Verhandlungen der Gesellschaft für Ökologie (Freising-Weihenstephan 1979) Band VIII 1980

Towards an ecological theory of nature management

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Naturschutz (Naturverwaltung) kann sich auf Pflanzen- und Tierarten (Populationen), auf Lebensgemeinschaften (Ökosysteme) oder auf Landschaftseinheiten (Ökosystemkomplexe) beziehen. In jedem Fall kann das Objekt unseres Schutzes als System, und können die Schutzmaßnahmen als Faktoren der Umwelt aufgefaßt werden.
Eine Lebensgemeinschaft, und so eine Pflanzengemeinschaft, aber auch eine Population ist als Subsystem eines Ökosystems zu verstehen, d.h. sie lebt in direkter Wechselwirkung mit einem inneren Milieu, in dem man ein oder mehrere Subsysteme unterscheiden kann. Für eine Pflanzen-(Produzenten-)gemeinschaft sind das z.B. Boden, Mikroklima, Konsumenten und Reduzenten, in bestimmten Auffassungen auch menschliche Einflüsse, soweit diese zum "steady state" des Ökosystems gehören bzw. dazu beitragen.
Die Stabilitätstypen "Persistenz" bzw. "Resilienz" sind Stufen von steady state-Dynamik, die an Stufen von niedriger bzw. hoher Umweltdynamik angepaßt sind, wobei das Niveau der Gesamtdynamik vor allem von der Dynamik der 3. Ordnung bedingt wird.
Die Erhaltung einer Pflanzengemeinschaft ist im Wesen eine Aufgabe der Erhaltung der zugehörigen Umweltdynamik. Wir können zwei Hauptgruppen von Naturschutzmaßnahmen unterscheiden: 1. Abschirmung von drohender extra-Dynamik der 3. Ordnung ("externe Verwaltung") und 2. Umwandlung von Dynamik der 3. Ordnung in die der 2. Ordnung ("interne Verwaltung").
Die steady state-Dynamik kann mittels Regulations- und Selektionsprozessen erhalten werden. Wir können Regulatoren und Selektoren sowohl innerhalb des Ökosystems unterscheiden ("interne Regulation") als auch außerhalb ("externe Regulation").
In den dynamischen Verhältnissen zwischen System und Umwelt gibt es vier Haupttendenzen von Störung, die wir aus einem "Source-sink"-Modell ableiten: "zuviel herein", "zu wenig herein", "zuviel heraus" und "zu wenig heraus". Regulierung ist immer auf eine oder mehrere dieser Tendenzen bezogen.

Nature conservation, nature management, ecological theory, environmental dynamics, regulation, diversity, stability stress.

1. Introduction

Theoretical ecological considerations on nature conservation and management have developed particularly in countries with a relatively heavy human impact on nature. Such countries are characterized by (cf. WESTHOFF 1977a):

- a small amount of near-natural to natural ecosystems
- emphasis on the preservation of semi-natural ecosystems (WESTHOFF, e.g. 1969, 1971a) in which man and nature are involved in a relatively stable balance ("man-made natural", van der MAAREL 1975)
- a great number of relatively small nature reserves which are relatively difficult to manage
- a concentration of rare and endangered species and vegetation types in these nature reserves (e.g. SUKOPP 1974, WESTHOFF 1976)
- a high recreational pressure on the reserves with its negative consequences (see LIDDLE 1975 for a review)
- a high susceptability of endangered species and communities even in the reserves for environmental changes in the surroundings due to agricultural and urban-industrial developments (e.g. WESTHOFF 1956; SUKOPP 1972; SUKOPP, TRAUTMANN 1976).

In view of this emphasis on nature conservation in largely cultivated countries we should make clear what we consider as nature and natural. With DASMANN (1972), USHER (1973) and DANSEREAU (1973), to mention three eloquent ecologists, we do not separate man from nature in our conception of nature conservation, but distinguish man as a special agent in nature. In the context of nature conservation and management we define natural (rather loosely) as "developing more or less independently from man's action". For natural ecosystems this means that man may act upon their structure and upon some undesired biotic influences (including human ones), but the majority of their populations develops spontaneously (hence the term "man-made natural").

