaska: the present vegetation cycle. *Ecology*, 4, 223–246.

Cooper, W.S. (1926). The fundamentals of vegetational change. *Ecology*, 7, 391–413.

Cooper, W.S. (1931). A third expedition to Glacier Bay, Alaska. *Ecology*, 12, 61–95.

Cooper, W.S. (1939). A fourth expedition to Glacier Bay, Alaska. *Ecology*, 20, 130–159.

Cowles, H.C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Bot. Gaz.*, 27, 95–117, 167–202, 281–308, 361–391.

Cowles, H.C. (1901). The physiographic ecology of Chicago and vicinity. *Bot. Gaz.*, 31, 73–108, 145–182.

Crocker, R.L. & Major, J. (1955). Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.*, 43, 427–448.

Dachnowski, A.P. (1912). *Peat Deposits of Ohio: Their Origin, Formation and Uses*. Geological Survey of Ohio Bulletin 16, Columbus, OH.

Dachnowski, A.P. (1926a). *Factors and Problems in the Selection of Peatlands for Different Uses*. U.S. Department of Agriculture Bulletin No. 1419, Washington, DC.

Dachnowski, A.P. (1926b). Profiles of peat deposits in New England. *Ecology*, 7, 120–135.

Dansereau, P. & Segadas-Vianna, F. (1952). Ecological study of the peat bogs of eastern North America. *Can. J. Bot.*, 30, 490–520.

Davidson-Arnott, R.G.D. (1988). Temporal and spatial controls on beach/dune interaction, Long Point, Lake Erie. *J. Coast. Res.*, Special Issue No. 3, 131–136.

Dech, J.P. & Maun, M.A. (2005). Zonation of vegetation along a burial gradient on the leeward slopes of Lake Huron sand dunes. *Can. J. Bot.*, 83, 227–236.

DeLuca, T.H., Nilsson, M.-C. & Zackrisson, O. (2002). Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia*, 133, 206–214.

van Dijk, P.M., Arens, S.M. & van Boxel, J.H. (1999). Aeolian processes across transverse dunes. II: Modelling the sediment transport and profile development. *Earth Surf. Proc. Land.*, 24, 319–333.

Downing, E.R. (1922). *A Naturalist in the Great Lakes Region*. University of Chicago Press, Chicago, IL.

Drury, W.H. & Nisbet, I.C.T. (1971). Interrelations between developmental models in geomorphology, plant ecology and animal ecology. *Gen. Syst.*, 16, 57–68.

Drury, W.H. & Nisbet, I.C.T. (1973). Succession. *J. Arnold Arbor.*, 54, 331–368.

Egler, F.E. (1954). Vegetation science concepts I. Initial floristics composition, a factor in old-field vegetation development. *Vegetatio*, 4, 412–417, 1952–1954.

Fastie, C.L. (1995). Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, 76, 1899–1916.

Fuller, G.D. (1912). The cottonwood dune association. *Trans. Ill. State Acad. Sci.*, 5, 137–143.

Gates, F.C. (1926). Plant successions about Douglas Lake, Cheboygan County, Michigan. *Bot. Gaz.*, 82, 170–182.

Goudie, A. (1989). *The Nature of the Environment*. Basil Blackwell Ltd., Oxford, UK.

Grunzweig, J.M., Sparrow, S.D., Yakir, D. & Chapin, F.S. (2004). Impact of agricultural land-use change on carbon storage in boreal Alaska. *Glob. Change Biol.*, 10, 452–472.

Harris, D. & Davy, A.J. (1987). Seedling growth in *Elymus farctus* after episodes of burial with sand. *Ann. Bot.*, 60, 587–593.

Hayashi, M. & van der Kamp, G. (2007). Water level changes in ponds and lakes: the hydrological processes. In: *Plant Disturbance Ecology: The Process and the Response* (eds Johnson, E.A. & Miyanishi, K.). Academic Press, San Diego, CA, pp. 311–339.

