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ON FOREST STABILITY

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## ON FOREST STABILITY

#### M. Van Miegroet

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Stability, is given a wide range of content in forestry. It is used to characterize a structural as well as a functional state and refers to the object as well as to its use. Because of the need for unequivocal definitions, it is advisable to give the object precedence over its use : Optimal forest use is only possible if the forest itself is in an optimal condition, both structural and functional.

Silvicultural research and treatment must also be given a broader background through confrontation of forestry opinion with contemporary ecological thought. Nature and the forest should be treated as realities, not as myths, means of social agitation and exclusive objects of economic use or financial gain.

#### 1. Stability

In applying the stability principle to ecosystems and plant communities, two lines of thought are followed : One basically goes out from species composition, the other from resistance of the plant community to disturbance.

#### 1.1. Species composition

<u>Clements</u> (1916), <u>Odum</u> (1969), <u>Horn</u> (1974), <u>Kuyken</u> (1979) a.o. consider stability as a relative steady-state equilibrium in the average species composition. It is reached after a period of variable length over a sequence of successive stages. The driving force behind the process is progressive community control of the physical environment or increasing homeostasis with it, resulting in maximal protection against perturbation (<u>Odum</u>, 1969). <u>Whittaker</u> (1970) considers such a state as the end point of succession, producing a climax community with a relatively stable species composition and a steady function. Species composition and function show a high degree of adaptation to the habitat and are essentially permanent. <u>Whittaker</u> (1970) links functional and structural aspects of succession and climax, although he thought this unadvisable before (Whittaker, 1965).

The opinions of Whittaker-Odum, concur with the convictions of Braun-Blanquet (1965), Braun (1950), Hudson (1957) and Daubenmire (1968) that stability reflects a particularly well-adjusted configuration of species as a consequence of uninterrupted evolution until a species combination is established, best suited to climate and site. Gleason (1926, 1927) expressed a nearly identical view, however adding that stable species composition and steady-state equilibrium were mainly reached as a consequence of running out of available species under the given conditions of time, site and space. This idea is indirectly supported by <u>Horn</u> (1974) stating that " ... stability is defined as the absence, or inverse, of species turnover and populations fluctuations." <u>Kuyken</u> (1979) also follows the line of thought of <u>Daubenmire-Whittaker-Odum</u>, expressing that a permanent species configuration is essential to the state of stability. He believes that increasing stabilization of the physical environment promotes species diversity, creating a higher degree of global stability on the broader ecosystem level, better and more complete as more time for adaptation is given.

Three types of community stability are distinguished :

Internal stability characterized by a certain permanence in numbers of species and individuals and thus by restricted change in time.

External stability expressed by the ability to resist external influences and characterized by its

resilience :	the ability of an ecosystem to return to the condition in which it was prior to disturbance ;	
elasticity :	the swiftness of recuperation ;	
amplitude :	the limits between which stability can be achieved or can be reconstructed.	

Cyclical stability or the evolution from disorder to order following well-defined and recurring cyclical patterns.

Internally stable systems are considered as very resistant against external natural disturbance, but highly sensitive to human intervention, especially if no time for adaptation is given (<u>Kuyken</u>, 1979). This is in fact a statement of opinion.

A more differentiated approach toward stability in species configuration is taken, among others, by <u>Clements</u> (1916). He makes the distinction between global stability when all successions on a site lead to a similar species combination at equilibrium and a state with <u>multiple</u> stable <u>points</u>, when different species combinations can be reached. <u>Clements</u> is a precursor to the mosaic theory, formulated later by <u>Aubréville</u> (1938,1969). He rejects the unidirectional character of succession and the unavoidable linking of a permanent set of species with a given physical environment as the ultimate stage of progressive community development.

12. Resistance

The concept of permanent species composition as a typical asset of the climax equilibrium, reached after an internally controlled, directional and undisturbed succession ( of

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species and/or stages) is opposed by <u>Raup</u> (1938,1964) <u>Lewon-tin</u> (1969), <u>Henry and Swan</u> (1974), <u>Connell</u> and <u>Slayer</u> (1977) and received with reserve by <u>Drury</u> and <u>Nisbet</u> (1973). They consider a system as stable if it persists despite perturbations (<u>Connell</u> and <u>Slayer</u>, 1977) and indirectly reject internal control of succession by the community. Stability, thus defined, can present two fundamental aspects (<u>Henry</u> and <u>Swan</u>, 1974):

adjustment stability when a system reacts by giving way to perturbation and subsequently recovering the original state ;

conservation, endurance or persistence when a system reacts by not giving way at all to perturbation.

Lewontin (1969), in agreement with the opinions of <u>Clements (1916)</u> and <u>Aubréville</u> (1938), accepts the possibility of quite different states of stability within a restricted space. He considers a point as stationary (stationary point) if a system does not change because the transformation vector at that point equals zero. If all transformation vectors nearby point to the stationary point, it is also a stable point. If the system returns to this stable point after any degree of perturbation it is <u>globally stable</u>. <u>Lewontin</u> (1969) expressed the relativety of stability

Lewontin (1969) expressed the relativety of stability and perturbation by drawing attention to the importance of scale. It is still more explicitly claimed by <u>Connell and Slayer</u> (1977) stating that all pronouncements about stability are of limited value unless the scales of time, space and intensity of perturbation are defined in relation to the organisms comprising the community. The latter restriction points to the necessity of changing space scales in the analysis of forest stability as the stand develops and the individual tree grows from seedling to maturity over a long period of time.

Connell and Slayer (1977) challenge the assertion of the existance of large tracts of climax unchanged over several generations as unrealistic, speculative and based only on impressions. They require as a basic condition for the stability of a system or a community that, on a scale of a generation time and over a large enough tract, early and late succession stages persist despite regular perturbation. The scale of time must be large enough to cover the generation period of the species with the highest average life expectancy and to permit the whole range and intensity of perturbations, typical for the site, to occur. The area under consideration must be large enough to assure sufficient diversity and to allow perturbations, opening up new sites, to take place at intervals no longer than the persistence period of early succession species.

The observations of Lewontin, Henry and Swan, Connell and Slayer cast doubt upon the validity of the approach by Daubenmire,Odum and their following, who assume, by necessity, but without sound proof, the homology between a spatial sequence, visible at one time, and a long-time sequence of vegetation types on a single site (Drury, 1973).

# 1.3. Evaluation

There is no generally accepted definition of ecological stability. It is not clear whether stability indicates a dampening in the fluctuation of the numbers of species and individuals or a long period of survival of actual species until their ultimate extinction ( Brookhaven Symposium, 1969 ). To explain the state, the pattern and the process of stability, the choice is between a determinist and an oppor-

tunist view.

The determinist model accepts the basic changableness or instability of the site ( cfr. Raup, 1964 ), as well as the close relationship between site and plant community as a driving factor. The site is subject to change by the community and an unavoidable and predictable combination of species arises at the end of evolutionary development, controlled by the plant community. Concurrence is replaced by coo-peration in the course of succession ( Kuyken, 1979 ) and more specialists make up the community ( <u>Odum</u>, 1969 ; niche specialization ). The dynamic decreases gradually and maximal homeostasis is reached at the end of the adaptation period.

This pattern corresponds to an internally controlled, closed system, reflecting the idea of conservation of nature without intervention. There is however no proof for the replacement of concurrence by the cooperation as a normal occurrence.

The determinist model is not based on direct observation. Long-term change must be deduced from the study of short-time spatial sequences, needing the substitution of time by space, judged acceptable and necessary by <u>Gleason</u> (1927), but re-jected by others ( <u>Drury and Nisbet</u>, 1973 ). Neither does this model of community development concur with silvicultural experience on forest evolution and stand growth. It is a seri-ous impediment to forest treatment. The opinion of <u>Odum</u> (1969) that diversity and niche specialization increase during transit from the developmental to the mature stage as a succession approaches climax, runs contrary to observations in the forest that species diversity and specialization reach a maximal level during the regeneration period when the dynamic of change is also maximal. The relative differences in height between individuals are maximal during the seedling phase. ( H. Van Miegroet, 1978 ; J.F. Verhegghen, 1979 ). In the early stages of forest regeneration seedlings are abundant ( up to 1 million/ha and more ), but very small in size. Their absolute space requirements are extremely limited, but relatively as high or higher as those of adult trees. Early root development is important and essential. Seedlings provisionally belong to the herbaceous stratum, where they are not well protected. In such a situation of stress, only individuals, establishing under conditions, best adapted to their specific requirements, have a chance to survive. Survival implies maximal equilibrium between migrants and micro-site conditions, resulting in a high degree of specialization. The main cause of frequent death during the first months and years, is the low degree of individual resistance to external influences and loss of resistance, due to bad establishment, marginal

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micro-site conditions and insufficient release of energy and nutrients. In mature stages the reduction ratio of stems can reach 1 : 200 to 1 : 2.000 or less. As the number of stems decreases, the remaining trees increase in volume, develop a bigger crown and require more space.

