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# Ecological stability of forests and sustainable silviculture

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**Abstract**

The ecological stability of forests is described and subsequently analyzed and discussed in relation to human impact. Forest management and utilization have a considerable influence on the stability and sustainability of forest ecosystems. Additionally, other human activities such as pollution and global climate change affect the present and future stability of our forests.

The main components of stability are resistance (inertia, immovability) and resilience (recoverability). These are analyzed with respect to genetic diversity within and between species and in relation to the biogeochemical cycle. The possibilities and constraints of silviculture are then discussed in relation to sustainable management practices and strategies, i.e. choice of provenances and species, including species mixtures, tree breeding, harvesting practices, as well as the silvicultural system applied. Finally, forest decline is discussed in relation to stability by means of a stress integration model.

*Keywords*: Forest ecosystem; Sustainability; Ecological stability; Silviculture; Forest decline; Management; Genetic variation; Biogeochemical cycle

## 1. Introduction

Extensive forest declines during the last decade, especially in Europe but also in other parts of the world, have initiated the discussion on the stability of forest ecosystems. Initially the forest decline discussion focused on single causes such as acid rain, ozone, climatic extremes, pests, etc. Today most scientists look upon the so-called 'novel forest decline' as a decrease in the stability of the ecosystem, caused by a number of partly interacting stresses, some of which are anthropogenic (Ulrich, 1987, 1989; Führer, 1990).

In forest management the traditional concept of stability focuses upon the trees and is defined mainly in relation to catastrophic events such as damage by snow and wind. Thus it lacks an ecological basis. The compartment 'trees' should not be considered in isolation but must be viewed as part of a complex interacting system of autotrophs, heterotrophs, and the physical environment. Hence the concept of forest stability must be expanded to embrace the general framework of ecological stability in order to recognize and solve ecosystem problems posed by present and future anthropogenic impacts.

We have to learn to manage ecosystems instead of stands in order to assure sustainability in a broad sense, which implies securing long term productivity and vitality, safeguarding biodiversity and protecting adjacent ecosystems. Hence, it is of outstanding importance to gain more basic information about the interactions between silvicultural measures and stability. Silviculturists must be aware that by manipulating forest structures, they may permanently interfere with fundamental, partly self-regulating processes of the ecosystem responsible for system stability and productivity.


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Consequently the aim of this article is to define and discuss the basic principles of ecological stability, to apply these principles in a forest ecosystem context, and to analyze silvicultural measures and the effect of other human activities such as pollution and global change within this conceptual frame.

## 2. Ecological stability

Ecosystems are open thermodynamic systems characterized by input and output of energy and matter. Stability may be defined as the ability of a system to remain near an equilibrium point or to return to it after a disturbance (Orians, 1975; Harrison, 1979). Hence, ecosystem stability is characterized by a dynamic equilibrium (steady state) achieved through interactions among functional groups of organisms and the physical environment. For example, the nutrient cycling results from the functional synchrony of autotrophs, heterotrophs, the atmosphere, and the soil compartment.

Ecosystems have numerous features, some are characterized as relatively stable, others are highly unstable. Hence it is important to define the feature (state variable) in focus when discussing stability. These variables can be divided into structural and functional features. Structural features include habitat diversity, floral and faunal diversity, biomass, age and size span, spatial distribution, etc. Functional features include among others energy dynamics such as net and gross production, production to respiration ratio, water use efficiency, energy flow in trophic structure, element cycling, and degree of organism interaction, etc.

Furthermore, stability must be viewed as a function of time and space. The persistence of species as a stability feature is closely connected with the spatial dimension of ecosystem (Grimm et al., 1992). The impact of different silvicultural measures and management systems on ecosystem stability suggests a certain spatial dimension (the mosaic cycle concept; Remmert, 1991), and that the temporal horizon should exceed more than one tree generation, thereby including the regeneration stage.

Stability within an ecosystem context must be analyzed in relation to perturbations (disturbances). Such perturbations may be defined as events (forcing functions) which do not naturally occur in the system, or as fluctuations beyond the 'normal' range of forcing functions defining the system.

Perturbations may be natural or anthropogenic (man made). Some natural perturbations include climatic fluctuations, variation in density of herbivores, predators, and pathogens, fire, wind, snow, and erosion. Anthropogenic perturbations may include system manipulation through utilization (clearing, harvesting, draining, use of pesticides and other chemicals, introduction of exotic species and unadapted populations), pollution (acid deposition, $SO_2$, ozone, and the $CO_2$ emission promoting a global change of climate), and the import of exotic (alien) organisms.

