

PATTERN, PROCESS, AND NATURAL DISTURBANCE
IN VEGETATION

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Made in United States of America

Reprinted from THE BOTANICAL REVIEW

Vol. 45, No. 3, July-September, 1979

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THE BOTANICAL REVIEW

VOL. 45

JULY–SEPTEMBER, 1979

No. 3

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ABSTRACT

Natural disturbances have been traditionally defined in terms of major catastrophic events originating in the physical environment and, hence, have been regarded as exogenous agents of vegetation change. Problems with this view are: (1) there is a gradient from minor to major events rather than a uniquely definable set of major catastrophes for each kind of disturbance, and (2) some disturbances are initiated or promoted by the biotic component of the system. Floras are rich in disturbance-adapted species. Disturbances have probably exerted selective pressure in the evolution of species strategies.

Heathland cyclic successions and gap-phase dynamics in forests have been viewed as endogenous patterns in vegetation. When death in older individuals imposes a rhythm on community reproduction, dynamics may indeed be the result of endogenous factors. However, documented cases of senescence in perennial plants are few and many cyclic successions and cases of gap-phase dynamics are initiated by physical factors. Forest dynamics range from those that are the result of individual tree senescence and fall, through those that are the result of blowdown of small groups of healthy trees, to those that are the result of large windstorms which level hectares of forest. The effect of wind ranges from simple pruning of dead plant parts to widespread damage of living trees. Wind speed is probably inversely proportional to occurrence frequency. Disturbances vary continuously. There is a gradient from those community dynamics that are initiated by endogenous factors to those initiated by exogenous factors. Evolution has mediated between species and environment; disturbances are often caused by physical factors but the occurrence and outplay of disturbances may be a function of the state of the community as well.

Natural disturbances in North American vegetation are: fire, wind-storm, ice storm, ice push on shores, cryogenic soil movement, temperature fluctuation, precipitation variability, alluvial processes, coastal processes, dune movement, saltwater inundation, landslides, lava flows, karst processes, and biotic disturbances. Disturbances vary regionally and within one landscape as a function of topography and other site variables and are characterized by their frequency, predictability, and magnitude. The landscape level is important in assessing disturbance regime. Disturbances and cyclic successions belong to the same class of events—that of recurrent dynamics in vegetation structure—irrespective

of cause. Dynamics may result from periodic, abrupt, and catastrophic environmental factors or they may result from an interaction of the changing susceptibility of the community and some regular environmental factor. In any case, the dynamics result in heterogeneous landscapes; the species adapted to this heterogeneity are numerous, suggesting their long time importance.

The importance of disturbance regime as part of the environmental context of vegetation means that allogenic and autogenic models of vegetation are difficult to apply. Species composition can be seen to be a function of disturbance regime, as well as other environmental variables. Competitive replacement in succession occurs, then, only as disturbances cease to operate and can be viewed as allogenic adjustment to a new disturbance-free environment. Competitive divergence, separation of role, and competition avoidance may, in fact, underlie successional patterns traditionally viewed as the competitive replacement of inferior species by superiorly adapted climax species.

The importance of ongoing dynamics is also difficult to reconcile with the concept of climax, founded as it is on the idea of autogenesis within a stable physical environment. Climax composition is relative to disturbance regime. Climax is only arbitrarily distinguished from succession. Climax as an organizing paradigm in plant ecology has obscured the full temporal-spatial dimensions important in understanding the vegetated landscape and the evolution of species which contribute to the landscape patterns.

Whittaker's coenocline concept is accepted with modifications: (1) natural disturbance gradients and Whittaker's complex gradient are intimately related, (2) temporal variation in the community should be viewed as an added axis of community pattern, and (3) ongoing dynamics have important effects on specificity of species to site relations and the predictability of vegetation patterns. Recent work has suggested an *r*-*K* continuum in species strategy. In general, colonizing ability is seen as a trade-off against specialization. Frequent disruption of the community and the creation of open sites seems to result in mixes of species that are fleeting in time and do not repeat in space. Species in such mixes are often tolerant of wide environmental extremes but are compressed into early successional time if disturbance ceases. The composition of such communities is not predictable from site characteristics. Even communities with low disturbance frequency lack complete environmental determinism, and historical events are important in understanding present composition. Communities vary in level of environmental determinism and species differ in niche breadth and degree of site specificity. Management implications of vegetation dynamics are discussed.

RÉSUMÉ

Les perturbations naturelles se définissent traditionnellement en fonction des événements catastrophiques majeurs dont l'origine se trouve dans l'environnement physique et que, de ce fait, l'on considère comme des agents exogènes des changements de la végétation. On peut opposer à ce point de vue les arguments suivants: (1) qu'il existe une gradation entre les événements mineurs et les événements majeurs au lieu d'un ensemble définissable de catastrophes majeurs pour chaque type de perturbation et (2) que quelques perturbations sont initiées ou promues par le composant biotique du système. Les flores sont riches en espèces adaptées aux perturbations. Les perturbations ont sans doute exercé une pression sélective sur l'évolution des stratégies que possèdent les espèces.

Les successions cycliques des landes et la dynamique du vide dans les forêts se sont considérées comme des configurations endogènes de végétation. Quand la mort des individus plus anciens impose un rythme sur la reproduction de la communauté, la dynamique peut bien être le résultat des facteurs endogènes. Cependant, il existe peu de cas documentés de la sénescence des plantes vivaces et bien des successions cycliques, et des cas de dynamique du vide sont initiés par des facteurs physiques. Les dynamiques des forêts s'étendent de celles qui résultent de la sénescence et de la chute d'un arbre individuel, à celles qui résultent de l'abattage par le vent de petits groupes d'arbres sains, jusqu'à celles qui résultent de grandes tempêtes qui nivellent des hectares de forêts. L'effet du vent va du simple élagage des parties mortes des plantes jusqu'aux dommages importants aux arbres vivants. Il est probable que la vitesse du vent est en rapport inverse avec sa fréquence. Les perturbations varient sans cesse. Il y a une gradation à partir des dynamiques de communauté initiées par les facteurs endogènes jusqu'à celles initiées par des facteurs exogènes. L'évolution a joué le rôle d'intermédiaire entre les espèces et l'environnement; les perturbations sont souvent dues aux facteurs physiques mais il se peut bien que les perturbations aient lieu et se terminent en fonction également de l'état de la communauté.

Les perturbations naturelles dans la végétation de l'Amérique du Nord sont les suivantes: le feu, les tempêtes, les tempêtes de glace, la poussée de la glace sur les côtes, le mouvement cryogène des sols, la fluctuation des températures, la variabilité de la précipitation, les procédés alluviaux, les procédés côtiers, le mouvement des dunes, l'inondation par les eaux de mer, les éboulements de terre, le flux de lave, les procédés karstiques, et les perturbations biotiques. Ces perturbations varient suivant la région et à l'intérieur d'un même paysage en fonction de la topographie et

d'autres inconstances du site et se caractérisent par leur fréquence, par leur prévisibilité et par leur grandeur. Le niveau du paysage a une importance pour l'évaluation du régime de la perturbation. Leur cause mise à part, les perturbations et les successions cycliques appartiennent à la même catégorie d'événements—celle de la dynamique périodique dans la structure de la végétation. La dynamique peut être le résultat des facteurs périodiques, brusques et catastrophiques dans l'environnement ou d'une action réciproque entre la susceptibilité changeante de la communauté et un facteur régulier dans l'environnement. En tout cas, des paysages hétérogènes en résultent; les espèces adaptées à cette hétérogénéité sont nombreuses, ce qui suggère leur signification à long terme.

L'importance du régime de perturbation comme partie du contexte environnant de la végétation signifie qu'il est difficile d'appliquer les modèles allogènes et autogènes de végétation. La composition de l'espèces peut se voir comme une fonction du régime des perturbations, ainsi que d'autres inconstants de l'environnement. Le remplacement compétitif dans la succession n'a donc lieu que lorsque les perturbations cessent d'exister et peut s'interpréter comme l'adaptation allogène à un nouveau environnement exempt de perturbations. La divergence compétitive, la séparation des rôles et le refus de la compétition peuvent, en fait, être à la base des configurations de succession considérées traditionnellement comme le remplacement compétitif d'une espèce inférieure par une espèce ortho-écologique adaptée de façon supérieure.

De plus, l'importance de la dynamique continue est difficile à concilier avec l'idée d'ortho-écologie qui est fondée sur l'idée de l'autogenèse dans un environnement physique stable. La composition ortho-écologique se rapporte au régime des perturbations. L'ortho-écologie ne se distingue qu'arbitrairement de la succession. L'ortho-écologie en tant que paradigme organisateur dans l'écologie des plantes a obscurci l'ensemble des dimensions temporelles et spatiales important à la compréhension du paysage végété et de l'évolution des espèces qui contribuent aux configurations du paysage.

Nous acceptons avec modifications le concept de cénocline ("coenocline") de Whittaker: (1) les gradations des perturbations naturelles et la gradation complexe de Whittaker sont intimement liées, (2) la variation temporelle dans une communauté doit se voir comme une dimension de plus dans la configuration d'une communauté, et (3) la dynamique continue a des effets importants sur la spécificité des rapports espèces-site et sur la prévisibilité des configurations de végétation. Des travaux récents suggèrent un continuum r-K dans la stratégie des espèces. En général, la capacité de coloniser est interprétée comme un échange contre la spécialisation. La perturbation fréquente de la communauté et la création des sites ouverts paraît avoir comme résultat des mélanges

d'espèces qui sont éphémères et qui ne se répètent pas dans l'espace. Les espèces dans de tels mélanges sont souvent très tolérantes de grandes extrêmes dans l'environnement mais se compriment tôt en temps de succession si la perturbation cesse. La composition de telles communautés ne peut pas se prédire suivant les caractéristiques du site. Même les communautés qui subissent une basse fréquence de perturbations manquent le plein déterminisme de l'environnement et les événements historiques sont importants à la compréhension de la composition actuelle. Les communautés varient quant au niveau de déterminisme de l'environnement et les espèces diffèrent quant à l'étendu de la niche et au degré de spécificité au site. L'importance de la dynamique de végétation pour le management écologique est discutée.

ZUSAMMENFASSUNG

Natürliche Störungen werden traditionsgemäß im Sinne von großen, in der physikalischen Umwelt entstehenden katastrophalen Ereignissen definiert und daher als exogene Erreger von Vegetationsveränderungen angesehen. Problematisch an dieser Auffassung ist folgendes: (1) Es gibt keinen einmalig bestimmbar Satz von Hauptkatastrophen für jede Störungsart, sondern einen Gradienten von kleinen bis zu großen Ereignissen, und (2) einige Störungen werden von der biotischen Komponente des Systems eingeleitet oder gefördert. Die Floren sind reich an störungsangepaßten Arten. Störungen haben wahrscheinlich einen Selektionsdruck bei der Evolution der Artenstrategien ausgeübt.

Die zyklische Sukzession im Heideland und die Dynamik der Bestandeslückenphase in Wäldern sind als endogene Vegetationsmuster betrachtet worden. Wenn das Absterben von älteren Individuen der Fortpflanzung der Pflanzengesellschaft einen Rhythmus auferlegt, dürfte die Dynamik allerdings das Resultat endogener Einflüsse sein. Die belegten Fälle von Altern in perennierenden Pflanzen sind jedoch wenige, und viele zyklische Sukzessionen und Fälle der Dynamik der Bestandeslückenphase werden durch physikalische Einflüsse hervorgerufen. Die Walddynamik umfaßt die Einflüsse, die sich aus den folgenden Situationen ergeben: Altern und Fall von einzelnen Bäumen, Windbruch von kleinen Gruppen gesunder Bäume und schließlich große Stürme, die Hektare von Wald ebene. Die Wirkung des Windes umfaßt sowohl das einfache Abbrechen von toten Pflanzenteilen als auch ausgedehnte Schäden an lebenden Bäumen. Die Windgeschwindigkeit ist der Aufttrittshäufigkeit wohl verkehrt proportional. Störungen variieren kontinuierlich. Es existiert ein Gradient von der von endogenen Einflüssen eingeleiteten zu der von exogenen Einflüssen eingeleiteten Gesellschaftsdynamik. Die

Evolution hat zwischen den Arten und der Umwelt vermittelt. Störungen werden oft durch physikalische Einflüsse verursacht, aber das Auftreten und das Abspielen von Störungen dürfte auch von dem Stand der Gesellschaft abhängen.

Natürliche Störungen in der Vegetation Nordamerikas sind Brand, Sturm, Eissturm, Eisschub an Ufern, Tieftemperatur-Bodenbewegung, Temperaturschwankung, Niederschlagsveränderlichkeit, alluviale und Küstenvorgänge, Dünenbewegung, Salzwasserpberflutung, Erdbeben, Lavaströme, Karstvorgänge und biotische Störungen. Die Störungen variieren regional und innerhalb einer Landschaft in Abhängigkeit von der Oberflächengestaltung und anderen Standortvariablen und werden durch ihre Häufigkeit, Vorausbestimmbarkeit und Größenordnung gekennzeichnet. Die Höhe des Geländes ist wichtig bei der Bewertung der Störungsbedingungen. Störungen und zyklische Sukzessionen gehören—unabhängig von der Ursache—der gleichen Ereignisklasse an: der wiederkehrenden Dynamik in der Vegetationsstruktur. Die Dynamik mag sich aus periodischen, abrupten und katastrophenartigen Umwelteinflüssen ergeben, oder aber sie mag aus der Wechselwirkung der sich ändernden Anfälligkeit der Gesellschaft und eines regelmäßigen Umweltfaktors resultieren. Auf jeden Fall führt die Dynamik zu heterogenen Landschaften. Die Arten, die sich dieser Heterogenität angepaßt haben, sind zahlreich, was auf ihre langwährende Bedeutung hinweist.

Die Wichtigkeit der Störungsbedingungen im Rahmen der Vegetationsumwelt deutet an, daß allogene und autogene Vegetationsmodelle schwer anzuwenden sind. Die Artenzusammensetzung kann in Abhängigkeit sowohl von Störungsbedingungen als auch von anderen Umweltvariablen betrachtet werden. Eine Konkurrenzersetzung in der Sukzession tritt dann nur auf, wenn die Störungen zu wirken aufhören, und kann als die allogenisches Anpassung an eine neue störungsfreie Umwelt verstanden werden. Konkurrenz-Divergenz, Rollentrennung und Konkurrenzvermeidung dürften tatsächlich den Sukzessionsmustern zugrundeliegen, die traditionsgemäß als die Konkurrenzersetzung von unterlegenen Arten durch überlegen angepaßte Klimaxarten verstanden werden.

Es ist auch schwer, die Bedeutung der fortwährenden Dynamik mit dem Begriff des Klimaxes in Einklang zu bringen, da letzterer auf den Begriff der Autogenese innerhalb einer stabilen physikalischen Umwelt begründet ist. Die Klimaxzusammensetzung ist in Bezug auf die Störungsbedingungen relativ. Klimax unterscheidet sich von Sukzession nur arbiträr. Die Klimax als Organisationsparadigma in der Pflanzenökologie hat die vollen zeitlich-räumlichen Dimensionen unklar gemacht, die für ein Verständnis der Vegetationslandschaft und der Evolution der zu den Landschaftsmustern beitragenden Arten wichtig sind.

Der Begriff des "coenocline" von Whittaker wird mit einigen Abän-

derungen angenommen: (1) Natürliche Störungsgradienten und der komplexe Gradient von Whittaker sind eng miteinander verwandt, (2) eine zeitliche Variation in der Gesellschaft sollte als zusätzliche Achse der Gesellschaftsmuster betrachtet werden und (3) die fortwährende Dynamik hat einen wichtigen Einfluss auf die Artenspezifität gegenüber den Standortverhältnissen und auf die Vorausbestimmbarkeit von Vegetationsmustern. Neuere Arbeiten weisen auf ein r-K-Continuum in der Artenstrategie hin. Im allgemeinen nimmt man an, die Fähigkeit zur Koloniebildung existiere auf Kosten der Spezialisierung. Das häufige Auseinanderreißen der Gesellschaft und die Schaffung lichter Standorte resultiert anscheinend in Artmischungen, die kurzfristig auftreten und sich räumlich nicht wiederholen. Die Arten in solchen Mischungen tolerieren oft weite Umweltextreme, werden aber in eine frühe Sukzessionszeit zusammengedrängt, wenn die Störung sich legt. Die Zusammensetzung solcher Gesellschaften kann nicht auf Grund der Standortskenngrößen vorhergesagt werden. Sogar Gesellschaften mit niedriger Störungshäufigkeit fehlt es an einem vollkommenen Umweltdeterminismus, und historische Ereignisse sind für das Verständnis der gegenwärtigen Zusammensetzung wichtig. Gesellschaften unterscheiden sich in dem Grad des Umweltdeterminismus, und Arten unterscheiden sich in der Nischenbreite und in dem Grad der Standortsspezifität. Es wird die Einbeziehung der Vegetationsdynamik in die Forstwirtschaftsführung erörtert.

INTRODUCTION

Vegetation is structurally dynamic. Dynamics are, in part, initiated by natural disturbances. Major objectives of this paper include the review of major kinds of natural disturbance important in North American vegetation and the building of an evolutionary framework for viewing the role of disturbance.

Traditionally, natural disturbance in plant communities is defined in terms of major catastrophic events originating in the physical environment—events which cause abrupt structural change in communities. Examples include fires, landslides, windstorms, and floods. This view is limiting; disturbance processes belong in a larger context. Problems with the traditional view include:

(1) For many kinds of disturbance there is a gradient from relatively minor to relatively major events. For example, wind effects in a forested ecosystem vary from simple pruning of branches to windthrow of standing dead trees to the extensive blowdowns caused by hurricanes and gales. Disturbances differ in frequency, predictability, and magnitude. Floods can be described in terms of their magnitude; e.g., the 50- or 100-year event. The spatial and temporal scale of a disturbance is relative to the community investigated. The burrowing activities of small mammals

may impact a grassland, or annual changes in water levels along a stream bank may periodically remove a bryophyte community.

(2) Some kinds of disturbance are initiated or promoted by the biotic component of the system. Fire magnitude depends not only on the source of ignition and weather conditions but also on the amount and combustibility of organic matter available. The evolution of strategies which initiate, promote, exploit, or resist disturbance means that the biotic and abiotic factors cannot be easily distinguished in many systems. The frequency, predictability, and magnitude, as well as the type of disturbance, may be selective forces in determining species strategies.

These two problems—the gradient in disturbance size relative to the community and the biotic role in disturbance—lead to reexamination of community concepts. Particularly important are the nature of climax and the controversy over autogenesis and allogenesi. These ideas, of course, are rooted deeply in the history of plant ecology.

The larger context for viewing disturbance processes is to see them as part of the general phenomenon of dynamics in community structure—whether they are more or less directed by environmental factors or by characteristics of the species present. These structural changes usually involve the death of plants or plant parts. The thesis will be developed here that such structural dynamics have implications for community properties, natural history characteristics of species, and the way communities are conceptualized.

This paper begins with a review of those temporal patterns traditionally seen as the result of factors endogenous to the community. Thereafter, natural disturbances (usually viewed as exogenous factors in vegetation) will be reviewed. These two sections will be drawn on in discussions of allogenesi, autogenesis, and the climax concept. A final section discusses a general model of the vegetated landscape and its management implications.

TEMPORAL PATTERN: ENDOGENOUS OR EXOGENOUS?

Many communities are characterized by compositional fluctuations, but even those that are compositionally stable show at least local structural changes as individual plants grow, die, and are replaced. Some temporal patterns seem to be initiated and maintained by characteristics of the plant species themselves, independent of environment. At the other extreme lie cases in which the causal factors of temporal pattern seem to lie outside the vegetation and are independent of its nature. This contrast in endogenous versus exogenous causal factors (Webb et al., 1972) underlies, as well, the distinction between autogenic and allogenic concepts of vegetational change (see Odum, 1971).

Endogenous Causal Factors: Heathland Pattern and Process

The most familiar examples of pattern apparently endogenously initiated and maintained come from studies on British heathland (Watt, 1947a, 1955, 1974; Knapp, 1974; Keatinge, 1975; Barclay-Estrup, 1970; Barclay-Estrup and Gimingham, 1969). Churchill and Hanson (1958) reviewed similar situations for tundra vegetation and also presented an overall scheme for describing temporal variation in plant communities. They used the term "cyclic replacement" for the endogenous pattern and process of the type reported in the heathland examples. Nonheathland examples have been described for a grassland community in North Dakota (Hanson and Whitman, 1937) and for the buildup and breakdown of peatslips in the Southern Hemisphere cold regions (Wace, 1961).

In these temporal patterns, individuals or colonies of one species senesce and are invaded by other species. These also become senescent eventually and are, in turn, invaded; the sequence leading back to the original species with as many as five phases replacing each other cyclically (Churchill and Hanson, 1958). The competitive abilities of the species vary as they age, and their reproduction is less competitive than the reproduction of other species on sites where they have held dominance.

Kershaw (1960) documented the senescence of *Alchemilla alpina* L. in Norway and underscored the central importance of senescence in understanding temporal pattern in plant communities, whether these patterns are cyclic or noncyclic. In Kershaw's particular case, *Alchemilla* becomes established as seedlings. Maximum seed production occurs between the eighth and twelfth year of development. Though individuals may live 23 years, the plants usually begin to senesce at about the age of 14. Soon the colonies disintegrate and new reproduction from seed becomes established on the resulting open sites.

When senescent individuals are replaced by younger individuals of the same species, as in Kershaw's example, species composition, even on local sites, remains constant although it is important to note that local structural changes (growth, death, replacement) are continuing to take place. This situation was termed "noncyclic replacement change" by Churchill and Hanson (1958) and corresponds to the way in which true climax communities are supposed to reproduce themselves.

Gap-Phase Reproduction

Gap-phase reproduction is another important kind of cyclic replacement. The parallel between this kind of forest dynamics and the heathland examples discussed above was drawn by Watt himself (1923, 1947a). Gap-phase work has resulted in a number of important observations: gap de-

pendent species are common in forest floras (Watt, 1923; Jones, 1945; Bray 1956, Williamson, 1975, Fox, 1977); tree distribution shifts within the forest as gaps are created, colonized, and the canopy reestablished (Forcier, 1975; Williamson, 1975; Vankat et al., 1975; Lorimer, 1977; Runkle, 1979); and gap size affects the community response; e.g., the diversity of species involved and the complexity and predictability of successional patterns in gaps (Jones, 1945; Monk, 1961b; Auclair and Cottam, 1971; Forcier, 1975; Ricklefs, 1977; Runkle, 1979). Gaps created by the fall of a shade tolerant species may serve to release shade tolerant reproduction (Brewer and Merritt, 1978) or may lead to replacement of shade tolerant species by more intolerant ones (Barden, unpublished manuscript). Runkle (1979) reported that gap size strongly influenced whether gaps resulted in species compositional change or just the release of the reproduction of canopy dominants.