This process of development produces a state of relative egalization and homogeneization regarding stratification, site occupation and species composition.

The experience that external factors drastically influence establishment and forest development is an argument in favour of early silvicultural intervention, especially before and during regeneration.

For the same reasons the opportunist model of stability is more acceptable from a silvicultural point of view. It recognizes fairly frequent major and minor perturbations, interrupting successions in course, often affecting and deeply modifying species configuration.

The acknowledgement of plant communities and forests as open systems concurs with widespread silvicultural opinion :

- Each intervention, well conceived and perfectly executed, is an induced minor perturbation or external influence, kept under control to produce maximal positive effects and reduce negative influences.
- Statements by <u>Clements</u> (1916) and <u>Lewontin</u> (1969) justify selection and early regulation of mixture.
- The viewpoint of <u>Connell and Slayer</u> (1977) that early and late succession stages must persist over large enough tracts to consider a community as stable, gives support to the general idea that forest stability must be achieved through an equilibrated pattern of age classes and optimal distribution of regeneration in time and space.

Even the view of <u>Odum</u> on the characteristics of mature stages are useful as an argument for the need to direct forest stand evolution toward quality selection. The same applies to the importance of the periode of adaptation or recuperation after disturbance (Kuyken, 1979). There is a real danger of not observing long enough recuperation periods in forest ecosystems under human treatment when forest management opts for quick growth, shortening of the regeneration period, drastic reduction of the rotation and diminishing the life span of trees and forests, thus increasing the vulnerability of the system.

Because sustained yield, as well as permanent and optimal forest use are only possible if the forests attain a high degree of ecological stability, all treatment and management must be directed toward perfect control of internal stress, the regulation of external influences and the good use of the potential for change, present in each living community.

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# 2. Patterns of Stability

The creation of a state of equilibrium takes time and a community must pass through several developmental stages to reach it (<u>Leibundgut</u>, 1970; <u>Weck</u> 1949, 1950). The initial phases of forest formation occur when a new site is spontaneously colonized. They also correspond with community restoration after accidental or wilful destruction of the forest. On most sites a considerable number of tree species is available to this end. Differences between the species in morphology, life history, longevity and requirements are responsible for the intricate patterns and combinations, in which they occur on a local or global level.

# 2.1. Succession

<u>Connell and Slayer</u> (1977) consider succession as a process of recovery of a community from perturbation. The rate of recovery is measured by the degree of return to the original species combination. Their view fundamentally differs from the opinion, held by <u>Daubenmire</u> (1966) that : " Succession consists of a unidirectional metamorphosis of a biocoenosis and its ecotope which allows different species to become established, or at least assert their dominance, in a sequence that has many predictable features "

Daubenmire believes that natural selection, by which plants are replaced by others better adapted to complete their life cycle under the new acquired conditions of the habitat, is the process, which controls evolution. Ultimately the population will be restricted to the species capable of completing their life cycle in face of intense competition. To express the functional aspect of succession <u>Mac Arthur</u> and <u>Connell</u> (1966) draw attention to the ( highly disputable and unproven ) fact, that each species alters the environment in such a way that it can no longer grow so successfully as others.

These classical ecological concepts refer to an internally controlled system. They further accept the modification of physical environment by the plant community as the driving force behind succession. Succession, thus conceived, is a consequence of internal stress and its release. The changes are considered as progressive and directional : The replacement of species is predictable ; the characteristics of the replacing species are well-known; it seems possible to recognize instable species; all species and associations are given an assigned place in successional order.

The idea of directional succession and a well-adjusted predictable configuration of species reflects the opinions of Braun-Blanquet (1964), Odum (1969) and Daubenmire (1966). Odum even believes that the same strategy applies to succession as to long-term evolutionary development of the biosphere. The primary base for assigning associations a place in succession are the size of the dominant plants, the number of species and the complexity of vegetation struc-

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ture. The concept of succession is thought to be inseparable from that of climax (<u>Whittaker</u>, 1965). In this view climax itself does not only correspond to a relatively stable species composition, but is also given a functional dimension, being considered as a steady-state, well adapted to the habitat and therefore essentially permanent (<u>Whit-</u> taker, 1970).

Serious objections can be raised against these rather controversial definition of succession and climax. Only <u>Daubenmire</u> (1966) takes natural selection, com-

Only <u>Daubenmire</u> (1966) takes natural selection, competition and concurrence into account. The influence of quasi normal and frequent disturbances or perturbations is nearly completely ignored, although <u>Tansley</u> (1935), as a precursor, already corrected the concept by distinghuishing between autogenic succession, comprising the changes brought about by the action of the plants themselves on the habitat, and allogenic succession, caused by external factors.

tat, and allogenic succession, caused by external factors. The thesis of Odum (1969) , that succession must conduct to a stabilized ecosystem with maximal species diversity and symbiotic links does not concur with silvicultural research on forest growth, stand development and mycorrhizal functions. Neither is there any concordance with observations that, in many cases, individual trees, which make up the ' climax forest ', are present from the start ( Clements, 1916 ; Niering and Egler, 1955 ; Hack and Goodlett, 1960 ; Marguis, 1967, 1973 ; Van Miegroet, 1979 ).

1ett, 1960; Marquis, 1967, 1973; Van Miegroet, 1979). It was demonstrated by Oliver (1978) that, in mixed stands in Central New England, the dominant species of the later stages of development ( red oak ) were established at the same time as the far more numerous and quick-growing species ( red maple and black birch ), which dominated the earlier stages.

There also is no doubt about repeated disturbances of pre-settlement forests of the U.S.A. over the past 1000 years : Full evidence is available that they were badly damaged or destroyed within the life span of the dominant conifers and at least once every 100 years ( <u>Connell and Slayer</u>, 1977 ). <u>Goodlett</u> (1954) and <u>Lutz</u> (1940) consider wind-throw as an active force in determining the structure of soils and Lutz even arrives at the conclusion that all soils, which bear or have borne forest stands, are more or less disturbed.

In the Black Rock Forest, comprising treated and untreated stands, <u>Raup</u> (1938) observes that actual forest types cross old boundaries of cutting and fire areas at random. Individual trees, more than 300 years old, are found on all kinds of site from straight stands on the lower slopes to brush-like stands on the top of hills. In all observed cases old trees match tree species and growth forms around them, suggesting that neither types nor sites changed much during their lifetime. <u>Raup</u> (1964) later objected against the substitution of time and space in ecological analysis, because this method is used as an engine running forward and backward at will. It created an imaginary picture of the forests of the past, used subsequently to evaluate actual forest conditions and predict future developments.

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There is, in fact, enough evidence that the plant community is not a closed but a fairly open system, especially the forest, composed of longlived species, subject to frequent minor and major disturbances. The behaviour of the community is determined by the life history of species and ecotypes available when the last major disturbance of the site took place.

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The fundamental instability of the site is an idea clearly expressed by <u>Raup</u> (1964) and undoubtly implied by the theories of <u>Daubenmire</u> - <u>Whittaker</u> - <u>Odum</u> on the modification of the physical environment by plant communities.

The presence of age-classes in the natural forest (<u>Raup</u>, 1964 : <u>Leibundgut</u>, 1945, 1959, 1960), the evidence on spatial dispersion of even-aged phases in Norwegian virgin forest (<u>Huse</u>, 1963), the doubts of <u>Mark</u> (1964) about structural stability in the selection forest and the constatation of a binomial diametre-class structure in the natural forests of Bosnia by <u>Drinic</u> and <u>Pintaric</u> (1959), all demonstrate the frequency of disturbance. The presence of more or less homogeneous and nearly even-aged phases on extended areas is proof of regeneration within a short time after localized forest degradation or destruction by natural agents. The proportional species content of a forest is more a consequence of major disturbance and of the relative presence of seedbearing species at the right moment, than of internal relationships within the community.

It must be admitted that practically all conceptions on succession and climax or nearly all schematic representations of forest development are, by utter necessity, deductions, not based on direct observation of a complete life cycle.

Forest or forest situations, corresponding to the speculative norms in use to characterize the climax or deduced form the steady-state situation, are quite rare, if existing at all.