The present contribution is mainly based on experiences in Great Britain, West Germany and the Netherlands (see USHER 1973, BUCHWALD, ENGELHARDT 1973 and BAKKER 1979 for general reviews). Within these countries the scientific basis for nature management is in part derived from the so-called relation theory developed by van LEEUWEN (1966, 1973; reviewed by van der MAAREL 1976). This theory has been developed in close connection with ideas on the relation between man and natural ecosystems by WESTHOFF (1955, 1969, 1971b, also van LEEUWEN 1979a). It has been connected with modern theory on the relation between diversity and stability (HOLLING 1973; MARGALEF 1968, 1975; ORIANS 1975; HABER 1972, 1979; van der MAAREL, DAUVELLIER, 1978). Finally the relation theory has been developed further by the originator towards a theory of "nature technique" with a technical terminology (van LEEUWEN 1979b, c; LAHAYE, van LEEUWEN 1979).

In the Netherlands the theoretical interest in diversity-stability problems found expression in the development of a general research theme "Structure and dynamics in vegetation" by the working group for plant ecology and vegetation science within the Netherlands' Organisation for Biological Research. This theme is elaborated on all levels of integration, as has been made clear at a special symposium (van der MAAREL 1979a). The present contribution is partly an expression of these organisational developments and at the same time a piece of information from Dutch to German language ecologists.

With structure and dynamics we have two broad concepts, which include those of diversity resp. stability, and to which we can relate nature management: as man's concern with the maintenance of the structure and dynamics of natural ecosystems.

2. On systems and surroundings

Nature management as applied ecology is concerned with ecosystems, on whatever level of abstraction, which are always systems of interaction between subsystems and their environment.

Nature management is usually directed to species populations, and biotic (usually plant) communities, but it may include ecosystem complexes or landscape units. At all levels the object of management is our subsystem and our management devices are factors within the complex of abiotic, biotic and anthropic factors which form the environment of the subsystem.

If we adopt an ecosystem compartment model such as that of ELLENBERG (1973, p. 3) we have to distinguish at least six biotic subsystems as to the type of matter and energy transferring organisms involved (cf. van der MAAREL, DAUVELLIER 1978): primary producers (autotrophic plants), primary consumers (herbivores), secondary consumers (carnivores), tertiary consumers (top carnivores), detritus decomposers (saprovores) and mineralizing decomposers. Two compartments of biomass may be added: the temporary detritus to be decomposed, and the permanent biomass (mainly wood and humus)

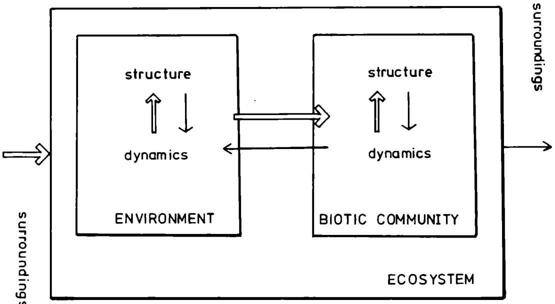

Fig. 1: Relations between a biotic community (synusia, population) with its direct abiotic-biotic environment and its wider (controlling) surroundings. Prevailing (entropy) directions of influences are indicated with double arrows, reverse (ectropy) directions of influences with single arrows, dynamic influences with double arrows and structural influences with single arrows. (According to van LEEUWEN, from van der MAAREL, DAUVELLIER 1978).

which builds up the concrete structure of a (terrestrial) ecosystem. According to DANSEREAU's (1973) ecosystem model these compartments represent levels of energy transfer (in his scheme only three, corresponding to vegetation, herbivores, and carnivores), the last mentioned compartment referring to the "investment" level. DANSEREAU also distinguished a basic level of mineral resources (in fact abiotic matter and energy resources) and a top level of "control", in which both abiotic (mainly climatic) and human controls are represented.

Clearly, communities representing one specific biotic compartment, or populations within these synusiae, are characterised by an own structural-dynamic behaviour towards the other compartments and towards the abiotic compartment within the ecosystem. All "other" compartments involved act as environment through which our management must operate in order to achieve our plan concerning the compartment to be managed (i.e. maintained, restored or developed). However, this abiotic-biotic environment is embedded in the wider surroundings of the ecosystem, which (to use DANSEREAU's term again) controls the ecosystem.