Numerous authors, working mainly with natural ecosystems, have defined stability in terms of buffer capacity, constancy, persistence, inertia, resistance, elasticity, cyclicity, integrity and resilience (Lewontin, 1970; Holling, 1973; Orians, 1975; Zonneveld, 1977; Haber, 1979; Harrison, 1979; Gigon, 1981; Ulrich, 1987; Kay, 1991; Jørgensen, 1992). However, the same term is often used by different authors for different aspects of stability, and a general agreement upon types and definition of ecological stability properties is still pending (Grimm et al., 1992).

When thermodynamic systems are moved away from their local equilibrium, they shift their state in a way which opposes the applied gradients and moves the system back towards its equilibrium attractor. In simple terms, systems have the ability to resist being moved from equilibrium and a tendency to return to the equilibrium state when moved from it (Schneider and Kay, 1993). The breakdown of stability into the two principal components resistance and resilience (as suggested by Webster et al., 1975) seems therefore appropriate to gain a certain degree of simplification in order to discuss and visualize the most important aspects of ecological stability. Correspondingly, (Grimm et al., 1992) rank resistance and resilience among the most important stability concepts related to specific properties and measures in ecological systems.

Resistance (inertia, immovability) comprises the ability of a system or the component in focus to resist external stress. An ecosystem feature that is easily changed has a low resistance, whereas one that is difficult to displace is resistant and in this sense stable. Resilience (recoverability) comprises correspondingly the ability of a system feature, when changed by a perturbation, to return to its former dynamic state. A

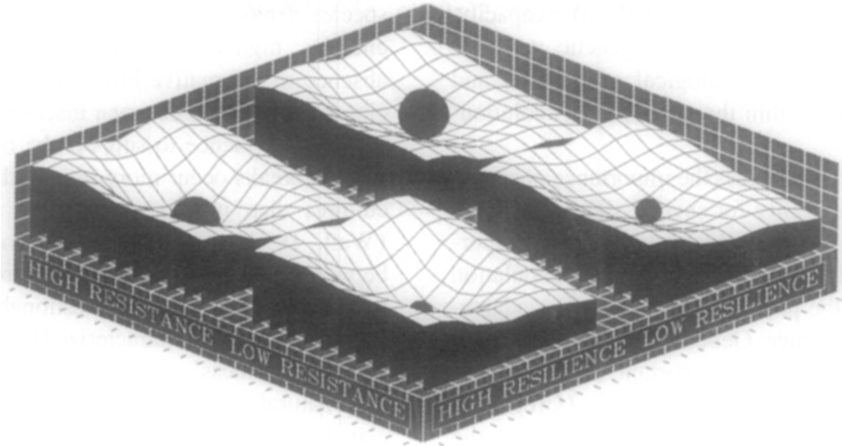


Fig. 1. Four images of stability are shown as combinations of resistance (the size of the marble: large, high resistance; small, low resistance) and resilience (the size of the hollow in the 'stability landscape': deep, high resilience; shallow, low resilience).

system that returns rapidly to its original steady-state is more resilient than one that responds slowly.

In order to visualize resistance and resilience, four images of stability are shown by means of potential energy in Fig. 1. In this very simplified way of illustrating these complex features, stability is shown as the ability to resist external forces in order to keep the marble (the system feature or the state variable focused upon) within a steady-state, respectively within its amplitude of recoverability or resilience (the hollow in the 'stability landscape'). Resistance is illustrated by the mass (graphically the size) of the marble. It requires a stronger perturbation to move the big marble (the highly resistant system) within the area of steady state (the bottom of the hollow) and to displace it outside the area of resilience (lift out of the hollow), than it does the small marble (the less resistant system). Resilience is denoted by the size and shape of the hollow in the 'landscape', illustrating the domain of attraction. More energy (a stronger perturbation) is required to displace the marble out of the deep hollow (the highly resilient system), than is required to move the marble out of the shallow hollow (the less resilient system).

Under unperturbed conditions, all four simplified ecosystems (hollow in the 'landscape' and marble) remain within their area of dynamic steady state (the bottom of the hollow). However, a perturbation might exceed the limits of local referential dynamics depending on the mass of the marble and the size of the hollow; hence the system or the ecological feature (structural or functional) focused upon will change permanently evolving into another dynamic equilibrium.