One of the most thoroughly investigated examples, and one which lends insight on an evolutionary level, is that of Forcier (1975) for northern hardwood forest. He reported that differing roles in gap regeneration allowed for coexistence of three tree species in a "climax microsuccession." The reproductive characteristics of the three species (e.g., number of seeds per crop, periodicity of seed crops, seed weight, dispersal, seed dormancy, microsite conditions for seedling establishment, and subsequent survivorship) complemented one another. Death in the understory itself resulted in heterogeneous environmental conditions (the most obvious being light undergaps) throughout the forest. The implicit suggestion is that the reproductive strategies of the three species reflected competitive divergence and niche specialization within the framework of this persistent, if locally shifting, spatial heterogeneity (see Pickett, 1976; Platt and Weis, 1977).

Recent work in mesic tropical forests suggests that gap-phase reproduction is also important in those systems and integrates with more extensive wind damage (Aubréville, 1971; Richards, 1952, 1955; Jones, 1955, 1956; Van Steenis, 1956; Budowski, 1963; Webb et al., 1972; Whitmore, 1974, 1975; Richards and Williamson, 1975; Foster, 1977; Strong, 1977; Hartshorn, 1977). Aubréville's (1971) theory of mosaic regeneration is based, in part, on the observation that canopy emergents often lack reproduction below closed canopies, an observation widely supported (see Dittus, 1977). Budowski (1970) related the reproductive characteristics of a series of tropical trees to the roles of the trees in vegetation dynamics.

Endogenous Pattern and Plant Senescence

It is clear that most gap-phase situations are not purely endogenous patterns, in that tree fall and/or tree death are often, if not *usually*, caused by environmental factors. As wind strength increases, the likelihood of

tree fall increases. A continuum can be envisioned from individual death and single tree gaps to larger scale blowdowns (Jones, 1945). Just such a situation has been described in the Solomon Islands (Whitmore, 1974) and can also be seen in the complementary studies of Forcier (1975) and Marks (1974) for northern hardwoods. Even in the case of individual death and single tree gaps, tree senescence independent of environment must be hypothesized in order to classify the pattern as truly endogenous. Death in trees, however, seems to result from the accumulation of exogenously caused injuries and diseases rather than senescence. A central problem is defining senescence in perennial plants since they possess ever-renewing meristems. A related question is whether plant longevity is under selective control (Harper, 1967; Harper and White, 1974).

A documented case of senescence has already been described above (Kershaw, 1960). An even more pertinent case of senescence in a discussion of gap-phase reproduction is that of Foster (1977). Foster termed the large leguminous tropical tree *Tachigalia versicolor* Standl. and Wms. "suicidal," in that, after attaining mature size without flowering, it flowers once, matures its wind-dispersed fruits, and dies. Foster suggested that this behavior results in a favorable environment for the seedlings produced from this one reproductive event. While seedling densities are high, it creates its own gap. Suicidal fall of the parent tree can also initiate disruption in adjacent parts of the canopy. Foster suggested that such a strategy may be of survival value "because most, if not all, tropical canopy species require an opening or "light-gap" in the forest canopy for successful maturation." Heavy insect predation of seeds and seedlings usually results in very low seedling densities for tropical trees. *Tachigalia* seedlings are at a high density when the gap is created. This suicidal pattern may be truly endogenous, except that windstorm may actually cause the tree fall or disrupt the adjacent canopy, thereby creating a larger opening.

Another case of programmed senescence in woody, perennial plants is that of bamboos (Janzen, 1976). Individuals and colonies remain nonreproductive for many years (even 100 or more). This vegetative period is followed by widespread synchronous flowering, seed dispersal, and senescence and death of the parent colonies. In this case the pattern may be a mechanism of escape from seed predation (Janzen, 1976).

A final pertinent example is that of *Acer pensylvanicum* (Hibbs et al., 1977). This species is frequent in northern hardwood forest as a suppressed shrub or small tree. In gaps these individuals are released and can reach heights of 40 feet. Apparently, sexual switching occurs during release. Plants are initially male, but as they attain maximum size during gap closure, they produce female flowers, fruit heavily, and senesce.

These cases of endogenous senescence stand as one extreme in kinds

of community dynamics. In some cases (e.g., Kershaw, 1960) composition is stable, even on local sites; in others, several species may be involved in cyclic succession (e.g., most gap-phase situations). In both cases, death in the older individuals imposes a rhythm on the establishment of new individuals. The structural dynamics themselves result in shifting patches of reproduction and internal heterogeneity in community environment. In the cyclic cases this heterogeneity has seemed to result in competitive divergence and complementary roles for different species in the community (Forcier, 1975; Fox, 1977). If, in some cases, no environmental factor is responsible for death and ensuing structural changes, then only an evolutionary necessity for death and sexual reproduction underlies such replacement. Fox (1977) viewed tree fall as an autogenic generator of stand heterogeneity and species diversity, an opinion shared by Strong (1977) for tropical forests.

NATURAL DISTURBANCE

Contrasting with the dynamics initiated by endogenous senescence are those temporal patterns initiated by factors external to the community. Traditionally, natural disturbances have been viewed as external agents of change. Accumulating evidence suggests both the wide-ranging importance of natural disturbance and problems with this view. This discussion will suggest that many natural disturbances are not independent of factors endogenous to the community; in fact, their outplay may often be governed by community properties.

Recurrent natural disturbances seem to characterize the environmental setting of many plant communities. Disturbances and the vegetation responses they initiate seem to be an integral part of the pattern in most landscapes. The kinds of natural disturbance vary regionally and also within one landscape as a function of topography, substrate, and the vegetation present.

One long-term proponent of the role of natural disturbance in vegetation has been Raup (1941a, 1956, 1957, 1964, 1967, 1975). In studies of temperate deciduous forest, boreal forest, and tundra, he has cited a variety of disturbances operating in each landscape: substrate instability (e.g., frost disturbance of tundra soils), flooding, water fluctuations and ice push on lake shores, drought, windstorm, ice storm, fire, insects, and disease outbreaks. Others, like Raup, associated with the Harvard forest have worked on the details of stand structure and disturbance in eastern temperate and boreal forests (Stephens, 1955a, b; Lyford and MacLean, 1966; Dix and Swan, 1971; Walker, 1972; Henry and Swan, 1974; Oliver and Stephens, 1977). Other workers have stated the case for the many kinds of disturbance recurrent in their study regions; e.g., areas as dif-

ferent as tundra (Churchill and Hanson, 1958), the Yukon (Douglas, 1974), temperate forest (Curtis, 1959; Franklin and Dyrness, 1969; Loucks, 1970; Marks, 1974), grasslands (Curtis, 1959; Vogl, 1974), and tropical forests (Ashton, 1969; Baker, 1970; Gómez-Pompa, 1971; Gómez-Pompa et al., 1976; Veblen et al., 1977). Age-patchiness in old-aged spruce-fir vegetation undisturbed by man has been widely reported (Cooper, 1913; Rhoades, 1961; Place, 1964); it has also been reported for temperate forests (Zedler and Goff, 1973; Williamson, 1975).

The following list of natural disturbances was drawn from the literature reviewed in this paper. No doubt this list can be added to with increasing awareness of natural disturbance. Natural disturbances important in North American vegetation are: fire, windstorm (including tornadoes and hurricanes), ice storm, ice push on shores, cryogenic movement of soil, temperature fluctuations (e.g., unusual frosts or hot spells); precipitation variability (e.g., droughts and wetter-than-normal periods) and resulting water-level fluctuations in drainage basins; alluvial erosion, deposition, and flooding; coastal erosion, deposition, and dune movement; saltwater unundation; landslides (including avalanches, earth movement); lava flows; karst processes; and biotic disturbances (e.g., destructive effects of larger animals, insect outbreaks, disease outbreaks, and destructive effects of vascular plants on one another).

Some kinds of disturbances are particularly regional in importance (e.g., freeze-thaw soil disturbance in the Arctic, and fire in chaparral, grasslands, western coniferous forests, and southeastern pine forests). Others are particularly associated with substrate and/or topography and occur throughout North America: alluvial erosion, deposition and flooding, coastal erosion and deposition, dune movement, and landslides. Pertinent literature is reviewed below for each of the disturbances listed above. No attempt has been made to integrate the accumulating literature on disturbance and sessile marine invertebrate communities (e.g., Wells, 1961; Dayton, 1971; Paine, 1974, Levin and Paine, 1975; Loya, 1976; Woodin, 1978); rather, the emphasis here has been placed on terrestrial vegetation and disturbance.

Fire

Fire is the best researched of the kinds of natural disturbance operating in North American vegetation. Recent symposia proceedings and major review articles testify to the amount of information now available on fire ecology (Ahlgren and Ahlgren, 1960; Komarek, 1966, 1968; Daubenmire, 1968b; Slaughter et al., 1971; Heinselman and Wright, 1973; Kozlowski and Ahlgren, 1974; Mooney and Conrad, 1977; Mooney et al., in press).

Fire is important in conifer dominated systems: boreal forest (Heinselman, 1973; Wright and Heinselman, 1973; Slaughter et al., 1971; Scot-

ter, 1972; Rowe and Scotter, 1973; Viereck, 1973; Johnson and Rowe, 1975), southeast pine forest (Chapman, 1932; Starker, 1934; Turner, 1935; Heyward, 1939; Wells, 1942; Garren, 1943; Oosting, 1944; Komarek, 1974), white pine forest (Lutz and McComb, 1935; Maissurow, 1935, 1941; Ahlgren, 1974; Little, 1974), pitch pine barrens (Little, 1946, 1974; Fahey, 1975); jack pine forest (Ahlgren, 1974; Yarranton and Yarranton, 1975), Southern Appalachian pine forests (Zobel, 1969), and western coniferous forest (Munger, 1940; Bailey and Poulton, 1968; Stone and Vasey, 1968; Franklin and Dyrness, 1969; Sherman and Chilcote, 1972; Lloyd and Gruell, 1973; Taylor, 1973; Houston, 1973; Habeck and Mutch, 1973; Lunan and Habeck, 1973; Kilgore, 1973; Rundel, 1973; Weaver, 1974).

Fire can be important in drier parts of the deciduous forest (Curtis, 1959; Raup, 1967; Henry and Swan, 1974). Fire maintains root-sprouting shade intolerant species over nonsprouting tolerant species (Buell et al., 1954; Brown, 1960; Monk, 1961b).

Fires may be less important in the tundra than boreal forests because biomass is lower and less combustible and soil profiles are often water saturated (Wein and Bliss, 1973). Fires do occur, however, and can be initiated by lightning or can spread to tundra from forest communities (Wein and Bliss, 1973; Cochrane and Rowe, 1969). Douglas and Ballard (1971) describe the effect of a fire on alpine tundra that had spread there from forest below.

Fire is fundamentally important in several other nonforest vegetation types. Reviews are available on the extensive literature for grasslands (Wells, 1965; Daubenmire, 1968b; Vogl, 1974) and chaparral (Hanes, 1971; Biswell, 1974; Christensen and Muller, 1975). Because deserts have lower biomass (less fuel) than these vegetation types, they have a lower fire frequency, but the fires that do occur can be severe (Humphrey, 1974). One interesting effect of fire on a species of cactus was described by Stelfox and Vriend (1977): fire burned spines off the cactus, which then became heavily browsed by pronghorn.

Fire importance is dependent on precipitation characteristics in two ways. There must be periods of low precipitation to dry out potential fuel in a given community. On the other hand, there must be enough precipitation for organic production to result in a buildup of biomass for fuel. Chaparral, western coniferous forests, central grasslands and their bordering oak and pine forests, the southern evergreen forest region, and dry substrates and topographic positions within the deciduous forest represent compromises in this twofold relationship of fire to precipitation.

Taxonomic difficulties have limited community studies in tropical America but it now appears natural fire is important, at least in more xeric vegetation (Munro, 1966; Budowski, 1966; Blydenstein, 1968; Lem-

on, 1968; Mount, 1969; West, 1971; Phillips, 1974; Foldats and Rutkis, 1975; Anderson and Fralish, 1975). Batchelder (1967) presented a map of fire occurrence in the tropics. Some have maintained that savannahs and grasslands in tropical America are the result of human use of fire in the landscape (Beard, 1945, 1953, 1955).

The papers cited above discuss basic features of fire disturbance regime and assess fire recurrence in the landscape. The occurrence of fire-promoting, -resisting, and -dependent traits has also been widely noted (Mutch, 1970; Shafi and Yarranton, 1973; Beasleigh and Yarranton, 1974; Gill, 1977), thus suggesting the selective force exerted by fire. The combustibility and buildup of organic matter and the fire-dependency exhibited by many species are phenomena which suggest that fire is not an entirely exogenous factor and may be as much a result of community structure and composition as of environment.

Windstorm

Wind disturbance is important in tundra vegetation (Churchill and Hanson, 1958; Anderson et al., 1966), temperate and boreal forest (Behre, 1921; Raup, 1941b, 1967; Cline and Spurr, 1942; Jones, 1945; Smith, 1946; Hutnik, 1952; Goodlett, 1954; Spurr, 1956a, b; Curtis, 1959; McIntosh, 1961; Monk, 1961a; Dix and Swan, 1971; Henry and Swan, 1974; Forcier, 1975; Lorimer, 1977b; Brewer and Merritt, 1978; Bormann and Likens, 1979; Runkle, 1979), balsam fir waves (Sprugel, 1976), coastal and dune vegetation (Olson, 1958; Martin, 1959; Wagner, 1964), and bog-mat vegetation (Curtis, 1959).

Workers at the Harvard forest (Stephens, 1955a; Swan, personal communication) have prepared a map of hurricane frequency in New England based on records for the period 1635–1959. At the Harvard forest there have been four major windstorms since 1730 plus several less severe windstorms, ice storms, and fires (Stephens, 1955a). Henry and Swan (1974) traced back the history of a stand in southwest New Hampshire in 1665 and found that episodes of fire and windstorm were more important than periods of tranquility in determining stand composition. Hurricane damage has been reported for New England (Smith, 1946; Spurr, 1956a), New Jersey (Reiners and Reiners, 1965), Mississippi River delta vegetation (Chabreck and Palmisano, 1975), the northern Gulf of Mexico coast (Stoneburner, 1978), and Puerto Rican forests (Wadsworth and Englerth, 1959). In the latter study, different species showed different degrees of wind damage, and insect infestations, decay, and liana importance all increased after hurricane damage. Fifty hurricanes have passed over some portion of Puerto Rico in the last 450 years. Windstorm is also important in the Solomon Islands (Whitmore, 1974) and Mauritius (Sauer,

1962). On a landscape level, Webb (1958) presented a detailed picture of cyclone effects on lowland rain forest in Australia. Storms averaged one per 7.2 years but varied locally in intensity. Depending on topographic position and the state of the vegetation, sites experienced disturbance-free periods of from 3 to 40 years. The most exposed sites experienced 100 mph winds, a higher storm frequency, and were dominated by a low cyclone scrub. On exposed knobs, fire could follow wind damage, particularly if the cyclone brought only moderate rains. Also taking a landscape view of wind, O'Cinneide (1975) reported that wind damage in Northern Ireland occurred from the stronger winds of the prevailing wind flow rather than from storm winds from other directions.

The dominance of intolerant species on wind exposed knolls and steep slopes in forested regions has been noted: In New England (Cline and Spurr, 1942; White, 1976) and Puerto Rico (Bannister, 1970). Wind effect varies with substrate and topography (Webb, 1958; Sauer, 1962; Whitmore, 1974). Wind-thrown trees result in pit and mound microrelief, providing an agent of soil mixing and producing different kinds of rooting sites for seedlings (Lutz, 1940; Hutnik, 1952; Stephens, 1956; Denny and Goodlett, 1956; Lyford and Maclean, 1966; Armson and Fessenden, 1973). The dependence of some species on mineral soil for seed germination or seedling survival and the ability of others to grow on rotting logs is well known (e.g., USDA, 1965).

Ice Storm

Warm fronts in winter with ground temperatures below freezing cause ice storms (Lemon, 1961; this paper presented a map of the extent of glaze storms in the continental United States). Some eastern trees are more prone to damage by ice storm than others (Illick, 1916; Ashe, 1918; Rogers, 1922, 1923). Ashe (1918) described how ice storms may limit the elevational range of some species in the Southern Appalachians; he noted that limb damage opens the way for wood-attacking fungi and insects and predicted that one ice storm would have effects on forest composition that would last 100 years. Others have also reported ice storm effects (Downs, 1938; Hough and Taylor, 1946; Carvel et al., 1957).

Ice Push

The destructive effect of ice push has been noted for the scouring of riversides (Lindsey et al., 1961) and lake shores (Raup, 1975).

Cryogenic Movement of Soil

Freeze-thaw cycle movement of soil causes the opening up of new surfaces, destruction of plant roots and whole plants, and changes in the

water table in both arctic (Polunin, 1934, 1935, 1936; Griggs, 1936; Hanson, 1950; Raup, 1951; Sigafos, 1951, 1952; Coombe and White, 1951; Muller, 1952; Johnson et al., 1966) and alpine tundra (Johnson and Billings, 1962; Price, 1971). Anderson (1967) saw the cyclic succession in *Dryas octopetala* communities as a response pattern to physical disturbance by freeze-thaw movement of soils plus the effect of wind. The vegetative cover also affects the pattern and intensity of frost action (Benninghoff, 1952; Wilson, 1952; Viereck, 1966).

Temperature Fluctuations

The profound effect of variability in spring weather on western alpine communities was described by Ehrlich et al. (1972). Unusual frosts in Brazil had a major effect on species composition of vegetation and plant geography in Brazil (Silberbauer-Gottsberger et al., 1977). Climatic fluctuation may be responsible for tree species shifts described for Minnesota over a 25-year period (Buell and Gordon, 1945; Buell, 1956; Buell and Martin, 1961; Westman, 1968). The effect of climatic variability has also been reported for European taiga communities (Korchagin and Karpov, 1974).

Precipitation Variability

Year to year changes in precipitation drive water-level fluctuations in swamps, bays, rivers, and lakes. Temperate climates at least seem to be characterized as much by variation as by mean precipitation figures; Janzen (1967) has suggested tropical climates are more constant.

Changing water levels cause flooding and erosion of vegetation during high water; drought and open sites for colonization during dry years. Shoreline vegetation is periodically destroyed (Raup, 1957); bog-mat vegetation advances during some years, but is broken apart and recedes in others (Buell and Buell, 1941; Curtis, 1959; Schwintzer and Williams, 1974; Reiners, personal communication; Buell et al., 1968; Buell and Buell, 1975).

During 55 years of change in a Michigan bog there was a succession from *Chamaedaphne* to a high shrub association with tree reproduction and back to *Chamaedaphne* as precipitation decreased, then increased again (Schwintzer and Williams, 1974). In small bogs in Minnesota, wet years caused formation of a moat around the central sphagnum-*Carex* central area and death of tree species; historical evidence suggested at least one similar formation of moats in the 1800's (Buell and Buell, 1975). Drury and Nisbet (1973) review work on similar cases and regard these as evidence of allogenic change and the lack of ongoing autogenesis in these systems taken by many as prime examples of hydric primary succession ("pond filling"). Wet years in the northern Great Lakes

caused increased growth of sphagnum; sphagnum can impede drainage, resulting in flooding and killing of forest trees. This "retrogressive succession" (Lewis and Dowding, 1926) was termed paludification by Heinselman (1970).

Rare rainstorms can have a long-lasting effect on desert community structure and composition (Zedler and Ebert, 1977). Rainstorms cause increased turbidity (causing reduction in photosynthesis) and an influx of nutrients (stimulating photosynthesis) in aquatic systems (Bishop, 1977).

Precipitation variability results, of course, in drought as well as flooding. Just as some topographic positions and substrates have a tendency for flooding, others have a tendency for drought. Visser (1949) presented a model of the American climate. He mapped drought tendency and showed a correlation between the driest years (e.g., 1871, 1894, 1910, and 1918) and widespread fires in the Great Plains, Rocky Mountains, and southeast coastal plain. Drought tendency is associated with certain regional climates and, even in the wetter areas of North America, develops on convex topography, permeable substrates, and other excessively drained sites. Droughts may occur with a frequency of less than 1 in 5 years and still be significant ecologically. The occurrence and importance of drought periods is obscured by the use of climatic means to represent regional climate.

Drought periodically reduces the importance of mesic species and causes irregular compositional fluctuations in forest (Hough and Forbes, 1943; Aikman and Smelser, 1938) and changes in growth rates of species (Buell et al., 1961). On a Missouri cedar glade, dry years favor annuals at the expense of perennials (Kucera and Martin, 1957). Perhaps the most thoroughly studied drought effects are those of the Dust Bowl years in the Great Plains (Weaver, 1950, 1958, 1968; Weaver and Albertson, 1943, 1944; Weaver and Bruner, 1945; Weaver et al., 1935; Albertson et al., 1957; Albertson and Tomanek, 1965; Albertson and Weaver, 1945; Coup-land, 1974; Stiles and Melchers, 1935). Borchert (1950; see also Transeau, 1935) related the prairie peninsula in the Midwest to the path of rain-bearing systems: rainy weather originating to the west often passes just to the north of the prairie peninsula, that originating in the Gulf of Mexico often passes just to the south. The peninsula itself thus has a higher probability of drought than land to the south or north.

Alluvial Erosion, Deposition, and Flooding

Stream migration, erosion, and deposition continually create new substrates and destroy old ones; shifting patterns of vegetation result in which species of varying colonizing ability, tolerance of flooding, and shade tolerance are distributed along the disturbance-created gradients

(Ware and Penfound, 1949; Buell and Wistendahl, 1955; Wistendahl, 1958; Weaver, 1960; Lindsey et al., 1961; Sollers, 1974; Bell, 1974; Lewis, 1975; Noble and Murphy, 1975; Johnson et al., 1976; Nanson and Beach, 1977; Bell and del Moral, 1977; Franz and Bazzaz, 1977). The importance of species found along rivers is correlated with flood frequency; in addition, the probability of different flood heights means that the gradient from river's edge to upland is a spatial gradient reflecting flood frequency (Bell, 1974; Bell and del Moral, 1977). Lewis (1975) claimed that silver maple colonization of sites created by deposition kept pace with meander destruction of mature silver maple trees. Kimmerer and Allen (1978) described disturbance to streamside bryophyte communities and species response.