Hayden, B.P., Santos, M.C.F.V., Shao, G. & Kochel, R.C. (1995). Geomorphological controls on coastal vegetation at the Virginia Coast Reserve. *Geomorphology*, 13, 283–300.

Heinselman, M.L. (1963). Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota. *Ecol. Monogr.*, 33, 327–374.

Hesp, P.A. (1988). Foredune morphology, dynamics and structures. *J. Sediment. Geol.*, 55, 17–41.

Hesp, P.A. (1996). Flow dynamics in a trough blowout. *Bound. Layer Meteorol.*, 77, 305–330.

Hesp, P.A. (2002). Foredunes and blowouts: initiation, geomorphology and dynamics. *Geomorphology*, 48, 245–268.

Hesp, P.A. & Martínez, M.L. (2007). Disturbance processes and dynamics in coastal dunes. In: *Plant Disturbance Ecology: The Process and the Response* (eds Johnson, E.A. & Miyanishi, K.). Academic Press, San Diego, CA, pp. 215–247.

Hotchkiss, S., Vitousek, P.M., Chadwick, O.A. & Price, J. (2000). Climate cycles, geomorphological change, and the interpretation of soil and ecosystem development. *Ecosystems*, 3, 522–533.

Jackson, S.T., Futyma, R.P. & Wilcox, D.A. (1988). A paleoecological test of a classical hydrosere in the Lake Michigan dunes. *Ecology*, 69, 928–936.

Johnson, E.A. (1979). Succession an unfinished revolution. *Ecology*, 60, 238–240.

Johnson, E.A., Miyanishi, K. & Kleb, H. (1994). The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta-Picea engelmannii* forest. *J. Ecol.*, 82, 923–931.

Johnson, W.C., Boettcher, S.E., Poiani, K.A. & Guntenspergen, G. (2004). Influence of weather extremes on the water levels of glaciated prairie wetlands. *Wetlands*, 24, 385–398.

van der Kamp, G., Stolte, W.J. & Clark, R.G. (1999). Drying out of small prairie wetlands after conversion of their catchments from cultivation to permanent brome grass. *J. Hydrol. Sci.*, 44, 387–397.

van der Kamp, G., Hayashi, M. & Gallen, D. (2003). Comparing the hydrology of a grassed and cultivated catchment in the semi-arid Canadian prairies. *Hydrol. Process.*, 17, 559–575.

Katz, N.J. (1926). Sphagnum bogs of central Russia: phytosociology, ecology and succession. *J. Ecol.*, 14, 177–202.

Keddy, P.A. (2007). *Plants and Vegetation: Origins, Processes, Consequences*. Cambridge University Press, Cambridge, UK.

Keever, C. (1950). Causes of succession on old fields of the Piedmont, North Carolina. *Ecol. Monogr.*, 20, 230–250.

Kent, M., Owen, N.W., Dale, P., Newnham, R.M. & Giles, T.M. (2001). Studies of vegetation burial: a focus for biogeography and biogeomorphology. *Prog. Phys. Geog.*, 25, 455–482.

Klinger, L.F. (1996). The myth of the classic hydrosere model of bog succession. *Arct. Alp. Res.*, 28, 1–9.

Krebs, C.J. (2001). *Ecology: The Experimental Analysis of Distribution and Abundance*, 5th edn. Benjamin Cummings, San Francisco, CA.

LaBaugh, J.W., Winter, T.C. & Rosenberry, D.O. (1998). Hydrologic functions of prairie wetlands. *Great Plains Res.*, 8, 17–37.

Law, B.E., Sun, O.J., Campbell, J., Van Tuyl, S. & Thornton, P.E. (2003). Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Glob. Change Biol.*, 9, 510–524.

Lichter, J. (2000). Colonization constraints during primary succession on coastal Lake Michigan sand dunes. *J. Ecol.*, 88, 825–839.