In the following discussion stability is analyzed in relation to its basic components. In this context an ecosystem may be defined by the two main components: 'information' and 'matter'. Thereby, 'information' means DNA and 'matter' the physical environment. By means of outside energy flux the information (the living organisms) 'organizes' the system, creating functions and structures in a locally reduced entropy state. Consequently, the discussion of the basic principles of ecosystem stability is related to (i) genetic diversity (information) and (ii) the biogeochemical cycle (matter).

### 2.1. Stability and genetic diversity

#### 2.1.1. Variation within species

Populations respond to spatial and temporal variation in the environment by selection and adaptation. Hence, the most important aspect of genetic variation is the buffering it provides against fluctuations in environmental conditions (Hattemer, 1994). Adaptation involves physiological and evolutionary aspects (Larsen, 1988): the individual reacts to a perturbation through physiological adaptation, which is limited by the homeostatic capacity of its genotype. If not all genotypes in a population are physiologically able to buffer the perturbation, selection processes will induce adaptation at the population level (Hattemer and Ziehe, 1987; Hattemer and Müller-Starck, 1989). The adaptability of a population, i.e. the potential buffer capacity, is therefore closely related to the genetic variation within the genotype (physiological adaptation) and between genotypes within the population (evolutionary adaptation).

Orians (1975) emphasizes the importance of spatial environmental variability for several stability properties of ecological systems. This may reflect the importance of maintaining genetic diversity at the population level to increase the potential (evolutionary) adaptability and thus resilience. Genetic diversity of individuals is correspondingly important in buffering environmental variability through time (Gregorius, 1985). This reflects the homeostatic capacity of the genotype, which is an important feature of resistance.

A reduction in the genetic resource base of species (genetic variation within and between individuals) may consequently have a profound effect on both ecosystem resistance and resilience. This is demonstrated by Larsen (1986, 1994) by explaining the decline of central European silver fir (*Abies alba* Mill.), pronounced during the last 15 years (and several other periods during the last centuries), as a result of genetic variation lost during the last glaciation. These results are supported by studies of genetic variation by means of polymorphisms of isozyme gene loci (Bergmann et al., 1990). Lagercrantz and Ryman (1990) postulate similar genetic 'bottle-neck effects' in central and southeast European Norway spruce (*Picea abies* (L.) Karst.).

### 2.1.2. Variation between species

One of the central doctrines in population ecology is that stability increases with the degree of interrelationship in the food web. Increased trophic web complexity leads to increased community stability (MacArthur, 1955; Elton, 1958; Pimentel, 1961). In nature population stability is not always associated with faunal and floral diversity. Correspondingly, May (1973) concludes that the relation between complexity and stability is substantially more complicated.

Floral diversity has been shown in many cases to reduce pest problems. Conversely, monocultures have often led to an increase in insect and disease problems (Gibson and Jones, 1977). Consequently, many scientists recognize outbreaks of pests or diseases as an ecological rather than a pathological problem (Vasechko, 1983). Several factors may dispose single species stands to insect attack including lack of natural enemies, high concentration of food (host plants), absence of alternative hosts and the development of closer coincidence between insect and plant phenologies. The evidence to support the opinion that insect pest outbreaks occur more frequently in forest monocultures than in mixed stands is still inconclusive (Watt, 1992). However, the common comparison between natural diverse (mixed) forest ecosystem and man-made monoculture is questionable, since the monoculture is not only characterized by simplicity but also by 'unnaturalness'.

In natural ecosystems resistance is apparently associated with diversity (species richness); this suggests that ecosystem response to perturbation primarily depends on the adaptive characteristics of the populations in the system. These characteristics reflect historical perturbations and the continual evolution of associated species. Selection acts to maximize fitness of populations in the system and not directly on stability properties of the system as a whole. Ecosystem response to environmental variability is consequently a complex product of coevolution. Coevolution may, depending upon the magnitude of perturbations and their distribution in time and space, therefore be of outstanding importance for stability of ecological systems.