Reproductive strategy and other ecological characteristics of flood plain trees are strikingly adjusted to disturbance regime. In particular, *Acer saccharinum* L., *Betula nigra* L., *Populus deltoides* Bartr., and *Salix nigra* Marsh., four outer flood plain species of the eastern deciduous forest, share the following characteristics: large regular yearly seed crops, light wind and water dispersed seeds, fast growth rates, low density wood, short life spans, low shade tolerance, ability to sprout when damaged, and high flood tolerance (McDermott, 1954; Hall and Smith, 1955; Hosner, 1957, 1960; Hosner and Boyce, 1962; U.S.D.A., 1965; McCleod and McPherson, 1973; Koevenig, 1976). Perhaps most striking is their early spring blooming period, early summer seed dispersal, lack of seed dormancy, and short viability periods (one to two weeks). *Betula nigra* may be the only birch species to fruit in early summer (Koevenig, 1976). *Acer saccharinum* and *Betula nigra* belong to genera in which upland, more shade tolerant species, by contrast, have later blooming dates, fall dispersed fruits, dormancy mechanisms, and longer viability periods. A possible explanation is that the outer flood plain species flower early (near spring flood time) so that as waters recede they are able to disperse to open mud banks and gravel bars. Fast growth rates (2–3 m/yr) enable the seedlings to become established during the summer and prior to the next year's spring floods. The lack of dormancy and short viability periods of outer flood plain trees contrast not only with upland shade tolerant trees but also with upland species that are (like the alluvial species) intolerant. The upland intolerant species have dormancy mechanisms and very long viability periods—longer than upland tolerant species as well (Marquis, 1975); e.g., 40+ years in *Prunus pensylvanica* L. f. (Marks, 1974) and 70+ years in *Comptonia peregrina* L. Coult. (Tredici, 1977).

A final example showing the dependence of species on alluvial disturbance regime and spatial shifts in erosion, deposition, and flooding is that of bottomland species such as *Taxodium* (Demaree, 1932) and *Nyssa* (Nixon et al., 1977; Skunk, 1939), which attain their best growth on sites

with permanent inundation but have seeds that need aerated sites not covered by standing water to germinate. Thus the species depend on the shifting occurrence of inundated and open sites.

Coastal Erosion, Deposition, and Dune Movement

Coastlines and dunal systems are continually altering under the influence of wind and water; often the greatest changes occur during storms (Nichols, 1920a, b; Martin, 1959; Wagner, 1964). Erosion-stabilization cycles have also been reported for inland dunes (Curtis, 1959; Olson, 1958).

Wagner (1964) described a cyclic series of events for *Uniola paniculata* L. on the foredunes of coastal North Carolina. Sand accretion stimulated plant growth; a mound of sand and the grass grew together until unusually high seas or strong winds eroded the sand. The exposed plant eventually died, allowing more sand to be eroded—and then deposited in new areas where the process began anew.

The influence of disturbance on salt marshes (Pethick, 1974) and mangrove swamps (Thom, 1967; Lugo, 1977; Craighead, 1971) has also been noted.

Saltwater Inundation

Storm-caused changes in salinity, and other saltwater flooding have been implicated as disturbances along coasts (Barbour and DeJong, 1977; Chesapeake Research Consortium, 1977; Chabreck and Palmisano, 1973).

Landslides, Avalanches, and Earth Movements

Landslides are a dramatic disturbance on steep slopes. Their frequency and the response of the vegetation has been studied in the White Mountains of New Hampshire (Flaccus, 1959), the Adirondacks (Bogucki, 1977), the Southern Appalachians (Bogucki, 1970), and the Pacific northwest (Swanston and Swanson, 1976). Intense rainstorms seem to be the major factor initiating landslides in the Great Smoky Mountains (Bogucki, 1970). Succession on water-saturated earth flow in Colorado was described by Langenheim (1956).

Lava Flows

Succession on lava flows has been studied by Eggler (1971), Smathers and Mueller-Dombois (1974), and Veblen et al. (1977). It is apparent from these references that there are species adapted to new sites created; whether primary successions lead to reestablishment of predisturbance "climax" vegetation is debated.

Karst Processes

The erosion of limestone in humid climates, causing instability in cliff faces and collapsing of and water table changes in sink holes, would seem to constitute an important disturbance type in some regions of the United States. I am unaware of vegetation papers describing community effects.

Biotic Disturbance

Animals may exert a continuous influence on vegetation or the effect may vary over time, causing periodic vegetation change; e.g., insect outbreaks (Swaine, 1933; Blais, 1954; Lejeune, 1955; Ghent et al., 1957; Morris, 1963; Macaloney, 1966). Insect infestations may follow damage caused by other disturbances such as wind (Gardiner, 1975) or ice storm (Ashe, 1918).

Burrowing animals are an important disturbance in grasslands (Curtis, 1959; Platt, 1975). Curtis (1959) referred to mounds in the prairie as "micro-gap-phases" and described local successional changes initiated by mound formation. Platt (1975) described the disturbance of prairie soil by badgers digging for ground squirrels in their burrows. Twenty years were required for succession to "undisturbed" prairie.

Buffalo were formerly important on grasslands (Weaver and Clements, 1929; Larson, 1940). The extinction or extirpation of larger animals makes the role of these species in original vegetation dynamics difficult to assess. For example, changes in habitat and removal of predators have led to changes in grazing pressure exerted by white-tailed deer in Minnesota and greatly decreased the importance of *Thuja occidentalis* L. in mature forests (Grigal and Ohmann, 1975). Other kinds of animal effects on vegetation include beaver flooding of stream valleys (Ives, 1942) and the impact of rabbits in Aspen parkland vegetation (Bird, 1930).

Periodic disease outbreaks are also potentially important and may have been the cause of postglacial fluctuation in *Tsuga* importance in the eastern United States (Lichens and Davis, 1975; Davis, 1976). Oak wilt in the Great Lakes region was reported on by Anderson and Anderson (1963).

Two interesting examples of promotion of disturbance by the effect of one vascular plant on another were recently described. Strong (1977) suggested that heavy epiphyte load in tropical forests increases wind damage. Siccama et al. (1976) showed that vines in a Connecticut woodland increased the damage suffered during ice storms, thus maintaining a patchwork of open areas which were themselves favorable sites for vine establishment and growth. In Puerto Rico, the importance of lianas was higher in patches of past hurricane damage than in undisturbed forest (Wadsworth and Englerth, 1959).

Disturbance: Emergent Points

The natural disturbance literature raises important points which are summarized in this section. These points are drawn from the many different kinds of disturbance reviewed above. Following this presentation, implications for community concepts will be discussed at greater length.

The following insights emerge from the natural disturbance literature: Supposedly exogenous disturbances often have an endogenous component; disturbances vary regionally and within one landscape; landscapes may be in dynamic equilibrium with local fluctuations canceling out over the whole; disturbances can be characterized by parameters such as frequency, predictability, and magnitude; disturbances are usually viewed as setting back succession and maintaining mixed vegetation; floras are rich in disturbance-adapted species. These points are discussed below.

Just as the pattern and process examples were seen to involve factors exogenous to the communities, so natural disturbance-initiated dynamics often have an endogenous component. The combustibility of plant parts may be adaptive and strongly influences the occurrence of fire (Mutch, 1970). The state of the community influences the effect of wind (Webb, 1958; Sprugel, 1976). Freeze-thaw disturbance of soils is influenced by effects of biomass on microclimate (Sigafos, 1952; Benninghoff, 1952; Viereck, 1966). Many of the papers that describe cases of natural disturbance make direct comparisons of the dynamics in their systems to the pattern and process literature (e.g., Thom, 1967; Anderson, 1967; Nanson and Beach, 1977). Some of the pattern and process papers themselves report gradients from local pattern to larger disturbances (e.g., Reiners and Lang, 1979; Wace, 1961). The gap-phase papers also refer to a gradient from small gaps through larger ones to large blowdowns (Jones, 1955; Webb et al., 1972; Whitmore, 1974; Marks, 1974; Forcier, 1975). The literature suggests the intrinsic similarity between heathland pattern and process, gap-phase dynamics, meandering rivers, mangrove dynamics, fire-influenced systems, and regions with recurrent windstorm. Only time and spatial scale separate these situations. They all seem to involve characteristics of both the species present and the environment.

Disturbances vary regionally. For example, tall, long-lived, thick-barked fire resistant trees in the western United States contrast with trees on mesic sites in the eastern United States, which are shorter lived, shorter in height, and thinner barked. Windiness in the East and dry summers and fires in the West may account for these differences. Of course, any given region may see several kinds of disturbance (Dix and Swan, 1971; Walker, 1972; Henry and Swan, 1974; Oliver and Stephens, 1977). It is also likely that disturbances are correlated with one another. Gardiner (1975) described infestations of wood-boring insects following

windstorm. Other examples are fire in a windthrown stand, windstorm damage following fungus attack on ice-storm damaged trees, and fire following drought.

Within one landscape, disturbance depends on topography substrate and vegetation. This has been reported for wind (Cline and Spurr, 1942; Webb, 1958; Sauer, 1962; Whitmore, 1974) and flooding (Bell, 1974). Hayes (1942) presented a model of contrasting fire danger on south- and north-facing slopes. Kessell (1976) has recently presented gradient models of fire occurrence. The effect of climatic drought depends on substrate. Diverse topography and substrate results in landscapes that contain both disturbance-prone and disturbance-protected situations; these act as refugia for species adapted to or sensitive to disturbance.

Disturbance may create landscapes that are in dynamic equilibrium with regard to composition and structure, as has been suggested for boreal forest (Shafi and Yarranton, 1973; Heinselman and Wright, 1973), subalpine fir forests (Sprugel, 1976), coastal systems (Martin, 1959), alluvial forests (Lewis, 1975; Bell and del Moral, 1977) and prairie (Curtis, 1959). Local floristic composition fluctuates greatly, but on the landscape level the region may be floristically stable except for long-term evolutionary changes, climatic change, or species migrations (Heinselman and Wright, 1973). For example, Cwynar (1978) showed that regional pollen spectra in his region of the boreal forest were stable for 1,200 years, despite a disturbance regime of one major fire per 80 years. The "shifting locus" of disturbance (Heinselman and Wright, 1973) may result in a relatively stable distribution of patches among various age classes within the landscape mosaic of community states. Temporal patches would then show a characteristic, if shifting, spatial distribution. Frequency in time becomes a predictor of distribution in space, given large enough areas and a constant disturbance regime. Disturbance recurrence itself may maintain a dynamic equilibrium in the landscape. In many cases, the changing state of the vegetation (e.g., fire fuel buildup in fire-prone systems and the aging of trees in wind-prone areas) results in a shifting susceptibility to disturbance and hence also contributes to dynamic equilibrium under constant disturbance regime. These dynamic equilibria of shifting patches of vegetation recall the cyclic dynamics in the pattern and process papers and have contributed to the frequent citing of such papers in the natural landscape literature. It also suggests that some landscapes show pulse-behavior in terms of stand reproduction and succession (e.g., Sprugel, 1976). Nanson and Beach (1977) found that geomorphological processes associated with meandering rivers initiated just such a situation as vegetation became established on open sites. The pulse-behavior persisted through several generations of trees, though with decreasing distinctness. Wavelike establishment was also reported by Hett and Loucks (1976) in a study of *Tsuga* and *Abies* population structure.

When disturbances generate mosaiclike patches of vegetation of different ages, such pulses of establishment (and often rapid early successional growth) may be important in landscapes. Disturbance-initiated patches may persist for long periods of time; e.g., patterned ground influences on environmental and community structure long after frost movement has ceased (Watt et al., 1966).

It is uncertain whether landscapes can be shown to have been in dynamic equilibrium condition (Connell and Slatyer, 1977). In any case, the maintenance of landscape heterogeneity on some level is indicated. Zedler and Goff (1973) proposed one method for quantifying such temporal-spatial relationships in their species association index.

Disturbances may alter sites by a drastic change in the physical factors (e.g., landslides) or simply by the removal of the effect of biomass on microclimate (e.g., blowdowns). Open competition-free sites may be created. In other situation, individuals already present may survive the disturbance and be involved in regrowth. In any case, competitive relations of species are altered.

Disturbance occurs on a wide range of scales. Whether the disturbance is viewed as occurring within one community or not depends on the investigator's definition of community. Gap-phase reproduction and heathland cyclic successions are most often treated as intracommunity patterns. On the other hand, large-scale and low frequency disturbances are viewed as producing temporal patterns, involving a series of communities as postdisturbance succession proceeds. This is an arbitrary decision, just as the definition of "community" itself is arbitrary.

Disturbances can be described by their frequency, predictability, and magnitude. For a given disturbance, frequency is the mean number of recurrences in a given time period; predictability is inversely related to the variation about mean recurrence interval. The prediction of fire occurrence and behavior has been a management goal for some time (Rothermel, 1972; Kessell, 1976). The frequency of floods of various magnitudes has been important in the planning of dams, flood plain zoning, and flood plain development. The recurrence interval of windstorms has been noted in a few regions (e.g., Stephens, 1955, 1956; Webb, 1958; Lorimer, 1977a).

Disturbance *magnitude* is more difficult to define. It is obvious, for example, that windstorms vary in physical force, size of area disturbed, and amount of damage done to vegetation. The time required for succession to restore the community to its predisturbance state may also vary with the "magnitude" of the disturbance. It is hard to find a unique and broadly applicable definition of magnitude. Water height or duration of floodwaters might be used for flooding; areal extent, hottest temperature reached, or amount of fuel consumed might be used for wilderness fires.

Though potentially independent, disturbance frequency, predictability,

and magnitude are often correlated. In particular, disturbance frequency is often inversely related to magnitude (e.g., the frequency distribution of flood height for rivers). These parameters are also correlated with topography and substrate (Kessell, 1976; Cline and Spurr, 1942; Hayes, 1942).

Most disturbances seem to show continuous gradients in magnitude. For example, wind is a part of the environmental setting of stands, and its effect varies from none to catastrophic (see discussion in Bormann and Likens, 1979; Major, 1974). Some insects exert a continuous effect to which plants are adapted; in other cases, insect species show dramatic population changes and cause widespread destruction in the vegetation. Climatic change (or fluctuation if trends are not sustained) can be gradual or abrupt. One end of these gradients in magnitude the disturbance itself melts into the normal setting of the community (Raup, 1941a). The plants are adapted; no dynamics are initiated (e.g., Reiners and Lang, 1979). With periodic disturbances of greater magnitude, dynamics are a characteristic feature of the landscape.

The gradient in disturbance frequency also has implications for community patterns. If disturbance frequency is very low, there will be a lack of compositional elements and structural modifications adapted to that disturbance. Such large-scale disturbance-dependent species as pin cherry become, in fact, locally extirpated (except for the storage of their seeds in the soil) in northern hardwood forests (Marks, 1974). If disturbance frequency is high, there may be a constant presence of species adapted to that disturbance and local extinction of species not so adapted. With highly frequent disturbance, the whole community may become structurally affected as well as compositionally adapted to the presence of the disturbance. Examples of this are the cyclone scrub of Webb (1958), krummholz on windswept eastern mountains (Reiners and Lang, 1979), the pygmy pine plains on sites of the highest burn frequency (Gill, 1975), and shrubby flood-battered riversides. Where disturbance is most frequent there is a lack of community dynamics. At either end of the frequency gradient there may be relative compositional stability. It is in the middle ground that there is an alternation of disturbance and disturbance-free periods and the variety of situations created by the interplay of disturbance and succession. Most communities fall within this middle ground and are composed of a mixture of species with different strategies in the temporal dynamics.

Disturbances have been viewed as setting succession back to earlier stages (Polunin, 1936; Cline and Spurr, 1942; Spurr, 1956b; Stout et al., 1975). In mesic temperate forests disturbance was seen as favoring oak over maple (Curtis, 1959; Buell et al., 1966). Shade tolerant species characteristic of vegetation with more open canopies may be successional on

mesic sites (Curtis, 1959). Climax adaptation scale seems also to be an index of moisture gradient in that mesic species are at the climax end of the scale and species characteristic of xeric, alluvial, or hydric successions are at the early successional end of the scale. The recurrence of disturbance dynamics in coastal environments and lack of evidence of ongoing autogenesis lead Lugo (1977) and Thom (1967) to abandon altogether a successional designation for mangrove vegetation.

Where disturbance is recurrent, communities that are mixtures of species of varying shade tolerance (or other measure of successional position) are maintained (Stearns, 1949; Buell and Wistendahl, 1955; Williamson, 1975; Stout et al., 1975; Forcier, 1975). With freedom from disturbance, many have noted that a drop in species diversity occurs as communities progress from midsuccessional mixed communities into climax communities (Drury and Nisbet, 1973). Only a subset of the flora is adapted to the extreme shady environment of late succession. Recurrent disturbance is therefore viewed as maintaining diversity (e.g., Loucks, 1970; Fox, 1977; Ricklefs, 1977; Connell, 1978).

Regional floras, from the tropics to the poles and from wet to dry climates, are rich in disturbance-dependent or adapted species. This implies the long range frequency and predictability of disturbances and their importance as a selective force in evolutionary history. Seedling strategies (Forcier, 1975), buried seed strategies (Clark, 1962; Leak, 1963; Wendel, 1972; Kellman, 1974; Marks, 1974; Marquis, 1975; Johnson, 1975; Tredici, 1977; Keeley, 1977; Keeley and Zedler, 1978; van der Valk and Davis, 1978), other reproductive characteristics (Harper and Ogden, 1970; Hedrick et al., 1976; Giesel, 1976; Runkle, 1979), woody plant branching patterns (Horn, 1971; Marks, 1975; Whitney, 1976), woody plant sprouting ability (Brayton and Woodwell, 1966; Trimble and Seegrift, 1973; Auclair, 1975), and herb species growth rates (Sobey and Borkhouse, 1977; Beasleigh and Yarranton, 1974) have all been related to species response during disturbance. It seems likely that understanding such natural history characteristics of species as reproductive strategy and geometry is of fundamental importance to understanding the communities they make up. Gill (1975) suggested that a short fire recurrence interval was important in the evolution of cone serotiny in local populations of *Pinus rigida* P. Mill. Fire-adapted traits have received much attention (Gill, 1977). There is an increasing awareness of the evolutionary significance of disturbance in understanding of natural history characteristics of tropical species (Gómez-Pompa, 1971; Gómez-Pompa et al., 1976). Bleakney (1972) reported that the importance of disturbance as a selective force was influenced by the relative length of recurrence interval compared to organism life span.

In general, disturbance-adapted species are seen as tolerant of envi-

ronmental extremes, intolerant of competition, and as good colonizers characterized by high reproductive potential, fast initial growth rates, and short life spans. This is the classic "r" strategy. It is usually contrasted with the conservative "K" strategy: fine-tuning to environment, strong competitive ability, low reproductive output, slow growth, and long life spans. Recent work has suggested that there is a continuum between these strategy types, or, in fact, other basic kinds of strategy (Grime, 1977; Harper, 1977; Whittaker and Goodman, 1979).

DISCUSSION: ALLOGENESIS, AUTOGENESIS, AND CLIMAX

The most important implications of the natural disturbance literature are those which affect basic views of vegetation. A dominant paradigm in plant ecology has been that of climax. The climax is the presumed result of autogenesis within a stable environment. Recently the concepts of autogenesis, allogenesiis, and succession have been critically reviewed (Drury and Nisbet, 1973; Horn, 1976). The natural disturbance literature aids a further investigation of these concepts and that of climax itself. These subjects are discussed in depth in the following sections.

Allogenesiis and Autogenesis

In this paper, natural disturbance has been classed with other kinds dynamics in community structure, irrespective of causal factor. Some phenomena, unlikely to be associated with disturbance by ecologists, also belong to this class of events. For example, senescence and death of deciduous leaves and the death of annual plants are ultimately cued to some environmental stimulus. What sets such biomass destruction apart from such readily acceptable disturbances as wildfire? Regularity of environmental stimuli and degree of species adaptation would seem to set such phenomena apart. In reality, some disturbances such as fire in chaparral or tall grass prairie are, to some degree, rhythmic (Philpot, 1977; Vogl, 1974), and the species present are quite well adapted to fires, if not promoting them. Senescence itself, whether of deciduous leaves, annual plants, or long lived perennials, may be under evolutionary control through selection by some factor of the environment.

If disturbance factors (in the broadest sense) are arranged in a series of decreasing frequency, it would become clear that a continuum of factors and community responses would be recognized. Annual photoperiodism, frost, variation in summer precipitation, ground fires, and major windstorm represent such a series for northeastern hardwood forests, in a general sense. At the beginning of the series, the factors are frequent (annual cycle) and regular (every year). At the end of the series, the

factors are infrequent and irregular. Community-wide adaptation is present in response to the first factors; there is a variety of adaptive responses to the effects of the latter part of the series. Phenological changes are certainly not succession (Mueller-Dombois and Ellenberg, 1974). The community responses to annual temperature regime (deciduous leaves) is certainly to be regarded as an endogenous rhythm. Likewise, communities highly adapted to frequent and predictable disturbance (i.e., fire in chaparral or tall grass prairie) may seem to lie on the endogenous end of the scale of causal factors discussed in an earlier section of this paper.

This view of disturbance factors, degree of disturbance, and degree of plant adaptation as continua leads to a logical problem: that of separating causal factors into strictly endogenous and exogenous categories. In every case of apparent endogenous process, some environmental factor can be identified as stimulating a response that leads to specific patterns in vegetation structure; if not directly, then through selection for adaptation in the long run. In many apparently exogenous disturbances, characteristics of the plants themselves are involved. Examples are the disturbance-promoting traits exhibited by fire-dependent trees (Gill, 1977) or simply the fact that the destructive potential of wind may be dependent on the state of the community. In the heathland examples, wind may merely erode senescing colonies, or it may be a causal factor of plant death; sometimes the distinction is an impossible one to make. Most canopy trees seem to be alive at the time of tree fall and gap initiation (see discussion in Runkle, 1979), but that is, of course, not always the case. Another pertinent example in which environment and species natural history are both involved in dynamics is that of fir waves (Sprugel, 1976). Important in the cyclic pattern are the short life span of fir, the floristic simplicity of the vegetation, an exposed position, shallow rocky soils, and the effect of wind.

While adapted to environment and controlled by environmental setting (including disturbance or freedom from it), species also affect environment, the expression of physical disturbance, and hence also affect the occurrence of other species. Those physical events which are recurrent, frequent, and predictable may lead to selection for adaptation. Those adaptations lend an endogenous component to the dynamics observed. Perhaps the only truly exogenous disturbances are those which are of such low frequency that they are unimportant in evolution of species adaptation. Some human disturbances may be totally new to vegetation. Bleakney (1972) reported that in a marine system, disturbance recurrence interval was longer than organism life span and that, therefore, there was no possibility for evolution of adaptations for either disturbance avoidance or exploitation. It seems best to recognize a continuum between community dynamics that are the result of species properties (i.e., those

involving senescence and pulse reproduction not directly stimulated by a sudden environmental event) and those which are the result of physical events uninfluenced by community properties. Natural communities seem to fall along such a continuum, rather than at either extreme.

The attempt to contrast exogenous and endogenous causal factors is related to the attempt to identify allogenes and autogenes in plant communities (Drury and Nisbet, 1973). Allogenes is community change driven by environmental change. The classic example is gradual and directional climatic change causing species distribution shifts and local community changes. Autogenes is community change driven by the properties of the species present and their effects on site environment (including edaphic changes). Succession, e.g., postglacial "pond filling," is classically described as autogenic. The attempt to classify agents of vegetation change as internal or external to the community is an old one (e.g., Gams, 1918; Cooper, 1926; Tansley, 1935).