According to van LEEUWEN the main direction of influences operating in the total system of ecosystem + surroundings is from surroundings via abiotic environment to the total biotic community. This direction represents the processes governed by the entropy law. Reverse influences originate in the biotic community as a result of building up of structure (ectropy). Influences of a dynamic character are more important than influences of a structural character (Fig. 1). This all means that

(1) the spatial arrangements of surrounding abiotic factors, notably temperature, rainfall, substrate texture and chemical properties determine the inner ecosystems environment, notably microclimate and soil properties;
(2) through this sequence the spatial arrangement of the biotic community is determined;
(3) the fluctuations in the controlling environmental factors are transferred to fluctuations in the inner environment;
(4) this sequence of fluctuations causes fluctuations in the biotic community;
(5) the determination of spatial patterns is governed by the fluctuations in the factors involved.

In short: "Dynamics governs structure".

In the usual case of concentrating our management on one particular compartment of the biotic community we have to differentiate the model of Fig. 1, with the autotrophic plant community as a first subsystem which governs in its turn the dependent subsystems.

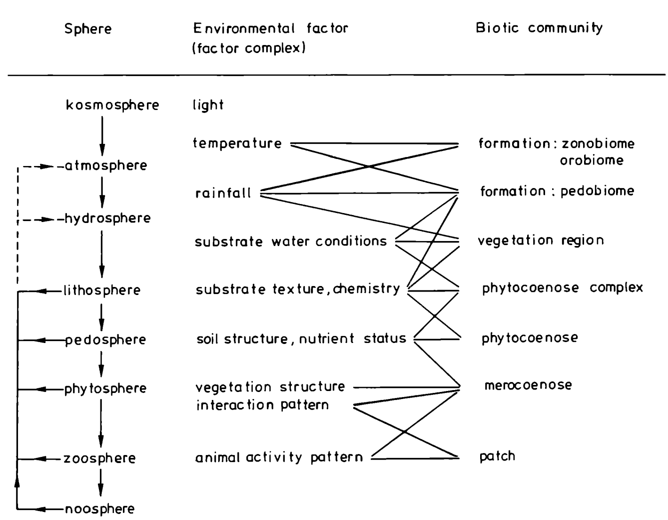

Fig. 2: Principal environmental factors and factor complexes arranged in a hierarchy of spheres operating on a biotic community.
(Redrawn after van der MAAREL 1976; biome terms after WALTER 1976).

According to van LEEUWEN the various controlling factors can be arranged in a sequence of spheres representing a hierarchy of impacts (Fig. 2). The practical interpretation of this scheme is as follows:

1) the higher the sphere of influence the more influential the factors are,
2) the fluctuations in environmental factors are more important for the biotic community as they operate from higher up in the hierarchy,
3) the biotic spheres can operate "backwards" and the noosphere, although originally down in the hierarchy of overall dependence, is extending its reverse impact.
4) Human activities usually imply changes (increases) in the dynamics of the environmental factors involved.
5) The higher the sphere a human impact is exerting on, the more profound the indirect impact on biotic communities governed by the environmental factors involved, and the more difficult the partly indirect effects can be predicted.

3. On environmental dynamics

In order to specify the statement "dynamics governs structure" van LEEUWEN distinguished three degrees (orders) of environmental dynamics (Fig. 3).

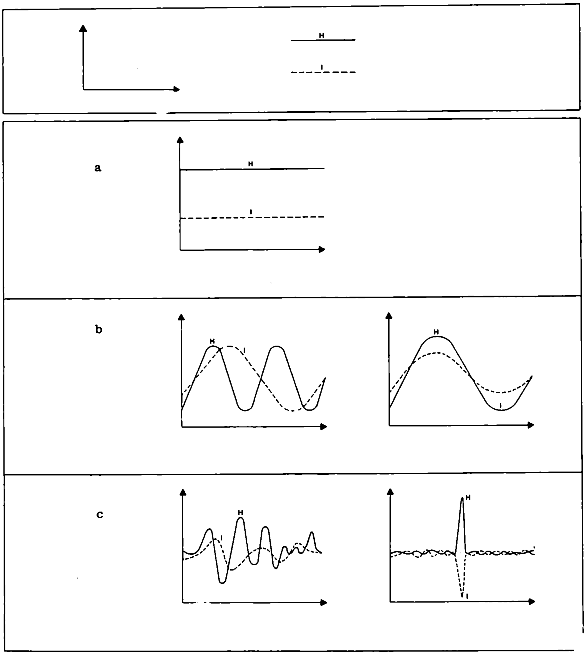

Fig. 3: Degrees of environmental dynamics (after van der MAAREL, DAUVELLIER 1978).
Level of a certain environmental factor is plotted on the Y-axis, time on the X-axis,
H = high level of dynamics, L = low level;
a: first degree: difference in level
b: second degree: difference in frequency or in amplitude
c: third degree: difference in irregularity with a catastrophic change as an extreme situation.