A stable (predictable) environment makes the development of a complex (mature) ecosystem through succession and coevolution possible. The development of ecosystem maturity is a function of higher energy and matter cycling, higher average trophic structure and web complexity, higher (bio)diversity, longer life cycles. In this context, complexity might be associated with system resistance, mainly owing to well developed biological population control mechanisms. A relatively simple system might develop under more unpredictable environmental conditions owing to the maintenance of simple (early) successional stages. Its robustness can in this context be attributed to system resilience. Consequently, complexity increasing resistance seems to act negatively upon system resilience, hence it is easier for a relative simple system than for a highly complex (interactive) system to return to its former state following a disturbance.

Species richness may additionally contribute to stability through risk alternation, since different species respond differently to biotic as well as abiotic stresses. Further, many insects and pathogens are spread more rapidly in homogeneous systems (monocultures) owing to contact (roots, crown) between individuals of the same (susceptible) species or clone (Heybroek, 1982).

### *2.2. Stability and the biogeochemical cycle*

The long-term productivity of forest ecosystems is closely linked with the nutrient cycle (Webster et al., 1975; Swank and Waide, 1980; Ulrich, 1987, 1989). For most natural ecosystems, recycling rates of nutrients limit primary production and regulate, at the source, biotic energy flow through the trophic structures.

Major perturbations may disturb the biogeochemical cycle through temporal and spatial aberration (decoupling) of biomass production and mineralization (Ulrich, 1987). The stability of sites following disturbance (natural or anthropogenic) is therefore closely related to the ability of the system to recycle nutrients and maintain structural and biotic integrity. Hence, perhaps the most important aspect of stability in managed forest ecosystems is the ability to retain soil fertility following pollution (soil acidification) and management-induced perturbation (harvest, cultivation). Monitoring nutrient loss rates may provide a useful indication of ecosystem response to disturbance.

Stability in this context is mainly due to resistance. Key features include nutrient and water storage capacity, the ability of the soil to buffer acidity formed during net nitrification, and to prevent or diminish the leaching of nitrate and other nutrients. This type of stability corresponds to Ulrich's 'elasticity' (Ulrich, 1987) or is simply expressed as 'buffer capacity' (Jørgensen and Mejer, 1977; Ulrich, 1992). System resilience can be conferred by mineral weathering, which provides the system with available nutrients. Weathering of silicate minerals is an important stability parameter, especially in managed forests characterized by a significant export of base cations due to harvest and deposition of acid compounds, since it is the main natural base cation source. Further, natural and anthropogenic (pollution) airborne sources of elements may contribute to nutrient supply and thereby to system resilience.

Species composition might affect the stability of the biogeochemical cycle, mainly due to species specific turnover and storage rates (Swank and Waide, 1980). Further, the forest floor vegetation plays an important role in the cycling and retention of nutrients (Bormann and Likens, 1979), especially in phases where the dominant vegetation (the trees) is affected owing to controlled (thinning, clear-cuts) or uncontrolled disturbances (wind throw, etc). The ground vegetation promotes the percolation of water, minimizes erosion and contributes to diversity and activity of heterotroph organisms including decomposers, thus stabilizing the biogeochemical cycle by balancing production and mineralization. Therefore, the quantity and quality of the ground vegetation may significantly contribute to biogeochemical stability.

## 3. Silviculture and stability

Most works dealing with ecological stability are based on theoretical rather than experimental research. Consequently, this theoretical knowledge has not been applied in management for stability in an ecological sense. The following discussion of possibilities through silvicultural measures to ensure stability of managed forests will primarily focus upon the stability of the tree species compartment in terms of structural features (genetic variation, species diversity, age and size, life span) and functional parameters (long term productivity including maintenance of biotic and abiotic resources).

In natural ecosystems there seems to be an inverse relationship between resistance and resilience. Hence biotic factors which tend to increase resistance (diversity, complexity, coadaptation) decrease resilience and vice versa. This interrelation between resistance and resilience seems to reflect the development of the ecosystem as response to the types of perturbation commonly encountered by the system and their distribution in time and space (see also Section 2.1.). However, man may influence resistance and resilience independently, since they are not obligatory functionally linked. This emphasises the danger that management, unaware of the basic principles of stability, might reduce both resistance and resilience and thus decrease stability. Numerous examples exist, including introduction of unadapted species and provenances, reduction of the genetic resource base through selection and breeding, large scale conversion of natural mixed forests into monocultures, the clearcutting system in combination with the use of herbicides, homogenization of structures beyond the 'natural' variation, shortening rotation age in combination with whole-tree harvesting, etc. However, this also pinpoints the possibilities to establish and to manage forests focusing on both resistance and resilience in order to increase system stability.

