# VEGETATION DYNAMICS IN EUROPEAN BEECH FORESTS

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ABSTRACT - Dynamic processes can be classified in terms of their time scale, their spatial scale, the elements observed, and the degree of human impact. Using these categories the regeneration of the tree layer, the regeneration of the herb layer as well as successional changes of supraregional importance (immissions, global change) are discussed.

A virgin (mixed) European beech forest consists of a mosaic of sub-stands that can be typified by their structure and developmental stage (phase) of the tree layer; in some phases the tree individuals of each sub-stand are rather even-aged. Natural cyclic regeneration of virgin (mixed) European beech forests mainly includes the tree species of the terminal phases, expecially the beech itself. Changes of tree species composition within the cycle are the exception; in European beech forests light-demanding pioneers seem to be restricted to rather small patches under natural conditions. In contrast, the sequence (1) felled-area flora, (2) pioneer shrub/pioneer forest and (3) terminal forest is a characteristic feature of managed deciduous forests as a consequence of soil disturbances.

During the cyclic regeneration of the tree layer of European beech forests the floristic content of the ground layer vegetation does not change fundamentally. Regeneration of many of the ground layer species of beech forests via generative diaspores is more or less restricted to micro-disturbances. In contrast disturbance of the topsoil and creation of open habitats for the establishment of saplings in the absence of competition is taking place all over a clear-cutting area.

European beech forests are subject to changes of floristic structure caused by immissions. Especially nitrogen, emitted over decades in large quantities, causes a successive change in floristics: species requiring high amounts of nitrogen are increasing in beech forests all over Europe. Most of them are rapidly and tall growing species, outcompeting the slower and smaller growing acid-indicators. Soil acidification, although taking place, is therefore often not reflected in changes in the vegetation cover. Up to now, syntaxonomic changes are usually restricted to the levels below the association. Additionally some proportion of (beech) forest stands are presently changing since the regeneration following the abandonment of degrading land use practices has not yet been completed.

As a consequence of changing climatic conditions ($CO_2$-content, air temperature, precipitation, storms) it is expected that European beech forests will change in the future. However, details of the floristic structure of future beech forest communities can not be predicted. Nevertheless, according to present knowledge, beech forests will remain the most important natural forests in Europe during the next century.

KEY WORDS - vegetation dynamics, European beech forests, *Fagus sylvatica*, fluctuation, cyclic regeneration, mosaic-cycle-concept, succession, immissions, global change.

## INTRODUCTION

The European beech forests were the subject of a scientific meeting of the working group "European Vegetation Survey" carried out in Rome in March 1997. The task set to this paper is to give a survey on vegetation dynamics in European beech forests. Vegetation dynamics means changes in both quality (floristic composition) and quantity (dominance, abundance) of the elements of vegetation units, the plant species, in time at a given place. Vegetation dynamics can be observed, analysed, interpreted and classified using very different points of view; the most important criteria to characterize vegetation dynamics are: (1) floristics and stand structure of the vegetation stand along the time axis, (2) the size of the area under observation, (3) the elements under observation and (4) the impact of man. In section 2 these criteria are discussed briefly. Using this theoretical background, in sections 3 to 5 the main results in the field of dynamic research concerning European beech forests are outlined. The presentation is focussed on the regeneration of the tree layer, on the regeneration of the herb layer and on successional changes of supraregional importance (immissions, global change).

# CLASSIFYING DYNAMIC PROCESSES IN VEGETATION

## TIME SCALE

Usually three major "types" or "classes" of vegetation dynamics are distinguished to characterize changes of vegetation in time (fig. 1):

(1) Fluctuation: Reversible short term (few years) changes of the number of plant individuals, the cover degree and/or the biomass of the species living on the site. Invasion or dying off of species does not occur (according to Rabotnov, 1974; Fischer, 1995). In short, fluctuations are undirected short-term changes in species quantities.

(2) Cyclic regeneration: Changes in vegetation stands concerning quality and quantity of species composition caused by ageing, dying and regrowing of plant individuals which lead back to the starting situation (supposing the site conditions have not changed in the meantime). An important example of cyclic regeneration is the sequence of developmental phases in forest regeneration cycles.