First order dynamics is an intrinsic characteristic of a factor, which is expressed in the (average) level of a factor. This is easy to understand only in factors such as temperature: a higher temperature is more dynamical than a lower one. For factors such as phosphate concentration, a very important dynamical factor in van LEEUWEN's considerations, we can understand the relation between concentration level and level of first order dynamics only as an indirect impact on the activity of organisms. *Second* order dynamics includes regular fluctuations in the level of a factor. Differences in second degree dynamics are expressed in differences in amplitude or in frequency. *Third* order dynamics concerns irregularity in the fluctuation of a factor. So far no clear measurement for the "amount of irregularity" has been suggested. The ultimate case of irregularity is the sudden very big change in the level of a factor ("catastrophy"). An extra complication with catastrophic changes is that they may exert an influence upon the ecosystem involved long after their occurrence (and usually before our investigation of the system starts).

The three degrees of environmental dynamics can be compared with each other as to their predictability. The notion of unpredictable environments and some ideas on adaptations of populations to such environments have been put forward by SLOBODKIN, SANDERS (1969), but they did not go into detail. MARGALEF (1974) discussed unpredictability in anthropogenic environmental changes, including the catastrophic event as a limit case, but he did not specify the concept either.

Clearly a first degree environmental dynamics is fully predictable, while organisms or rather populations can become adapted to second degree dynamics, such as tidal fluctuations in chloride concentration or seasonal meteorological fluctuations.

In his recent studies van LEEUWEN (1979b, 1979c; LAHAYE, van LEEUWEN 1979) reconsidered the difference between surroundings and environment as shown in Fig. 1 in terms of the unpredictability of the environmental factors involved. He now includes all predictable environmental factors in the inner ecosystems environment as far as the biotic community has developed adaptations to the rhythmic (second degree) fluctuations. Such conditions co-determine the steady state of an ecosystem and hence van LEEUWEN now speaks of steady state dynamics (as distinct from unpredictable dynamics).

For nature management this view means that rhythmic human activities, particularly yearly mowing can in the long run be adapted to and hence belong to the steady state of a semi-natural ecosystem.

In the further interpretation of environmental dynamics we may include the notion of the hierarchy of spheres: fluctuations of factors from higher spheres will have a stronger impact on the biotic community. Moreover it seems that the unpredictability of such fluctuations increases as well. Thus cosmospheric fluctuations can be considered the most important ones, but since they are largely unpredictable they can hardly be included in the actual study of ecosystem dynamics. Atmospheric fluctuations come next and they can be studied effectively in their direct and indirect impacts.

4. On species response curves in relation to environmental dynamics

In view of the difficulties in measuring "amount of environmental fluctuations" it is necessary to approach the impact of dynamics through the behaviour of populations and communities. For populations there is evidence and theory concerning the distribution along environmental gradients. The usual model is of the Gaussian type (Fig. 4a), which goes back to SHELFORD (1913) and has been documented particularly by WHITTAKER (1967, 1975, 1978). Recent considerations, observations and experiments (e.g. MUELLER-DOMBOIS, ELLENBERG 1974; GRIME 1973, 1979, AUSTIN 1976, summarized by AUSTIN 1980) show that bimodal and wedge-type response curves (response usually measured as absolute or relative biomass) are also possible and existent.