The idea of autogenes necessitates the definition of stable "normal" environments, for it is within such an environment that community development towards some inevitable climax can occur. Changing environments prevent autogenes; in fact, they drive allogenic change. The "normal" environment must also be nondisruptive to succession; disturbances are viewed as setting back succession. Succession is a period of nonequilibrium with an adjustment to the given stable and "normal" environment, in this view.

There are several problems with the concept of autogenes. Environments seem, on the whole, neither stable nor nondisruptive. This is, of course, not a criticism of the basic concept, but just a statement that it rarely goes to completion. Drury and Nisbet (1973) have made a more fundamental criticism. They present allogenic models of primary successions. These are discussed below in the discussion section "Monoclimax."

Another problem with the concept of autogenes concerns the role of disturbance in vegetation. Disturbances are part of environments and communities. Disturbance dynamics are prominent where disturbance and disturbance-free periods alternate. It might be argued that successional vegetation is fleeting, not due primarily to autogenes but rather to the fleeting operation of an exogenous factor, disturbance. Where disturbance is more frequent, the disturbance-adapted species are more prominent. Hence, as in allogenic vegetational change, disturbance dynamics can be described by changes in the operation of extra community factors. Postdisturbance succession is analogous to vegetational change with climatic change. There are time lags in this system. The disturbance-adapted species yield during a period of succession to disturbance-sensitive species, and the vegetation adjusts to a new "normal" (disturbance-

free) environment. Certainly, competitive replacement in successional time and within stable environments occurs. After natural or human disturbance in forested regions, the production of shade, soil development, and changes in mineral cycling and energy flow are all seen as community-driven processes that accompany autogenic development of "climax" communities. However, the brief operation of disturbance characterizes this situation. Where disturbance is particularly frequent, as in yearly fires in grassland or cryogenic movement of soil in the Arctic, the disturbance itself blends in with the concept of the "normal" environment that controls the "climatic climax" composition. Species adapted to the disturbance are permanent members of these communities.

The basic question can be phrased as follows: Do disturbances set back succession or do they redefine climax environmental setting? Traditional views have tended to conceptualize disturbances as external to the community and as destroying climaxes or interrupting autogenesis. Where disturbances are infrequent, at least compared to human life spans, this has been seemingly simple and logical. On the other hand, in regions with more frequent disturbance, such as grasslands (Vogl, 1974), boreal forests (Raup, 1941a; Rowe, 1961; Zach, 1950), and tundra (Churchill and Hanson, 1958), the traditional succession and climax oriented views are more difficult to maintain and have generated controversy. These traditional views have also been challenged for desert (Noy-Meir, 1973) and tropical systems (Hewetson, 1956).

Vogl (1974) found problems applying successional theory to grasslands. He suggested that much of the evidence for the development of the theory of succession in grasslands came from fire excluded areas. He also concluded that shade tolerance is not important in the development of grassland communities and that the definition of climax vegetation becomes difficult in light of the disturbance-related dynamics. He stated:

A more reasonable approach is to dismiss successional classification of grassland species and classify them as increasers, decreasers, neutrals, invaders, or retreaters (Vogl 1964), depending upon their responses to such factors as grazing, droughts, or burnings In summary, succession can be better understood if the traditional concepts and terms are discarded and if grassland succession is considered a cyclic or circular phenomenon in which fire, or its ecological equivalent, is essential.

An advantage in Vogl's terminology is that the terms are keyed to specific environmental factors. Instead of being considered either successional or climax, there are many designations that can be applied, depending on the environmental factor examined. The floristic composition of the grassland landscape contains species which respond differently to each of the disturbances cited above, as well as to environmental gradients static in the landscape during disturbance-free periods. It should be apparent that Vogl's terminology is oriented to a concept of exogenously driven vege-

tation dynamics. There is no one "increaser" in all environmental situations; rather there is an "increaser" for each set of environmental situations.

Enlarging on Vogl's terminology, competitive ability and dominance can be seen as dependent on the environmental setting. This model stresses exogenous causal factors: Environmental setting determines community properties. An extreme statement of this view was that of Gleason (1927) in his tongue-in-cheek reference to an open water forest climax for the northeastern sea coast where rising sea level had drowned areas once dominated by forests and salt marshes.

Another basic question, then, is this: What shapes vegetation—disturbance-free periods of competition and succession or repeated disturbance and environmental fluctuation? Henry and Swan (1974) traced the history of a stand in southwestern New Hampshire back to 1665 and stated:

As summary and hypothesis for forests of the Pisgah region we can say that tranquility does not appear to be an important mediator of change, but that external events (fire and windstorm) are extremely important. The vegetational composition on one site may change considerably over time, and studies that examine compositional change associated with disturbance may provide a key to predicting its progress.

This statement echoes that of Raup (1957):

The ideas of community structure and the expression of dominance, that of biological succession, and finally, that of climax, are based largely upon the assumption of long term stability in the physical habitat . . . I see the community, not as the product of long term, slow development in a relatively stable physical habitat, but rather as the product of repeated major disturbances by factors largely external to vegetation. I must think of such disturbances, not as unusual departures from the normal, but as part of the normal itself.

A rough estimate of the time necessary for development on undisturbed climax *sensu strictu* (i.e., the most shade tolerant species, excluding even gap-phase species) in mesic temperate and tropical forests is 200–1,000 years (Webb, 1958; Curtis, 1959; Poore, 1968; Daubenmire, 1968a). The time needed in prairie has been estimated at 20 years (Platt, 1975) on patches of fresh soil dug by badgers. Many workers have reported regional disturbances of higher frequency than the disturbance-free periods required (Raup, 1941a, 1951, 1956, 1957, 1964, 1967; Dix and Swan, 1971; Walker, 1972; Henry and Swan, 1974; Oliver and Stephens, 1977). However, Lorimer (1977a), using land survey records, found that frequency of fire and blowdown in Maine was of low enough frequency to allow widespread development of climax communities. This assessment was shared by Bormann and Likens (1979) for northern hardwood forest in New Hampshire. Disturbance regime varies regionally; at present more work is needed before details of the effect of disturbance in the landscape will be known.

Both the controversy over exogenous and endogenous causal factors and that over allogenesi and autogenesi are grounded in the notion of a community-environment duality. Ecologists have searched for first causes of natural systems in either the biotic or abiotic components. Such a search seems futile, and the community-environment duality artificial in systems where evolution has resulted in species which influence disturbance frequency, predictability, and magnitude. There would seem to be a continuum from factors that are relatively endogenous to those that are relatively exogenous in vegetation composition, and, in addition, a continuum from chronic, normal, environmental factors, to acute, catastrophic ones. Classifications posed for phenomena along these continua (e.g., Tansley, 1935; Dansereau, 1974; Rabotnov, 1974; Major, 1974) lend an artificiality to vegetation concepts that depend on them.

The Climax Concept

The climax paradigm as an organizing generalization in plant ecology has long attracted controversy. The natural disturbance literature provides insights that are used below to cast climax and its controversy into a clearer light. The historic definitions of climax (monoclimax, polyclimax, and climax pattern) will be discussed first. Thereafter, an attempt is made to list all elements generally implied in use of the term climax. A final section in this discussion develops the idea that complementary reproductive strategies may be the result of coevolution (Forcier, 1975; Whittaker, 1977) within communities under disturbance regimes and that the recognition of self-reproducing vegetation, on which the recognition of climax often depends, is more complicated than is usually considered.

According to the classical view of succession, development within communities results in a self-reproducing terminal community. The species composition of this community is under the control of regional climate. This climatic climax dominates the landscape except where succession is chronically slowed down or continually interrupted, but even here the climax is seen as potential and inevitable in the long run. The emphasis is on the directional nature of the change and on the self-regulated terminal stage. The climax is seen as an important focus of community integration and species evolution. The climax species are seen as the best competitors in a regional flora, and it is assumed that they cause the local extinction of successional species. Their dominance is evidence of their evolutionary adaptation to the environmental setting. Compositional stability and self-reproduction are central to the recognition of climax.

Nearly every landscape varies topographically and geologically. Site to site variation was early recognized as an important control of com-

munity composition within one climatic region. Two schools became polarized over the problem of many community types within a single climax area: monoclimax and polyclimax. Later, Whittaker (1953) incorporated continuous models of species distributions in his concept of climax pattern. The review of the climax concept presented here is not intended to present a complete synopsis of work that has been done. For more extensive reviews see Whittaker (1953, 1974), Selleck (1960), Langford and Buell (1969), Drury and Nisbet (1973), Mueller-Dombois and Ellenberg (1974), Knapp (1974), and Horn (1976).

Monoclimax

Faced with landscapes of diverse vegetation, monoclimax ecologists took refuge in two concepts: that of ultimate base-leveling through long-term geomorphological processes, and that of convergence of soils through long term, autogenic, vegetational development. These two processes were seen as resulting in independence from initial site conditions. Hence, control of vegetation composition would shift directly to climate.

The debate on the validity of the monoclimax concept is not only concerned with the obvious observation that landscapes are not now dominated by monoclimax communities, but also with whether there is an ongoing process of development, however slow. Diverse communities were linked together in successional schemes. Extrapolation of successional processes predicted convergence on the climatic climax. However, rates of some successions were slow and others were continually set back to earlier stages. Hence, some ecologists chose to regard climax as a potential state, not necessarily one which had ever dominated or ever was likely to dominate whole landscapes. Viewing the climax as an ideal, never-attained state is still one of the alternatives available (see discussion of this issue in Langford and Buell, 1969). Curtis (1959) reported that white pine, a shade intolerant species, would die out without disturbance but continued:

Uninterrupted successions of this sort must have been very rare in presettlement times, since the time period of 800 to 1,000 years necessary from initial stand to final forest is so long that the chances of no catastrophe are practically nil.

In this view, the process of succession to climax is undeniable, even if the process does not always or ever go to completion. In the monoclimax concept, the climatic climax has an innate "representativeness," even if it remains dominant in only a small part of the landscape.

There are questions as to whether either base-leveling or soil convergence is a real process in nature. An alternative hypothesis to base-leveling is the dynamic equilibrium model of Hack (1960). Implications of

these ideas for plant ecology have been discussed by Hack and Goodlett (1960), Goodlett (1969), Drury and Nisbet (1971), Thom (1967), and Heinzelman and Wright (1973). Short term erosion is viewed as a real process, but observation in the short run of this process alone cannot be extrapolated to validate the peneplain concept as a developmental model. This note of caution is extended by the papers cited above to plant ecologists: succession is observed, but short term change is not enough to validate the climax concept (Selleck, 1960).

Soil convergence has been critically reviewed by Drury and Nisbet (1973), who suggested that some short-term convergence may occur, but the process slows down and does not result in independence from initial site conditions. The idea that long-term soil development would produce convergence in soils of different parent materials and topographic situations was challenged by Olson (1958) for postglacial landscape development on Lake Michigan sand dunes. This vegetation had also been studied by Cowles (1899), one of the early developers of ideas of the climax concept. In Olson's study, it was local site conditions and topography which determined the direction and extent of soil and vegetation development.

A perspective on the postglacial development of vegetated landscapes that is different than that of monocl原因 succession is implicit in Olson's work and other studies reviewed by Drury and Nisbet (1973). Assuming for the moment that climate is stable and recurrent natural disturbance unimportant, soil and vegetation develop on open sites, but the rate and extent of the development varies with initial site conditions. A steady state is reached in which environmental gradients and community gradients continue to lace through the landscape. This is the climax pattern of Whittaker (1953). Beyond this initial adjustment, there is no ongoing trend to dominance by shade tolerant mesic species across the landscape. Rather, these species only dominate mesic situations where topography and soil texture insure moist and well-drained soils. The landscape remains gradient rich. The establishment of these gradients is the end point of succession. Ongoing climatic change and recurrent natural disturbance overlie this picture of the steady state, gradient rich landscape, and complicate the acceptance of Whittaker's (1953) concept of the pattern as climax. At any rate, it is heterogeneous landscapes, not peneplain surfaces and monocl原因es, that are important as the environmental setting in evolution.

Hydric and xeric primary successions, in the monocl原因 view, were supposed to converge on the climatic climax. Olson's study can be taken as an examination of one case of succession on xeric sites. The incorporation of organic matter in soil development on the sandy parent material increases the moisture holding capacity of the substrate. The mono-

climax view is that this trend toward mesicness can be extrapolated to long time spans and so predict eventual dominance by the mesic climax. In addition, according to this view, the change is generated by the action of the plant community: it is autogenic. In Olson's analysis, as just described, the trends did not continue. If the climate became moister, the mesic species would continue to expand their ranges. Such change, however, would be allogenic. Taylor (1963) presented an allogenic model of supposed primary succession on xeric volcanic soils. He found that vegetation development was best on the sites where physical accumulation of volcanic dust had occurred. Webb (1968) found that succession did not result in a change from oligotrophic to entrophic nutrient conditions in soils; rather, fertility-demanding species came to dominate those sites that were eutrophic to begin with.

Pond-filling is an example of autogenic succession on wet sites. Organic matter is seen as gradually raising the substrate above the water table, with eventual production of mesic conditions. Again it is agreed that developmental change does take place. Shore lines become vegetated. Organic matter and siltation build plant substrate on places previously open water. Indeed, some ponds may fill by organic matter production and siltation. But others do not. Again it is suggested that a dynamic steady state is reached and that the extent of development is dependent on overall climate and initial site conditions (in this case, hydrology, chemistry, and morphometry of the drainage basin). Returning again to a postglacial forested landscape, community development in drainage basins results in a spectrum of communities from closed forest wetland to open meadow or dwarf shrub vegetation without open water to various degrees of fringing vegetation around open water, depending on initial conditions. Zonation around the center of the basin should then be interpreted as a reflection of the physical environment, not ongoing succession (Drury and Nisbet, 1973). Zonation does not necessarily reflect time, as is so often suggested.

Some of the changes that do take place can be described as autogenic. Organic matter is important as a substrate in wetlands. Organic matter in soils changes the properties of the soil. Forest shade creates a more mesic and temperature-buffered environment than in the open. This influence on site does affect the distribution of species. Mesic species might indeed grow beyond the indefinite bounds of "mesic topography" in the shade of xeric species dominated canopies. Organic matter in the soil may result in mesic species extending their range to the periphery of this "mesic topography." It is suggested here that such change is predictable given the facts of overall climate and physical conditions of site. It is not the result of a continuing trend towards monoclimate.

Polyclimax

Polyclimax ecologists proposed the recognition of many edaphic and topographic climaxes, and to distinguish these from the climatic climax a system of modifiers and prefixes were used (see Egler 1947, p. 389, for an enumeration). This view has two problems. First, many separate climaxes are seen as occurring, mosaic fashion, in the landscape. Where environmental gradients are continuous, it would now seem likely that vegetation distribution will also be continuous (resulting again in Whittaker's [1953] notion of the climax as pattern; see also Whittaker, 1974). The second problem of the polyclimax concept is that it leads to a proliferation of climax types, such that all kinds of vegetation characteristic of a particular set of environmental variables and persistent within the given environmental context are considered climax. Where does this process stop?

In 1942, Wells asked the question, "Is there a salt spray climax?" Wells' question concerned climax in coastal North Carolina and whether salt spray could be viewed as an environmental factor controlling the presence of a distinctive climax. On a broader level the question is asked again here: Is there a climax for each combination of environmental factors? Is each set of species characteristic of a given environmental setting and persistent within that setting a climax? If the answer to these questions is yes, a proliferation of climax types results. The term "climax" has lost its original meaning and means something like "adapted to" with reference to the environmental factors controlling species distribution. The acceptance of disturbance climaxes means that even shade intolerant species maintained by recurrent disturbance are climax (e.g., Cline and Spurr's [1942] white pine climax on wind exposed sites).

If the answer to Wells' question is yes, environmental setting determines species persistence and climax. There is nothing wrong with this view except that "climax" has lost meaning. Every species is climax in that it evolved within some environmental setting and is extant within that setting. If temporal dynamics and natural disturbance are taken into account, every species is persistent in the landscape within the full temporal-spatial context. Zedler and Goff (1973) analyzed the association of species and population structure within increasingly large sample blocks. With large sample blocks that encompassed patches with different disturbance histories, shade tolerant and intolerant species were associated. They commented:

In fact, at this large scale, nearly all species would be "climax", since they form a mixture with a population structure which is probably just as stable as that of the most undeniably "climax" forest at a smaller scale.

Climax has then become an evolutionary term and means "adapted to"

with reference to environmental setting. Indeed it might be argued that present-day species are not climax, since evolution is ongoing. Even within their own environmental setting, present day species may prove to be fleeting as evolution proceeds.

If the answer to Wells' question is no, then it must be shown that succession to regional climatic climax is indeed a real process and that other kinds of vegetation are inherently unstable. Polyclimax ecologists answered the question yes with the resulting proliferation of climax types. Polyclimax ecologists did recognize one climatic climax on mesic well-drained sites. Vegetation workers differed on whether this was the predominant regional vegetation on average sites or whether it was mesic vegetation, irrespective of how many places it was found in a landscape (in some landscapes it was absent entirely). They also differed on whether ongoing disturbance ought to be considered in the definition of climate of the climatic climax.

Apparent autogenesis within some "normal" environment characterizes the development of the climax. The key issue is that climax concept necessitates a definition of some "normal" environmental setting of a community. The key question is thus: Should disturbances be considered part of the definition of this "normal" environmental setting? Certain climates are strongly associated with high probabilities of periodic destructive events: violent windstorms, fire, frost movement of soils, and the like. Where these occur with a frequency of less than one per year (and especially where they occur with a low frequency compared to human life spans), they may seem extraneous to a definition of climate and to exert unusual effects on the plant community. On the other hand, other disturbances to vegetation, such as year-to-year fluctuations in precipitation and resulting changes in tall grass prairie structure and composition, are more obviously related to regional climate. Fire is a function of climate: lightning strikes initiate natural fires, and drought creates fire prone situations. Should fire be considered a feature of regional climate in fire prone regions?

This dilemma is perfectly exemplified by the continuing dialogue over climax in the southeastern coastal plain region (Chapman, 1932; Starker, 1934; Turner, 1935; Heyward, 1939; Wells, 1942; Garren, 1943; Oosting, 1944; Lemon, 1949; Quarterman and Keever, 1962; Blaisdell et al., 1973; Komarek, 1974; Veno, 1976; Delcourt and Delcourt, 1977; McGinty and Christy, 1977). There is a full range of opinions expressed in these papers from the view that fire is part of the environmental setting of the true climax to the view that fire recurrently prevents development of the climax. Churchill and Hanson (1958) present a review of the papers dealing with climax in the tundra landscape, another region in which the literature is replete with a full range of opinions as to the dilemma of recurrent disturbance and climax definition.

If disturbance is excluded from the definition of climax, we often are ruling out factors important both within present day landscapes and as selective forces in species evolution. Climax status is conferred on the group of species which are disturbance-sensitive, which are able to increase during disturbance-free periods. In forests, for example, climax becomes synonymous with a kind of reproductive strategy, shade tolerance. Are gap-phase reproducers part of the climax? Some hold they are, considering normal tree death maintains them in the stand (Forcier, 1975). What seems to be ignored here is that whether the extremely shade tolerant, moderately shade tolerant, or intolerant species predominate is a function of disturbance frequency, which is a function of regional environmental setting. In frequently disturbed forests (e.g., southeastern pine forests), the search for shade tolerant species leads to the recognition of climax types which may never have existed as vegetational associations or which have no potential for replacing pine except on wetter, fire protected sites. Here again, disturbance regime influences the direction and completion of successional trends. In nonforest communities (e.g., grassland) the definition of climax without disturbance becomes even more difficult. One could identify the K-strategists as climax (i.e., those with strong competitive ability within specified environments) but here again some reference must be made to environmental setting, including disturbance. Further, do all communities have K-strategists? Are the K-strategists of one community as attuned to environment as those of another? If there is often an r-K continuum (Grime, 1977), then deciding where to draw the line between climax and nonclimax species becomes arbitrary.

To exclude disturbance from the environmental setting of the climax is unsatisfying because we must define some regional set of "most competitive" species. In so doing, we have ruled out one important factor in competition—response to various disturbances. This is possible only in communities with low disturbance frequency.

If disturbance is included within the "normal" environment defining climax, the term "climax" loses all meaning, because all species that are persistent within some environmental context are climax. This situation is the same one that polyclimax ecologists created: a climax for each definable set of environmental factors. What, then is not climax? Even early successional communities are persistent in landscapes where some factor of the environment recurrently creates open sites.

Climax Pattern

The best choice among the spectrum of climax definitions is that of Whittaker (1953): the climax as pattern. Whittaker's thorough discussion is one of the best available on the dilemmas of the climate concept. Some of his arguments which have bearing on the current discussion are reviewed below.

It is clear that, for Whittaker, landscape gradients and the distribution of species populations are the important facts to recognize in conceptualizing vegetation pattern: "There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients and to other factors All climaxes are edaphic, as well as topographic and climatic, climaxes All are part of the climax pattern . . . adapted to climate and all other non-catastrophic factors of environment." In the last part of this quote Whittaker means to rule out large scale infrequent disturbance which initiates a dramatic change in species composition, but not all kinds of disturbance, as will become clear in the discussion below. He specifically cites frost movement in the tundra, and periodic fire and insect outbreaks in forests as examples which lead to temporal pattern and spatial patchiness within climax vegetation. Whittaker makes it clear that some climaxes are unstable and are characterized by recurrent natural disturbance and periodic reproduction.

The present analysis agrees with Whittaker that there is a gradient from particularly predictable and frequent disturbances to relatively long term disturbances:

. . . and it may then be difficult to draw a distinction between fire (and windfall, etc.) as environmental factors to which some climaxes are adapted and as disturbance introducing still greater instability and initiating succession in others. A continuous series from climaxes fully adapted to fire and scarcely affected by a single burn, through climaxes in which minor changes are produced by each burning and those in which vegetation structure is altered, but not destroyed, to climaxes which are entirely destroyed by a single fire, may be expected. Without attempting to draw a clear line where none exists, it may be thought that, in fire-adapted climaxes, fire either does not destroy the dominant population or does not cause replacement of the dominant growth form, as in other climaxes Other stands may have windfall permitting reproduction as a normal part of their relation to environment.

Because of the fact that community composition is relative to position along spatial environmental gradients and also to this continuous gradient in disturbance regimes, Whittaker concludes, "There are no distinctions between climax and succession, or, more concretely, between climax and seral stands, except relative instability and relative significance of directional change No completely rigorous definition of climax and its distinction from succession has been found, and apparently none need be expected." Daubenmire (1968a) made a similar point with reference to the gap-phase to larger blowdown gradient: "It is a matter of opinion as to how many trees must blow down to initiate a sere (*intercommunity*) rather than a serule (*intracommunity*)."