It is practically impossible to complete the study of theoretical forest models by factual analysis of concrete forest succession on account of the long life expectancy of most tree species and the puzzling problem of decreasing numbers.

Considering the undisputable frequency and intensity of regularly recurring perturbations, it is acceptable to consider and to treat the forest as a relative unstable system, in which it is advisable to direct ecologically based management toward cyclical change over a maximal period of time.

#### 2.2. The sequence of species

The integral acceptance of the climax-principle must imply that for every region a self-perpetuating climax exists (<u>Raup</u>, 1964), dominated by species, capable of regeneration, that also produced the climax. This deduction is at the origin of the picture of the climax forest as of an all-aged, dense forest, in constant regeneration and dominated by very old surviving trees. The same arguments, used to prove that the european selection forest (Plenterwald) is an abstraction or the result of purposeful technical intervention (<u>Leibundgut</u>, 1945,1946,1959; <u>Van Miegroet</u>, 1965), permit to conclude that the forest with maximal biomass and stability, in a permanent steady-stage equilibrium and with a constant species configuration, is also a construction of the mind. It results from backward projection of actual situations along lines of non-observed succession.

In this view, cyclical change and cyclical stability in managed or unmanaged forests, within limits set by the physical environment, are however not excluded. The cyclical development follows predictable sequences of species, influenced by type, intensity and area of disturbance ( or cutting ), the intrinsic qualities of available species and their life history at the given time and site.

Observations on light and nutrient requirements of tree species, periodicity, intensity and possibilities of dispersal and establishment, reaction and impact on the site, allow to distinguish, within limits, two groups of species :

Early succession species = successional species ; intolerant sp. ; light demanding sp., pioneer sp.

Positive characteristics : large numbers of propagules; early and frequent fructification; good to excellent dispersal powers; potential for long-time survival in a dormant state; germinate and establish without protection; grow quickly to maturity.

Negative characteristics : short life span ; often replaced ; do usually not establish, grow and survive on already occupied sites ; offspring seldom survives in the permanent presence of parents and other adults.

Late succession species =tolerant species ; climax sp.

Positive characteristics : survive in presence of early pioneer species; able to stand more shadow than the species, under the cover of which they establish; long life span; not so often replaced; tend to accumulate.

Negative characteristics : low number of heavy propagules; slow dispersal restricted in space; late and not so frequent fruc-tification.

Controversial characteristics : grow slowly to maturity ; can block resources, eventually preventing establishment of other species and survival of own offspring.

Tolerance is closely related to the efficiency of light absorption and transformation as well as to site conditions. Tolerance and light requirements are variable within populations and species ; they change in the course of time ( Van Miegroet, 1965 ; Van Miegroet and Vyncke, 1969 ).

Based on supposed light requirements, Leibundgut (1970, 1959,1960) accepted the sequence " light demanding species light demanding sp. + tolerant sp. -> tolerant sp. + light demanding sp. -> tolerant sp. -> " to explain cyclical as well as longterm evolutive development in the forest.

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In his opinion forest treatment must maintain, as long as possible, the maturity phase, dominated by relatively more tolerant species, promote the cyclical transition " maturity  $\longrightarrow$  old age  $\longrightarrow$  regeneration  $\longrightarrow$  maturity " and prevent the linear development " maturity  $\longrightarrow$  old age degradation —> " . He believes that relative tolerant, slower growing species, with a longer life expectancy serve stability in different ways.

This line of management concurs, curiously enough, with Horn's opinion (1974), that the forest equilibrium is domi-nated by very shade tolerant species and corresponds to a model of increasing competitive ability. His statement would be more correct if the term " relative tolerant species " were used : Moderately tolerant species are in fact in the majority (<u>Stephens and Waggoner</u>, 1970). The common view on the moment of establishment of

tolerant species needs also some correction as it is necessary to reckon with eventual periods of suppression of 20-180 years ( Van Miegroet, 1965 ), especially important for fir in Europe ( Van Miegroet, 1964 ).

During the suppression period, tolerant species survive in a state of suspended or restricted activity. They are unconspiciously present under the cover of less tolerant species of the same or of a lesser age. They retain, for a long time, the ability to react on release by quick emergen-cy ( Mlinsek, 1967 ). They often support more than one period of suppression and can emerge repeatedly. ( Horvath-Marolt 1978, Priv. comm. ). The phenomen was also observed with less tolerant species such as ash ( Fraxinus excelsior L. ), surviving during more than 40 years under a dense oak-horn-beam cover. Seedlings reached less than 50 cm of height but were able to react on release, even to gain dominant status ( Van Miegroet and Lust, 1972 ; Lust 1973 ). There is however some doubt about the real nature

of the first stages of forest establishment and on the exclusive role of pioneer-species. Clements (1916,1928) observed that in the secondary space, such as fire areas and fallow fields, seeds of species, belonging to different stages of succession, were present. In some cases even seeds and fruits of the dominants of all stages, including climax, were pre-sent at the time of initiation. Evidence of invasion of opened-up space by species, representative for the later stages of development at the same time or previous to species, normally dominant in earlier stages, was also found in Connecticut ( Niering and Egler, 1955 ). Simultaneous regeneration and establishment of tree species with widely different light and nutrient requirements, following a variable pattern of dispersal and species configuration, occurs even on the poorest sites ( Van Miegroet 1979 ; Verhegghen 1979 ).

It is therefore inopportune to accept a single or prevailing pattern of establishment ( <u>Connell and Slayer</u>, 1977 ), as it seems evident that the sequence of species is not exclusively conditioned by the modification of the site by the plant community, the highly variable degree of tolerance of the species or their inhibitive powers, but by a combination of all these and other factors. " Time " and " Space "

their impact and relationship are extremely important. Irreversible changes

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occur, biomass is translocated, resources are blocked or released by the sheer passing of time. Space is relevant for the quantity of available resources and the conditions for dispersal and establishment of species, affecting numbers and relationships, interspecific and intraspecific. Therefore it is more logical to explain the sequence

Therefore it is more logical to explain the sequence of species and their combination at maturity by the degree of disturbance of community or site and the actual life history of available components. Depth and development of the root system, resistance against fire and natural ennemies, vitality and reproductive powers at the right moment, are of primordial significance.

Silvicultural treatment can influence most of these phenomens. Regulation of mixture, genetic and phenotypical selection, promotion of deep-rooted species with a dense wood structure, resistant against drought, stormwind, snow and insects can be undertaken quite early. Relative slow growth can be aimed at and put to good use as quick juvenile growth is no warrant for optimal community development.

In the relative open forest system, treatment has various opportunities to make the right choice of species and individuals, to influence their growth, to control relations between site and trees, to direct the sequence of species, to create the best spatial combinations in the ultimate stage of maturity and to perpetuate an acceptable type of cylical equilibrium.

#### 2.3. Disturbance

Disturbance is a rupture of structural and functional equilibrium, seriously changing or destroying the plant community. In the process biomass decreases drastically, the number of components is severely affected and the combination of species profoundly modified.

Disturbances or perturbations are quite frequent (<u>Connell and Slayer</u>, 1977) short cuts to succession. They are associated with man since early times, but also occur without human interference, often provoked by spontaneous fire, flood, landslide, storm, grazing etc. The causes of disturbance are widespread. Even before the appearance of man and beyond his realm, succession was and is frequently stopped or profoundly modified. This leads <u>Raup</u> (1938) to conclude that most sites are fundamentally unstable. The prevalence of even-aged phases and of age-classes in forests, considered as untouched by man ( pre-settlement forest in the U.S.A., european virgin forests), proves the frequency, intensity and extension of disturbance.

The opinion that the actual species content of the forest is more closely related to major disturbance than to relationships within the community, (<u>Raup</u>, 1938), which also expresses the prevalence of external influences over internal control, is acceptable.

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The existence of dominant, widely spaced age-classes resulting from regeneration bursts after perturbation is confirmed by <u>Connell and Slayer</u> (1977). Evidence on disturbances and their effects in the U.S.A. is impressive (<u>Stephens</u>, 1955; <u>Goodlett</u>, 1954; <u>Raup</u> 1954 ; <u>Denny and Goodlett</u> 1954 ; <u>Lutz</u>, 1940,1956, 1959 ; <u>Malin</u> 1956 ). The observations of <u>Raup</u> (1938) on the crossing of actual

The observations of <u>Raup</u> (1938) on the crossing of actual forest types of the old boundaries of cutting and fire areas were mentioned before. After floods in Virginia <u>Hack</u> and <u>Goodlett</u> (1960) observed sycomore and black locust rapidly covering the scarred areas, but 6 years after the disturbance most tree species, typical for the undamaged mature forest, were present again. The seedlings, first colonizing land slides, were identical to species on older, even on pre-Colombian lands slides. On clearcuttings of older mixed hardwood stands, <u>Marquis</u> (1967) found, 5 year after exploitation, shade-tolerant climax species next to intermediate and intolerant succession species in a rate 1 : 1. It is highly probable that the mature stand, arising from such regeneration, will be dominated by the long-lived original species, most important components of the clearcut stands, but also of the regeneration made possible by clearcutting.