Litvak, M., Miller, S., Wofsy, S.C. & Goulden, M. (2003). Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest. *J. Geophys. Res.*, 108. Doi:10.1029/2001JD 000854.

Loope, W.L. & Arbogast, A.F. (2000). Dominance of an ∼150-year cycle of sand-supply change in late Holocene dune-building along the eastern shore of Lake Michigan. *Quatern. Res.*, 54, 414–422.

Martínez, M.L. & Moreno-Casasola, P. (1996). Effects of burial by sand on seedling growth and survival in six tropical sand dune species from the Gulf of Mexico. *J. Coast. Res.*, 12, 406–419.

Maun, M.A. (1996). The effects of burial by sand on survival and growth of *Calamovilfa longifolia*. *Ecoscience*, 3, 93–100.

Maun, M.A. (2004). Burial of plants as a selective force in sand dunes. In: *Coastal Dunes: Ecology and Conservation* (eds Martinez, M.L. & Psuty, N.P.). Springer-Verlag, Berlin, pp. 119–135.

Maun, M.A. & Lapierre, J. (1984). The effects of burial by sand on *Ammophila breviligulata*. *J. Ecol.*, 72, 827–839.

Maun, M.A. & Lapierre, J. (1986). Effects of burial by sand on seed germination and seedling emergence of four dune species. *Am. J. Bot.*, 73, 450–455.

Maun, M.A. & Perumal, J. (1999). Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecol. Lett.*, 2, 14–18.

McNaughton, S.J. & Wolf, L.L. (1973). *General Ecology*. Holt, Rinehart and Winston, Inc., New York, NY.

McQuilkin, W.E. (1940). The natural establishment of pine in abandoned fields in the Piedmont Plateau region. *Ecology*, 21, 135–147.

Miyanishi, K. & Johnson, E.A. (2007). Coastal dune succession and the reality of dune processes. In: *Plant Disturbance Ecology: The Process and the Response* (eds Johnson, E.A. & Miyanishi, K.). Academic Press, San Diego, CA, pp. 249–282.

Molles, M.C.J. (2002). *Ecology: Concepts and Applications*. McGraw-Hill, New York, NY.

Moreno-Casasola, P. (1986). Sand movement as a factor in the distribution of plant communities in a coastal dune system. *Vegetatio*, 65, 67–76.

Morrison, R.G. (1973). *Primary succession on sand dunes at Grand Bend, Ontario.* PhD Dissertation, University of Toronto, Toronto, ON.

Myster, R.W. & Pickett, S.T.A. (1990). Initial conditions, history and successional pathways in ten contrasting old fields. *Am. Midl. Nat.*, 124, 231–238.

Namikas, S.L. & Sherman, D.J. (1998). AEOLUS II: an interactive program for the simulation of aeolian sedimentation. *Geomorphology*, 22, 135–149.

Odum, E.P. (1953). *Fundamentals of Ecology*. Saunders, Philadelphia, PA.

Olson, J.S. (1958). Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot. Gaz.*, 119, 125–170.

Oosting, H.J. (1942). An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Midl. Nat.*, 28, 1–126.

Oosting, H.J. (1956). *The Study of Plant Communities: An Introduction to Plant Ecology*, 2nd edn. W. H. Freeman and Company, San Francisco, CA.

Payne, A.M. & Maun, M.A. (1981). Dispersal and floating ability of dimorphic fruit segments of *Cakile edentula* var. *lacustris*. *Can. J. Bot.*, 59, 2595–2602.

Pearsall, W.H. (1920). The aquatic vegetation of the English Lakes. *J. Ecol.*, 8, 163–201.

Pickett, S.T.A. (1982). Population patterns through twenty years of oldfield succession. *Vegetatio*, 49, 45–59.

Pickett, S.T.A. (1983). Absence of an Andropogon stage in oldfield succession at the Hutcheson Memorial Forest. *Bull. Torrey Bot. Club*, 110, 533–535.