The present analysis of the role of natural disturbance in plant communities leads to complete agreement with Whittaker's description of

vegetation. However, in view of the continuous gradients in disturbance regime both geographically and within one landscape (disturbance factors being correlated with other variables of complex landscape gradients), the arbitrariness of the climax-succession distinction becomes overwhelming. Often overlooked in the debates over climax status or composition is the true description of disturbance regime, regionally and topographically, and the analysis of population distribution along the temporal, disturbance-initiated dimension of plant communities. The evolutionary significance of disturbance is obscured.

Definitions and Applications of "Climax"

General summaries follow for the historic climax concepts discussed. Thereafter, an attempt is made to describe the meanings and applications of the term as found in current usage.

Monoclimax: the climax as an ideal, never attained state.—This view suggests that disturbance prevents climax development and that the closest approach to climax occurs on certain microsites (i.e., mesic disturbance-protected sites). The stringent application of this definition eliminates gap-phase reproducers in forests and essentially results in the term "climax" being a kind of reproductive strategy. This is most readily identified in temperate forests: the extreme shade tolerant strategy. As easy as it is to apply this definition of climax to temperate mesic forests, it always has become controversial in other regions (e.g., in deserts [Noy-Meir, 1973], grasslands [Vogl, 1974], boreal forest [Raup, 1941a; Rowe, 1961; Zach, 1950], tundra [Raup, 1941a; Churchill and Hanson, 1958], and tropical systems [Hewetson, 1956; Thom, 1967]). In communities with frequent disturbance the climax reproductive strategy may be absent entirely from the flora.

Some workers modified this extreme view by accepting cyclic successions, like gap-phase reproduction, within the single climax (Bormann and Likens, 1979). In this definition of climax, the climax is seen as compositionally dynamic on local sites. On enlarging the perspective to larger blocks of landscapes, the local patterns may cancel out, with the landscape as a whole showing relative compositional stability. Watt's (1947a) pattern and process cyclic successions, including gap-phase dynamics, are allowable within this climax concept. The smaller scale disturbances and disturbance-dependent species are included in this notion of climax.

Polyclimax, including disturbance climaxes.—In this view, frequent disturbance does not *prevent* climax; rather it defines a new kind of climax, the dis-climax. Here, disturbance becomes another one of the "normal" environmental factors that control climax composition.

Climax pattern.—Whittaker modified previous views with the notion of continuous compositional gradients along environmental gradients. The decision as to whether a given disturbance was part of the normal environmental setting controlling climax composition or was a nonnormal factor initiating succession was seen as arbitrary and dependent on disturbance scale, relative significance of directional change after disturbance, and change in growth form of the dominant plants.

None of these concepts of climax can be universally applied. On one level, this problem itself is a function of variable disturbance regimes across a spectrum of communities and landscapes. In hypothetical communities with no disturbance, composition may be stable. Where disturbance is highly frequent and its effects constantly present, disturbance can be seen as just another one of the environmental factors which control composition. As before, composition may be stable within such a constant environment. It is in the middle ground between these two extremes that climax is most controversial. It is in this part of the disturbance frequency gradient that directional change occurs during disturbance-free periods and disturbance-dependent species dominate after disturbances. The idea of climax, founded as it is on a notion of environmental constancy and a vegetation-environment compositional equilibrium, will always be controversial as applied to environmental settings which are characterized by ongoing, recurrent, or periodic change. Dynamics in structure, if not composition, are intrinsic to all vegetation. Any climax is stable only in a relative sense. How much variation and what kinds of dynamics are allowable within the definition of climaxes (Churchill and Hanson, 1958)? This forms a basic, philosophical question that must be faced by those using the concept.

In addition to the broad and historical definitions of climax discussed above it is apparent from current literature that the term "climax" has been put to a variety of more particular uses. While most of the implied definitions of the term overlap in meaning, the following basic elements can be segregated out (see also Whittaker, 1974).

(1) *Climax as distinguishing the presettlement, old aged vegetation.*—Human disturbance has deflected the vegetation from this state; succession reestablishes it. Land surveys, explorers' notes, and remnant stands are used to describe the presettlement state of the vegetation. The effect of past natural disturbance and the influence of edaphic conditions are not usually used to invalidate climax status as they are in other uses of the term.

(2) *Climax as the predicted end point of primary or secondary succession.*—Composition of vegetation of varying successional age and intra-stand reproduction are used as evidence; eventual climax composition is predicted by extrapolation under the assumption of a stable environment.

(3) *Climax as compositionally stable, equilibrium, persistent, self-reproducing vegetation.*—The usual evidence for climax status is the comparison of dominant to reproductive status. Long-term survivorship information is usually lacking; hence, actual self-reproduction is rarely proved. This definition of climax is hard to apply except in shady, mesic, disturbance-protected vegetation. Here the most shade tolerant species are recognized as climax, and gap-phase reproducers are usually not included. Time spans for total dominance of the most shade tolerant species is ca. 200–1,000 years (Webb, 1958; Curtis, 1959), and such self-reproducing stands were probably rare, given small scale gap-phase dynamics as well as larger disturbances. Logging and agricultural disturbance and subsequent succession have created uniform youthful to submature canopies. Shade tolerant species thrive in the understory of these stands. Human disturbance has eliminated patchiness on a local level in mesic temperate landscapes and has created large and uniform stands of successional species above shade tolerant reproduction. Using these stands to predict climax composition has resulted in widespread acceptance of uniform stands of the most shade tolerant species as climax.

(4) *Climax as characteristic, regional vegetation of average sites.*—This definition is used in mapping. Küchler (1964) preferred the phrase, “potential natural vegetation,” because of the confusions over climax definition. Choices of vegetation are often arbitrary and depend on mapping scale. The effect of human disturbance is ignored, but widespread edaphic situations (e.g., in the Florida everglades, alluvial forests along the Mississippi River, and boreal muskeg) are mapped. These are treated as successional in other uses of climax described here.

(5) *Climax as predominant regional, upland vegetation.*—Edaphic situations are ignored for the most part, and their vegetation is treated as successional. The vegetation of average upland sites is used to define the climax.

(6) *Climax as regional, mesic vegetation.*—With this use of climax, “mesic” must be defined. Alternatives are: average moisture conditions for the region, and most favorable moisture conditions attainable during autogenic succession. In the latter case, vegetation of moist and well-drained sites is often proposed as regional climax although it may be limited to valleys, ravines, or sites with favorable soil texture.

These applications of “climax” all suggest, to one degree or another, a concept of relatively persistent, regionally characteristic vegetation. These applications all connote appealing notions of age and equilibrium and differentiate between human impacted landscapes and natural states. Nonetheless, there are so many different shades of meaning that investigators should point out their own perception of the meaning of “climax” and the kinds of evidence they are basing their decisions on. If the con-

cept is to be used, it seems necessary to include a description of that environmental context, including disturbance, within which the designated climax can replace other species. It would also seem necessary to spell out the small-scale dynamics allowable within the climax community.

The climax concept implies that there is some vegetation-environment equilibrium mediated by evolution and that stable vegetation will exist within some "normal" regional environment. All climates show fluctuation and many result in forces destructive to community structure, thus changing local environmental conditions, if only through the elimination of the effect of community structure on microclimate. The species adapted to such conditions are numerous, suggesting the long evolutionary history of their occurrence. Even in environments which lack destructive factors, the very necessity of death and turnover of individuals insures some persistent local structural dynamics. Reconciling such dynamics with the climax concept has generated much controversy. Is the climax concept useful (Whittaker, 1974)? It would seem that its use must be explicitly defined by investigators; alternatively, it could be abandoned in favor of a less controversial concept, e.g., "potential natural vegetation" of a defined environmental context.

Reproductive Strategy and the Concept of Self-reproduction

Implicit in the climax concept is relative compositional stability and, hence, self-reproduction. It is apparent that structural dynamics insure heterogeneity in the community. Even compositionally stable vegetation seems to be made up of species with a variety of reproductive characteristics that are adapted to various aspects of this heterogeneity. The "climax strategy" of copious reproduction below the dominance of parents does not seem to be absolutely better than other strategies except under certain conditions within this heterogeneous pattern.

In forests, species have been described by their "shade tolerance." The most obvious candidates for climax status are those species that have shade tolerant reproduction. However, the use of shade tolerance as a measure of successional trends, simple as it seems to be, involves several complications. The categorization of species by tolerance is usually done by observation of where their reproduction survives in the field, not by measurement of their behavior in experimental light regimes in which other variables are held constant. Species may vary across their geographical range in shade tolerance, and response to light in a given situation may depend on other environmental factors. Forest canopies alter other environmental variables of sites; e.g., temperature, wind, and moisture regimes, and these may be as important or more important than their

influence on light climate in determining seed germination and seedling survival. Shade tolerance is perhaps better described as shade persistence, since mortality among even shade tolerant seedlings is high, and suppressed individuals must be released by increased light to reach the canopy (Brewer and Merritt, 1978). Finally, there are many kinds of vegetation where competition for light is irrelevant. Search for a single major variable of community competition that results in autogenic successional change in an analogous fashion has often been deemed fruitless (Churchill and Hanson, 1958; Rowe, 1961; Vogl, 1974).

The work of Forcier (1975) and Marks (1974) illustrates these points as they apply to mesic temperate forest. Seeds of *Fagus grandifolia* Ehrh. carry a heavy energetic investment in seed germination on a shady, litter covered forest floor. The price of this investment seems to be a low colonizing ability—Forcier's study showed that *Fagus* had the lowest rate of advance after disturbance in the forest he sampled. *Betula lutea* Michx. f., on the other hand, has very light seeds to disperse widely, resulting in dominance of *Betula* in the first year seedling class. These seedlings suffer almost complete mortality except on disturbed sites with exposed mineral soil and on moss mats on rotting logs and rocks from which *Betula lutea* puts down trailing roots which reach the forest floor. The strategy of *Fagus grandifolia*, which is the climax species in the strict sense, consists of persistence and slow growth on a site waiting for canopy openings to develop. The *Betula lutea* strategy seems to consist of attempting yearly to disperse to canopy gaps. Enlarging this picture to larger scale disturbance response, *Prunus pensylvanica* L. f., insures persistence in the landscape by the accumulation of its long dormant seeds in the soil. The different geometry of these species (e.g., *Betula*'s spur branches) and other morphological-physiological characteristics of the species are probably also involved in this response system.

Extreme shade tolerance and heavy investment in seedling survival is only one possible strategy in the northern hardwood forest. Under certain conditions it makes the shade tolerant species the "most competitive" species. However, in many gaps (particularly larger ones?), such species are outcompeted, either in terms of colonizing ability or because of the faster growth rate of gap-phase species in full light. There are many adjustments that can be made among the variables of longevity, seed crop size, dispersal mechanisms, and seed weight. More information on the basic natural history of species is needed if the composition and dynamics of communities is to be unraveled. Shade tolerance is one of many possible modes of existence, even in closed crown forests.

Prediction of climax composition in forests has traditionally relied on the comparison of overstory to understory composition. The understory is, expectably, made up of shade tolerant species. *Acer saccharum*

Marsh., for example, over a wide range of the eastern deciduous forest produces prolific numbers of seedlings in communities where seed trees are present in the canopy. Trends toward *Acer* dominance are widely reported (e.g., Dansereau, 1946; Dix, 1957; Langford and Buell, 1969). It is suggested here that such prediction of successional trends needs further analysis.

First, survivorship curves of species are not rigid but vary with changing conditions, including death and fall of canopy trees (Forcier, 1975). Any age-class distribution can result in increase, decrease, or stasis for a population depending on survivorship. The abundant first-year seedlings of *Betula lutea* only foreshadow an increase for that species under conditions of increased light and a disturbed forest floor (Forcier, 1975).

Shade results in a forest floor that is cooler and moister than open sites. In regions south of its main dominance, as in *Quercus* forests, the mesophyte, *Acer saccharum*, may exist in relatively stable populations of a few canopy seed trees and abundant seedlings and saplings growing beneath a predominantly *Quercus* canopy. During the dry years (and closest to the driest edge of its distribution), *Acer* may be restricted to ravines, north slopes, and concave topography. Trees in these situations may send reproduction out into the forests beyond on sites where shade ameliorates the moisture stress that would be experienced in the direct sunlight of the canopy level (where temperature also fluctuates more widely). During wetter years *Acer* reproduction may expand the distribution of the species. During drier years, a contraction of this distribution may occur. In any given year the observation of *Acer saccharum* reproduction does not necessarily predict gradual succession to that species. (See Whittaker [1953] for a similar point about the interpretation of mixtures of mesic and less mesic species.) In general, the possibility of ongoing climatic change is uncorrected for in most studies of succession.

In forest climates the physical biomass of the community alters environmental characteristics of the site. The creation of deep shade is peculiar to these forest climates and communities. The magnitude of the effect of microsite may be unique to forests when other environmental variables are considered in addition to light. Mesic forests, with their absence of fire and long disturbance cycle, may be the only community type where shade tolerance is a characteristic strategy. The necessity of turnover in the canopy insures that sites within even these forests must see changing light levels over time. The occurrence of species which are members of shady environments of mesic forests, like understory trees in a tropical rain forest and shrubs and herbs in a temperate forest, suggests that adaptation to moist shady temperature-buffered microclimates is important as one component of the regional picture. The other component, of course, is the species adapted to conditions created by tree

fall (Fox, 1977; Grubb, 1977). Mesic shade tolerant tree species are unique in having to traverse or persist within a shady forest environment on the way to eventual position in a full-light canopy position.

VEGETATION AND LANDSCAPE

A picture of the vegetated landscape emerges from this discussion. Communities are structurally dynamic. There is a continuum of causal factors from those that are apparently endogenous to those that are apparently exogenous. The structural dynamics of communities result in dynamics in environmental factors, if only because community structure affects site microenvironment. These structural dynamics differ regionally; they also vary within one landscape as a function of topography and other site variables.

Spatial and temporal heterogeneity in environment seems to have been important in the ecological setting of species evolution. Reproductive strategies, among other autecological characteristics, seem to show adaptations for persistence in landscapes characterized by such heterogeneity. Regional floras show a spectrum of reproductive characteristics that suggest competitive divergence and adaptation to disturbance/structural dynamics patterns.

The Coenocline Concept and Community Dynamics

According to Whittaker's (1975) coenocline concept, environmental factors, in general, change continuously across the landscape, influencing the distribution of plant populations. The continuous multifactored environmental gradient is termed a *complex gradient*. Species populations are, in this view, continuously distributed. Communities (*phytocenoses*) are arbitrary positions along this gradient of continuous compositional change. The landscape continuum of communities is termed the *coenocline*.

Niche specialization through competitive divergence along "significant" gradients is viewed as the evolutionary process responsible for the coenocline (Whittaker, 1972). These "significant" gradients need not be spatial environmental gradients, though in most instances this is the kind of gradient reported. Species niche separation could consist of different blooming periods or pollinators (Snow, 1965; Mosquin, 1971; Gentry, 1974). Such separation could allow for coexistence in space and positive associational patterns. The same can be said for the complement of species involved in gap-phase dynamics (Forcier, 1975; Fox, 1977) or for species occupying different strata (Whittaker, 1975). Such separation of role implies an escape from competition and hence the pressure for di-

vergence claimed in Whittaker's model. This separation does not necessitate separation along any additional gradients, although it seems most often true that species have unique distributions with separate optima along many gradients.

The natural disturbance literature suggests ways that the coenocline concept can be extended. Three main points will be raised.

(1) Natural disturbance and the complex gradient are intimately related.

(2) Temporal dynamics can be seen as another axis of the coenocline.

(3) Ongoing dynamics have important implications for the specificity of species to site relations expectable within the coenocline.

That natural disturbance and the landscape complex gradient are intimately related can be seen in those studies which focus on the landscape level (Albertson et al., 1957; Webb, 1958; Heinselman and Wright, 1973; Vogl, 1974; Fahey, 1975; O'Kinneide, 1975; Bell and del Moral, 1977; Veblen et al., 1977; Zackrisson, 1977; Reiners and Lang, 1979; Runkle, 1979). The frequency, regularity, and magnitude of disturbance, as has been already suggested, depends on topography, substrate, and the state of the vegetative cover. Landscapes contain a continuum from disturbance-prone situations to particularly protected ones. Both extremes on this gradient act as refugia and seed sources when conditions change in surrounding vegetation. At the local community level, species composition will depend on age, disturbance history, and spatial relations with such refugia.

The occurrence of species in closed forest which are more commonly found in other habitats such as streamsides and rock ledges might at first be interpreted as noise in the process of seed dispersal and plant survival. In fact, such individuals may be indicative of the fundamental niche of the species. With disturbance the species may be able to expand across the coenocline. Rocky knolls and outcrops and wetlands harbor many species in landscapes which may be important in disturbance recovery in the surrounding vegetation.

Species sparsely distributed through midsuccession and older communities may seem to play minor roles in the community when examined in the narrow context of present composition. Such species may explode into prominence following a major disturbance, resulting in rapid revegetation and nutrient conservation for the community as a whole (Marks, 1974; Newton et al., 1968; Zavitkovski and Newton, 1968).

Although vegetation is locally dynamic, on larger scales there may be a characteristic and relatively stable distribution of land into various disturbance, regrowth, and old-age classes (Heinselman and Wright, 1973). On this larger scale, the landscape may be in a steady state, as long as disturbance regime remains constant in its overall expression. In such a landscape there may be local elimination of species, but no regional

extinction (Zedler and Goff, 1973). Both successional and climax species have spatially shifting distributions.

The second extension of the coenocline concept is to view succession as a coenocline in time (Whittaker, 1975; Austin, 1977; Pickett, 1976). In temporal dynamics, the interaction of species populations is another dimension to the coenocline pattern in the landscape. Phytocoenoses are arbitrary positions along this axis as well in vegetation variation. The regional matrix of communities and the total flora that contribute to this matrix (the gamma diversity of Whittaker, 1975) represent the full range of environments and biological interactions. Evolution and niche divergence is presumed to be important within this full context of environment gradients, including those that are determined by dynamics of communities or cause those dynamics (Harper, 1977).

Elimination during disturbance or ensuing succession is not extinction. Early successional species locally eliminated in one community in the landscape often have dispersed to some newly disturbed site. In a larger sense, are such species poor competitors? Many of them have competition avoidance mechanisms or low energetic investment in seedlings which suffer high mortality under adverse conditions. Disturbance is one of the factors that controls species prominence. An evaluation of competitive ability must be keyed to specific environmental situations, including to disturbance. A suggested conclusion is that species distribution along a successional dimension represents diversification and competition avoidance (Pickett, 1976; Platt and Weis, 1977) and only direct competition in a narrow present-time sense.

The final implication that natural disturbance has for the coenocline concept is the effect of periodic disturbance on the specificity of species to site relations. This also has implications for the kinds of strategies (Grime, 1977; Harper, 1977) that will be adaptive in the variety of situations present and the overall predictability of vegetation patterns.

The role of chance historic events in species-rich tropical forest has been noted by Poore (1968) and Knight (1975). Gap-phase processes and other disturbances are seen as overlying any strict correlation of species and site in a spatial sense and, further, as preventing any strict correlation of species to temporal gradients as well. The list of species potentially important in any one gap is large. Which species becomes established in a particular gap is related to a series of probabilistic events, including timing of tree fall, proximity of seed trees, irregularity of seed crop size, and success or failure of dispersal agents. The role of historic events has also been noted in temperate and boreal vegetation (Raup, 1951, 1956, 1957, 1964, 1975; Stephens, 1955a; Walker, 1972; Henry and Swan, 1974; Korchagin and Karpov, 1974; Coupland, 1974; Harper, 1977; Oliver and Stephens, 1977). Auclair and Cottam (1971) described the role of black cherry in Wisconsin and stated that patterns of species replacement dur-

ing disturbance recovery are not "orderly and predictable, but irregular as a result of chance dispersal and local catastrophe." As discussed earlier, Forcier (1975) saw his cyclic succession, not as an unvarying pattern, but as a representation of the general roles of the three species involved. The question then becomes: To what degree can species distribution in time and space be predicted given facts of both landscape environmental gradients and stand history? The answer to this question is likely to be different for different species and communities. In fact, comparing different communities in their level of environmental determinism might be a way to answer these kinds of questions. Sutherland (1974) has summarized the evidence from a variety of plant and animal communities in suggesting that many communities can exist in several compositional states.

An extreme situation in this regard is that reported by Raup (1975) for plant distribution in shore habitats of Lake Athabaska. He found no repeating definable zones or communities along the shore, but rather completely individualistic associations of species. The fluctuating mix of species was the result of recurrent disturbance. There were no predictable relations of species to microsite. Raup showed that the most specialized plants (halophytes and aquatics) were the least "versatile" species in his study area. This implies a trade-off between specialization and flexibility in disturbance response. Griggs (1936) also found that disturbance resulted in highly variable and fluctuating associations in tundra vegetation.

Raup's case stands as a critical reference point at one end of a gradient in degree of environmental determinism in vegetation pattern. Most communities show a balance of historic chance events and competition-mediated environmental determinism in their composition. The historic hypothesis long maintained by Raup and others associated with the Harvard forest leads to acceptance of Gleason's individualistic association (Gleason, 1926). A further implication suggested here is that ongoing variation in both the physical and competitive environment of species, as well as the role of chance events, maintains population variability that might otherwise be eliminated during intense interspecific competition. This maintenance of species variability may result in vegetation patterns predictable only to a certain degree, since gradient distribution of a species might therefore be expanded and show more overlap with neighboring species. It often seems that ecologists expect species to be entities that are not internally variable. Mathematical models of species distribution in the landscape might fail, not due to failure to include some measurement of environment, but to a lack of recognition that the underlying control of composition involves accidents of history. In this regard, the biological meaning of lack of site correlation (i.e., the degree of spread of species along a gradient) is equally important to what environmental

determinism can be found (i.e., specific adaptations to a certain range of conditions on a gradient, with peak performance located at a definable point).

Competition along spatial and temporal gradients may result in pressure for species specialization and increasingly tight species to site relations. The temporal dynamics of spatial environmental gradients, plus chance events and the role of disturbance along the temporal gradient, may maintain population variability and/or niche breadth (Slatkin and Lange, 1976). Instead of apologizing for the failure of mathematical models to predict the distribution of species, we should ask what evolutionary facts underlie these problems. Disturbance may result in a variable relationship of the realized to fundamental niche and hence lessens the predictability of species from site variables when an index of stand history is not available. How do species, communities, and landscape patterns compare in their level of environmental determinism? The necessary maintenance of variability may counterbalance the trend for competitive divergence and tight species to site relations.

Niche specialization through competitive divergence is seen by some (e. g., Forcier, 1975; Fox, 1977; Whittaker, 1977) as a process of coevolution in communities that results in community integration. Communities are seen as made up of species, with different and complementary roles. Opposing this view are those who see details of composition as due more to stand history than competitive interaction, whether those interactions are on a successional or evolutionary time scale (e.g., Raup, 1975).