(3) Succession: Directional sequence of plant communities (that means changes in floristic composition!) on a spot as a consequence of the changing site conditions (Fischer, 1995). According to Miles (1979) successions are "tending away from the initial notional mean" (for detailed description of succession see Falinski, 1986).

This differentiation helps to simplify scientific discussion on vegetation dynamics, but it is to realize that "there are no hard and fast dividing lines between any different kinds of change ... All changes result from the continuous flux in populations of individual species..." (Miles, 1979, p. 36).

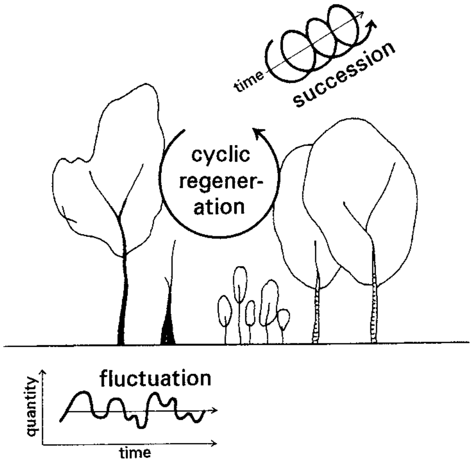



Fig. 1 - The three main types of vegetation dynamics: fluctuation, cyclic regeneration and succession.

SPATIAL SCALE

In contrast to tree-less ecosystems like steppes, alpine meadows or bogs, forests are characterized by a marked vertical stand structure. The most important parts of this structure are (1) the tree and shrub layer (shrub layer often consisting of small, young or suppressed trees) and (2) the herb (and cryptogamic) layer. The tree layer is very important in shaping living conditions of the herb layer (shading, deposition of litter, stand climate), but reversily the herb layer may influence the tree layer, too, by modifying the tree species composition during regeneration via competition. Both components of the forest stand are involved in dynamical processes and are subject of studies on vegetation dynamics. To analyse vegetation dynamics of the herb layer (inside as well as outside the forest) plots of a size of less than 1 square meter up to several square meters are used (see Klotz, 1996); the plot size to analyse the dynamics of the tree layer is often 100 square meters, several hundred square meters up to some hectares (e.g. Fischer, 1992; Mayer *et al.* 1980). Studies on (forest) vegetation types (communities) are working on a landscape level, studies on vegetation formations on a continental or global level.

OBJECTS UNDER INVESTIGATION

Usually one of the following hierarchical levels is the object of studies in vegetation dynamics:

(1) The individuals and populations of selected species (i.e. tree species, herb layer species); this is the working level of population biology.

(2) The tree layer: Forest sciences are especially working in this compartment of the ecosystem; parallel, the focus can be on the herb layer, the moss layer or further synusiae (e.g. synusie of epiphytes).

(3) The phytocoenosis: Community ecology, especially phytosociology is focussed on that element.

(4) The biocoenosis as a total, relevant especially concerning nature conservation sciences.

(5) The biogeocoenosis or ecosystem, studied in functional aspects of site/vegetation relationships in the course of dynamics.

HUMAN IMPACT

Most of the world's vegetation stands have been used by man more or less intensively, and that is true for the European beech forests for two or more millennia.

The tree layer is directly influenced, the herb layer both directly and indirectly. We have to assume that vegetation dynamics in managed forests will follow different pathways than in virgin forests. Most of our knowledge on vegetation dynamics in European beech forests is based on studies in managed forests; forest stands suited to study natural dynamic processes are very rare.

It should be stressed that all the criteria mentioned above can be applied simultaneously to each dynamical process under observation; which criterion will be chosen depends on the goal of the study.

## THE REGENERATION OF THE TREE LAYER

The detailed study of regeneration of forest stands faces methodological problems owing to the very long time period involved. However, by interpreting the forest structure of recent forest stands growing side by side as subsequent stages in time it becomes possible to formulate some essential hypotheses on forest dynamics. Using increment core analysis additional information on the age and fate of both individual trees and tree populations can be obtained.