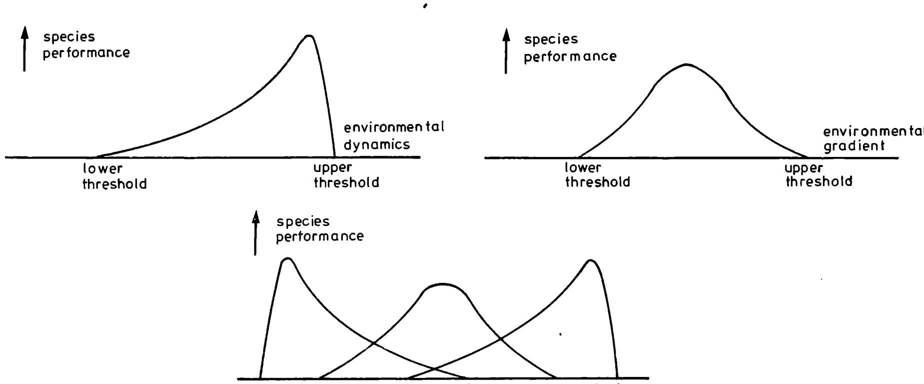

Fig. 4: Models for species population performance along environmental gradients.
a) Gaussian response function
b) Supposed wedgetype response along a gradient of environmental dynamics
c) Possible differentiated response curves at different ranges of the gradient of environmental dynamics (van der MAAREL 1976).

Part of this evidence can be combined with van LEEUWEN's suggestion of a wedge-type population response to a gradient of increasing environmental dynamics (Fig. 4b), as elaborated by van der MAAREL (1976, van der MAAREL, DAUVELLIER 1978). The idea behind this model is based on the observation that in extremely dynamical environments (such as on wind-exposed beaches), populations of especially adapted species such as *Ammophila arenaria* may show their greatest development towards the source of dynamics. Maybe (Fig. 4c) this only applies to situations of high dynamics, while at lower levels a reversed wedge-type response is more feasible. In fact GRIME (1973) presented a similar model based on the different dominance behaviour of species: at low levels of environmental dynamics ("stress" in GRIME's terms) due to competitive ability, at high levels of dynamics due to physiological tolerance.

As AUSTIN (1980) made clear, the type of response is largely dependent on the type of environmental gradient. He even spoke of confusion concerning such types. In view of van LEEUWEN's statement about first order dynamics which is not traced as such there is indeed confusion.

A still further complicating aspect is the fluctuation in the populations involved. For plant species there is only little evidence for the course and the mechanisms of fluctuations in relation to environmental fluctuations (see MILES 1979 for a recent review). For animal populations both description and models are much more advanced, but the understanding of the details of environmental fluctuations is ill-developed (see various contributions in CODY, DIAMOND 1975).

5. On the development of environmental gradients

The gradual increase or decrease in a certain environmental factor (such as in AUSTIN's [see 1980] experiments with increasing nutrient concentrations) is not always found in the field. According to van LEEUWEN a real environmental gradient with a gradual increase or decrease in at least one factor only occurs under special circumstances, which he summarizes as follows: first, a unidirectional flow of water is necessary and second, the level of environmental dynamics must decrease "upflow". Fig. 5 shows the basic conditions and the specification for a number of well-known factors considered as master factors.

TOPOGRAPHICAL GRADIENT	high		►		low
SUBSTRATE GRADIENT	sand	►	loam	►	clay
SOIL GRADIENTS					
- moisture	dry		►		wet
- lime content	poor in lime		►		rich in lime
- pH	acid		►		basic
- organic matter	peaty, humus rich		►		mineral, humus poor
- nutrients (N,P,K)	oligotrophic		►		eutrophic
- chloride	fresh		►		saline
MICROCLIMATE GRADIENTS					
- light	shady		►		light
- temperature	cool		►		warm
CULTURAL GRADIENTS					
- cutting	less		►		more
- mowing	less		►		more
- manuring	less		►		more
- treading	less		►		more
GRADIENTS OF ENVIRONMENTAL DYNAMICS	less		►		more

Fig. 5: Development of ecologically effective environmental gradients on the basis of a topographical gradient in a humid climate according to van LEEUWEN (modified after van der MAAREL, DAUVELLIER 1978).

Clearly environmental gradients can develop on various scales. Usually the environmental variation is considered on the meso-scale, i.e. including a series of different communities. For the understanding of the relations within a community we need data on micro-heterogeneity in the major environmental factors. The available evidence (e.g. van der MAAREL 1971) suggests that the species diversity of a plant community may be dependent on environmental micro-heterogeneity to a larger extent than is usually assumed.

In the context of van LEEUWEN's relation theory such a fine grained community pattern with relatively many species occurring in small quantities and a dispersed distribution is bound to relatively low levels of environmental dynamics (limes divergens environment, van LEEUWEN 1966, see also van der MAAREL 1976).