If disturbance maintains mixes of species of varying strategy, it is tempting to conclude that disturbance (including gap-phase dynamics) maintains or generates species diversity in vegetation (Grubb, 1977; Fox, 1977). In a short-term sense it is undoubtedly true that disturbance maintains diversity. The problem with evaluating this claim in a longer term sense is that the species so maintained may not have evolved in the first place without recurrent disturbance to closed canopies. Disturbance is at once the reason for this landscape maintenance as it is for the evolutionary existence of such species. In fact, in a longer term sense, ongoing disturbance may act to limit potential diversity if it does maintain niche breadth and population variability. Greater climatic instability with distance from the equator is, indeed, one hypothesis for lower species diversity and more wide-ranging species along this gradient (Janzen, 1967). Particularly specialized species with low population variability would seem the most susceptible to extinction due to a variable environment and ongoing disturbance.

Although it was suggested earlier that successional time was another dimension of the coenocline, it should be pointed out that it may be a fundamentally different kind of gradient compared to spatial-envi-

mental ones. When disturbance creates open, competition-free sites it promotes species of high reproductive effort, strong colonizing ability, tolerance of widely fluctuating initial site conditions, fast initial growth rates, and short life span. Armstrong (1976) reports a microcosm experiment in which two species of fungi, one a superior competitor and the other a superior colonizer, formed a stable coexistence under conditions of disturbance-produced patchiness. Studies of intertidal and marine communities of sessile invertebrates support the idea that relative colonizing ability and on-site competitive ability may be evolutionary trade-offs and that mixtures of species variously adapted to disturbance-produced patchiness may exist as dynamic, steady-state communities (Dayton, 1971; Loya, 1976). In other cases, disturbance may also involve pressure for specialization; e.g., cone serotiny (Gill, 1975).

Grime (1977) identifies three primary strategies in plants. These are the ruderal, competitive, and stress-tolerant. He identifies these, in the order named, with a continuum between r-type strategies and K-type strategies. The ruderal strategy is characteristic of frequently disturbed but potentially productive habitats. The competitive strategy is associated with productive and less disturbed habitats. The stress-tolerant strategy is associated with continuously unproductive situations. This fits the model of disturbance presented here: in the most disturbed habitats, such as windswept krummholz or flood-battered riverbanks, the community is often depauperate in both biomass and diversity. Here, disturbance is so constant as to prevent high production, and the plants must be structurally resistant to the disturbance. In periodically disturbed sites, the disturbance-free period determines the relative balance of the ruderal and competitive strategies, as they are defined by Grime. It is also important to note that Grime recognizes intermediate strategies to the three primary ones. Grime and Hunt (1975) used the same concept in exploring relative growth rates of different species in a local flora. Whittaker and Goodman (1979) recently published a discussion of species strategy and environmental heterogeneity. Their results support Grime's recognition of three basic strategy types. Genetic implications of heterogeneous environments have been recently discussed (Wiens, 1976; Leven, 1976; Slatkin and Lange, 1976; Giesel, 1976; Hedrick et al., 1976).

Madison (1977) described adaptive radiation within *Monstera*, a genus of tropical lianas. He found that there was a continuum from small, rapidly growing, early maturing, short-lived species characteristic of abundant but ephemeral habitats (twigs and small branches) to massive species with slow growth rates, late maturation, and long life spans, which occupy rare but stable habitats (boles of large forest trees).

Competitive divergence along temporal gradients might have very different implications for niche structure than, for example, divergence

along a spatial moisture gradient. This would be true, for example, if the degree of specialization/efficiency within a defined context (usually referred to as competitive ability) is a trade-off against colonizing ability. Is environmental fine-tuning a trade-off against reproductive output? Evidence suggests that it is but the question is not yet fully resolved. At any rate, niche breadths along gradients versus the relative height and narrowness of peaks representing species optima along these same gradients are affected by evolution within structurally dynamic communities. Genetic diversity within species populations as well as species diversity within communities are influenced by evolution in a dynamic setting. Is population variability inversely related to species diversity in communities? Are niche breadth, specialization, and population genetic diversity related? Can we build a predictive model of these population and community level characteristics as outcomes of evolution? These questions are as yet unresolved.

Management Implications

Landscape perspective is important in the management of our dwindling wilderness area. The natural area concept (Chapman, 1947) suggests that it is important to preserve a matrix of communities, not just old aged communities, and, in addition, that it is necessary to allow natural processes such as disturbance to occur. The preservation of such matrices is important to wildlife management. It has been long noted that forest edges, wetlands, shrub lands, and early successional vegetation are crucial for animal species, though none of these are "climax" situations. Perhaps the lack of strict correlation of animal species and plant communities (i.e., the inability of ecologists to assign associations of animals to climaxes [Shelford and Olson, 1935]) suggests itself that old aged communities were always part of a regional matrix of communities between which animals traveled (Peek, 1974; Krefting and Ahlgren, 1974). Patches of fast growing successional vegetation are extremely important as animal habitat and for herbivore food sources; patches of senescent vegetation (e.g., tree snags as nesting sites for birds or as forage areas for insect-eating birds) are also important (DeGraaf, 1978). These relations again imply the long range evolutionary significance of heterogeneous vegetation.

In an ideal sense, the preservation of species is dependent on the preservation of natural processes (Dolan et al., 1978). The situation, of course, is more complicated than allowing, for example, each natural fire to burn due to political pressure, recreational use, past fire suppression, and constraints imposed by the areal extent of the preserved area. This underscores the need for investigations of the biological realities of the

systems preserved. Understanding disturbance in the landscape is needed for practical management concerns as well as for the resolution of abstract vegetation questions (Wright, 1974). Research into fire management has lead the way (Kessell, 1976) but flood management and its effect on vegetation has also received attention (Hall and Smith, 1955; Harris and Marshall, 1963; Franz and Bazzaz, 1977). Other disturbances, such as dune movement and coastal erosion (Schroeder et al., 1976), have always been management problems, particularly when human life and property are situated where disturbance is inevitable and its prevention impossible, costly, and damaging to natural systems.

Disturbance suppression has been attempted for several kinds of the natural disturbances reviewed here; fire, alluvial erosion and flooding, dune movement and coastal erosion, and natural pest population cycles. In each case, suppression has caused unexpected problems. Fire suppression allows the buildup of fire fuels such that subsequent fires are more intense than normally would occur (Mutch, 1970; Mooney et al., 1979). In addition, disturbance-dependent species may be lost from sites that are not allowed to burn. Removal of spring floods altered meander pattern and resulted in a decline in native vegetation (Johnson et al., 1976). Dune stabilization lead to establishment of a woody community which was not salt-spray resistant and was vulnerable to extreme storms. Erosion potential was greater in the long run than it had been with shifting dunes and grass-dominated vegetation (Schroeder et al., 1976). Pesticide control of pest outbreaks can lead to decline in natural control mechanisms and result subsequently in more drastic outbreaks (Brown, 1961).

Human perturbations in the landscape have included both disturbance suppression (e.g., fire suppression and subsequent succession to woody plants in the prairie) and physical destruction of communities. One bias in the study of natural disturbance has been the association of this phenomenon with the disasters produced by settlement, agriculture, and industry. Many ideas about the unnaturalness of disturbance stem from observation of the present altered landscape. Human disturbance in some cases may mimic natural disturbance. In others it certainly does not and may, in fact, produce new selection pressures and evolution (e.g., tolerance of heavy metals in grasses, Antonovics, 1971) or exceed the absolute biological limits of adaptation. Human disturbance may be a possible selective force in the evolution of such weeds as *Hieracium* and *Taraxacum* species. The recent burst in recognized forms in *Craetagus* has been attributed by Dansereau (1957) to human disturbance. Many open habitats created by human disturbance are colonized by a mixture of native and introduced species. The native species are most often characteristic of natural communities that occurred in open habitats in the landscape (i.e., riverbanks, wetlands, cliff faces) or were important in the

natural disturbance regime of closed communities. When human disturbance mimics natural disturbance, native successional species (along with the introduced weeds that follow human civilization) may thrive in such situations. The most dangerous case is, of course, where human disturbance creates new situations to which species are not adapted.

CONCLUSION

The notions of autogenesis, allogenesi, and climax are all based on the idea that first causes of community characteristics can be found in either biotic or abiotic variables. This is artificial in systems where species are adapted to and influence environment. Climax can only be defined with reference to a specific environmental context; this context cannot be defined without including disturbance and other dynamics-producing characteristics. Hence, the climax concept necessarily generates controversy. An arbitrary decision becomes imperative: how much change is allowable within the notion of a stable climax?

Abiotic factors can only be artificially classified as normal, gradually changing, and abruptly changing. This may do no great harm in some systems with long periods of relative stability and in which community reproduction corresponds closely in composition to dominant species composition, but in other systems it simply cannot be applied. The climax concept is basically classificatory in philosophy. The natural world is characterized, in the main, by continuous variation. Classifications are not necessarily bad in themselves, but they do introduce artificiality into our perceptions. If the climax concept is used it must be referenced to specific environmental situations, including natural disturbance regime and other dynamic properties.

Communities are always structurally dynamic and often compositionally so. Dynamics range from individual death to large scale change. If only because of changing influence of biomass on site, community environment is also dynamic. Temporally dynamic and spatially heterogeneous environments have been important in evolution. Many species are dependent on structural dynamics for their continued existence in the landscape. Whether dynamics are viewed as within or between communities depends entirely on the investigator's idea of scale and definition of community. Gap-phase reproduction in forests has been alternately treated as maintaining successional, intermediately tolerant, species in the community, and as part of the normal equilibrium of a self-reproducing community. Tree falls have been alternately viewed as due to an exogenous factor, wind, and as the result of the senescence of community dominants. Given a broad view, communities and landscapes may be in dynamic equilibrium with local changes cancelling out over the whole.

Hence, they may possess relative floristic stability. Local sites may see temporal, cyclic, change; there may be a characteristic pattern of patches in space.

Natural disturbances vary in kind, as well as the continuous parameters of frequency, predictability, and magnitude. Disturbance regime is defined as the sum of disturbances operating in a given landscape. Environmental factors involved in dynamics vary from chronic and normal to acute and catastrophic. These factors interact with community state such that most vegetation dynamics are neither purely endogenous nor exogenous rhythms. Plant senescence, difficult to define, is central to the conceptualization of endogenously driven change.

Species have evolved strategies in the dynamics of their communities, strategies which promote, resist, or avoid disturbance, for example. The terminology of Vogl (1974) is more useful for describing species roles than the traditional succession-climax distinction, since it recognizes the essential importance of environmental context. Species are described as increasers, decreasers, invaders, retreaters, or neutrals with reference to specific community situations. The notion of climax forces an absolute choice in a search for the best adapted competitor; Vogl's terminology is relativistic in approach. Each strategy in a community contributes to the pattern of coexistence we now observe.

Vegetation forms a coenocline in time as well as in space. Landscape complex gradients which underlie the spatial coenocline also contribute to the temporal pattern. Natural disturbances and other vegetation dynamics vary regionally and within one landscape as a function of topography, soil, other site characteristics, the state of the vegetation, and such other biotic factors as plant-disease and plant-animal interactions. Dynamics in vegetation seem to result in vegetation patterns which are not precisely predictable from environmental variables without knowledge of stand history. Intrinsic dynamics have implications for the specificity of species to site relations and other characteristics of niche. A need for a better perspective on the temporal dimension of communities is apparent.

ACKNOWLEDGMENTS

I would like to especially thank William A. Reiners, who reviewed all drafts of this paper, assisted in the early formulation of the ideas presented, and encouraged me to prepare it for publication. I am also indebted to Susan P. Bratton who edited the final drafts and made many helpful suggestions about organization and structure. I am grateful to Alwyn Gentry, Leonette Edwards, Jack Schultz, and Fred and Holly Hickler for editing and discussions of earlier drafts. All these friends gave

freely of their time to help me improve the manuscript. I also benefitted from presentation of these ideas at Dartmouth College, Missouri Botanical Garden, St. Louis University, and Uplands Field Research Lab.

LITERATURE CITED

- Ahlgren, C. E. 1974. Effects of fires on temperate forests: North Central United States. Pages 195–223 in T. T. Kozlowski and C. E. Ahlgren (eds.), *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Ahlgren, I. F. and C. E. Ahlgren. 1960. Ecological effects of forest fires. *Bot. Rev.* **46**: 304–310.
- Aikman, J. M. and A. W. Smelser. 1938. The structure and environment of forest communities in central Iowa. *Ecology* **19**: 141–148.
- Albertson, F. W. and G. W. Tomanek. 1965. Vegetation changes during a 30-year period in grassland communities near Hays, Kansas. *Ecology* **46**: 714–720.
- , ———, and A. Riegel. 1957. Ecology of drought cycles and grazing intensity on grasslands of Great Central Plains. *Ecol. Monogr.* **27**: 27–44.
- and J. E. Weaver. 1945. Injury and death or recovery of trees in a prairie climate. *Ecol. Monogr.* **15**: 395–433.
- Anderson, D. J. 1967. Studies on the structure in plant communities. IV. Cyclical succession in Dryas communities from northwest Iceland. *J. Ecol.* **55**: 629–635.
- , R. C. Cooke, T. T. Elkington, and D. J. Read. 1966. Studies in structure in plant communities. II. The structure of some dwarf-heath and birch-copse communities in Sjald-Fannardalur, north-west Iceland. *J. Ecol.* **54**: 781–793.
- Anderson, G. W. and R. L. Anderson. 1963. The rate of spread of oak wilt in the Lake States. *J. For.* **63**: 823–825.
- Anderson, R. C. and J. S. Fralish. 1975. An investigation of palmetto, *Paurotis wrightii* (Griseb. and Wendl.) Britt., communities in Belize, Central America. *Turrialba* **25**: 37–44.
- Antonovics, J. 1971. The effects of a heterogeneous environment on the genetics of natural populations. *Am. Sci.* **59**: 593–599.
- Armson, K. A. and R. J. Fessenden. 1973. Forest windthrows and their influence on soil morphology. *Soil Sci. Soc. Am. Proc.* **37**: 781–783.
- Armstrong, R. A. 1976. Fugitive species: experiments with fungi and some theoretical considerations. *Ecology* **57**: 953–963.
- Ashe, W. W. 1918. Note on "Ice Storms in the Southern Appalachians" by Verne Rhoades. *Mon. Weather Rev.* **46**: 374.
- Ashton, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* **1**: 155–196.
- Aubréville, A. 1971. Regeneration patterns in the closed forest of the Ivory Coast. Pages 41–55 in S. R. Eyre (ed.), *World vegetation types*. Macmillan Press, Ltd., London. 264pp.
- Auclair, A. N. 1975. Sprouting response in *Prunus serotina* Ehrh.: multivariate analysis of site, forest structure, and growth rate relationships. *Am. Midl. Nat.* **94**: 72–87.
- and G. Cottam. 1971. Dynamics of black cherry (*Prunus serotina* Ehrh.) in southern Wisconsin oak forests. *Ecol. Monogr.* **41**: 153–177.
- Austin, M. P. 1977. Use of ordination and other multivariate descriptive methods to study succession. *Vegetatio* **35**: 165–176.
- Bailey, A. W. and C. E. Poulton. 1968. Plant communities and environmental interrelationships in a portion of the Tillamook burn, northwestern Oregon. *Ecology* **49**: 1–13.
- Baker, H. G. 1970. Evolution in the tropics. *Biotropica* **2**: 101–111.
- Bannister, B. A. 1970. Ecological life cycle of *Enterpe globosa*. Gaertn. Pages 299–314 in H. T. Odum (ed.), *A tropical rainforest*. U.S. A.E.C., Div. Tech. Inf. Washington, D. C.

- Barbour, M. A. and T. M. DeJong. 1977. Response of West Coast beach taxa to salt spray, seawater inundation, and soil salinity. *Bull. Torrey Bot. Club* **104**: 29–34.
- Barclay-Estrup, P. 1970. The description and interpretation of cyclical processes in a heath community. II. Changes in biomass and shoot production during the *Calluna* cycle. *J. Ecol.* **58**: 243–249.
- and C. H. Gimingham. 1969. The description and interpretation of cyclical processes in a heath community. I. Vegetational change in relation to the *Calluna* cycle. *J. Ecol.* **57**: 737–758.
- Barden, L. S. Tree replacement in small canopy gaps of a southern Appalachian forest. (Unpublished manuscript.)
- Batchelder, R. B. 1967. Spatial and temporal patterns of fire in the tropical world. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **6**: 171–707.
- Beard, J. S. 1945. Some ecological work in the Caribbean. *Emp. For. J.* **24**: 40–46.
- . 1953. The savanna vegetation of northern tropical America. *Ecol. Monogr.* **23**: 149–215.
- . 1955. The classification of tropical American vegetation types. *Ecology* **36**: 89–100.
- Beasleigh, W. J. and G. A. Yarranton. 1974. Ecological strategy and tactics of *Equisetum sylvaticum* during a postfire succession. *Can. J. Bot.* **52**: 2299–2318.
- Behre, C. E. 1921. A study of windfall in the Adirondacks. *J. For.* **19**: 632–637.
- Bell, D. T. 1974. Tree stratum composition and distribution in a streamside forest. *Am. Midl. Nat.* **92**: 35–46.
- and R. del Moral. 1977. Vegetation gradients in the stream-side forest of Hickory Creek, Will County, Illinois. *Bull. Torrey Bot. Club* **104**: 127–135.
- Benninghoff, W. S. 1952. Interaction of vegetation and soil frost phenomena. *Arctic* **5**: 34–44.
- Bird, R. D. 1930. Biotic communities of the aspen parkland of central Canada. *Ecology* **11**: 356–442.
- Bishop, J. W. 1977. Effects of rainstorms on phytoplankton production in Westhampton Lake, Virginia. Abstract in *Bull. Ecol. Soc. Am.* **58**(2): 52.
- Biswell, H. H. 1974. Effects of fire on chaparral. Pages 321–364 in T. T. Kozlowski and C. E. Ahlgren (eds.). *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Blais, J. R. 1954. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. *Ecology* **35**: 62–71.
- Blaisdell, R. S., J. Wooten, and R. K. Godfrey. 1973. The role of magnolia and beech in forest processes in the Tallahassee, Florida, Thomasville, Georgia area. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **13**: 363.
- Bleakney, J. S. 1972. Ecological implications of annual variation in tidal extremes. *Ecology* **53**: 933–938.
- Blydenstein, J. 1968. Burning and tropical American savannas. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **8**: 1–15.
- Bogucki, D. J. 1970. Debris slides and related flood damage with the September 1, 1951, cloudburst in the Mt. LeConte–Sugarland Mountain area, Great Smoky Mountains National Park. Ph.D. Thesis, Univ. Tennessee, Knoxville. 165 pp.
- . 1977. Debris slide hazards in the Adirondack Province of New York State. *Environ. Geol.* **1**: 317–328.
- Borchert, J. R. 1950. The climate of the central North American grassland. *Assoc. Am. Geogr. Ann.* **40**: 1–39.
- Bormann, F. H. and G. E. Likens. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York. 253 pp.
- Bray, J. R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology* **37**: 598–600.
- Brayton, R. D. and G. M. Woodwell. 1966. Effects of ionizing radiation and fire on *Gaylussacia baccata* and *Vaccinium vacillans*. *Am. J. Bot.* **53**: 816–820.
- Brewer, R. and P. G. Merritt. 1978. Windthrow and tree replacement in a climax beech-maple forest. *Oikos* **30**: 149–152.
- Brown, J. H. 1960. The role of fire in altering the species composition of forests in Rhode Island. *Ecology* **41**: 310–316.

- Brown, W. L.** 1961. Mass insect control programs: Four case histories. *Psyche* **68**: 75–111.
- Budowski, G.** 1963. Forest succession in tropical lowlands. *Turrialba* **13**: 42–44.
- . 1966. Fire in tropical American lowlands. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **5**: 5–22.
- . 1970. The distinction between old secondary and climax species in tropical Central American lowland forests. *Trop. Ecol.* **11**: 44–48.
- Buell, M. F.** 1956. Spruce-fir, maple-basswood competition in Itasca Park, Minnesota. *Ecology* **37**: 606.
- and **H. F. Buell.** 1941. Surface level fluctuations in Cedar Creek Bog, Minnesota. *Ecology* **22**: 317–321.
- and ———. 1975. Moat bogs in the Itasca Park area, Minnesota. *Bull. Torrey Bot. Club* **102**: 6–9.
- , ———, and **W. A. Reiners.** 1968. Radial mat growth in Cedar Creek Bog, Minnesota. *Ecology* **49**: 1198–1199.
- , ———, and **J. A. Small.** 1954. Fire in the history of Mettler's Woods. *Bull. Torrey Bot. Club* **81**: 253–255.
- , ———, ———, and **C. D. Monk.** 1961. Drought effect on radial growth of trees in the William L. Hutcheson Memorial Forest. *Bull. Torrey Bot. Club* **88**: 176–180.
- and **W. E. Gordon.** 1945. Hardwood-conifer contact zone in Itasca Park, Minnesota. *Am. Midl. Nat.* **34**: 433–439.
- , **A. N. Langford, D. W. Davidson, and L. F. Ohmann.** 1966. The upland forest continuum in northern New Jersey. *Ecology* **47**: 416–432.
- and **W. E. Martin.** 1961. Competition between maple-basswood and fir-spruce communities in Itasca Park, Minnesota. *Ecology* **42**: 428–429.
- and **W. S. Wistendahl.** 1955. Flood plain forests of the Raritan River. *Bull. Torrey Bot. Club* **82**: 463–472.
- Carvel, K. L., E. H. Tryon, and R. P. True.** 1957. Effects of glaze on the development of Appalachian hardwoods. *J. For.* **55**: 130–132.
- Chabreck, R. H. and A. W. Palmisano.** 1973. The effects of Hurricane Camille on the marshes of the Mississippi River delta. *Ecology* **54**: 1118–1123.
- Chapman, H. H.** 1932. Is the longleaf type a climax? *Ecology* **13**: 328–334.
- . 1947. Natural areas. *Ecology* **28**: 193–194.
- Chesapeake Research Consortium, Inc.** 1977. The effects of tropical storm Agnes on the Chesapeake Bay estuarine system. John Hopkins Univ. Press, Baltimore. 639 pp.
- Christensen, N. L. and C. H. Muller.** 1975. Effects of fire on factors controlling plant growth in *Adenostoma* Chaparral. *Ecol. Monogr.* **45**: 29–55.
- Churchill, E. D. and H. C. Hanson.** 1958. The concept of climax in arctic and alpine vegetation. *Bot. Rev.* **24**: 127–191.
- Clark, F. B.** 1962. White ash, hackberry, and yellow poplar seed remain viable in the forest litter. *Indiana Acad. Sci. Proc.* **72**: 112–114.
- Cline, A. C. and S. H. Spurr.** 1942. The virgin upland forest of central New England: A study of old growth stands in the Pisgah Mountain section of southwestern New Hampshire. *Harv. For. Bull.* **21**: 58 pp.
- Cochrane, G. R. and J. S. Rowe.** 1969. Fire in the tundra at Rankin Inlet NWT. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* 292 pp.
- Connell, J. H.** 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310.
- and **R. O. Slayter.** 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**: 1119–1144.
- Coombe, D. E. and F. White.** 1951. Notes on calcicolous communities and peat formation in Norwegian Lapland. *J. Ecol.* **39**: 33–62.
- Cooper, C. F.** 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* **30**: 129–164.
- Cooper, W. S.** 1913. The climax forest of Isle Royale, Lake Superior, and its development. *Bot. Gaz.* **55**: 144; 115–140; 189–235.
- . 1926. The fundamentals of vegetational change. *Ecology* **7**: 391–413.
- Coupland, R. T.** 1974. Fluctuations in North American grassland vegetation. Pages 235–241 in R. Knapp (ed.). *Vegetation dynamics*. Dr. W. Junk, The Hague.

- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part I. Geographical relations of the dune floras. *Bot. Gaz.* **27**: 95–117; 167–201; 281–308; 361–391.
- Craighead, F. C., Sr. 1971. The trees of South Florida. I. The natural environments and succession. University of Miami Press, Coral Gables, Florida. 212 pp.
- Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 pp.
- Cwynar, L. C. 1978. Recent history of fire and vegetation from laminated sediment of Greenleaf Lake, Algonquin Park, Ontario. *Can. J. Bot.* **56**: 10–21.
- Dansereau, P. 1946. L'érablière laurentienne. II. Les successions et leurs indicateurs. *Can. J. Res. Sect. C, Bot. Sci.* **24**: 235–291.
- . 1957. Biogeography, an ecological perspective. Ronald Press Co., New York. 394 pp.
- . 1974. Classification of successions and of their terminal stages. Pages 125–135 in R. Knapp (ed.), *Vegetation dynamics*. Dr. W. Junk, The Hague.
- Daubenmire, R. F. 1968a. Plant communities: A textbook of plant synecology. Harper and Row, New York. 30 pp.
- . 1968b. Ecology of fire in grasslands. *Adv. Ecol. Res.* **5**: 209–266.
- Davis, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geosci. Man* **13**: 13–26.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**: 351–389.
- DeGraaf, R. M. 1978. New life from dead trees. *Nat. Wildl.* (June 1978): 29–31.
- Delcourt, H. R. and P. A. Delcourt. 1977. Presettlement magnolia-beech climax of the Gulf Coastal Plain: Quantitative evidence from the Apalachicola River Bluffs, north-central Florida. *Ecology* **58**: 1085–1093.
- Demaree, D. 1932. Submerging experiments with *Taxidium*. *Ecology* **13**: 258–262.
- Denny, C. S. and J. C. Goodlett. 1956. Microrelief resulting from fallen trees. In C. S. Denny (ed.), *Surficial geology and geomorphology of Potter County, Pennsylvania*. U.S. Geol. Surv. Prof. Pap. 288.
- Dittus, W. P. J. 1977. The ecology of a semi-evergreen forest community in Sri Lanka. *Biotropica* **9**: 268–286.
- Dix, R. L. 1957. Sugar maple in the climax forests of Washington, DC. *Ecology* **38**: 663–665.
- and J. M. A. Swan. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. *Can. J. Bot.* **49**: 657–676.
- Dolan, R., B. P. Hayden, and G. Soucie. 1978. Environmental dynamics and resource management in the U.S. National Parks. *Environ. Manage.* **2**: 249–258.
- Douglas, G. W. 1974. Montane zone vegetation of the Alsek River region, Southwestern Yukon. *Can. J. Bot.* **52**: 2505–2532.
- and T. M. Ballard. 1971. Effects of fire on alpine plant communities in the North Cascades, Washington. *Ecology* **52**: 1058–1064.
- Downs, A. A. 1938. Glaze damage in the birch-beech-maple-hemlock type of Pennsylvania and New York. *J. For.* **36**: 63–70.
- Drury, W. H. and I. C. T. Nisbet. 1971. Inter-relations between developmental models in geomorphology, plant ecology, and animal ecology. *Gen. Syst.* **16**: 57–68.
- and ———. 1973. Succession. *J. Arnold Arbor. Harv. Univ.* **54**: 331–368.
- Eggler, W. A. 1971. Quantitative studies of vegetation on sixteen young lava flows on the Island of Hawaii. *Trop. Ecol.* **12**: 66–100.
- Egler, F. E. 1947. Arid Southeast Oahu vegetation, Hawaii. *Ecol. Monogr.* **17**: 383–435.
- Ehrlich, P. R., D. E. Breedlove, P. F. Brussard, and M. A. Sharp. 1972. Weather and "regulation" of subalpine populations. *Ecology* **53**: 243–247.
- Fahey, J. J. 1975. Fire in the forests of Maine and New Hampshire. Abstract in *Bull. Ecol. Soc. Am.* **56**: 41.
- Flaccus, E. 1959. Revegetation of landslides in the White Mountains of New Hampshire. *Ecology* **40**: 692–703.

- Foldats, E. and E. Rutkis. 1975. Ecological studies of chapparo (*Curatella americana* L.) and manteco (*Byrsonima crassifolia* HBK) in Venezuela. *J. Biogeogr.* 2: 159-178.
- Forcier, L. K. 1975. Reproductive strategies and the co-occurrence of climax tree species. *Science* 189: 808-810.
- Foster, R. B. 1977. *Tachigalia versicolor* is a suicidal neotropical tree. *Nature* 268: 624-626.
- Fox, J. F. 1977. Alternation and coexistence of tree species. *Am. Nat.* 111: 69-89.
- Franklin, J. F. and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S.D.A. For. Serv. Res. Pap. PEW 80: 1-216.
- Franz, E. H. and F. A. Bazzaz. 1977. Simulation of vegetation response to modified hydrologic regimes: A probabilistic model based on niche differentiation in a flood plain forest. *Ecology* 58: 176-183.
- Gams, H. 1918. Principienfragen der Vegetationsforschung Viertelsjahrsschr. Naturf. Ges. Zürich 67: 132-156.
- Gardiner, L. M. 1975. Insect attack and value loss in wind-damaged spruce and jack pine stands in northern Ontario. *Can. J. For. Res.* 5: 387-398.
- Garren, K. H. 1943. Effects of fire on vegetation of the southeastern United States. *Bot. Rev.* 9: 617-654.
- Gentry, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6: 64-68.
- Ghent, A. W., D. A. Fraser, and J. B. Thomas. 1957. Studies of regeneration of forest stands devastated by the spruce budworm. I. *For. Sci.* 3: 184-208.
- Giesel, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7: 57-80.
- Gill, A. M. 1977. Plant traits adapted to fires in Mediterranean land ecosystems. Pages 17-26 in H. Mooney and C. E. Conrad (eds.). Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3. Washington, D.C.
- Gill, D. E. 1975. Spatial patterning of pines and oaks in the New Jersey pine barrens. *J. Ecol.* 63: 291-298.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7-26.
- . 1927. Further views on the succession concept. *Ecology* 8: 299-327.
- Gómez-Pompa, A. 1971. Posible papel de la vegetación secundaria en la evolución de la flora tropical. *Biotropica* 3: 125-135.
- , S. del Amo R., C. Vazquez-Yanes, and A. Butando (eds.). 1976. Investigaciones sobre la regeneración de selvas altas en Veracruz, México. Cia. Editorial Continental, SA. Calz. de Tlalpan Núm. 4620, México 22, D.F. 676 pp.
- Goodlett, J. C. 1954. Vegetation adjacent to the border of Wisconsin drift in Potter County, Pennsylvania. *Harv. For. Bull.* 25: 93 pp.
- . 1969. Vegetation and the equilibrium concept of landscape. Pages 33-44 in K. N. H. Greenidge (ed.). Essays in plant geography and ecology. Nova Scotia Museum, Halifax.
- Grigal, D. F. and L. F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecol. Monogr.* 45: 389-407.
- Griggs, R. F. 1936. The vegetation of the Katmai district. *Ecology* 17: 380-417.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1194.
- and R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.* 63: 393-422.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* 52: 107-145.
- Habek, J. R. and R. W. Mutch. 1973. Fire-dependent forests in the northern Rocky Mountains. *Quat. Res.* 3: 408-424.
- Hack, J. T. 1960. Interpretation of erosional topography in humid temperate regions. *Am. J. Sci.* 258A: 80-97.
- Komarek, E. V. 1974. Effects of fire on temperate forests and related ecosystems: South-

- and J. C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U.S. Geol. Surv. Prof. Pap. 347.
- Hall, T. F. and G. E. Smith. 1955. Effects of flooding on woody plants. West Sandy Dewatering Project, Kentucky Reservoir. J. For. **53**: 281–285.
- Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. Ecol. Monogr. **41**: 27–52.
- Hanson, H. C. 1950. Vegetation and soil profiles in some solifluction and mound areas in Alaska. Ecology **31**: 606–630.
- and W. Whitman. 1937. Plant succession on solonetz soils in western North Dakota. Ecology **18**: 516–522.
- Harper, J. L. 1967. A Darwinian approach to plant ecology. J. Ecol. **55**: 247–270.
- . 1977. Population biology of plants. Academic Press, New York. 892 pp.
- and J. Ogden. 1970. The reproductive strategy of higher plants: I. the concept of strategy with specific reference to *Senecio vulgaris* L. J. Ecol. **58**: 681–689.
- and J. White. 1974. The demography of plants. Ann. Rev. Ecol. Syst. **5**: 419–463.
- Harris, S. W. and W. H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. Ecology **44**: 331–343.
- Hartshorn, G. 1977. Neotropical forest dynamics. Abstract in Bull. Ecol. Soc. Am. **58**: 29.
- Hayes, G. I. 1942. Difference in fire danger with altitude, aspect, and time of day. J. For. **40**: 318–323.
- Hedrick, P. W., M. E. Ginevan, and E. P. Ewing. 1976. Genetic polymorphism in heterogeneous environments. Ann. Rev. Ecol. Syst. **7**: 1–32.
- Heinselman, M. L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands. Ecol. Monogr. **40**: 235–261.
- . 1971. The natural role of fire in northern conifer forests. Pages 61–72 in C. W. Slaughter, R. J. Barney, and G. M. Hansen (ed.). Fire in the northern environment—a symposium. Pac. Northwest For. Range Exp. Stn., Portland, Oregon.
- . 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. **3**: 329–382.
- and H. E. Wright, Jr. (eds.). 1973. The ecological role of fire in natural conifer forests of western and northern North America. Quat. Res. **3**: 317–318.
- Henry, J. D. and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material—An approach to the study of forest succession in southwest New Hampshire. Ecology **55**: 772–783.
- Hett, J. M. and O. L. Loucks. 1976. Age structure models of balsam fir and eastern hemlock. J. Ecol. **64**: 1029–1044.
- Hewetson, C. E. 1956. A discussion on the "climax" concept in relation to the tropical rain and deciduous forest. Emp. For. Rev. **35**: 274–291.
- Heyward, F. 1939. Relation of fire to stand composition of longleaf pine forests. Ecology **20**: 287–304.
- Hibbs, D. H., B. C. Fisher, and B. F. Wilson. 1977. The survival strategy of striped maple. Abstract in Bull. Ecol. Soc. Am. **58**: 47.
- Horn, H. S. 1976. Succession. Pages 187–204 in R. M. May (ed.). Theoretical ecology: Principles and applications. Blackwell, London.
- Horn, H. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, New Jersey. 144 pp.
- Hosner, J. F. 1957. Effects of water on seed germination of bottomland trees. For. Sci. **3**: 67–69.
- . 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. For. Sci. **6**: 246–251.
- and S. G. Boyce. 1962. Relative tolerance to water saturated soil of various bottomland hardwoods. For. Sci. **8**: 180–186.
- Hough, A. F. and R. D. Forbes. 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. Ecol. Monogr. **13**: 299–320.
- Hough, A. F. and R. F. Taylor. 1946. Response of Allegheny northern hardwoods to partial cutting. J. For. **44**: 30–38.

- Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* **54**: 1111–1117.
- Humphrey, R. R. 1974. Fire in the deserts and desert grassland of North America. Pages 365–400 in T. T. Kozlowski and C. E. Ahlgren (eds.). *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Hutnik, R. J. 1952. Reproduction on windfalls in a northern hardwood stand. *J. For.* **50**: 693–694.
- Illick, J. S. 1916. A destructive snow and ice storm. *For. Leaves* **15**: 103–107.
- Ives, R. L. 1942. The beaver-meadow complex. *J. Geomorphol.* **5**: 191–203.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* **101**: 233–249.
- . 1976. Why bamboos wait so long to flower. *Ann. Rev. Ecol. Syst.* **7**: 347–392.
- Johnson, A. W., L. A. Viereck, R. E. Johnson, and H. Melchior. 1966. Vegetation and flora. In N. J. Wilimorsky and J. N. Wolfe (eds.). *Environment of the Cape Thompson region, Alaska*. U.S. A.E.C.
- Johnson, E. A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. *Can. J. Bot.* **53**: 2933–2941.
- and J. S. Rowe. 1975. Fire in the subarctic wintering ground of the Beverley caribou herd. *Am. Midl. Nat.* **94**: 1–14.
- Johnson, P. L. and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to Cretaceous processes and patterns. *Ecol. Monogr.* **32**: 102–135.
- Johnson, W. C., R. L. Burgess, and W. R. Keammerer. 1976. Forest overstory vegetation and environment on the Missouri River Floodplain in North Dakota. *Ecol. Monogr.* **46**: 59–84.
- Jones, E. W. 1945. The structure and reproduction of the virgin forest of the North Temperate zone. *New Phytol.* **44**: 130–148.
- . 1955. Ecological studies on the rain forest of Southern Nigeria. I. *J. Ecol.* **43**: 564–594.
- . 1956. Ecological studies on the rain forest of Southern Nigeria. II. *J. Ecol.* **44**: 83–117.
- Keatinge, T. H. 1975. Plant community dynamics in wet heathland. *J. Ecol.* **63**: 163–172.
- Keeley, J. E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* **58**: 820–829.
- and P. H. Zedler. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *Am. Midl. Nat.* **99**: 142–161.
- Kellman, M. 1974. Preliminary seed budgets for two plant communities in coastal British Columbia. *J. Biogeogr.* **1**: 123–133.
- Kershaw, K. A. 1960. Cyclic and pattern phenomena as exhibited by *Alchemilla alpina*. *J. Ecol.* **48**: 443–453.
- Kessell, S. R. 1976. Gradient modeling: a new approach to fire modeling and wilderness resource management. *Environ. Manage.* **1**: 39–48.
- Kilgore, B. M. 1973. The ecological role of fire in Sierran conifer forests. *Quat. Res.* **3**: 496–513.
- Kimmerer, R. W. and T. F. H. Allen. 1978. The role of disturbance in the structure of a riparian bryophyte community. Abstract in *Bull. Ecol. Soc. Ann.* **59**: 88.
- Knapp, R. (ed.). 1974. *Vegetation dynamics*. Dr. W. Junk, The Hague. 356 pp.
- . 1974. Cyclic successions and ecosystem approaches in vegetation dynamics. Pages 92–100 in R. Knapp (ed.). *Vegetation dynamics*. Dr. W. Junk, The Hague.
- Knight, D. H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecol. Monogr.* **45**: 259–284.
- Koenig, J. L. 1976. Effect of climate, soil physiography, and seed germination on the distribution of river birch (*Betula nigra*). *Rhodora* **78**: 420–437.
- Komarek, E. V., Sr. 1966. The meteorological basis for fire ecology. Pages 85–126 in *Proc. Annu. Tall Timbers Fire Ecol. Conf.*
- . 1968. Lightning and lightning fires as ecological forces. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **8**: 169–197.
- Komarek, E. V. 1974. Effects of fire on temperate forests and related ecosystems: South-

- eastern United States. Pages 251–277 in T. T. Kozlowski and C. E. Ahlgren (eds.), *Fire and Ecosystems*. Academic Press, New York. 542 pp.
- Korchagin, A. A. and V. G. Karpov. 1974. Fluctuations in coniferous taiga communities. Pages 227–231 in R. Knapp (ed.), *Vegetation dynamics*. Dr. W. Junk, The Hague.
- Kozlowski, T. T. and C. E. Ahlgren (eds.). 1974. *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Krefting, L. W. and C. E. Ahlgren. 1974. Small mammals and vegetation changes after fire in a mixed conifer-hardwood forest. *Ecology* **55**: 1391–1398.
- Kucera, C. L. and S. C. Martin. 1957. Vegetation and soil relationships in the glade region of the Southwestern Missouri Ozarks. *Ecology* **38**: 285–291.
- Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. *Am. Geogr. Soc. Spec. Publ.* **36**. 116 pp.
- Langenheim, J. H. 1956. Plant succession on a subalpine earthflow in Colorado. *Ecology* **37**: 301–317.
- Langford, A. N. and M. F. Buell. 1969. Integration, identity, and stability in the plant association. *Adv. Ecol. Res.* **6**: 83–135.
- Larson, F. 1940. The role of the bison in maintaining the short grass plain. *Ecology* **21**: 113–121.
- Leak, W. B. 1963. Delayed germination of white ash seeds under forest conditions. *J. For.* **61**: 768–772.
- Lejeune, R. R. 1955. Population ecology of the larch sawfly. *Can. Entomol.* **87**: 111–117.
- Lemon, P. C. 1949. Successional responses of herbs in the longleaf-slash pine forest after fire. *Ecology* **30**: 135–145.
- . 1961. Forest ecology of ice storms. *Bull. Torrey Bot. Club* **88**: 21–29.
- . 1968. Effects of fire on African Plateau grassland. *Ecology* **49**: 316–322.
- Levin, S. A. 1976. Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.* **7**: 287–310.
- and R. J. Paine. 1975. The role of disturbance in models of community structure. Pages 56–67 in S. A. Levin (ed.), *Ecosystem analysis and prediction*. Philadelphia, Pennsylvania.
- Lewis, F. J. and E. S. Dowding. 1926. The vegetation and retrogressive changes of peat areas ("muskegs") in central Alberta. *J. Ecol.* **14**: 317–341.
- Lewis, K. P. 1975. Community analysis and the dynamics of establishment of *Acer saccharinum* L. (silver maple) on flood plains of the unglaciated Appalachian Plateau. Abstract in *Bull. Ecol. Soc. Am.* **56**: 489.
- Lichens, G. E. and M. B. Davis. 1975. Post-glacial history of Mirror Lake and its watershed in New Hampshire, USA: An initial report. *Verh. Int. Ver. Limnol.* **19**: 982–993.
- Lindsey, A. A., R. O. Petty, D. K. Sterling, and W. Van Asdall. 1961. Vegetation and environment along the Wabash and Tippecanoe Rivers. *Ecol. Monogr.* **31**: 105–156.
- Little, S. 1946. The effects of forest fires on the stand history of New Jersey's pine region. *Northeast. For. Exp. Stn., For. Manage. Pap.* **2**. 45 pp.
- . 1974. Effects of fire on temperate forests: Northeastern United States. Pages 225–250 in T. T. Kozlowski and C. E. Ahlgren (eds.), *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Lloyd, L. L. and G. E. Gruell. 1973. The ecological role of fire in the Jackson Hole Area, northwestern Wyoming. *Quat. Res.* **3**: 425–443.
- Lorimer, C. G. 1977a. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* **58**: 139–148.
- . 1977b. Stand history and dynamics of a southern Appalachian virgin forest. Ph.D. Thesis, Duke Univ. 200 pp. Univ. Microfilms No. 77-18. 778. Ann Arbor, Michigan.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. *Am. Zool.* **10**: 17–25.
- Loya, Y. 1976. Recolonization of red sea corals affected by natural catastrophes and man-made perturbations. *Ecology* **57**: 278–289.
- Lugo, A. 1977. Mangroves: succession or steady-state? Abstract in *Bull. Ecol. Soc. Am.* **58**: 29.
- Lunan, J. S. and J. R. Habeck. 1973. The effects of fire exclusion on ponderosa pine communities in Glacier National Park, Montana. *Can. J. For. Res.* **3**: 574.

- Lutz, H. J.** 1940. Disturbance of soil resulting from uprooting of trees. *Yale Univ. Sch. For. Bull.* **45**: 37 pp.
- and **A. L. McComb.** 1935. Origin of white pine in virgin forest stands in northwestern Pennsylvania as indicated by stem and basal branch features. *Ecology* **16**: 252–256.
- Lyford, W. H. and D. W. MacLean.** 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harv. For. Pap.* **15**.
- Macaloney, H. J.** 1966. The impact of insects in the northern hardwoods type. U.S.D.A. For. Serv. Res. Note NC-10. 3 pp.
- Madison, M.** 1977. A revision of *Monstera* (Araceae). *Contrib. Gray Herb. Harv. Univ.* **207**. 100 pp.
- Maissurow, D. K.** 1935. Fire as a necessary factor in the perpetuation of white pine. *J. For.* **33**: 373–378.
- 1941. The role of fire in the perpetuation of virgin forests in northern Wisconsin. *J. For.* **39**: 201–207.
- Major, J.** 1974. Kinds and rates of changes in vegetation and chronofunctions. Pages 8–18 in R. Knapp (ed.). *Vegetation dynamics*. Dr. W. Junk, The Hague.
- Marks, P. L.** 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* **44**: 73–88.
- 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. *Bull. Torrey Bot. Club* **102**: 172–177.
- Marquis, D. A.** 1975. Seed storage and germination under northern hardwood forest. *Can. J. For. Res.* **5**: 478–484.
- Martin, W. E.** 1959. The vegetation of Island Beach State Park, New Jersey. *Ecol. Monogr.* **29**: 1–46.
- McCloud, K. W. and J. K. McPherson.** 1973. Factors limiting the distribution of *Salix nigra*. *Bull. Torrey Bot. Club* **100**: 102–110.
- McDermott, R. E.** 1954. Effects of saturated soil in seedling growth of some bottomland hardwood species. *Ecology* **35**: 36–41.
- McGinty, D. T. and E. J. Christy.** 1977. Turkey oak ecology on a Georgia sand hill. *Am. Midl. Nat.* **98**: 487–491.
- McIntosh, R. P.** 1961. Windfall in forest ecology. *Ecology* **42**: 834.
- Monk, C. D.** 1961a. The vegetation of the William L. Hutcheson Memorial Forest, New Jersey. *Bull. Torrey Bot. Club* **88**: 156–166.
- 1961b. Past and present influences on reproduction in the William L. Hutcheson Memorial Forest, New Jersey. *Bull. Torrey Bot. Club* **88**: 167–175.
- Mooney, H., J. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners (eds.).** 1979. Fire regimes and ecosystem properties. U.S.D.A. For. Serv. Gen. Tech. Rept. Washington, D.C. (In press.)
- and **C. E. Conrad (eds.).** 1977. Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. U.S.D.A. For. Serv. Gen. Tech. Rept. WO-3. Washington, D.C. 498 pp.
- Morris, R. F. (ed.).** 1963. The dynamics of epidemic spruce budworm dynamics. *Entomol. Soc. Can. Mem.* **31**. 352 pp.
- Mosquin, T.** 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* **22**: 398–402.
- Mount, A. B.** 1969. Eucalypt ecology as related to fire. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **9**: 75–108.
- Mueller-Dombois, D. and H. Ellenberg.** 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.
- Muller, C. H.** 1952. Plant succession in arctic heath and tundra in northern Scandinavia. *Bull. Torrey Bot. Club* **79**: 296–309.
- Munger, T. T.** 1940. The cycle from douglas fir to hemlock. *Ecology* **21**: 451–459.
- Munro, N.** 1966. The fire ecology of Caribbean pine in Nicaragua. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **5**: 67–84.
- Mutch, R. W.** 1970. Wildland fires and ecosystems—a hypothesis. *Ecology* **51**: 1046–1051.
- Nanson, G. C. and H. F. Beach.** 1977. Forest succession and sedimentation on a meandering river flood plain, northeast British Columbia, Canada. *J. Biogeogr.* **4**: 229–252.