Such evidence casts a new light on the real impact of perturbation. It also relativates the functional aspects of the modification of the site by successional species as a prerequisite for succession : In many cases perturbation promotes cyclical evolution, as, quite often, tree species and even individual trees, which will build up the ultimate " climax forest ", are present from the start.

Disturbance is nearly always followed by a burst of regeneration, due to the sudden release of various resources in considerable amounts. In the same way as transition from one life form to another is known to be accompanied by an increase in species diversity, the same phenomen occurs during forest regeneration, whether skilfully planned, directed and executed or spontaneously appearing after minor and major perturbations. In both archetypal regeneration forms, the site is quickly colonized by individuals of about the same age, quite often belonging to extremely different species, eventually blocking resources and preventing further additional invasion for many years. Under very special conditions of site, climate and opportunities for establishment, the presence of a single species, ready for reproduction, can have such an impact that an evenaged, homogenous stand arises after perturbation. Such is the case of massive regenerations of Pinus strobus after the catastrophes of the 17th century in some parts of the U.S.A., with undisputed dominance of this species over a period of 200 to 250 years as a consequence ( Henry and Swan, 1974 ). Analogous effects of grazing and insect damage are equally well known. Oliver and Stephens (1977) by their study of the influence of huricanes between 1500 and 1952 on age-class distribution also concluded that large and small-scale disturbances were basic to the structure of the Central New England forest. The allogenic pattern of succession prevails over the autogenic pattern.

All these observations and experiences tend to prove that perturbation and disturbance are normal phenomens, permanently to be reckoned with. They repeatedly occur within the life span of a tree, the average duration of a development

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cycle or the rotation period of a forest stand. Perturbations must be met properly and put to maximal use by forest treatment. The analysis of perturbation and recovery, of their type, intensity and spatial pattern, of the modifications, they provoke, and the functional relationships, they destroy, gives basic information to silvicultural practice. Forest treatment can be a correction of a spontaneous disturbance, but also a controlled provocation of a minor perturbation. It is a technique to regulate the impact in time and space of disturbance and consists of a set of interventions to reduce negative and to enhance positive effects of change, whether spontaneous or induced. Perturbation is an asset of managed and unmanaged forests, indicating their character of relatively open systems. It is an argument in favour of intensive treatment.

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From an ecological and silvicultural point of view, intensity and location in time and space of disturbance determine the amount of resources released, the opportunities for establishment, the degree of protection and the rate of hindrance, suffered by young plants colonizing the openedup site. Indirectly, they also determine pattern, rate and swiftness of recovery, and, under certain conditions, new species combinations as well as the eventual return to a previous situation.

The same type of analysis, used by <u>Connell and Slayer</u> (1977) to study the hypothetical course of regeneration in their proposed basic models on the sequence of species, can be applied to work out a general picture on the possible consequences of spontaneous disturbance but also of cutting, stand treatment and regeneration practice. The transposition is based on the analogy between area of disturbance and cutting area (A), as well as between intensity of disturbance and I from severe or big (+) to slight or small (-) a simplified outline can be deduced.

## I (+)A(+)

Ecological situation : Large disturbance ( fire, flood, landslide ) with near complete destruction of all vegetation. Silvicultural situation : Clearcutting ( Kahlschlag )

#### Prognosis

Fairly long period of recuperation until a new complete cover is established, as return to the original situation or its equivalent takes time.

Regeneration comes predominantly from the outside :

 The first to establish are species with fairly heavy seeds already present before the disappearance of the forest cover, directly followed by migrating species with a great amount of light seeds and a high potential for dispersal.
 The first phase of establishment is closed within a couple of years.  Climax species, tolerant species or species with infrequent seed production and heavy seeds, not present at the start, move in rather slowly, spreading from the edges toward centre. Prevailing winds have a minor effect.

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# I (-)A(+)

Ecological situation : Wind throwing most of the subdominant and/or dominant trees, but not directly destroying undergrowth and suppressed trees.

Silvicultural situation : Regeneration under cover.(Schirmschlag ).

#### Prognosis

Restricted change of actual species configuration. Fairly slow recovery. Regeneration from in- and outside nearly equally important, the eventual shifting of the balance depending on density and quality of the remaining cover :

- If not directly suppressed by undergrowth, semi-tolerant but fast growing species (beech) are able to establish. They can temporarily suppress more tolerant, but slower growing species, already present as seeds or seedlings (fir).
- Emergency of surviving tolerant species after a long period of suspended or restricted growth activity.
- Slow invasion of tolerant species if space and resources are still available.

# I (+) A(-)

Ecological situation : Destruction of all individuals over a rather small space ( wind, lightning, disease ).

Silvicultural situation : Group regeneration ( Femelschlag )

## Prognosis

Profound local change, eventually producing general change over a large area and/or a long period ( regeneration period; chronic disease) by repetition in time and space. Regeneration comes from the outside :

- Simultaneous establishment of neighbourhood species with restricted dispersal possibilities and by nearby and more distant species with light seed.
- Restricted emergency of tolerant species.
- Slow to feeble growth of intolerant species, depending

on the extent of the area, as the release of resources is restricted by the presence of surrounding adults.

 Relatively tolerant species dominate more and earlier (relative and absolute numbers of individuals)as area is decreasing.

# I (-)A(-)

Ecological situation : Death of a single adult. Silvicultural situation : Selection forest ( Plenterwald )

# Prognosis

Due to limited release of resources the potential for change is reduced and of local importance, creating a confusing picture of general stability :

 The first and most important ensuing phenomen is the stimulation of growth of surviving adults and subdominant components. 1922

- Emergency of tolerant species, eventually released after a supression period of up to 100 years or more.
- Little actual regeneration and no outside invasion as the level of available space and resources is too small

Further exploration of these hypothetical patterns can be a source of inspiration for forest treatment. The choice of cutting space and intensity is an excellent means to manipulate a forest system without endangering its existence. It serves to determine the attainable degree of forest stability, the swiftness of recovery from spontaneous or induced perturbation, the configuration of species, the structural features of a stand and the time needed to create a desirable state.

# 3. Parameters of stability

#### 3.1. Diversity

An essential point of difference between developmental and miture stages of a plant community, as conceived by <u>Odum</u> 1969, is diversity in species and form and their increase with succession. This partly reflects the hypothesis of <u>Margalef</u> (1968), that diversity often increases with succession to reach a certain level and then to decrease again toward the final stages of development, <u>Margalef</u> believes that fluctuations slow down and rythms change as a consequence of reactions directly induced by external factors and as an indirect response to stimuli, associated with ecologically im-

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portant factors. He admits in this way, that plant communities and forests are open systems, responding to induced change. The thesis that diversity can be a reflection of external influences is supported by the observations of <u>Harper</u> (1969) on the influence of myxomatose on species diversity and the work of <u>Milton</u> (1940) on the effects of grazing, confirmed by cynegetic research in Europe.

Increasing diversity over a complete succession-period is, in any case, not a general phenomen. Whittaker (1965) found instances were diversity was as high in disturbed forests as in mature stable forests of the same environment. He also notes a difference in degree of diversity and in reaction to changing physiographic conditions between the tree stratum and the herbaceous stratum.

The study of <u>Hack and Goodlett</u> (1960) on the floodplains of the Little River in N. Virginia confirms previous findings: the youngest and most unstable forests are the most diverse in comparison to those on more stable surfaces, which show the relative lowest diversity.

The review of current opinion indicates that succession does not consist in replacement of a weak community by a better adapted one. Recent ecological and silvicultural research permit to formulate a triple hypothesis to be tested on its practical validity :

- Replacements in the forest occur on the basis of species not of communities.
- The endpoint of forest development can be a state of relative stability over a variable period of time. It is characterized by a fairly stable and functional combination of species. There is no evidence of an unavoidable, long-time or permanent steady-state with maximal diversity as the result of succession.
- The influence of external factors on change is important, but versatile.