### *3.1. The choice of species and provenances*

Species selection is probably the most important single manageable factor in securing future stability. The main prerequisite for choosing plant material is to select species and to use provenances which are adapted to the biotic (pests) and abiotic (climate, soil) environment of the specific site including man made perturbations.

Local species and populations ensure a certain degree of adaptedness, since the population genetic structure reflects the fluctuations in local environmental forcing functions. In contrast, numerous examples demonstrate the dangers of using unadapted species and provenances. Even comprehensive species and provenance trials may lead to erroneous conclusions, since not all parameters affecting survival and productivity (mostly extremes) are encountered during the period of testing. A major weakness is that the testing period is too short compared with the rotation age of the species. Further, species and provenance trials normally cover only a small number of potential sites, making spatial extrapolation of the results rather uncertain. As a consequence, introduced species and provenances often contribute to a reduced system stability due to lack of adaptedness (resistance). Changes in the environmental forcing functions caused by climate changes and the introduction of exotic alien organisms (pests) may drastically reduce adaptedness of local species and populations.

Fig. 2 illustrates the proposed concept of stability in relation to climate change. A system, which in the 'good old days' ('1990') was stable (high resistance and resilience), loses stability owing to decreasing climatic adaptedness of its organisms (populations) and reduction in both physiological and evolutionary buffer capacity. Resistance and resilience decrease, and the system develops into a susceptible state ('2040', and especially '2090'). Consequently perturbations, which might exceed earlier 'normal' levels, eventually lead to permanent changes.

The question of adaptability is the main problem in clonal forestry. Stands with only one or a few genotypes have a greatly reduced adaptability on the population level (evolutionary adaptability) leading to lack of resilience. Forest stands with one or a few genotypes especially selected for good performance in a particular environment, are unlikely to have enough buffering capacity in an uncertain future (Perry and Maghembe, 1989).

Artificial regeneration traditionally using a limited number of plants raised in modern plant production systems limits the possibilities of natural selection against undesirable (selfings) and poorly adapted genotypes during stand development. This might lead to reduction in both resistance and resilience, thereby affecting future structural stability. These problems are discussed by Hattemer and Müller-Starck (1988), Hattemer (1994) and Ackzell and Lindgren (1994). However, the ecological significance of such limitations in the selection potential in artificial established stands is only insufficiently analyzed and far from understood.

### *3.2. Forest tree breeding*

Selection for certain phenotypic characters increases the risk of an uncontrolled change of the genetic resource base, thereby promoting the possibility of diminishing the potential adaptability (Gregorius et al., 1979; Ziehe and Hattemer, 1989). This is of special importance in relation to the present atmospheric pollution situation (Gregorius, 1986). Traditional forest tree breeding is based upon the assumption, that the local environment and its amplitude of fluctuation in the past can be extrapolated into the future. Hence progeny testing, which provides the basis for future breeding populations, is basically retrospective (Larsen, 1990).

Hence, the breeding goal, in the context of stability, aims to increase resistance by optimizing local adaptedness. The increasing anthropogenic impact upon the global environment (pollution and the $CO_2$ increase promoting a climate change) makes the occurrence of unpredictable changes in the local growing environment highly probable, even within the next tree generation. Traditional breeding for maximal growth and

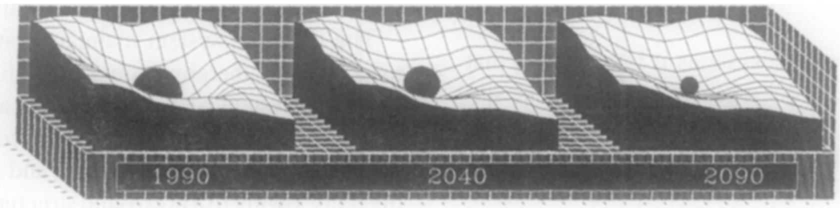


Fig. 2. Forced by climate change, the ecosystem resistance and resilience decrease over time as a result of a reduction in adaptedness and adaptability of its populations, and the system develops into a susceptible state.

local adaptedness might, under these circumstances, develop into a 'no through road'.