### NATURAL CYCLIC REGENERATION

It was K. Rubner who pointed out in 1925 that many forest stands, even in the absence of differentiation of the abiotic site conditions, consist of a number of different sub-stands with distinct structural characteristics. In the fifties, Leibundgut (1959) substantiated this idea by documenting the different physiognomy of forest patches graphically and analysing the growth behaviour of the trees (increment core analysis) in detail. He interpreted these structural types of forest vegetation as "phases" within a developmental process of the forest. The most important phases are:

| | |
|---|---|
| * Verjüngungsphase | regeneration phase: young trees are establishing, |
| * Jugendphase | juvenile phase, characterised by juvenile trees, |
| * Optimalphase | phase characterized by a closed tree layer canopy of middle-aged trees; only few very old and few very young trees present, |
| * Plenterphase | phase of simultaneous presence of trees of all age classes, |
| * Zerfallsphase | phase of decay of trees and tree layer. |

Zukrigl *et al*. (1963) used this method to analyse virgin forests of the northern Alps in Austria. Figure 2 represents the four main phases of the virgin forest Rothwald/ Austria, belonging to the mixed mountain beech forests.

Mayer *et al*. (1980, p. 59) presented a map of the "distribution of the developmental phases in the untouched centre of Corkova Uvala" (fig. 3), a spruce-fir-beech forest ("*Abieti-Fagetum illyricum*") from Croatia. This map demonstrates clearly that natural mixed beech forests possess an intricate spatial structure that can be destribed as a mosaic of forest regeneration phases.

Within some of the patches the trees are rather even-aged; such sub-stands represent what German foresters call "Altersklassenwald". The size of each sub-stand has a wide range from a fraction of a hectare up to several hectares (Remmert, 1992: in beech forests one to two hectares).

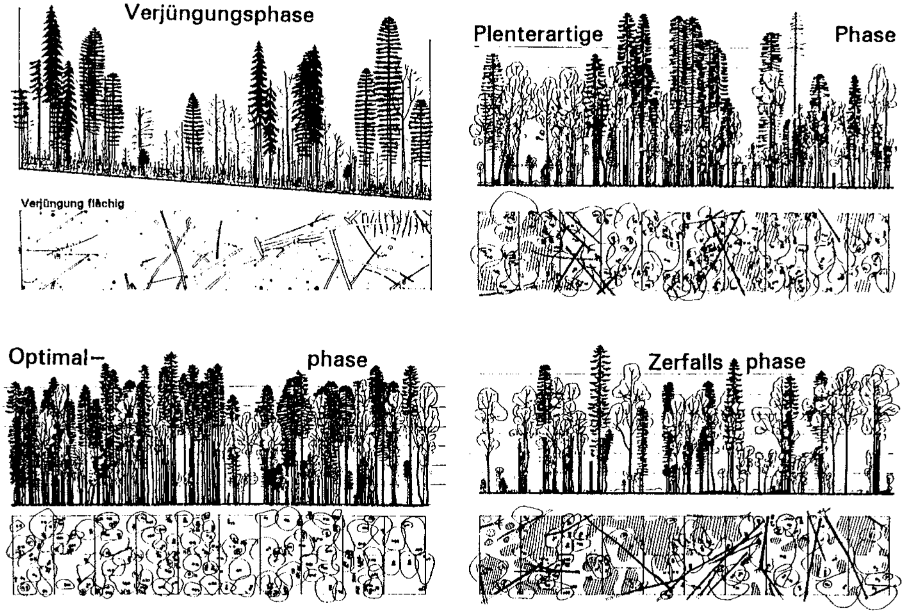



Fig. 2 - Phases of regeneration of the virgin forest “Rothwald” in Austria (from Zukrigl et al. 1963, modified).