Silvicultural practice has repeatedly observed that regeneration, induced by opening-up of the forest over a sufficient large area, nearly always provokes a sudden increase in the number of species. The same applies to site colonization after forest destruction or clear-cutting. The principal reason for this provisional enrichment, next to release of multiple resources, is the temporary neutralization of concurrence and inhibition. It is eventually favored by the migration of species with a high potential for dispersal ( birch, willow, alder ) and by the establishment of tolerant or intolerant species, with heavy or light seeds, already present before the site was uncovered.

From a functional point of view two sets of phenomens, occuring simultaneously or consecutively, promote increasing diversity :

a. Temporary consolidation of the very first migrations of fast growing species, not yet threatened by slow growing, emergent species, with a dense crown and a longer life span.

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 Periodical addition of more tolerant species with restricted opportunities for dispersal.

The level of maximal diversity and its subsequent culmination are induced by :

- Early culmination of growth of the relative light demanding species, often speeded up by the restoration of the forest cover.
- Progressive emergency to subdominant and dominant status of relative tolerant species.
- Multiple selection, affecting all species and populations and provoking a quick and important decrease in the numbers of species and individuals.

By the sheer fact of decreasing numbers of individuals, provided the remaining trees grow well, unrest tends to disappear, the dynamic of change decreases and a temporary state of relative stability and lower diversity in species and forms is attained. A certain degree of homogeneization of the dominant tree stratum by treatment can be therefore acceptable, not in the least because relative homogeneity corresponds with a natural state in the maturity-phase. It can be compensated by greater diversity in the lower tree strata. There is in fact and there should not necessarily be any correlation between diversity in different strata : Their reaction to ecological conditions can be quite different ( Whittaker, 1965 ) and their functions are obviously not identical ( Van Miegroet, 1976 ). For all these reasons a homogenized, although not ne-

For all these reasons a homogenized, although not necessarily homogeneous dominant tree stratum is not to be rejected as a matter of principle from an ecological point of view, provided global stratification is maintained and due attention paid to diversity in the lower tree strata and even in the herbaceous layers.

When evaluating diversity, it is erronous to restrict all considerations to a static situation, to neglect functional aspects and to minimalize the impact of " time " and " space ".

In this respect the relation theory by <u>Van Leeuwen</u> (1966) deserves broad attention. On stability in plant communities he states that constancy in time is always correlated with variability in space and that uniformisation in space is equilibrated by variation in time.

The time factor is directly linked up with growth and change. Due to the fact that the periodicity of seed production, seed morphology, dispersal possibilities and the power of intrusion of species are different, the periodicity of intrusion and the number of opportunities to profit from an advantageous situation are also different.

The interference between time and space compels silviculture and forest management to make choices. The promotors of the selection forest in Europa (Ammon, 1951,55; Dannecker, 1959,1950,1949; Pockberger, a.o.) reject such a choice as irrelevant. They tend to abolish the notion of time and space and believe a forest can be maintained inde-

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finitely in a state, thought to be close to the original natural situation. The application of analysis, based on the relation theory of <u>Van Leeuwen</u>, proves the inconsistency of such statements.

The fundamental choice to be made is in fact between stability in space, corresponding to short-time technological and financial requirements, and stability in time, correlated with long-time social and economic benefit.

Stability in time serves broader human interests. It requires a high degree of activity, sound planning, good manipulation of the forest and an equilibrated relation between time and space.

- presence, at the same time, of all stages of stand development on areas correlated with the duration of each phase;
- choice of regeneration period and regeneration area in function of a desirable initial and/or ultimate combination of species in the dominant stratum;
- regular progress of regeneration, based on the relation between total forest area, life expectancy of the dominant trees and regeneration period;
- distribution and location of the annual or periodical regeneration area in function of spatial equilibrium.

The choice of the conditions of time and space must be completed by selective interventions at any moment, but especially during the early phases of stand establishment and formation. The relation between species and between individuals must be regulated continually. Unsuitably occupied space must be freed by cutting undesirable species and individuals. Treatment can also promote the establishment of valuable species with restricted dispersal opportunities.

The analogy between natural and induced stand evolution is the fundamental characteristic of forest management based on ecological considerations : Treatment anticipates the course of phenomens. It chooses or creates the most favorable circumstances for optimal development. The impact of the external factor on succession, diversity and species combination, recognized by contemporary ecology, is the main argument for intensive stand treatment.

#### 3.2. Production and productivity

The absence of a significant correlation between productivity and diversity is not surprising, because it should imply the linking of functional and structural characteristics. Furthermore it is undeniable that in the mature stages of community development and in stable, well structured and dense forests, relatively huge quantities of resources and nutrients are blocked. Even Odum (1960,1969) has cited cases of gradual and permanent change of species diversity in the course of normal succession in a community where, functionally, a temporary steady-state was reached over a relatively long period. This means at least that productivity and production do not necessarily change with species diver-

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sity or inexorably increase during succession.

Whittaker (1965) has furnished proof that production and diversity are not significantly correlated. More specifically, no increase of production with increasing diversity can be demonstrated. Bio-energetic research ( Margalef, 1968 ) and the analysis of forest growth, show that current production and productivity are, in the first place, a time func-tion. Biomass ( = production ) increases during succession, but the ratio of primary production to total biomass de-creases, as does current production ( = increment ). The study of forest growth show that only during the first stages of development and for a short time current increment ( = primary production ) increases gradually. Increment, in fact, culminates quite early ( between 30 to 70 years for oak and 35 to 65 years for spruce in Europe ). In a developing forest ecosystem the decrease of current production, and of productivity, as indicated by the changing ratio of energy flux to standing biomass, is strongly influenced by the blocking of resources in standing biomass. This culmination of growth in forest stands corresponds with the bio-energetic characteristics of mature stages of plant communities, as described by Odum (1969). The evolution of gross and net primary production, respiration losses and total biomass concur with an explain the evolution of increment and standing stock.

The absence of a positive correlation between diversity and productivity is, however, no argument in favour of forest homogeneization without restriction or a reason to neglect mixtures. It is a fundamental error, often made by forestry, to link structural ( mixture, homogeneity, stratification, etc ), and functional ( production, productivity, sustained yield, etc. ) aspects of the forest presence without further exploration.

Likewise, the decrease of total and net current primary production in the course of succession, the evolution of assimilation and respiration toward nearly equal levels and the continually increasing biomass pro unit of energy flow are no proof for the advisability of shorter rotations. These aspects refer only to purely material aspects of growth, but give no information on real value production or functional importance.

On the other hand, the increase of production through homogenization, admissable under certain conditions, is done by favouring individuals and species with the highest bioenergetic yield. Sometimes it may be useful to stablize a combination of species in a sub-climax arrangement or beneath the level of maximal production. This process of stabilization poses no technical problems, but it has ecological consequences.

As to forest treatment it should be kept in mind that its principal mission is to maximalize all positive effects and to reduce the impact of undesirable influences by putting into application the results of ecological and bioenergetic research :

- Fixation of a forest at a high level of total production is feasible, but it mostly corresponds with a sub-maximal level of productivity and current production.

- Increase of current production and productivity is nearly always a consequence of perturbation or the interruption of a relative state of maturity.
- To minilalize the impact on the total community of an induced transition and of stand regeneration, it is necessary to reduce perturbation in two aspects :
  - a. The area, annually or periodically coming up for regeneration, must be determined by the ratio between total forest area and rotation ( or average life span of the dominant trees or duration of the prefixed regeneration period ).
    - b. The annual or periodical regeneration space is to be distributed over a number of regeneration groups, depending upon the most desirable species combination, a satisfying rate of progress of regeneration and the necessity to maintain over-all forest stability.
- Forest stability is best served by the decrease of both annual regeneration space and the space of the individual regeneration group.

Regular forest regeneration and measures to induce or to provoke it are necessary to increase ecological and economic productivity. It permits the choice of new combinations of species and makes structural improvements possible.

The reduction of its ecological effects requires the restriction of the primary regeneration space and the almost simultaneous lengthening of regeneration period and rotation. Under these conditions a state of cyclical stability can be created over a fairly long period of time and maintained. This state of equilibrium can be combined with maximal diversity, advisable from an ecological, social and ethical point of view.