Increasing stability by breeding for potential adaptability may therefore be the only possibility to 'prepare' our forest tree populations for an uncertain future (Larsen, 1991). The multiple population breeding concept (Namkoong et al., 1980) might be a promising strategy to increase genetic variation at the population level. This should increase the evolutionary adaptive potential, increasing resilience by promoting the buffer capacity of the population. However, since only small losses of plants owing to natural selection can be tolerated, this strategy has a limited potential in practical forestry. Breeding for the physiological adaptive potential, i.e. increasing the homeostatic capacity and thereby the resistance of the single tree, might in this context be more promising (Larsen, 1991). However, adequate methods for testing physiological adaptability to uncertain environmental changes are still lacking.

### 3.3. Species mixtures

The decomposer activity is reflected in the humus form, which is partly dependent upon the vegetation. Even aged conifer forests (spruce, larch and pine) have a tendency to accumulate litter (raw humus), which indicates a temporal decoupled matter cycle. Other more nutrient demanding species are characterized by a higher activity of decomposers, leading to better humus forms (mull and moder) and more balanced matter cycles. By choosing site specific appropriate species it is possible to a certain extent to improve the biogeochemical cycle, thereby increasing stability.

By mixing different species, including trees, shrubs and herbs, it is possible within certain limits to avoid the temporal decoupling of biomass production and mineralization, as a mixture of litter types assures a continuous decomposition, thus preventing phases of humus accumulation and net mineralisation. Morgan et al. (1992) and Brown (1992) demonstrated higher mineralization rates in litter of species mixtures (larch/pine and pine/spruce, respectively) compared with pure species, reflecting higher activity among decomposers in litter mixtures. Other studies, however, contradict these findings (Chapman et al., 1988). Depending upon species-specific characteristics, mixed forests may contribute to ecological stability by increasing resistance and resilience and additionally decreasing the potential magnitude of perturbation owing to mineralization or acidification pushes as defined by Ulrich (1987).

Mixed stands may have greater species diversity in other compartments of the ecosystem. This might lead to an increased resistance, especially in relation to better controls of pests. It must be emphasised, however, that this higher resistance is mainly due to the complexity of energy flow developed through coevolution among functional groups of organisms. Species mixtures should support existing food web interactions (Vasechko, 1983). Hence, the artificial creation of more complex structures by mixing species, without taking coevolutionary relationships into account, may therefore not lead per se to higher system resistance (Roberts and Tregonning, 1980).

Another aspect of system stability is the possibility of increasing the potential depth of the rooting zone by introducing species characterized by a deeper rooting ability (Ulrich, 1987). Such species might work as a pump of nutrients (mainly base cations) from deeper soil horizons, thus increasing the weathering potential and the storage capacity of the system and thereby both resilience and resistance. Information about species-specific capability to expand the rooting zone in relation to soil characteristics are still very sparse, however.

### *3.4. Silvicultural systems*

In managing forest ecosystems it is important that stability also includes the regeneration stage. The stability problems in the regeneration phase are mainly connected to the biogeochemical cycle, due to accelerated mineralization and reduced uptake leading to losses of nutrients. These problems depend upon the silvicultural system adopted.

To obtain a high production of fast growing species, forest management often promotes extreme structural homogenization, usually even aged mono-specific systems. Such homogeneous systems, however, also occur in natural forest ecosystems due to large scale destruction by natural causes (fire, wind, insects). These ecosystems exhibit cyclic stability through time (Orians, 1975). This type of stability is of minor importance in man managed forests, since they are characterized by major (uncontrolled) disturbances, and consequently may not satisfy the requirement of sustainability in terms of production.

Clearcutting corresponds to a major disturbance leading to heavy changes in biotic regulation and physical environment (micro climate) and initiating a long period of recovery with release of energy and lost control of the hydrological and biogeochemical cycle (Bormann and Likens, 1979; Vitousek et al., 1979; Nykvist and Rosén, 1985; Hornbeck et al., 1987; Swank and Crossley, 1988; Emmett et al., 1991). Alterations in soil biology, including changes in the structure of microorganism community (Jones and Richards, 1977) and declines in mycorrhiza (Amaranthus and Perry, 1987) as well as nutrient losses to stream and ground water (Bormann and Likens, 1979; Martin et al., 1985; Swank, 1988) are further consequences of larger clearings. The acceptability of clear-cuttings should therefore be carefully analyzed according to the local conditions, especially in relation to the biogeochemical cycle (weathering rates, losses of nutrients, storage capacity, acidification, erosion, etc.).