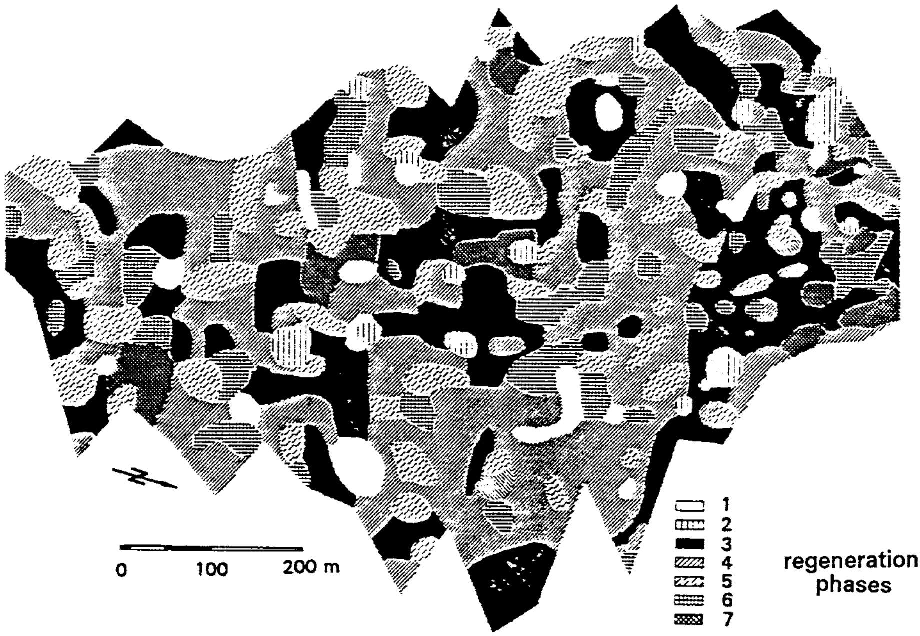



Fig. 3 - Mosaic of regeneration phases in the croatian virgin forest Corkova Uvala (Mayer et al. 1980, modified).

Each sub-stand is subject to a developmental cycle of its own; using the words of Remmert (1991) a forest is a mosaic of “desynchronized cycles as the structural units in a mosaic-like ecosystem” (p. 18). - This is the central statement of the mosaic-cycle-concept, introduced by Aubreville (1936) and promoted by Remmert (1991, 1992).

An important consequence for forestry is that harvesting the wood step by step by extracting small groups of trees (e.g. “Femelschlag”, “Lochhieb”) comes rather close to the natural situation; in contrast (medium and large scale) clear-cutting as well as fixing a completely mixed tree age structure all over a forest stand for decades or centuries (“Plenterwald”) is more artificial.

Apart from this main statement of the mosaic-cycle concept, which seems to be widely accepted, a special aspect of the concept is under discussion over several years: Does the tree species composition change more or less fundamentally within each cycle or not? Concerning the European beech forests Remmert (1991; 1992) postulated the following sequence of events and tree species:

(1) A fraction of a beech forest stand becomes disturbed (e.g. by windfall).
(2) The first phase of the tree layer regeneration is dominated by pioneer trees, especially by the white-barked birch (*Betula* spec.). While young birch occupies the open space of the disturbed area the old beech trees along the border of the open area are going to dy off owing to “sunburn” (the cambium of the exposed beech trunks dies, but not in the case of birch because of its white, reflecting bark).
(3) Dying beech is successively replaced by birch.
(4) Step by step birch becomes substituted by tree species with rough bark (*Ulmus, Fraxinus, Acer, Prunus, Quercus*); within the growing forest stand sunburn is no longer a problem.
(5) In the shadow of these trees beech starts to regenerate and to build up a new forest stand again dominated by beech.

In his 1991 publication Remmert finished the description of this cycle with the words: “Very often there is a short-cut in the cycle, and beech follows beech” (p. 5).