#### 3.3. Structure and stratification

The idea that forest stability in a self perpetuating state is reflected in forest structure is wide-spread. <u>Daubenmire</u> (1968,1959) holds the opinion that an ageclass distribution, characterized by the abundance of very young individuals with successively older individuals, rapidly diminishing in number following a geometric rate of decline, is a common attribute of a stable population. Inherent to this opinion is the assumption that the age of a tree is reflected by its measurements, more specifically by the diametre of its stem. <u>Oliver</u> (1978) tries to put an end to this misunderstanding and dubious interpretation : " Increasing evidence of stratification and/or broad distribution in mixed deciduous stands does not necessarily indicate an all-aged condition, but may also exist in even aged stands ". This conviction and the necessity to determine age unequivocally

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in retrospective analysis of forest stands, is illustrated by his assessment of age at the root collar of the tree and at 1.40 m of height (<u>Oliver and Stephens</u>, 1977 ; <u>Oliver</u>, 1978).

The idea of geometric age-class distribution is furthermore linked with the picture of a very old, all-aged, extremely mixed, very irregular, highly stratified, undisturbed, natural forest. Raup (1964) considers this as an abstraction, obtained by letting run backward in time a theoretically conceived and never really observed model of succession.

The view of ecologists as <u>Daubenmire</u> a.o. on the optimal forest structure corresponding with maximal stability comes, however puzzling, close to the visionary concept of <u>Anmon</u> (1951,1955) of the selection forest. (Plenterwald) To the geometric rate of decline of each successive class a mathematical expression was given for the first time by <u>de Liocourt</u> (1793). This idea is retained in many attempts to describe and analyse structural stability (<u>Biolley,1920;</u> <u>Schaeffer</u> and <u>Gazin and d'Alverny 1930; Schaeffer</u>, 1937; <u>de Lemps</u>, 1951; <u>Colette 1932; 1951; 1960; Boudru</u>, 52,56, 57). Neither of them, however, did confound or assimilate age with diametre; they all based their analysis of structure on the factual distribution of diametre classes.

There is ample evidence that the picture of the allaged, highly stratified and untouched natural forest is not realistic and does, in no case, correspond with a steady state of maximal stability.

In several European virgin forests, Leibundgut (1945,1959, 1960,1970 ) found unstratified phases covering vast areas nearly always belonging to a single age-class or with a restricted age-class distribution. Most pre-settlement forests in the U.S.A. also seem to be even-aged or comprise a restricted number of well defined age-classes. The frequency of site disturbance and bursts of regeneration after each major disturbance, combined with the inhibition power of certain species (<u>Connell and Slayer</u>, 1977), account for the horizontal dispersion of widely spaced age-classes. <u>Oliver and Stephens</u> (1977) demonstrated that stratification in the deciduous forests of central New-England is allogenic in origin and reflects the intensity of disturbance. They found 6 distinguishable age-classes in the Harvard Forest, correlated with major hurricanes in 1938,1951,1815,1730/1750, 1635 and 1500 or earlier. They conclude that a large disturbance, removing dominant trees, allows establishment of new trees. Species arising together after a large disturbance create a distinct vertical stratification. A small disturbance does not lead to new recruitment, but to accelerated growth of remaining trees. Smaller disturbances, preventing new establishment, but accelarating growth of understory trees, do not provoke vertical stratification - they should rather dampen it but create forest with a mixed upper canopy. The result is a mosaical structure of post-disturbance stands.

Concerning the structure of european selection forests, <u>Mitscherlich</u> (1959), <u>Susmel</u> (1956) and <u>Lust</u> (1966,1968) express serious doubts on the uniqueness of the geometric rate of decline between diametre classes. They neither accept the similarity between the untouched natural forest and the selection forest. Their constatations imply rejection of

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unidirectional and internally controlled forest succession, confirming the views of <u>Oliver</u> and <u>Stephens</u> (1977) : The structure of the selection forest is the result of a sum of minor disturbances. Their analysis can also be used as proof that treatment equals disturbance. <u>Mitscherlich</u>, <u>Susmel</u> and <u>Lust</u> accept a variety of possible rates of decline between diametre classes, each corresponding to a different state of equilibrium, structure and productivity. <u>Lust</u> (1968) even proved that the theoretical state of equilibrium depends upon the maximal tree diametre to be obtained, the number of trees pro ha, the maximal diametre class and the span of each class, all objects of free choice by forest management. It stands to reason that time and space are important

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It stands to reason that time and space are important factors in evaluating the significance of an equilibrium curve. The probability of a geometrically declining rate of classes ( age or diametre ) increase as the period under consideration is shorter and the area bigger. The comparison between actual and theoretical equilibrium curves is even a useful technique to plan management of larger forest areas (<u>Van Miegroet</u>, 1979). <u>As to vertical stratification</u>, proof exists that it is

As to vertical stratification, proof exists that it is mainly caused by age differences, fundamental differences between species and individuals and early specialization during establishment and growth, relating to microcosmic differences in site and growing conditions. The latter phenomen explains the differences in growth between individuals of the same species and age, leading to evident stratification.

The importance of slight differences in age and growth during the first stages of forest development has been repeatedly demonstrated (Van Miegroet 1956, II. Van Miegroet, 1978.) Individuals of the very first wave of establishment, have bigger chances of belonging to the population from which the dominant trees will ultimately arise, whereas latecomers of the same species have more chances to die prematurely. If regeneration periods are short, differences in age become less important within a short time on account of the swift decrease of numbers of individuals and the death of the weakest components, which, in some instances, are also the youngest. In the case of longer regeneration periods, age differences however can be significant because of slow opening-up of the site or the predominance in regeneration of species with heavy seeds, long intervals between fructification or great distances to be covered during migration.

To explain structural stand features, differences between species are normally more important than age differences. The potential for height growth of species and their specific growth rhythms determine stratification to a high degree. Quick growing species with good dispersal facilities, although early culminating in growth are mostly dominant, at least visually, during the first years of stand formation. They are gradually replaced in the dominant story by slower growing, later culminating and more tolerant species, inconspiciously present from the start, but emerging later, or really establishing later, due to infrequent seed production and/or big migration distances.

Whatever the case, stratification is more than a structural quality of the forest stand. It is an essentiel functional characteristic, largely determining forest stability in the ecological and physical sense. Stratification and the degree of forest stability arising from it, are determined by the nature, the extension and the intensity of perturbation, the process of regeneration or establishment, the growth rhythms of major species and their present life history. These aspects are controlable by silvicultural intervention or belong to its field.

Thus human intervention can become a wilful, mild, systematic perturbation, skilfully executed to produce a desirable and predetermined change. By reasoned choice of species, regulation of mixture, good regeneration practice, sound cuttings and permanent control of growth relations between species and individuals in all strata, silvicultural treatment influences and determines the structure of a forest and, consequently, its stability.

The horizontal distribution of space by forest management aiming at maximal stability, is conditioned by available tree species and the accepted time scale, reflected in rotation or given by the physical age or the exploitability of dominant species and individuals. The longer the average period of time between establishment and death or cutting ( rotation ) of the dominant trees, the more time for cyclical regeneration is available and the longer the effective regeneration period RP can be.

Any increase in duration of RP directly produces a decrease of the annual or periodical regeneration area. It indirectly influences the area of the individual regeneration unit or group (AG), which reflects the regeneration method.

The relationship between the surface of the regeneration group and the length of the regeneration period is typical for the management or treatment type :

RP	AG	Туре
Maximal	Minimal	Selection forest (Plenterwald)
Long	Small	Group regeneration (Femelschlag)
Long	Big	Regeneration under cover ( Schirm- schlag )
Minimal .	Maximal	Clear-cutting ( Kahlschlag ).

Long rotations and long regeneration period, especially if combined with small regeneration groups, tend to favour slow growing and more tolerant species. A long regeneration period increases the chances for the establishment of species with long fructification intervals. It favours emergency of tolerant species and, usually, makes growing conditions for intolerant species less attractive.

A high degree of forest stability can be created by promoting vertical stratification and optimal distribution in time and space of all stages of forest stand development. It is obtainable through a system of group stratification, making maximal use of structural and functional differences within populations, based on sound knowledge of the local life history of available tree species.

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#### Conclusions

A forest is not and has never been a closed system. The long\_term evolutionary processes and the short\_term developmental changes it suffers, are partly caused by the relief of internal stress, but mostly by minor perturbations and major disturbances, spontaneously occurring or directly and indirectly induced by man. The relative importance of internal control and external influences depends upon the quality of the site and the fundamental characteristics, numbers and life histories of available tree species. The level of energy resources has a direct influence on species diversity, structural complexity and longevity of individuals and species. It determines, in a way, the resistance of the community against perturbations. Maximal homeostasis of the community with its physical environment, attained in the course of development, but not necessarily at its climax, seems to act in the same sense.