- Newton, M., B. A. el Hassan, and J. Zavitzovski. 1968. Role of red alder in western Oregon forest succession. Pages 73–84 in J. M. Trappe, J. F. Franklin, A. F. Tarrant, and G. M. Hansen (eds.). *Biology of alder*. Pac. Northwest. For. Range Exp. Stn., U.S.D.A. For. Serv. Portland, Oregon.
- Nichols, G. E. 1920a. The plant associations of eroding areas along the seacoast. *Bull. Torrey Bot. Club* **47**: 89–117.
- . 1920b. The associations of depositing areas along the seacoast. *Bull. Torrey Bot. Club* **47**: 511–548.
- Nixon, E. S., R. L. Willett, and P. W. Cox. 1977. Woody vegetation of a virgin forest in an Eastern Texas river bottom. *Castanea* **42**: 227–237.
- Noble, R. E. and P. K. Murphy. 1975. Short term effects of prolonged backwater flooding on understory vegetation. *Castanea* **40**: 228–238.
- Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Ann. Rev. Ecol. Syst.* **4**: 25–51.
- O'Cinneide, M. S. 1975. Aspect and wind direction as factors in forest stability: The case of Northern Ireland. *J. Biogeogr.* **2**: 127–139.
- Odum, E. P. 1971. *Fundamentals of Ecology*, 3rd ed. Saunders, Philadelphia. 574 pp.
- Old, S. M. 1969. Microclimate, fire, and plant production in an Illinois prairie. *Ecol. Monogr.* **39**: 355–383.
- Oliver, C. D. and E. P. Stephens. 1977. Reconstruction of a mixed species forest in Central New England. *Ecology* **58**: 562–572.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot. Gaz.* **119**: 125–170.
- Oosting, H. J. 1944. The comparative effect of surface and crown fire of a loblolly pine community. *Ecology* **25**: 61–69.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93–120.
- Peek, J. M. 1974. Initial response of moose to a forest fire in northeastern Minnesota. *Am. Midl. Nat.* **91**: 435–438.
- Pethick, J. S. 1974. The distribution of salt pans on tidal salt marshes. *J. Biogeogr.* **1**: 57–61.
- Phillips, J. 1974. Effects of fire in forest and savanna ecosystems of Sub-Sahara Africa. Pages 435–481 in T. T. Kozłowski and C. E. Ahlgren (eds.). *Fire and Ecosystems*. Academic Press, New York. 542 pp.
- Philpot, C. W. 1977. Vegetative features as determinants of fire frequency and intensity. Pages 12–16 in H. Mooney and C. E. Conrad (eds.). *Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems*. U.S.D.A. For. Serv. Gen. Tech. Rept. WO-3. Washington, D.C.
- Pickett, S. T. A. 1976. Succession: an evolutionary interpretation. *Am. Nat.* **110**: 107–119.
- Place, I. C. M. 1964. Structure of old growth forest stands in eastern Canada. Abstract 10th Int. Bot. Congr. 1964, pp. 273–274.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecol. Monogr.* **45**: 285–305.
- and I. M. Weis. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. *Am. Nat.* **111**: 479–513.
- Polunin, N. 1934. The vegetation of Akpatok Island, I. *J. Ecol.* **22**: 337–395.
- . 1935. The vegetation of Akpatok Island, II. *J. Ecol.* **23**: 161–209.
- . 1936. Plant succession in Norwegian Lapland. *J. Ecol.* **24**: 372–391.
- Poore, M. E. D. 1968. Studies in Malaysian rain forest, I. The forest on triassic sediments in Jengka Forest Reserve. *J. Ecol.* **56**: 143–196.
- Price, L. W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. *Ecology* **52**: 638–647.
- Quarterman, E. and C. Keever. 1962. Southern mixed hardwood forest: Climax in the southeastern coastal plain, USA. *Ecol. Monogr.* **32**: 167–185.
- Rabotnov, T. A. 1974. Differences between fluctuations and successions: examples in grassland phytocoenoses of the U.S.S.R. Pages 20–24 in R. Knapp (ed.). *Vegetation dynamics*. Dr. W. Junk, The Hague.

- Raup, H. M.** 1941a. Botanical problems in Boreal America. *Bot. Rev.* **7**: 147–248.
- . 1941b. An old forest in Stonington, Connecticut. *Rhodora* **43**: 67–71.
- . 1951. Vegetation and cryoplanation. *Ohio J. Sci.* **51**: 105–116.
- . 1954. Some botanical problems of arctic and subarctic regions. *Arctic* **7**: 229–235.
- . 1956. In report of meeting Int. Un. Conserv. Nature, Edinburgh, 1956. *Nature* **178**: 175–177.
- . 1957. Vegetational adjustment to the instability of site. Pages 36–48 in *Proc.*, 6th Tech. Meet. 1956, Int. Un. Conserv. Nature Nat. Resources, Edinburgh.
- . 1964. Some problems in ecological theory and their relation to conservation. *J. Ecol.* **52**(suppl.): 19–28.
- . 1967. American forest biology. *J. For.* **65**: 800–803.
- . 1975. Species versatility in shore habitats. *J. Arnold Arbor. Harv. Univ.* **55**: 126–165.
- Reiners, N. M. and W. A. Reiners.** 1965. Natural harvesting of trees. William L. Hutcheson Mem. For. Bull. **2**: 9–17.
- Reiners, W. A. and G. E. Lang.** 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. *Ecology* (In press.)
- Rhoades, R. W.** 1961. The distribution of White Spruce, *Picea glauca*, in New Hampshire. M.S. Thesis, Univ. New Hampshire, Durham. 52 pp.
- Richards, P. W.** 1952. The tropical rain forest. Cambridge, England. 450 pp.
- . 1955. The secondary succession in the tropical rain forest. *Sci. Progr.* **43**(169): 45–57.
- Richards, P. and G. B. Williamson.** 1975. Treefalls and patterns of understory species in a wet lowland tropical forest. *Ecology* **56**: 1226–1229.
- Ricklefs, R. E.** 1977. Environmental heterogeneity and plant species diversity: a hypothesis. *Am. Nat.* **111**: 376–381.
- Rogers, W. E.** 1922. Ice storms and trees. *Torreya* **22**: 61–63.
- . 1923. Resistance of trees to ice storm injury. *Torreya* **23**: 95–99.
- Rothermel, R. C.** 1972. A mathematical model for predicting fire spread in midland fuels. USDA For. Serv. Res. Pap. INT-115. 40 pp.
- Rowe, J. S.** 1961. Critique of some vegetational concepts as applied to forests of north-western Alberta. *Can. J. Bot.* **39**: 1007–1017.
- and **G. W. Scotter.** 1973. Fire in the boreal forest. *Quat. Res.* **3**: 444–464.
- Rundel, P. W.** 1973. The relationship between basal fire scars and crown damage in giant sequoia. *Ecology* **54**: 210–213.
- Runkle, J. R.** 1979. Gap phase dynamics in climax mesic forests. Ph.D. Thesis, Cornell Univ. Ithaca, New York. 289 pp.
- Sauer, J. D.** 1962. Effects of recent tropical cyclones on the coastal vegetation of Mauritius. *J. Ecol.* **50**: 275–290.
- Schroeder, P. M., R. Dolan, and B. P. Hayden.** 1976. Vegetation changes associated with barrier-dune construction on the Outer Banks of North Carolina. *Environ. Manage.* **1**: 105–114.
- Schwintzer, C. R. and G. Williams.** 1974. Vegetation changes in a small Michigan bog from 1917 to 1972. *Am. Midl. Nat.* **92**: 447–459.
- Scotter, G. W.** 1972. Fire as an ecological factor in boreal forest ecosystems of Canada. Pages 15–24 in *Fire and the Environment*, Symp. Proc. USFS, USDA, Denver, Colorado.
- Selleck, G. W.** 1960. The climax concept. *Bot. Rev.* **26**: 534–545.
- Shafi, M. I. and G. A. Yarranton.** 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology* **54**: 897–902.
- Shelford, V. E. and S. Olson.** 1935. Sere climax and influent animals with special reference to the transcontinental coniferous forest of North America. *Ecology* **16**: 375–402.
- Sherman, R. J. and W. W. Chilcote.** 1972. Spatial and chronological patterns of *Purshia tridentata* as influenced by *Pinus ponderosa*. *Ecology* **72**: 294–298.
- Siccama, T. G., G. Weir, and K. Wallace.** 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. *Bull. Torrey Bot. Club* **103**: 180–183.
- Sigafos, R. S.** 1951. Soil instability in tundra vegetation. *Ohio J. Sci.* **51**: 281–298.

- . 1952. Frost action as a primary physical factor in tundra plant communities. *Ecol.ogy* **33**: 480–487.
- Silberbauer-Gottsberger, I., W. Morawetz, and G. Gottsberger. 1977. Frost damage of Cerrado plants in Botucatu, Brazil, as related to the geographical distribution of species. *Biotropica* **9**: 253–261.
- Skunk, I. V. 1939. Oxygen requirements for germination of seeds of *Nyssa aquatica*, tupelo gum. *Science* **90**: 565–566.
- Slatkin, M. and R. Lange. 1976. Niche width in a fluctuating environment—density independent model. *Am. Nat.* **110**: 31–55.
- Slaughter, C. W., R. J. Barney, and G. M. Hansen (eds.). 1971. Fire in the northern environment—a symposium. Pac. Northwest. For. Range Exp. Stn., For. Serv., USDA, Portland, Oregon. 275 pp.
- Smathers, G. A. and D. Mueller-Dombois. 1974. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. National Park Service, Sci. Monogr. Series No. 5.
- Smith, D. H. 1946. Storm damage in New England forests. M.S. Thesis, Yale Univ., New Haven, Connecticut. 173 pp.
- Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in a tropical forest. *Oikos* **15**: 274–281.
- Sobey, D. G. and P. Barkhouse. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick-Nova Scotia border region. *Can. Field-Nat.* **91**: 377–383.
- Sollers, S. C. 1974. Substrate conditions, community structure, and succession in a portion of the flood plain of Wissahickon Creek. *Bartonia* **42**: 24–42.
- Sprugel, D. G. 1976. Dynamic structure of wave-generated *Abies balsamea* forests in the northeastern United States. *J. Ecol.* **64**: 889–912.
- Spurr, S. H. 1956a. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* **37**: 443–451.
- . 1956b. Forest associations in the Harvard Forest. *Ecol. Monogr.* **26**: 245–262.
- Starker, J. T. 1934. Fire resistance in the forest. *J. For.* **32**: 462–467.
- Stearns, F. W. 1949. Ninety years change in a northern hardwood forest in Wisconsin. *Ecology* **30**: 350–358.
- Stelfox, J. G. and H. G. Vriend. 1977. Prairie fires and pronghorn use of cactus. *Can. Field-Nat.* **91**: 282–285.
- Stephens, E. P. 1955a. The historical-developmental method of determining forest trends. Ph.D. Thesis, Harvard Univ., Cambridge. 36 pp.
- . 1955b. Research in the biological aspects of forest production. *J. For.* **53**: 183–186.
- . 1956. The uprooting of trees: a forest process. *Proc. Soil Sci. Soc. Am.* **20**: 113–116.
- Stiles, E. H. and L. E. Melchers. 1935. The drought of 1934 and its effect on trees in Kansas. *Trans. Kans. Acad. Sci.* **38**: 107–127.
- Stone, E. C. and R. B. Vasey. 1968. Preservation of coast redwood on alluvial flats. *Science* **159**: 157–161.
- Stoneburner, D. L. 1978. Evidence of hurricane influence on Barner Island slash pine forests in the Northern Gulf of Mexico. *Am. Midl. Nat.* **99**: 234–238.
- Stout, B. B., J. M. Deschenes, and L. F. Ohmann. 1975. Multispecies model of a deciduous forest. *Ecology* **56**: 226–331.
- Strong, D. R., Jr. 1977. Epiphyte loads, tree-falls, and perennial disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. *J. Biogeogr.* **4**: 215–218.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *Am. Nat.* **108**: 859–873.
- Swaine, J. M. 1933. The relation of insect activities to forest development as exemplified in the forests of eastern North America. *Sci. Agric.* **14**: 8–31.
- Swanston, D. N. and F. J. Swanson. 1976. Timber-harvesting, mass erosion, and steep land form geomorphology in the Pacific Northwest. Pages 199–221 in D. R. Coats (ed.). *Geomorphology and Engineering*. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania.

- Tansley, A. G.** 1935. The use and abuse of vegetational concepts and terms. *Ecology* **16**: 284–308.
- Taylor, B. W.** 1963. An outline of the vegetation of Nicaragua. *J. Ecol.* **51**: 27–54.
- Taylor, D. L.** 1973. Some ecological implications of forest fire control in Yellowstone National Park, Wyoming. *Ecology* **51**: 1394–1396.
- Thom, B. G.** 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. *J. Ecol.* **55**: 301–343.
- Transeau, E. N.** 1935. The prairie peninsula. *Ecology* **16**: 423–437.
- Tredici, P. del.** 1977. The buried seeds of *Comptonia peregrina*, the sweet fern. *Bull. Torrey Bot. Club* **104**: 270–275.
- Trimble, G. R., Jr. and D. W. Seegrist.** 1973. Epicormic branching on hardwood trees bordering forest openings. U.S.D.A. For. Serv. Res. Pap. NE-261. 6 pp.
- Turner, L. M.** 1935. Catastrophes and pure stands of southern shortleaf pine. *Ecology* **16**: 213–215.
- U.S.D.A.** 1965. Silvics of forest trees of the United States. For. Serv., USDA Agric. Handb. 271. 762 pp.
- Van der Valk, A. G. and C. B. Davis.** 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**: 322–335.
- Vankat, J. L., W. H. Blackwell, Jr., and W. E. Hopkins.** 1975. The dynamics of Hueston Woods and a review of the question of the successional status of the southern beech-maple forest. *Castanea* **40**: 290–308.
- Van Steenis, G. G. G. J.** 1956. Basic principles of rain forest sociology. Pages 159–163 in *Study of tropical vegetation*. Proc. of the Kandy Symp., UNESCO, Paris.
- Veblen, T. T., D. H. Ashton, F. M. Schlegel, and A. T. Veblen.** 1977. Plant succession in a timberline depressed by vulcanism in south-central Chile. *J. Biogeogr.* **4**: 275–294.
- Veno, P. A.** 1976. Successional relationships of five Florida plant communities. *Ecology* **57**: 498–508.
- Viereck, L. A.** 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecol. Monogr.* **36**: 181–199.
- . 1973. Wildfire in the taiga of Alaska. *Quat. Res.* **3**: 465–495.
- Visher, S. S.** 1949. American dry seasons: their intensity and frequency. *Ecology* **30**: 365–370.
- Vogl, R. J.** 1974. Effects of fire on grasslands. Pages 139–194 in T. T. Kozlowski and C. E. Ahlgren (eds.), *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Wace, N. M.** 1961. The vegetation of Gough Island. *Ecol. Monogr.* **31**: 337–367.
- Wadsworth, F. H. and G. H. Englerth.** 1959. Effects of the 1956 hurricane on forests in Puerto Rico. *Caribb. For.* **20**: 38–51.
- Wagner, R. H.** 1964. The ecology of *Uniola paniculata* L. in the dune-strand habitat of North Carolina. *Ecol. Monogr.* **34**: 79–96.
- Walker, B. H.** 1972. Vegetation-site relationships in the Harvard Forest. *Vegetatio* **29**: 169–178.
- Ware, G. H. and W. T. Penfound.** 1949. The vegetation of the lower levels of the flood plain of the South Canadian River in central Oklahoma. *Ecology* **30**: 478–484.
- Watt, A. S.** 1923. On the ecology of British beechwoods with special reference to their regeneration. *J. Ecol.* **11**: 1–48.
- . 1947a. Pattern and process in the plant community. *J. Ecol.* **35**: 1–22.
- . 1947b. Contributions to the ecology of bracken. IV. The structure of the community. *New Phytol.* **46**: 97–121.
- . 1955. Bracken versus heather: a study in plant sociology. *J. Ecol.* **43**: 490–506.
- . 1974. Senescence and rejuvenation in ungrazed chalk grassland (grassland B) in Breckland: The significance of litter and of moles. *J. Appl. Ecol.* **11**: 1157–1172.
- , **R. M. S. Perrin, and R. G. West.** 1966. Patterned ground in Breckland: structure and composition. *J. Ecol.* **64**: 239–258.
- Weaver, H.** 1974. Effects of fire on temperate forests: Western United States. Pages 279–319 in T. T. Kozlowski and C. E. Ahlgren (eds.), *Fire and ecosystems*. Academic Press, New York. 542 pp.
- Weaver, J. E.** 1950. Stabilization in midwestern grassland. *Ecol. Monogr.* **20**: 251–270.

- . 1958. Summary and interpretation of underground development in natural grassland communities. *Ecol. Monogr.* **28**: 55–78.
- . 1960. Flood plain vegetation of the central Missouri Valley and contacts of woodland with prairie. *Ecol. Monogr.* **30**: 37–64.
- . 1968. Prairie plants and their environment: a 50-year study in the Midwest. Univ. Nebr. Press, Lincoln. 276 pp.
- and F. W. Albertson. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. *Ecol. Monogr.* **13**: 63–117.
- and ———. 1944. Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecol. Monogr.* **14**: 393–479.
- and W. E. Bruner. 1945. A seven-year quantitative study of succession in grassland. *Ecol. Monogr.* **15**: 297–319.
- and F. E. Clements. 1929. *Plant ecology*. 2nd ed., 1938. McGraw-Hill, New York. 520 pp.
- , L. A. Stoddart, and W. Noll. 1935. Response of the prairie to the Great Drought of 1934. *Ecology* **16**: 612–629.
- Webb, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, north Queensland. *Aust. J. Bot.* **6**: 220–228.
- . 1968. Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* **49**: 296–311.
- , L. G. Tracey, and W. T. Williams. 1972. Regeneration and pattern in the subtropical rain forest. *J. Ecol.* **60**: 675–695.
- Wein, R. W. and L. C. Bliss. 1973. Changes in arctic *Eriophorum* tussock communities following fire. *Ecology* **54**: 845–852.
- Wells, B. W. 1942. Ecological problems of the southeastern United States coastal plain. *Bot. Rev.* **8**: 533–561.
- Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecol. Monogr.* **31**: 239–266.
- Wells, P. V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains region. *Science* **148**: 246–249.
- Wendel, G. W. 1972. Longevity of black cherry seed in the forest floor. U.S.D.A. For. Serv. Res. Note NE-149. 4 pp.
- West, O. 1971. Fire, man, and wildlife as interacting factors limiting the development of climax vegetation in Rhodesia. *Proc. Annu. Tall Timbers Fire Ecol. Conf.* **11**: 121–145.
- Westman, W. E. 1968. Invasion of fir forest by sugar maple in Itasca Park, Minnesota. *Bull. Torrey Bot. Club* **95**: 172–186.
- White, P. S. 1976. The upland forest vegetation of the Second College Grant, New Hampshire. Ph.D. Thesis, Dartmouth College, Hanover, New Hampshire. 295 pp.
- Whitmore, T. C. 1974. Change with time and the role of cyclones in tropical rain forest of Kolombangara, Solomon Islands, Univ. Oxford Commonwealth Forestry Institute. Institute Paper No. 46.
- . 1975. *Tropical rain forests of the Far East*. Clarendon Press, Oxford. 282 pp.
- Whitney, G. G. 1976. The bifurcation ratio as an indicator of adaptive strategy in woody plant species. *Bull. Torrey Bot. Club* **103**: 67–72.
- Whittaker, R. H. 1953. A consideration of climax theory; the climax as a population and pattern. *Ecol. Monogr.* **23**: 41–78.
- . 1972. Evolution and measurement of species diversity. *Taxon* **21**: 213–251.
- . 1974. Climax concepts and recognition. Pages 138–154 in R. Knapp (ed.), *Vegetation dynamics*. Dr. W. Junk, The Hague.
- . 1975. *Communities and ecosystems*, 2nd ed., Macmillan, New York. 385 pp.
- . 1977. Evolution of species diversity in land communities. *Evol. Biol.* **10**: 1–67.
- and D. Goodman. 1979. Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. *Am. Nat.* **113**: 185–200.
- Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* **7**: 81–120.

- Williamson, G. G. 1975. Pattern and seral composition in an old-growth beech-maple forest. *Ecology* **56**: 727–731.
- Wilson, J. W. 1952. Vegetation patterns associated with soil movement on Jan Mayen Island. *J. Ecol.* **40**: 249–264.
- Wistendahl, W. A. 1958. The Hood plain of the Raritan River, New Jersey. *Ecol. Monogr.* **28**: 129–153.
- Woodin, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. *Ecology* **59**: 274–284.
- Wright, H. E., Jr. 1974. Landscape development, forest fires, and wilderness management. *Science* **186**: 487–495.
- and M. L. Heinselman. 1973. The ecological role of fire in natural conifer forests of western and northern North America—Introduction. *Quat. Res.* **3**: 319–328.
- Yarranton, M. and G. A. Yarranton. 1975. Demography of a jack pine stand. *Can. J. Bot.* **53**: 310–314.
- Zach, L. W. 1950. A northern climax, forest or muskey? *Ecology* **31**: 304–306.
- Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. *Oikos* **29**: 22–32.
- Zavitkovski, J. and M. Newton. 1968. Ecological importance of snowbrush (*Ceanothus velutinus*) in the Oregon Cascades. *Ecology* **49**: 1134–1145.
- Zedler, P. H. and T. A. Ebert. 1977. Shrub seedling establishment and survival following an unusual September rain in the Colorado desert. Abstract in *Bull. Ecol. Soc. Am.* **58**(2): 47.
- and F. G. Goff. 1973. Size-association analysis of forest successional trends in Wisconsin. *Ecol. Monogr.* **43**: 79–94.
- Zobel, D. B. 1969. Factors affecting the distribution of *Pinus pungens*, an Appalachian endemic. *Ecol. Monogr.* **39**: 303–333.