Even aged stands combined with large-scale clear felling offer little spatial variation in structural and functional ecological features promoting a low diversity and periods of matter and nutrient imbalances exaggerating these above mentioned ecological problems during the regeneration stage. Various silvicultural measures can shorten this period of acute entropy, and the introduction of more adapted (tolerant) and adaptable species offers increased potential stability.

The selection system maintains rather fixed structural features thereby promoting a functional steady state. The system is characterized by a good control of the biogeochemical cycle determined by the limited release of space for regeneration and by a rather high diversity, owing to a horizontal structure and individual mixture. The selection system is probably the silvicultural system most closely related to the 'shifting-mosaic steady state' defined by Bormann and Likens (1979), except that old trees are not allowed to fall and decompose.

Group regeneration and strip regeneration exhibit ecological features intermediate between the clearcutting and the selection system. Depending upon the size of the clearings the nutrient cycle remains more or less closed. Regeneration under cover (canopy) implies a mild disturbance with only small changes in matter balance of the system maintaining control of the nutrient cycle. Further the micro climate created by the forest cover remains almost unchanged.

### *3.5. Harvesting practices and stand treatment*

The effects of harvesting on long-term productivity by means of management impact evaluation studies through modeling have attracted little attention until recently (Kimmins, 1977, 1986; Dyck et al., 1986). If the export of nutrients (mainly base cations, phosphorus and micro nutrients) via harvesting exceeds deposition and inputs from weathering of minerals, the deviation of the nutrient balance from the steady-state will indicate that the ecological carrying capacity has been exceeded. Thus, sustainability is lost and stability decreases. In many acid forest ecosystems in Europe, harvesting may remove more base cations than are replaced by mineral weathering. According to Ulrich (1987, 1991), the existence of these systems is mainly due to atmospheric inputs from pollution and they are highly unstable.

The common stem-only harvesting system limited the amounts of nutrients lost to the system, whereas whole-tree harvesting methods may lead to considerably more soil disturbance (erosion) and nutrient export. Substantial increases in nutrient losses by whole-tree compared with stem-only harvesting have been calculated (Sterba, 1988; Mann et al., 1988;

Fahey et al., 1991a,b). This indicates that harvesting method might be one of the most important single factors responsible for management induced nutrient losses. The actual effect upon long-term productivity depends upon the export–import balance and the nutrients stored. In many tropical forest ecosystems with very limited nutrient storage and weathering capacity, harvesting has a significant effect on system stability. Hence, harvesting practices must be analyzed and reconsidered in relation to the biogeochemical status of the actual ecosystem.

The structural and functional features of the ecosystem depends upon the control of regeneration and upon the temporal regulation of space and relations between species. In this context, methods, frequency and intensity of thinning play an important role by controlling the forest floor. Especially in plantation forestry, characterized by phases of pronounced build-up of raw humus (dense stands of spruce, larch and pine) a stabilizing effect on the biogeochemical cycle might be obtained by a thinning practice, which gives sufficient light to assure the existence of a continuous ground vegetation. The use of herbicides may affect stability negatively (Likens et al., 1970), especially in phases of afforestation and recultivation after clear-cutting where the nutrient cycle mostly is disturbed. The introduction of suitable ground vegetation in order to stabilize the nutrient cycle might under such circumstances be considered.

Ecosystem stability can be increased by chemical and biological soil amelioration (Ulrich, 1989). Such technical measures include soil cultivation and application of fertilizers and lime. By improving the physical and chemical properties of the soil, mainly resistance (nutrient and water storage capacity) but also resilience (weathering potential) can be increased.

## 4. Stability and forest decline

Research during the last 10 to 15 years on the causes of the widespread forest declines shows a rather heterogeneous and complex pattern. It is therefore generally accepted that these unspecific declines are caused by a number of partly interacting stresses, some of which are of anthropogenic origin.

Fig. 3 illustrates the concept of stability in relation to a multiple stress integration model, where the stresses are grouped into predisposing, inciting and contributing factors as proposed by Manion (1991). Manion's model, which was developed to explain tree decline, is in this context applied to ecosystems. A stable system (stand) depicted by high resistance and resilience is, according to Fig. 3, characterized by well adapted populations, i.e. its species and provenances are adapted to the specific ecological site conditions, biotic as well as abiotic. Further, stand structures and treatment are system and species adapted.