There are so many examples demonstrating that the short-cut (*sensu* Remmert) is generally the rule, while the long run appears as the exception in European deciduous forests:

(1) One of the best documented virgin (mixed) beech forests of Central Europe is the “Rothwald” in the northwestern Alps of Austria (elevation about 1.000 m obove sea level; Zukrigl *et al*. 1963). All the phases of this primeval forest are built up by *Fagus sylvatica, Abies alba* and *Picea abies*. In this forest *Ulmus scabra* and *Acer pseudoplatanus* occur as scattered individuals only; pioneer tree species are completely missing. Five documented stands representing the most important regeneration phases of this forest include only *Fagus, Abies* and *Picea*. The same applies to a mixed beech forest in Croatia (Mayer et *al*., 1980).
(2) In 1995 Korpel published extensive results on the virgin forests in the Western Carpathians. The numerous exampels of beech and mixed beech forests presented in this study document the complete lack of pioneer-dominated phases in the regeneration cycle; beech, fir and spruce are dominating all the regeneration phases. *Acer* is characterised by Korpel as an “admixed” species (p. 300). The virgin forest at the Kubany-mountain in the Bohemian Forest/Chech

Republic is a further example of this regeneration type.

(3) Beech forest dynamics in the well known natural forest reserve "Heilige Hallen" in Mecklenburg/Germany (120 to 140 m above sea level) show the same tendency; pioneer trees are restricted to the root plates of fallen trees (Knapp & Jeschke, 1991).

(4) East of the area settled by beech, mixed *Carpinus-Quercus-Tilia*-forests occur. The Bialowieza National Park in Eastern Poland contains good examples of close-to-nature *Carpinion* forest stands (*Tilio-Carpinetum*). Here again, phases with dominance of pioneer trees are not known (Falinski, 1986).

These observations are supported by modelling of the tree species composition during the regeneration process. The most important parameters in competition amongst trees are (1) height increment and (2) shading capacity combined with shade tolerance. The European beech is a shade tree, and according to the yield tables, middle-aged and old grown beech (as well as spruce) have high rates of annual height increment. Using these two parameters of competition as well as the life span of the species Roloff & Peik (1990; see in Roloff, 1992) modelled the tree layer regeneration, starting with a "pioneer forest", dominated by *Betula*, *Acer* and *Fraxinus* under the ecological conditions of Lower Saxonia in NW-Germany (fig. 4). After 150 years the model creates a pure beech forest! The pioneer trees had disappeared to a great extent, and from year 400 onwards they are missing completely.

As a consequence (and in contrast to Remmert's specification of the mosaic-cycle-concept!) it can be stated that cyclic regeneration of (mixed) virgin European beech forests regularly includes only the tree species of the terminal phases, expecially the beech itself. The "short-cut" *sensu* Remmert (1991) is the rule, changes of species composition within the cycle are the exception. Under natural conditions in (mixed) deciduous forest regeneration cycles light-demanding pioneers seem to be restricted to small forest patches in short episodes.

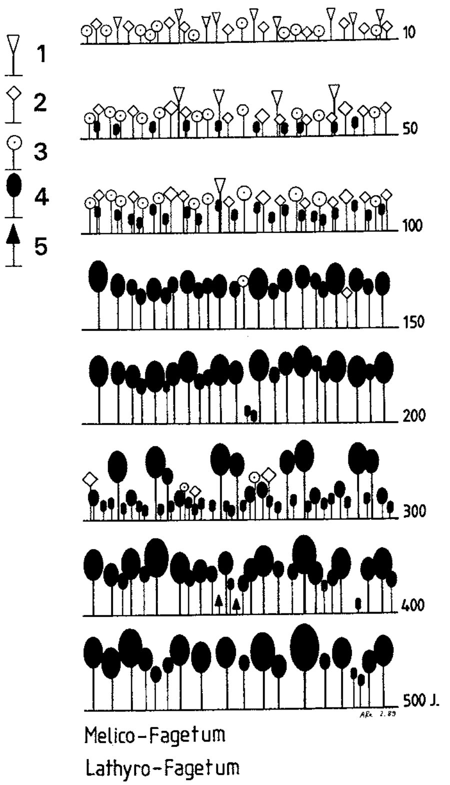



Fig. 4 - Simulated succession from pioneer forest to beech-dominated forest; running time 500 years. 1 *Betula* spec., 2 *Acer* spec., 3 *Fraxinus excelsior*, 4 *Fagus sylvatica*, 5 *Picea abies* (Roloff, 1992).