Perturbations are frequent and, mostly, occur independently from forest development. The rupture of internal equilibrium, structurally and functionally, can however cause external perturbation through loss of individual and collective resistance or, at least, magnify its effect in intensity, time and space.

Maximal diversity in species or forms and maximal productivity are not typical for the steady-state equilibrium, characterized, on the contrary, by a certain degree of homogeneization, structural egalization and maximal blocking of resources.

Disturbances nearly always provoke a burst of regeneration and a significant increase in diversity following the release of resources, change in concurrence relationships and temporal neutralization of inhibitive powers. They often create good conditions for the emergency of suppressed trees, the development of seeds and seedlings, already present, and the migration of other species, tolerant and intolerant. The intensity of disturbance and the extent of its area, determine the sequence of species and developmental stages, the life history of species taken into account. In most cases re-occupation of opened up sites is completed within a fairly short time, explaining the relatively even-aged or ageclass structure of some natural or so-called undisturbed forests.

Responsible forest treatment must find its inspiration in the course of natural phenomens. Its primary task is to keep internal stress in the forest community under control by regulating concurrence and selection, to prevent or to reduce the chances for undesirable and destructive disturbances, to build up individual and collective resistance against external influences, to minimalize their negative effects and to put their positive effects to maximal use. Treatment acts as a planned and skilfully executed perturbation under permanent control. It not only serves forest regeneration, but, by the choice of intensity and area of cuttings, it helps to determine, within limits set by physical environment and available material, the species composition. It subsequently undertakes continual selection between species and individuals, creates a structural and functional equilibrium and promotes maximal homeostasis between the forest community and its physical environment. There can be no serious opposition against a certain degree of homogenization and egalization, especially in the dominant canopy, provided it is counterbalanced by optimal vertical straitification and a reasonable distribution in time and space of developmental stages or age-classes. The ultimate aim of forest treatment should be to create and maintain cyclical stability around the maturity stages, promoting sufficient species diversity, productivity and multiple value production.

Optimal structural and functional stability does not concur with the picture of a very dense, uneven-aged, intimately mixed forest, based on extreme reduction of individual regeneration space. Neither does this picture correspond with a steady-state equilibrium in untouched natural forests : It is to be considered as a fixation of a developmental stage, characterized by structural degradation.

The promotion of ecological stability is the primordial mission of silvicultural intervention : From the relative stability of the object depends the relative stability of its use.

#### BIBLIOGRAPHY

1. AMMON W. : 1951. Das Plenterprinzip in der Forstwirtschaft. Bern/Stuttgart. 158 pp. 2. Id. : 1955. Die Erforsrechnung wird aktuell. Schweiz. Zeitschr. Forstw. <u>106</u> (5/7) : 367-373. 3. AUBREVILLE A. : 1938. La forêt coloniale : Les forêts de l'Afrique occidentale française. Ann. Acad. Sci. Colon. 9 : Id. : 1965. Les bois dans l'économie de l'Afrique 1-245. noire; Europe, France, Outre-Mer. Paris. 5. BACKMAN G. : 1945. Wachstum und organische Zeit. Bios. 15. 6. BIOLLEY H. : L'aménagement des forêts par la méthode expérimentale et specialement par la méthode du contrôle. Paris/Neufchatel. 90 pp. 7. BOUDRU M. : 1952. Considération sur la futaie jardinée de chêne. Bull. Inst. Agron/ Gembloux. 20 : 155-177. 8. Id. : 1956, Quelques exemples de futaie jardinées de chêne, Bull. Inst. agron. Gembloux. 24 (2) 109-120. 9.Id. : 1956. Evolution d'une forêt de chêne d'âges multiples soumise à un aménagement contrôlé. Bull. Soc. R. For. Belg. 63 (8/9) : 373-385. 10.Id.: 1957. Futaie jardinée et futaie par bouquets. Ann. de Gemboux. 63 (3) : 165-172. 11. BRAUN E.L. : 1950. Deciduous forests of eastern North Amerida. Philadelphia. 596 pp. 12. Id. : 1964. Pflanzensoziologie. 3. Aufl. Wien/New York. 865 pp. 13. BRAY W.L. : 1915. The development of the vegetation of New York State. N.Y. State Coll. of For. Techn. Bull. No. 3. 14. BROWN M. : 1970. The social responsibility of the sientist. London 282 pp. 15. CLEMENTS F.E. : 1916. Plant succession. Carnegie Inst. Washington. 512 pp. 16. Id. : 1916. Plant succession and in-Washington. 512 pp. 16. Id. : 1916. Plant succession and in-dicators. New York. 453 pp. 17. COLETTE L. : 1932. Aménagement des futaies jardinées par la méthode du contrôle. Bull, Soc. R. For. Belg. 39 : 105-177. 18. Id. : 1951. Le développement du hêtre-type en futaie jardinée. Bull. Soc. R. For. Belg. 58 : 415-420. 19. Id. : 1960. Trente années de contrô-

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le en hêtrale jardinée. Stat. Rech. E.F. Groenendaal. Sér. B. No. 25. 20. COMMONER BARRY : 1971. The closing circle. New York 212 pp. 21. CONNELL J.H. & SLAYER R.O. : 1977. Mechanisms of Succession in Natural Communities and their Role in Community and Organization. The American Naturalist. 982. 1119-1144. 22.DANNECKER K. : 1949. Um das Plenterprin-zip in Sudwestdeutschland. Schweiz. Zeitschr. Forstw. 100 (9): 414-429. 23.Id.1950. Waldbau ohne Zeitbegriffe. Al-gel. Forstzeitschr. <u>5</u> (26/27): 295-297. 24. Id.: 1959. Lehrreiche Waldbeispiele im schwäbisch-fränkischen Weisstannenbereich, Allg. Forstzeitschr. <u>14</u> (31) : 548-549. 25. DAUBEN-MIRE R.F. : 1959. Plant and environment. New York. 422 pp. 26. Id. : 1968. Plant Communities. New York. Evanston and London 300 pp. 27. DENNY C.S. & GOODLETT S.C. : 1956. Microrelief resulting from fallen trees. U.S. Geol. Surv. Prof. Paper. 288. 28. DRURY W.H. & NISBET C.T.T. 1973. Succession. J. Arnold Arbor. 54 (3) : 331-368. 29. DUVIGNEAUD P. & TANGHE M. : 1962. Ecosystèmes et BIosphère, Bruxelles 128 pp. 30. FREY-WYSSLING A. : 1949. Stoffwechsel der Pflanzen. Zurich. 283 pp. 31. GLEASON H.A. : 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club. 44 : 463-481. 32. Id. : 1927. Further views on the succession concept. Ecology. 8 : 299-326. 33. GOODLETT J.C. : 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County. Penn. Harvard. For. Bull. 25, 34. HACK J.T. & GOODLETT J.C. : 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. Y.S. Geol. Surc. Prof. Pap. 347,64 pp. 35, HARPER J.L. : 1969. The role of predatiovegetational diversity. Brookhaven Sympos. Bio. 22 22 : 36. HENRY J.D. & SWAN M.A. : 1974. Reconstructin 48-61. forest history from live and dead plant material. Ecology 55 : 772-783. 37. HORN H.S. : 1974. The ecology of secondary succession. Ann. Rev. Ecolg. Syst. 5: 25-27. 38. HUDSON J.P. : 1957. Control of the Plant Environment. London 240 pp. 39. HUSE S. : 1963. Die letzten Urwaldvorkommen Norwegens. Schweiz, Zeitschr. Forstw.111 (7) : 394-404. 40 KUYKEN E. 1979. Wetenschappelijke achtergronden van het natuurbehoud. Ref. Symposium Vereniging voor Groenvoorziening. Mechelen 1979. 21 pp. 41. LEEUWEN C.G., VAN : 1966. A relation theoretical approach to pattern and process in vegetation, Wentia 15 : 25-46. 42.LEIBUNDGUT H. : 1945. Waldbauliche Untersuchungen über den Aufbau von Plenterwäldern. Mitt. eidg. Anst. Forstl. Versuchsw. XXIV : 219-236. Id. : 1946. Femel-Anst. Forstl. Versuchsw. XXIV : 219-236. schlag und Plenterung. Schweiz. Zeitschr. Forstw. 97 (7) : 306-317. 44. Id. : 1959. Ueber Zweck und Methodik der Struktur- und zuwachsanalyse von Urwäldern. Schweiz. Zeitschr. Forstwes. <u>110</u> (3) : 111-135. 45. Id. : 1960. Résultats d'études de forêts vierges européennes. Italia For. & Mont. <u>XV</u> (6) : 213-218. 46. Id. : 1970. Der Wald eine Lebensgemeinschaft. Frauenfeld 197 pp. 47. Id. : 1978. Ueber die Dynamik europäischer Urwälder. All Forst. Zeitschr. Sonder-helft nr. 24 (686-690). 48. LEMPS F. de : 1951. Futaie jardinée par bouquets et futaies de chêne par bouquêts. Rev For. Française 9 : 577-578. 49. LEWONTIN R.C. : 1968. Diversity and stability in ecological systems. Brookhaven symp. Bio.22. 50.LIOCOURT F. de : 1898. De l'aménagement des sapinières. Bull. Soc. For. De Franche Comté et de Belfort. 51. LUST N.: 1966. Theoretische studie van het plenterevenwicht meer in het bijzonder in de bossen van het gebied van de Venetiaanse

