

1988

# From Community Ecology to Vegetation Management: Providing a Scientific Basis for Management

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## Recommended Citation

van der Valk, A. G., "From Community Ecology to Vegetation Management: Providing a Scientific Basis for Management" (1988). *Botany Publication and Papers*. 106.

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# From Community Ecology to Vegetation Management: Providing a Scientific Basis for Management

## **Abstract**

What relevance has theoretical community ecology to vegetation managers? The answer to this question has at least two parts. One, community ecology provides a framework for understanding how communities are put together; i.e., what determines their composition, structure and location. Two, community ecology provides insights into what type of data and research are needed to perceive, predict or produce vegetative change. The second part of the answer has direct applications to vegetation management. If mechanisms that cause vegetation change are understood, then they can be exploited to manipulate vegetation, and the results of these manipulations can be predicted more reliably.

I will first consider briefly both parts of contemporary reductionist answers, and then illustrate with examples from wetland ecology how reductionist models of communities can be translated into better management. Management in this paper is restricted to what Milton Weller (1978) has called "natural" management; i.e., the manipulation of natural forces that control the composition and dynamics of vegetation. This approach involves manipulating either water levels, fire frequency or grazing intensity to alter the composition or structure of vegetation.

## **Disciplines**

Botany | Ecology and Evolutionary Biology | Terrestrial and Aquatic Ecology

## **Comments**

This is a proceeding from van der Valk, A. G. 1988. From community ecology to vegetation management: providing a scientific basis for management. Transactions of the Fifty-third North American Wildlife and Natural Resources Conference, March 18-23, 1988, Louisville, Kentucky. Posted with permission.

# From Community Ecology to Vegetation Management: Providing a Scientific Basis for Management

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## Introduction

What relevance has theoretical community ecology to vegetation managers? The answer to this question has at least two parts. One, community ecology provides a framework for understanding how communities are put together; i.e., what determines their composition, structure and location. Two, community ecology provides insights into what type of data and research are needed to perceive, predict or produce vegetative change. The second part of the answer has direct applications to vegetation management. If mechanisms that cause vegetation change are understood, then they can be exploited to manipulate vegetation, and the results of these manipulations can be predicted more reliably.

I will first consider briefly both parts of contemporary reductionist answers, and then illustrate with examples from wetland ecology how reductionist models of communities can be translated into better management. Management in this paper is restricted to what Milton Weller (1978) has called "natural" management; i.e., the manipulation of natural forces that control the composition and dynamics of vegetation. This approach involves manipulating either water levels, fire frequency or grazing intensity to alter the composition or structure of vegetation.

## What is a Plant Community?

Although there is not yet unanimity among plant ecologists about the nature of plant communities, there does seem to be consensus developing. Since the 1950s, the reductionist community concept put forward during the first third of the twentieth century by Gleason (1917, 1926, 1939) in North America and others in Europe has become the dominant community paradigm among plant ecologists, and it is gaining favor among animal ecologists (McIntosh 1985, 1987). Gleason's views can be summarized in his own words (Gleason 1917): "1. All phenomenon of vegetation, i.e., of numbers of individuals, depend upon the phenomenon of the individual plant. 2. The plant population of any area is determined by environmental selection of immigrants from the surrounding population. 3. Because of similarity of environmental selection and of available sources of immigration, areas of uniform vegetation are developed, known as plant associations. 4. Effective change in the environment or in the surrounding population may lead to significant changes in the vegetation of an area. If these changes involve the establishment of a new association, the phenomenon is known as succession."

Gleason's "individualistic" concept of plant communities had its first major impact in the 1950s on how plant ecologists sampled and classified vegetation. It challenged the old typological approaches, and resulted in the development of alternative approaches, collectively known as ordinations (Whittaker 1962, 1967, McIntosh, 1967, 1985). It is generally not until the 1970 and 1980s that plant ecologists interested in other aspects of community ecology began to recast various concepts or problems in Gleasonian terms, including two perennial problems, the nature of the community and succession. Many other ecologists contributed ideas, insights and data that influenced this reformulation, particularly the American community ecologists F. E. Egler (1954), H. M. Raup (Stout 1981) and R. H. Whittaker (1975), and the British population ecologists A. S. Watt (1964) and J. L. Harper (1977).