Pickett, S.T.A. (1988). Space-for-time substitution as an alternative to long term studies. In: *Long-term Studies in Ecology* (ed. Likens, G.E.). Springer, New York, NY, pp. 110–135.

Pickett, S.T.A., Parker, V.T. & Fiedler, P.L. (1992). The new paradigm in ecology: implications for conservation biology. In: *Conservation Biology: the Theory and Practice of Nature Conservation, Preservation and Management* (eds Fiedler, P.L. & Jain, S.K.). Chapman and Hall, New York, NY, pp. 65–88.

Poulson, T.L. (1999). Autogenic, allogenic, and individualistic mechanisms of dune succession. *Nat. Areas J.*, 19, 172–176.

Quarterman, E. (1957). Early plant succession on abandoned cropland in the central basin of Tennessee. *Ecology*, 38, 300–309.

Ranwell, D.S. (1958). Movement of vegetated sand dunes at Newborough Warren, Anglesey. *J. Ecol.*, 46, 83–100.

Ricklefs, R.E. (1990). *Ecology*, 3rd edn. W.H. Freeman and Company, New York, NY.

Roberts, M., Reiss, M. & Monger, G. (1993). *Biology: Principles and Processes*. Nelson, Surrey, UK.

Rode, A.A. (1961). *The Soil Forming Process and Soil Evolution*. Israel Program for Scientific Translations, Jerusalem, Israel.

Roozen, A.J.M. & Westhoff, V. (1985). A study on long-term salt-marsh succession using permanent plots. *Vegetatio*, 61, 23–32.

Rose, M.R. & Mueller, L.D. (2006). *Evolution and Ecology of the Organism*. Pearson Education, Inc., Upper Saddle River, NJ.

Salisbury, E.J. (1925). Note on the edaphic succession in some dune soils with special reference to the time factor. *J. Ecol.*, 13, 322–328.

Schwintzer, C.R. (1978). Vegetation changes and water levels in a small Michigan bog. In: *Wetlands: Ecology, Values, and Impacts* (eds DeWitt, C.B. & Soloway, E.). Institute for Environmental Studies, University of Wisconsin Madison, WI, pp. 326–336.

Seabloom, E.W. & van der Valk, A.G. (2003). The development of vegetative zonation patterns in restored prairie pothole wetlands. *J. Appl. Ecol.*, 40, 92–100.

Seabloom, E.W., Moloney, K.A. & van der Valk, A.G. (2001). Constraints on the establishment of plants along a fluctuating water-depth gradient. *Ecology*, 82, 2216–2232.

Shelford, V.E. (1911). Ecological succession. II. Pond fishes. *Biol. Bull.*, 21, 127–151.

Shelford, V.E. (1963). *The Ecology of North America*. University of Illinois Press, Urbana, IL.

Smith, R.L. & Smith, T.M. (2001). *Ecology and Field Biology*, 6th edn. Benjamin Cummings, San Francisco, CA.

Stiling, P. (2002). *Ecology: Theories and Applications*, 4th edn. Prentice-Hall, Upper Saddle River, NJ.

Sykes, M.T. & Wilson, J.B. (1990). An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand. *Acta Bot. Neerl.*, 39, 171–181.

Tansley, A.G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, 16, 284–307.

Tansley, A.G. (1939). *The British Isles and Their Vegetation*. Cambridge University Press, Cambridge, UK.

Transeau, E.N. (1903). On the geographic distribution and ecological relationships of the bog societies of northern North America. *Bot. Gaz.*, 36, 401–420.