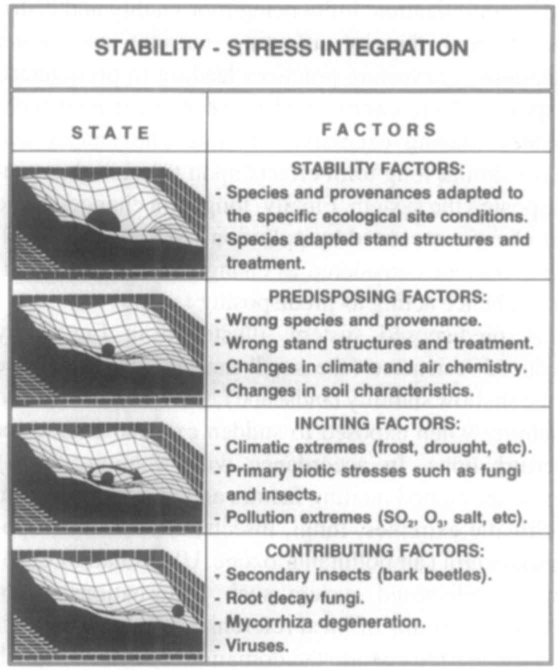


Fig. 3. Forest decline is illustrated in relation to the stability concept by means of a multiple stress integration model. The stresses are grouped into predisposing, inciting and contributing factors as proposed by Manion (1991).

In case the above mentioned prerequisites are not fulfilled, the system is predisposed, which in terms of stability means that resistance and resilience are reduced owing to lack of adaptedness of its population caused by diminished physiological and evolutionary buffer capacity. A similar reduction in the stability of the system may occur by long term changes in the ecological site conditions, such as climate changes and changes in soil characteristics. Under these aspects the running changes in the soil chemical properties should be mentioned, which are forced by acid deposition and lead to soil acidification, base cation depletion and

$Al^{3+}$-mobilization, influencing root vitality and distribution and thereby affecting nutrient and water relations. Harvesting practices leading to pronounced export of base cations and stand management techniques causing excessive leaching phenomena will have similar long term effects upon the soil, thus predisposing the system. Finally, long term changes in the air chemistry caused by pollution ($SO_2$, ozone, PAN, etc.) may be considered as changes in the site conditions, hence acting as predisposing factors.

A predisposed system, illustrated in Fig. 3 by reduced resistance (the small marble) and resilience (the shallow stability landscape), will show its reduced stability when exposed to sudden external stresses or perturbations. In accordance with Manion (1991) these are named inciting factors and may be of natural (climatic extremes, fungi, insects, etc.) or anthropogenic origin (air pollutants, ozone, UV-radiation, etc.). In a predisposed system such perturbations might exceed the limits of local referenial dynamics displacing the marble outside the domain of attraction, which in terms of decline means the occurrence of visible symptoms.

A predisposed and, because of stresses, degenerating system, might be further destabilized through a number of contributing factors such as secondary insects (bark beetles), pathogens, and the degeneration of important symbiotic relationships (mycorrhiza). The marble is placed outside the domain of attraction and moves into another dynamic equilibrium characterized by substantial changes in structural and functional features, which means that the forest declines beyond the limit of recovery.

## 5. Sustainability in a broad sense and aspects of future silviculture

Sustainability as a management goal was developed in Germany (in German: Nachhaltigkeit) during the 18th century, aimed at sustained production of wood. Today the products and demands of forests are much more diverse, and include wood, shelter, recreation, nature and habitat protection, species and gene conservation, etc. Consequently the criteria for sustainable forest management as defined at the CSCE Conference in Montreal in 1993 include biodiversity, production, vitality and health, soil and water conservation, and global ecological cycles. This stresses the importance of expanding the meaning of sustainability by embedding it within a general framework of ecological stability. Further, the possibilities of an increase in climatic variation within the next tree generation emphasize the importance of ecosystem flexibility and stability.

Until now silviculture has been based upon information gained partly through local management experiments. Thus silviculture is mainly based upon empirical knowledge limited in time and space and lacking a basis of ecological understanding. This has led to the development of management systems which exceed the ecological carrying capacity and lead to losses in sustainability and even to pronounced decline phenomena.

A new scientific approach is needed to develop a program of forest management which satisfies sustainability in its broad sense. Silviculture must develop from the empirical manipulation of stand structures into a science of ecosystem management founded upon knowledge of system processes and interactions. Today this knowledge is still very sparse, and much more research in systems ecology is needed.

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