In the opposite situation the limes convergens develops. Here the environmental fluctuations are large and if topographical gradients occur, there is an increase in dynamics upflow the gradient (Fig. 5). Such a situation is characterized by relatively few species occurring in large quantities and clumped distributions and with large temporal variations.

6. On diversity and stability

Within this framework, at least some attention should be paid to the controversial item of diversity - stability relations. To shorten the discussion the recent contribution by HABER (1979) in the same symposium series can be referred to. HABER's description of two contrasting types of stable ecosystems is very well in accordance with the above typology of environments. The persistent (resistent) diverse ecosystems are bound to relatively constant (divergent) environments and can, under such circumstances, develop a rather rich and constant species assemblage. The elastic (resilient) dominance ecosystems are bound to relatively fluctuating (convergent) environments and can only develop a poor and fluctuating species assemblage.

As a direct elaboration of the statement "dynamics governs structure" we can summarize the relation between diversity and stability as follows: stability of the external ecosystem environment governs diversity in the biotic community and the latter determines in turn stability in the internal environment (along the lines of MACARTHUR's 1955 original thoughts).

7. On regulation and selection

From the beginning the concepts regulation and selection have been essential in van LEEUWEN's theory. In his recent work (van LEEUWEN 1979c; LAHAYE, van LEEUWEN 1979) the concepts have been elaborated in such a way that a better understanding of an idea by MARGALEF (1968), which remained obscure, is now possible. MARGALEF considered that mature ecosystems can only develop at the expense of less mature, pioneer ones, by "exploiting" them. We can now interpret this statement as follows: mature ecosystems need rather stable (constant) surroundings.

These surroundings consist not only of parts of the abiotic spheres but also of other ecosystems. If such ecosystems are in part of the resilient type they are able to neutralize part of the environmental dynamics. An example of such a situation is found in coastal dunes (e.g. those in the Netherlands, cf. van der MAAREL 1979b) where the relative persistence of tall scrub with *Crataegus monogyna* and woodland with *Quercus robur* and *Betula verrucosa* in the inner part of the dunes, at a small distance to the sea, is facilitated by the zonation of younger and more elastic ecosystems in the direction of the beach: lower scrub of *Hippophaë rhamnoides* and *Ligustrum vulgare*, low scrub of *Hippophaë* only, open grassland with *Ammophila arenaria*. The damping of environmental dynamics, notably sand movement and wind action by these younger ecosystems is obvious.

The regulating action of man in nature management is equally clear: the maintenance of an ecosystem (usually only the plant community component is directly concerned) is essentially the maintenance of the required level of environmental dynamics. This means in present day practice that the ecosystem to be managed is either protected against possible (third order) dynamics brought about by human action outside the area, or regulated by the transformation of unavoidable third order dynamics into more regular dynamics e.g. by ground water regulation or controlled grazing and mowing. These two forms of management are examples of what is called external and internal management (e.g. WESTHOFF 1971b, BAKKER 1979, van der MAAREL 1979b).

The basic idea on selection and regulation is elucidated in Fig. 6; Selection and regulation processes leading to an increase in spatial variation and a decrease in temporal variation of an ecosystem respectively. Such processes act in the opposite direction as thermodynamics suggest: ("dynamics governs structure") a decrease in spatial variation or homogenization, and an increase in temporal variation or disregulation (see also HABER 1978).

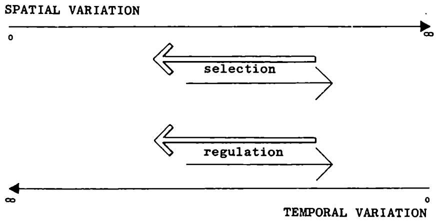

Fig. 6: Selection and regulation as processes leading to an increase in the spatial variation and a decrease in the temporal variation of an ecosystem. (according to van LEEUWEN, after van der MAAREL, DAUVELLIER 1978).

Regulation and selection occur often together, i.e. regulating mechanisms often act as selectors at the same time. Regulation may be considered the most important process since it effects environmental dynamics. In his recent considerations van LEEUWEN distinguished four types of regulation, which are directed towards an ecosystem embedded in a surrounding acting both as a source and as a sink (Fig. 7). Each type of regulation counteracts a possible disregulation in the matter and energy metabolism of the system. The four disregulations can be laconically described as:

1) "too little into",
2) "too little out of",
3) "too much into" and
4) "too much out of" the system.