TREE LAYER REGENERATION AND MAN

At present, forestry represents the most important impact of man on the dynamics of regeneration cycles in European beech forests. In the course of timber extraction, especially during clear-cuts, but also during small scale extracting procedures, the tree layer disappears (more or less), ground vegetation as well as seedlings and saplings of trees are partly destroyed, open places for the establishment of invading individuals are created. Anemochorous (and zoochorous) pioneer trees may immigrate. The result is a "pioneer forest", dominated by species of the genus *Betula, Salix, Populus* and *Sambucus*, a feature that is well known from all over Europe.

## THE REGENERATION OF THE HERB LAYER

Floristic composition and ecological adaptation of the ground vegetation of European beech forests are to a high degree determined by the beech tree layer. This is especially true in respect of the regeneration process. Again two aspects of regeneration are to be distinguished: (1) within the undisturbed cycle of the tree layer and (2) caused by external disturbance.

There are two important "compartments" of the forest ecosystem which are the resources of ground vegetation regeneration: (1) the recent stock of gound layer plants and (2) the soil seed bank.

One of the earliest studies on forest soil seed banks all over the world was carried out in forests near Göttingen (Göttinger Wald/Germany) by Peter (1893, 1894). Peter studied the soil seed bank of forest stands (beech forests and spruce forests) which had been used as arable fields or meadows in former times. Fischer (1987) documented the regeneration following "small scale disturbance" (plots of 0.25 m2 each; ground vegetation destroyed mechanically - dug soil), comparing it with recent soil seed bank and seed rain in managed beech forests (*Hordelymo-Fagetum/Melico-Fagetum*). As a general conclusion from studies of this type it can be stated that there is only small floristic similarity between the recent ground layer vegetation and the soil seed bank, both qualitatively and quantitatively (fig. 5). On the one hand only a few forest ground layer species are represented in the soil seed

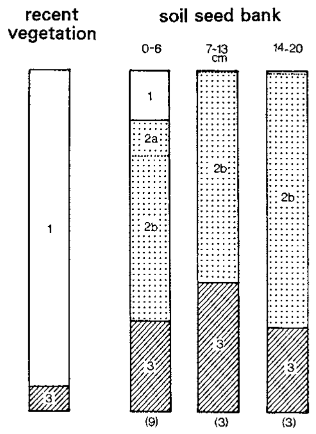
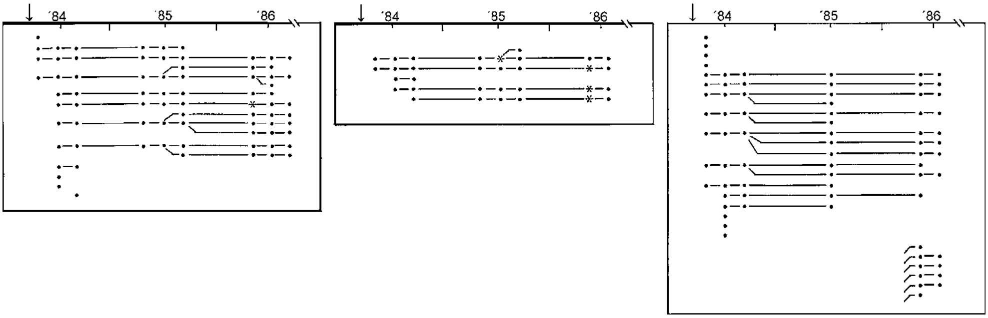



Fig. 5 - Floristic composition both of the recent ground layer vegetation (left hand) and of the soil seed bank (0-6 cm, 7-13 cm, 14-20 cm depth; right hand) in a managed beech forest stand (Hordelymo-Fagetum allietosum) near Giessen/Germany, 220 m above sea level.
Ecological groups: (1) forest species, (2) felled area species (2b: Juncus-species) and pioneer forest species, (3) miscellaneous species.
Quantities (as percentage of the ecological groups): recent vegetation: cover degrees added; soil seed bank: number of viable seeds.
(Fischer, 1987, modified).

bank (in the case of *Hordelymo-Fagetum allietosum,* e.g. *Allium ursinum, Viola reichenbachiana, Melica uniflora, Scrophularia nodosa, Stachys sylvatica*), and on the other hand most of the soil seed bank species are misssing in the recent vegetation. Qualitatively the soil seed bank is absolutly dominated by felled-area species (e.g. *Rubus idaeus, Hypericum hirsutum, Juncus* div. spec.), which are often completely missing in the recent vegetation stand.