Tyndall, R.W., Teramura, A.H., Mulchi, C.L. & Douglass, L.W. (1986). Seed burial effect on species presence along a mid-Atlantic beach. *Can. J. Bot.*, 64, 2168–2170.

van der Valk, A.G. (1974). Environmental factors controlling the distribution of forbs on coastal foredunes in Cape Hatteras National Seashore. *Can. J. Bot.*, 52, 1057–1073.

van der Valk, A.G. (1981). Succession in wetlands: a Gleasonian approach. *Ecology*, 62, 688–696.

van der Valk, A.G. (1994). Effects of prolonged flooding on the distribution and biomass of emergent species along a freshwater wetland coenocline. *Vegetatio*, 110, 185–196.

van der Valk, A.G. (2005). Water-level fluctuations in North American prairie wetlands. *Hydrobiologia*, 539, 171–188.

van der Valk, A.G. (2007). Development of post-disturbance vegetation in prairie wetlands. In: *Plant Disturbance Ecology: The Process and the Response* (eds Johnson, E.A. & Miyanishi, K.). Academic Press, San Diego, CA, pp. 341–370.

van der Valk, A.G. & Davis, C.B. (1976). Seed banks of prairie glacial marshes. *Can. J. Bot.*, 54, 1832–1838.

van der Valk, A.G. & Davis, C.B. (1978). The role of the seed bank in the vegetation dynamics of prairie glacial marshes. *Ecology*, 59, 322–335.

van der Valk, A.G. & Welling, C.H. (1988). The development of zonation in freshwater wetlands: an experimental approach. In: *Diversity and Pattern in Plant Communities* (eds During, H.J., Werger, M.J.A. & Willems, J.H.). SPB Academic Publishing, The Hague, Netherlands, pp. 145–158.

Van Breemen, N. (1995). How *Sphagnum* bogs down other plants. *Trends Ecol. Evol.*, 10, 270–275.

Vitousek, P.M., Turner, D.R. & Kitayama, K. (1995). Foliar nutrients during long-term soil development in Hawaiian montane rain forest. *Ecology*, 76, 712–720.

Walker, R.E. (1940). Biotic succession in a coastal salt marsh. *Proc. Oklahoma Acad. Sci.*, 20, 95–97.

Walker, D. (1970). Direction and rate in some British post-glacial hydroseres. In: *Studies on the Vegetational History of the British Isles* (eds Walker, D. & West, R.G.). Cambridge University Press, London, pp. 117–139.

Warming, E. (1895). *Plantesamfund. Grundtræk af den økologiske plantegeografi*. P.G. Philipsen, Copenhagen.

Weaver, J.E. & Clements, F.E. (1929). *Plant Ecology*, 1st edn. McGraw-Hill Book Company, Inc., New York, NY.

Whitford, H.N. (1901). The genetic development of the forests of Northern Michigan. *Bot. Gaz.*, 31, 289–325.

Winter, T.C. (1989). Hydrological studies of wetlands in the northern prairie. In: *Northern Prairie Wetlands* (ed. van der Valk, A.G.). Iowa State University Press, Ames, IA, pp. 16–54.

Winter, T.C. & Rosenberry, D.O. (1995). The interaction of ground water with prairie pothole wetlands in the Cottonwood Lake area, east-central North Dakota, 1979-1990. *Wetlands*, 15, 193–211.

Winter, T.C. & Rosenberry, D.O. (1998). Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood Lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrological records. *Clim. Change*, 40, 189–209.

Wolfe, F. (1932). Annual rings of *Thuja occidentalis* in relation to climatic conditions and movement of sand. *Bot. Gaz.*, 93, 328–335.

Woo, M.-K. & Rowsell, R.D. (1993). Hydrology of a prairie slough. *J. Hydrol.*, 146, 175–207.

Zhang, J. & Maun, M.A. (1990). Sand burial effects on seed germination, seedling emergence and establishment of *Panicum virgatum*. *Holarct. Ecol.*, 13, 56–61.

Zobel, M. & Kont, A. (1992). Formation and succession of alvar communities in the Baltic land uplift area. *Nord. J. Bot.*, 12, 249–256.