-27-

republick. Thesis R.U.G. Gent. 120 pp. 52. Id. : 1968. Le calcul du coefficient de gradation Q d'après de Liocourt à l'aide du volume total et du diamètre maximal. Sylva Gan-davensis. 19-18 pp. 53. Id. : 1973. La respiration et la photosynthèse de frênes qui poussent dans des conditions différentes. Sylva Gandavensis, 36, 17 pp. 54. Id. : 1973. Etuse sur la teneur en pigment de fênes qui croissent dans les conditions différentes. Sylva Gandavensis. 37. 19 pp. 55. LUTZ H.J. : 1940. Disturbance of forest soil resulting from the uprooting of trees. Yale School of For. Bull. 45 56. Id. : 1956. The effects of forest fires in the interior 57. Id. : of Alaska. U.S. Dept. Agric. Techn. Bull. 1133. 1959. Aboriginal man and white man as historical causes of fire in the boreal forest. Yale Univ. School of For. Bull. 65. 58. MAC ARTHUR R.H. & CONNELL J.H. : 1966. The biology of Populations. New York. 200 pp. 59. MALIN J.C. : 1956. The Grassland of North America. New York ( via 28 ). 60. MARGALEF R. : 1963. On certain unifying principles in ecology. Am, Nat. 97 : 357-374. 61. Id. : 1968/ Perspectives in ecological theory. Univ. Chicago. Press Chicago. 111 pp. 62. MARK J, : 1964. Die gegenwärtige waldbauliche Situation. Allgem. Forstztg. 75 (19/20) : 214-216. 63. MARQUIS D.A. : 1967. Clearcutting in northern hardwoods. U.S. Forest Service Res. Pap. N.E. 85 13 pp. 64. Id. : An appraisa of clear-cutting on the Monogahella National Forest. U.S.D.A. For. Serv. NE For. Exp. Stat. 55 p. 65. MIEGROET H. van : 1978. Differentiatieverschijnselen in spontane verjongingen van esdoorn, Thesis R.U.G. Gent. 91 pp. 66.MIEGROET M. van : 1956. Untersuchungen über den Einfluss der waldbaulichen Behandlung 66.MIEGROET M. van : 1956. und der Umweltsfaktoren auf den Aufbau und die morphologischen Eigenschaften von Eschendickungen in schweizerischen Mittelland. Mitt. Schweiz, Anst. Forstl. Versuchsw. 32 (6) : 230-370. 67. Id. : 1964. Die Position der Weisstanne in Belgien. Schweiz. Zeitschr. Forstw. 115 (9/10) : 492-517. 68 Id. : 1965. De toepassing van de Plentering in Nederland. Nederl. Bosb. Tijdschr. 37 (10) : 310-334. 59. Id. : 1965. Die Lichttransgression und die Lichtreflektion bei Blättern einiger Laubbaumarten. Schweiz. Zeitschr. Forst. <u>116</u> (7) 556-589. 70. MIEGROET M. Van & VYNCKE G. : 1969. Die Transgression der Lichtsprahlung durch Baumblätter unter verschiedenartigen Kunstlichtbedingungen zur Entwikclung gekommen. Sylva Gandavensis. 13. 37 p. 71. MIEGROET M. van & LUST N. : 1972. Aufbau, Wacnstum und Reaktionsvermögen von unterdrückten Eschenverjüngungen. Sylva Gandavensis. 34. 38 pp. 72. MIEGROET M, van : 1979. Voorlopig verslag over de bosbouwkundige analyse van het Neigembos, als uitgangspunt voor een verantwoord beleid en beheer. Onderzoekscentrum voor Bosbouw? R.U.G. 86 pp. 73. Id. : 1979. The initial stages of spontaneous establishment of species under forst cover and on poor stands. Sylva Gandavensis. ( In printing ). 74. Id. : 1979. The basis concept of forest stability. MAB-UNESCO-IUFRO Symposium on the Stability of SPruce Stands. BRNO. 35 pp. 75. MILTON W.E.J. : 1940. The SPruce Stands, BRNO. 35 pp. effect of manuring grazing and cutting on the yiel botanical and chemical composition of natural hill pastures. Journ. Ecol. 76. MITSCHERLICH G. : 1959. Kritische Unter-28 : 326-356. suchungen oder Spekulationen über den Plenterwald. Forst u. Holzw. 14 (24) : 522-523. 77. MLINSEK D. : 1967. Verjungung und Entwicklung der Dickungen im Tannen-Buchen Urwald " Rog ' I.U.F.R.O. Congress München 1967. Sect. 23. 78. Id. : 1967.

-28-

Wachstum und Reaktionsfähigkeit der Urwamldbuchen auf der Balkan-Halbinsel.I.U.F.R.O. Congress. München 1967. Sect.23 79. NIERING W.A. & EGLER F.E. 1955. A shrub community of Viburnum lantago, stable for twenty-five years. Ecology. 36 : 80. ODUM E.P. : 1969. Fundamentals of ecology. hyladelphia. 546 pp. 81. Id. : 1960. Organic pro-356-360. 2nd. Ed. Phyladelphia. 546 pp. duction and turnover in old field succession. Ecology. 41 : 82. Id. : 1960. The strategy of Ecosystem Develop-34-48. ment. Science, 164 : 262-270. 83. OLIVER C.D. & STEPHENS E.P. : 1977. Reconstruction of a mixed-species forest in Central New England, Ecology, 58. : 562-572, 84. OLIVER C.D.: 1978. The development of red oak in mixed stands in Central New England, Yale Univ. School of For. Environm. Stud. Bull. 91. 63 pp. 85. PINTARIC K. : 1959. Urwald in Jugoslawien. Schweiz. Zeitschr. Forstwes. 110 (3) : 163-168. 86. POCK-BERGER P. : 1950. Forstwirtschaft und Waldnatur. Allgem. Forstzeitschrift. 14 (5) : 75-78. 87. RAUP H.M. : 1938. Botanical studies in the Black Rock Forest. Black Rock Forest Bull, nº7. 88. Id. : 1963. Some problems in ecological theory and their relation to Conservation. J. Ecol. 52 : 19-28. 89. SCHAEFFER, A., GAZIN A. & d'ALVERNY. 1930. Sapinières. Le jardinage par contenance. Paris, 100 pp. 90, SCHAEFFER L. : 1937. Le jardinage appliqué aux essences feuillues. Bull. Soc. R. For. Belg. <u>44</u> (7) : 366-373. 91. STEPHENS E.P. : 1955. The historical Developmental Method of Determining Forest Trends, Doc, Thesis. Harvard Univ. 228 pp. 92. STEPHENS G.R. & WAGGONER P.E. : 1979. The Forest anticipated from 40 years of natural transition in mixed hardwoods. Bull. Connecticut Agr, Exp, Sta, nº 17 : 1-58. 93. SUSMEL L. : 1956. Leggi di variozione del parametri della foresta disetanea normale. It for. e mont. 94. TANSLEY A.G. : 1935. The use and abuse of vegetational concepts and 95. VERHEGGHEN J.F. : 1979. terms. Ecology. 16 : 284-307. De verjonging van de es in het Almoeseneiebos te Gontrode, meer bepaald na 1976. Thesis RUG Gent. 87 pp. 96. WECK J. : meer bepaald na 1976. Thesis RUG Gent. 87 pp. 1949. Gestaltung von Bestandesgefüge und Bestandesmischung als Grundlage zum Aufbau eines Dauerhochleistungswaldes. Schweiz, Zeitschr. f. Forstwes, 100 : 486-501. 97 Id. Naturgemässer Wirtschaftswald, Allgem. Forstzeitschr. 5. 97 Id. : 1950. (26/27) : 303/304.

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