For these situations the following terms are proposed: (1) hypotrophy, (2) congestion, (3) hypertrophy, and (4) exhaustion and for the four corresponding regulation types: (1) suppletion, (2) discharge, (3) interception, and (4) retention. It will be clear that between (1) and (4) and between (2) and (3) a direct connection exists. In practice regulation mechanisms may have combined effects.

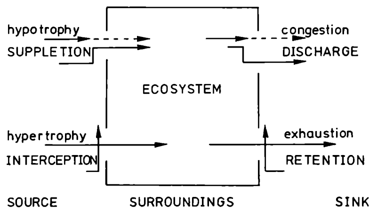

Fig. 7: Four types of regulation of an ecosystem in its surroundings through source and sink relations.

Although van LEEUWEN did not say this explicitly these four situations should be understood as temporal changes in the external conditions of an ecosystem. Some examples are: (1) temporal shortage of water, interruption in the supply of nutrients (e.g. in an *Ammophiletum)*, (2) concentration of dead material, blowing in of sand, (3) unexpected inundation and eutrophication, and (4) overgrazing. Van LEEUWEN did not restrict the idea of "source-sink" disturbances to the level of biotic community. In fact many examples can be mentioned for the individual plant or animal.

So far no clear elaboration of regulation in this sense is made regarding the localization of the regulating mechanism. Van LEEUWEN mentioned examples of very different kinds such as the forming of reserve organs, stomata, mimicry, formation of levees, building of dikes and storage of water by bogs.

If we concentrate on regulation mechanisms on the ecosystem level for the purpose of the present theme, we may distinguish between internal and external regulation. Internal regulation is performed by the biotic community and leads to overall stabilization of the ecosystem (e.g. through tempering of microclimate and formation of humus). External regulation is performed by an agent from the surroundings. Of course man is an important external regulator in many ways. (Note that if one accepts the definition of steady state dynamics as suggested by van LEEUWEN some of the human regulations must be called internal).

An interesting case of external regulation is provided by peat bogs which store water that can be taken from nearby water-dependent ecosystems in dry years. In fact exploitation by or protection of mature ecosystems in the sense mentioned by MARGALEF (1968) and exemplified above with the vegetation zonation in coastal dunes, can be interpreted as regulation of one ecosystem through processes in neighbouring ecosystems. This aspect should be elaborated and considered in a wider landscape ecological context, where many so-called horizontal relations can be distinguished.

8. On disturbance and stress

In the above section the word disturbance was used as the "disregulation" to be regulated. Like the concept of regulation that of disturbance should be further elaborated. Again some recent contributions can be mentioned which may help us in this elaboration. First ODUM, FINN, FRANZ (1979) made clear how perturbation can be used as a general term for the deviation of a normal or expected ecosystem state. The normal state is apparently what others consider the steady state (cf. van LEEUWEN, but also for instance LOOMAN 1976, who refers to the cycling of matter and energy, and BORMANN, LIKENS [1979] who refer to the production/respiration ratio).

If we refer perturbation to a particular environmental factor we can distinguish an interval (sometimes very small) where an increase in the value of the factor stimulates production; this is the "subsidy" interval. Beyond that an increase would reduce production, and here we have a stress interval. Hence ODUM et al. (1979) speak of a subsidy-stress gradient. Of course "production" is not the only parameter to compare along the subsidy-stress gradient, another possibility mentioned by the authors would be diversity.

Another relevant contribution is that by GRIME (1979 and some earlier papers). This author distinguished between disturbance and stress. Stress includes all influences from the environment which limit photosynthesis, disturbance includes all destructive influences on the plants. (This approach has been developed primarily in relation to plant populations, but could of course be extended to animal populations and to entire biotic communities.)

GRIME postulated four possible strategies in plants to cope with the various combinations of high and low levels of disturbance and stress:

		intensity of stress	
		low	high
intensity of disturbance	low	competition	stress-tolerance
	high	ruderal strategy	no viable strategy

GRIME elaborated this typology by distinguishing a number of combined or intermediate strategies, which cannot be discussed here. For our present purpose it is sufficient to make some general observations.