A large number of papers and books in the last decade or so dealing with disturbance, palaeoecological change and the population biology of plant species have influenced the development of contemporary formulations of reductionist concepts of plant communities whose origins can be traced back to Gleason. Of these, the most important and influential, arguably, are: Grubb (1977) on the importance of dispersal, seed germination and seedling survival for understanding community development and persistence; P. S. White (1979) on the ubiquity of disturbance; Noble and Slatyer (1980) on predicting successional changes from life-history characteristics of species; Tilman (1980) on relative efficiency of nutrient uptake as the basis for predicting the outcome of competition among species; Davis (1981) migrational patterns of tree species in eastern North America during the quarternary; the book, *Ecological Communities: Conceptual Issues and the Evidence*, edited by Strong et al. (1984); the book edited by Diamond and Case (1986) on *Community Ecology*, particularly the chapter by Chesson and Chase on nonequilibrium community theory; the book edited by J. White (1985) on *The Population Structure of Vegetation*; Johnstone (1986) on plant invasions and the definition of succession; and the book *Landscape Ecology* by Forman and Godron (1986).

It is beyond the scope of this paper to analyze the specific contributions made by the each of these papers or books, but I will summarize what is, from my perspective, their overall message: that plant communities are impermanent assemblages of species that are not in equilibrium with their environment; that they are constantly recovering from disturbance(s) (i.e., that communities have a history); that the characteristics of a community are those of its constituent species; that communities can undergo several different kinds of changes; and that understanding and predicting all kinds of changes requires a knowledge of the life-history characteristics of species whose invasion, growth and elimination cause them.

## **Vegetation Change**

Several types of community change are recognized—succession, maturation and fluctuation (van der Valk, 1985, 1987). Succession is defined as the "observed change with time in species number and type in an assemblage" (Johnstone 1986) or, in more operational terms, any change in the species in an area from year to year (van der Valk 1985). It is caused by species invading an area and/or established species being eliminated. Change due to the growth of plants are classified as either maturations or fluctuations (van der Valk, 1985, 1987). Maturation is the accumu-

lation of biomass on a site from year to year. It is caused by the growth of plants from one year to the next. Fluctuation is a change in the relative contribution of species to the total biomass of an area from year to year (van der Valk 1985). It is due to differences in rates of vegetative propagation of species from year to year due to differences in environmental conditions from year to year. I will restrict myself here to a consideration of contemporary concepts of succession and its implications for management.

Since succession is caused by either the invasion or extirpation of a species, it is these two population-level phenomena that must be studied to understand and predict changes in the composition of vegetation in an area, i.e., its future compositional states. Neither phenomenon has received a great deal of attention in the literature (Johnstone 1986). What makes it possible for a plant to invade an area is the presence of a "safe site," an area whose environmental conditions are suitable for its establishment, usually as a result of seed germination (Harper 1977). Four types of safe sites have been recognized by Johnstone (1986)—default, stable, temporary, and future. These are defined in terms of barrier type (vegetation and environment) and barrier selectivity (selective and universal).

An invasion window is a time-dependent safe site that is defined in terms of type of barrier and its selectivity. A default invasion window (universal, environmental barrier) means that no safe site exists. Habitat creation is needed to change a default window to some other type. Stable windows exist whenever an environmental barrier to invasion is removed, e.g., geographical isolation, fire, flooding, etc. Whenever a universal, vegetative barrier to invasion is removed, a temporary invasion window is opened. This window remains open only for a short time after the vegetation on a site has been eliminated by fire, overgrazing, wind throw, etc. Future windows involve the removal of a selective, vegetative barrier. A species can reach or become established in a vegetated area, but remains suppressed until an opening occurs in the vegetation due to disturbance or the death of a plant. This classification scheme provides a framework for examining the kind of invasion window a particular species requires for its establishment, and when is this likely to occur. In a management context, it provides a framework for determining what barrier must be removed to get a desirable species established.

The extirpation of species from a site has received even less theoretical consideration than the invasion of species. Classifications of species on the basis of their potential longevity are primitive (annuals, biennials, perennials without vegetative propagation, perennials with vegetative propagation). The potential longevity of species under specific conditions is rarely known. This may not be of any great significance, since disturbance seems to cut short the life span of most species (White 1979).

Understanding and predicting successional change requires a knowledge of both the life-history characteristics of species (seed dispersal, seed longevity, seed-germination requirements, age at which sexual reproduction begins, vegetative propagation, potential life span, etc.) and of the type and frequency of disturbance events that create potential invasion windows and/or eliminate species. Noble and Slatyer (1980) used this type of information to predict the composition of postfire forest vegetation, and van der Valk (1981) used a similar system to predict the composition of wetland vegetation after a change in water level.