Although only small quantities of forest ground vegetation species are represented in the soil seed bank, the seedlings that emerge after small-scale disturbance beneath the beech canopy generally belong to these species (see Fischer, 1987, p. 147, 152). The survival rate of such seedlings emerging immediately after the disturbance is surprisingly high, with the seedlings that germinate first tending to dominate the micro-stand in the future (fig. 6). Additionally the disturbed plots are colonized vegetatively from the surrounding vegetation (see fig. 6: *Stachys*).

In the shadow of the beech tree layer the felled area species, which are present




Oxalis acetosella    Viola reichenbachiana    Stachys sylvatica

Fig 6 - Development of individual plants of 3 species; seedlings emerged after digging the soil on small experimental plots (0.5 x 0.5 m) within an old grown forest (Hordelymo-Fagetum; soil seed bank see fig. 5). All the individuals of the 3 species present on the plot were recorded (Fischer, 1987, modified).
dot: plants registered
only 1 dot: plant individual only registered once.
dots connected by lines: plants present during a time period.
star: plant flowering.
fork: vegetative reproduction.
Time of disturbance: spring 1984 (arrow); end of recording: summer 1986.

in the soil seed bank at high densities do not germinate; apparently lack of light inhibits their germination. In the course of (clear-)cutting the upper soil layers will be disturbed mechanically in many places. In managed forests micro-disturbances of the type mentioned above tend to be spread all over the forest floor. Additionally the timber extraction procedure creates new conditions concerning micro-habitat (micro-climate, nutrient availability): (1) higher quantity and better quality of light, (2) larger daily and annual amplitudes in temperature regime, (3) increased humus mineralisation rate. Therefore, wherever soil becomes disturbed and viable seeds of the soil seed bank become exposed to full light, the felled-area species will start germination and establishment.

Additionally the disturbances produced by logging procedures create open space free from competition, which can be used by species invading from outside, such as *Betula, Populus* and *Salix*. These trees and shrubs occupy new space among the felled-area flora, e.g. *Epilobium, Senecio* and *Calamagrostis*.

In summary, it can be pointed out that during the cyclic regeneration of the tree layer of the European beech forests the floristic content of the ground layer vegetation does not change fundamentally. Regeneration of many of the ground layer species of beech forests via generative diaspores is more or less restricted to micro-disturbances. In contrast disturbance of the topsoil and creation of open habitat for establishment of saplings without competition is a common event all over a clear-cutting area. Therefore the well known sequence (1) felled-area flora, (2) pioneer shrub and/or pioneer forest and (3) terminal forest, documented e.g. by Dierschke (1988), is a characteristic feature of managed (European beech) forests.

In forests without any direct human impact this sequence is restricted to very small patches such as the root plates of fallen trees; this situation has been documented by Fischer (1992, 1996) for spruce forest ecosystems, too. Again forest harvesting procedures like “Femelschlag” and “Lochhieb”, working on rather small patches, tend to possess characteristics of natural processes: only small scale establishment of felled-area and pioneer species.

Natural large scale disturbances are of high importance to forest vegetation dynamics in the boreal forest zone. Plochmann (1956) for example indicated that pioneer trees like *Populus balsamifera, P. tremuloides* and *Betula papyrifera* are common components of (semi-) natural forests of the boreal zone of Northwest Alberta/Canada depending on forest fire. While in boreal forest ecosystems forest fire is a natural element, it does not play an important role in European beech forests.

Windfall may be another important disturbance factor, but it is hard to estimate its large scale influence on European beech forests. An analysis of the quantities of fallen wood during the storms from February 1990 in Bavaria led to the result, that related to the total stand volume of the tree species spruce had been thrown five times, pine two times as much as beech and fir (König, Mössmer and Bäumler, 1995). The conclusion seems to be justified that storm (large-scale windfall) is not of overriding importance in European beech forest ecosystems.