1) Competition is to be expected in environments with both a low level of stress and a low level of disturbance. As was briefly mentioned above (GRIME 1973) this situation may lead to a dominance ecosystem, i.e. an ecosystem with a high portion of the plant biomass produced by only one species. This fits only partly in the ideas on the development of dominance in relation to environmental dynamics put forward by van LEEUWEN (1966, 1979b and HABER 1979). In the relation theory (see Fig. 4) dominance is first-of-all related to a high level of environmental fluctuation. The difference between the two approaches is found in the fact that in GRIME's "competition environment" a high level of fertility is involved. This means a high level of first-order environmental dynamics for most other species except for the potential dominant (in terms of ODUM et al. 1979 for those species the transition between subsidy and stress would be reached).
2) The ruderal strategy, including a high potential growth-rate and a short life-cycle, is bound to a relatively high level of fertility (i.e. supply of N, P and K). In many grasslands under heavy grazing we may find a very high species diversity with a predominance of species without a real ruderal strategy (e.g. van der MAAREL 1971). Here one of GRIME's intermediate categories, i.e. "stress-tolerant ruderals" would be more appropriate, but the corresponding environmental conditions, i.e. moderate intensities of stress and disturbance do not seem to correspond well.
3) The relevance of these observations for our present considerations is twofold: first we are in need of an extension of the stress-disturbance model with a separate line of variation reflecting nutrient conditions; second it is not altogether simple to extrapolate from the individual population strategy to a community strategy.

9. Some conclusions

The maintenance of a variety of ecosystems should be the aim of any regional nature conservation policy. Within this variety the varied, diversified ecosystems are of special interest because they harbour most of our rare and endangered species. At the same time we recognize that this type of ecosystem is bound to a high level of environmental heterogeneity and/or a low level of environmental dynamics. Such subtle conditions are easily disturbed by homogenization and/or disregulation. Increased anthropogenic dynamics often operates as stress in the sense of limiting the production of plants and in the end limiting the number of species which are able to survive. In such cases man-induced "stress-dynamics" overrules originally existing spatial variety.

Therefore a major task for nature management will be the interception of anthropogenic dynamics around potential or actual nature reserves. If we could succeed in forming a buffer zone around a nature reserve in which a gradient or decreasing human impact could be established, we would even be able to contribute to the overall variation in the region involved.

We may summarize these considerations in the form of seven guidelines for nature management. They are taken from van der MAAREL 1975 who derived them from van LEEUWEN (1966, see also 1979a) and WESTHOFF (1969, 1971b, see also 1977a, b and BAKKER 1979).

Guideline 1: Check the gradient structure of the environment and its dynamic properties, whether natural or anthropogenic.

Guideline 2: Keep steady-state diverse semi-natural systems in that state by continuing the former management, probably an agricultural one.

Guideline 3: Gradients of human influence may be induced in sufficiently large semi- to near-natural areas.

Guideline 4: Ecoclines have to be protected from ecotone disturbance, especially eutrophication, by buffering them.

Guideline 5: Ecoclines can be established or amplified by creating oligotrophic conditions dominating over meso- or eutrophic ones.

Guideline 6: If a rather constant environment is inevitably getting into a more dynamic state the changes should be damped as much as possible.

Guideline 7: Where natural dynamics occur we should not tame them, and whenever this is inevitable we should replace the natural dynamics by a comparable form of cultural dynamics, for example introducing grazing on a cut-off desalinating natural salt marsh.

Finally we may plea for an amalgation of the conservation-ecological ideas exposed here with both ecosystem-function based ideas on environmental management (e.g. WATT 1973 and HOLLING, CLARK 1975 who also presented guidelines) and with biogeographical theory as developed by MACARTHUR (e.g. 1972) and applied by DIAMOND (e.g. 1975) and WILSON, WILLIS (1975) to the designing of nature reserves. How effective simple comparative studies of nature reserves of different size and age can be was shown by PETERKEN (1974). Such work is almost lacking in West European conservation ecology!

Beyond nature conservation and management we have to develop an environmental planning, in which the ecologist's strategy changes from a more passive adaptive approach to a more active directive approach. The previous Symposium of the Gesellschaft für Ökologie was partly devoted to this new development, which we find represented both in Germany and the Netherlands (ANON. 1977; SCHREIBER 1977; van der MAAREL, DAUVELLIER 1978; LAHAYE et al. 1979). Environmental zoning (van der MAAREL 1978) is becoming a major tool here to which nature management may be linked very well.

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