## Management Applications

A reductionist community model assumes that characteristics of constituent species determine community characteristics (composition, structure, biomass, etc.). Consequently, research emphasis is placed on comparative studies of the life-histories of species. Life-history studies of different types of freshwater species have revealed many important characteristics of those species that determine how they behave in the field. These include the fact that many have long-lived seed and thus are abundant in seed banks, and that seeds of most emergents and annuals germinate only when there is no standing water (van der Valk 1981). For these groups of species, recruitment is possible only during a drawdown when a stable invasion window occurs. Comparative information on the life-histories of species (dispersal syndromes, seed-germination traits, growth rates, etc.), particularly their safe requirements, can be used to analyze and predict succession.

Because in some wetlands species are recruited primarily from seed banks, predicting the composition of drawdown vegetation solely from seed bank data is feasible. For managers, this is important because drawdowns are used routinely to re-establish emergents and annuals in these wetlands (Weller 1978). If, for some reason, the seed bank of such a wetland does not contain desirable species, *a priori* predictions of the composition of drawdown vegetation can prevent management mistakes. The discrepancy, if any, between predicted and actual seedling densities also is an indicator of how well factors controlling recruitment from the seed bank during drawdown are understood.

Comparative seed-germination studies of wetland species (e.g., Galinato and van der Valk 1986) have indicated that species of the same life form can differ significantly in their germination traits. These differences can be exploited potentially in the field by manipulating environmental conditions to alter the composition and structure of wetland vegetation.

As two examples of the management benefits to be gained from a reductionist approach to succession, I will outline how this approach permits *a priori* predictions of the densities of emergent species at various elevations in a prairie lacustrine wetland during a drawdown, and how exploiting seed-germination traits can be used to prevent the establishment of undesirable species in moist soil units.

### *Predicting Future States of Vegetation*

A reductionist model of wetland succession of freshwater prairie wetlands (van der Valk 1981) has been used to predict the composition of drawdown vegetation in a series of experimental marshes (Table 1). In these marshes, the emergent vegetation was eliminated by flooding them 1 meter above normal for two years, and then the marshes were drawn down for one or two years (Murkin et al. 1985). Prior to raising the water levels, the seed banks of these marshes at various elevations were investigated (Pederson 1983). This was done by placing seed bank samples (collected at random) in trays in a cold frame during the growing season, keeping the samples moist and counting the number of seedlings that emerged. Predictions of the composition of the drawdown vegetation were made solely from these seed bank data. This is feasible because recruitment during drawdowns is almost exclusively from their seed banks (Welling 1986). Seedling densities during the first year of the

Table 1. Mean predicted and actual shoot densities (per m<sup>-2</sup>) of dominant emergents during the first year of a drawdown at different elevations in experimental cells of the Marsh Ecology Research Project, Delta, Manitoba, Canada.

Elevation (m)	<i>Scirpus lacustris</i>		<i>Typha glauca</i>		<i>Scolochloa festucacea</i>		<i>Phragmites australis</i>	
	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted	Actual
248.0	0	0	72	0	17	7	25	0
247.9	0	0	49	0	7	1	26	0
247.8	60	80	150	0	10	140	12	1
247.7	150	160	110	4	27	340	10	1
247.6	530	15	310	1	51	170	14	1
247.5	2,100	200	360	16	69	230	25	2
247.4	800	1,600	610	12	20	23	8	2
247.3	360	310	140	130	0	0	3	1
247.2	290	50	18	7	0	0	1	0
247.1	130	2	32	0	0	0	4	0
Mean	440	240	190	17	20	91	13	1

drawdown were obtained from 80 permanent quadrants at known elevations located at random in the experimental marshes (Welling 1986).

The predicted and the actual mean densities of four dominant emergent species (*Scirpus lacustris*, *Typha glauca*, *Scolochloa festucacea* and *Phragmites australis*) at different elevations in eight experimental marshes are presented in Table 1. For *Scirpus lacustris*, *Typha glauca*, and *Phragmites australis*, predicted mean seedling densities were lower than those found in the field by 44, 91, and 93 percent, respectively. Mean *Scolochloa festucacea* seedling density, on the other hand, was higher in the field than predicted by 400 percent. Rank order correlations between predicted and actual seedling densities at different elevations were 0.93 for *Scolochloa festucacea*, 0.76 for *Scirpus lacustris*, 0.44 for *Typha glauca* and only 0.03 for *Phragmites australis*. Environmental conditions along the elevation gradient seem to have influenced the recruitment of each species differently. Their seed germination traits are different. This was confirmed by Galinato and van der Valk (1986) in a series of laboratory studies.

Seed bank data allows managers to make quite detailed predictions about the composition of drawdown vegetation. Having such data takes most of the uncertainty out of this type of management manipulation. Nevertheless, there remain discrepancies between predicted and actual densities of seedling during the drawdown. These suggest that factors controlling the recruitment in the field were different from those under which the seed banks were examined, particularly for *Phragmites australis* and *Typha glauca*. This will always be a problem with predictions from seed bank data. It is impossible to know precisely what field conditions will be during a drawdown, so that they can be simulated exactly in the seed bank study.

### Seed Germination Traits and Community Composition

The impact of soil moisture levels on the recruitment of species in moist soil units in the Mingo National Wildlife Refuge, Missouri, has been studied by Naim (1987). These units are managed to produce seeds for overwintering waterfowl, by drawing them down in summer and reflooding them in the fall (Fredrickson and Taylor 1982).

In the field, soil moisture changes, after the initiation of a drawdown, were monitored for a month, as were the emergence of seedlings for four dominant species (Table 2).

Seeds of each species began to germinate when soil water matrix potentials had dropped to a particular level: *Polygonum* seeds began to germinate while there was still some standing water (0 kPa); *Eleocharis* at about  $-3$  kPa; *Echinochloa* at about  $-13$  kPa; and *Xanthium* at about  $-25$  kPa. Experimental studies of the impact of soil water matrix potential on seed germination parallel the field results: *Polygonum* seeds germinate in the wettest soils ( $> -10$  kPa); *Eleocharis* seeds between  $-10$  and  $-20$  kPa; *Echinochloa* seeds germinated over a wide range of soil matrix potentials, but best around  $-25$  kPa; and *Xanthium* seeds best between  $-40$  and  $-60$  kPa (Naim 1987). These results indicate that a slow drawdown is preferable to a fast one, because it keeps soil moisture higher longer. This favors the recruitment of such desirable species as *Polygonum* and *Echinochloa*, but prevents the recruitment of such undesirable species as *Xanthium*.

Many other examples of manipulating natural forces (water level, fire and grazing) to manage vegetation are available whose consequences can best be understood and predicted in a reductionist perspective (e.g., Basset 1980, Bakker and Ruyter 1981, Neckles et al. 1985, Thompson and Shay 1985). Since reductionist models require comparative information about species, they often cannot be developed yet, because the information needed is not available. To predict under what circumstances species can invade, persist or be eliminated, the key features of the life-history of species in a given situation must be identified, and research done to obtain the required information about each relevant species. Reductionist models based on comparative life-history data will provide the best possible foundation for vegetation management.

## Conclusions

In reductionist community models, the characteristics of a community are a function of its constituent species. The composition of of community at any time and its change with time are consequences of the difference between rates of establishment and extirpation of species. The more information that is available about life-history features (dispersal, seed-germination traits, age at which sexual reproduction begins, etc.) of species in an assemblage and in the surrounding area, the better future states (composition, structure, biomass, etc.) of that assemblage can be predicted. To

Table 2. Emergence (%) of seedlings of four species in June 1985 during a drawdown in a moist soil unit at the Mingo National Wildlife Refuge, Missouri. Soil moisture is expressed as soil water matrix potential (kPa)—the more negative the value, the drier the soil (data from Naim 1987).

Week	Soil moisture	<i>Polygonum hydropiperoides</i>	<i>Eleocharis obtusa</i>	<i>Echinochloa crusgalli</i>	<i>Xanthium pensylvanicum</i>
0	0	5	0	0	0
1	$-10$	73	20	0	0
2	$-31$	100	72	30	8
3	$-60$	100	93	60	62
4	$-76$	100	100	100	100

predict when changes of state will occur, however, the environmental changes or disturbances that are needed to open potential invasion windows must also be known. In a management context, this information is needed to determine what environmental factor(s) must be manipulated (i.e., what barriers must be removed) to produce a desirable change in the composition or other states of an assemblage. Reductionist models stress the basic ecological realities—recruitment and elimination of individuals—that are ultimately the cause of all vegetation change. A reductionist perspective provides a more realistic foundation for understanding, evaluating and planning management schemes. Since managers can predict the future state of vegetation, often in detail, it eliminates much of uncertainty associated with managing vegetation.

## Acknowledgments

This is paper number 42 of the Marsh Ecology Research Program of the Delta Waterfowl and Wetlands Research Station and Ducks Unlimited Canada. I would like to thank Chip Welling, Roger Pederson and Parvaiz Naim for the use of some of their unpublished data, and the Delta Waterfowl and Wetlands Research Station and its staff for their support, advice and encouragement.

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