## SUCCESSIONAL CHANGES OF SUPRAREGIONAL IMPORTANCE

Changing environmental conditions cause successional changes of (forest) vegetation stands, that means changes of the floristic composition. Two topics of relevance throughout the area of European beech forests to be discussed here are (1) the influence of pollution and/or nutrient input and (2) the influence of changing climate (caused by anthropogenic emissions).

### FORESTS AND IMMISSIONS

Since the 1960s an increasing number of publications described floristic change in phytocoenoses in the surroundings of industrial complexes (e.g. Trautman, Krause and Wolf-Straub, 1970). European (mixed) beech forests have been studied in detail during the last one or two decades in this context. Tab. 1 summarizes some of these studies and their main results.

It had been expected that as a consequence of "acid rain" the importance of acid indicator species should increase and the corresponding mean Ellenberg indicator value (Ellenberg *et al*. 1991) decrease (hypothesis: "acid rain supports acid indicator species"; see Buck-Feucht, 1986). Indeed a decrease of acid indicator value was reported by Wittig *et al*. (1985; millet grass-beech forests of the Westphalian bight/NW-Germany) and Schmidt (1993; Osterzgebirge/E-Germany); but against all expectations the acid indicator species in the ground layer of beech forests did not generally increase during the last decades. On the contrary, rather often the number and cover degree of acid indicator species was reduced! On the other hand in most cases the nitrogen indicator species increased. Light indicating species either increased or decreased.

Studying forest vegetation changes between 1950 und 1990 in the Luzulo-Fagetum of the Rhön/Germany, Röder *et al*. (1996) found a strong positive correlation of mean acidity indicator and mean nitrogen indicator values. The nitrophilous species are not depending on acid soils, but are fast growing and productive species, outcompeting the less productive growing acid indicators. Therefore parallel to the invasion of N-indicators the acidity-value increases independently of the soil pH. In fact, in southern Sweden the acid indicator species did not increase, although pH decreased significantly (average decrease: 0.78 pH-units; Falkengren-Grerup, 1986), but nitrogen indicator species did increase.

The studies summarized in tab. 1 show, that European beech forests are subject to general changes of floristic structure caused by immissions. Especially nitrogen, usually a minimum factor under natural conditions, but emitted for decades in large quantities, causes a successive change in floristics. The nitrogen-indicators do not prefer (do not indicate!) acid soils, but tolerate them; therefore with increasing importance of the nitrogen indicator species at the cost of acid indicators the soil acidity indicator value decreases independently of recent soil pH.

The synsystematical position of the forests under immissions usually did not change on the level of the association till the present time, but they did on the level of subtypes. While in the Luzulo-Fagetum of the Rhön in 1950 a "Calluna-subtype"

TABLE 1 SURVEY OF FLORISTICAL AND/OR ECOLOGICAL CHANGES IN EUROPEAN BEECH FORESTS DEPENDING MAINLY ON IMMISSIONS. ↓ : DECREASING; ↑ INCREASING.

| landscape/country | author(s) | forest type | period of time | number of releve pairs | qualitative description of changes |
|---|---|---|---|---|---|
| Westphalian Bight/ NW-Germany | WITTIG et al. 1985 | millet grass-beech forest | 1976 → 1983 | 44 | no. of species per relevé ↑ (+3)<br>no. of acid indicator species ↑ (+1,3)<br>mR-value ↓ |
| Osterzgebirge/ O-Germany, NSG Wachholderwald dto, abandoned gardens | SCHMIDT 1993 | Galio odorati-Fagetum, Luzulo-Fagetum, Tilio-Acerion | 1956 → 1991 | 9<br><br><br>67 | mR-value ↓ (-1,1)<br>no. of species per relevé ↓<br>mN-value +- constant |
| Southern Sweden | FALKENGREN-GRERUP 1986, 1989 | deciduous forests, Fagus dominant in most sites, representing all types of beech forests in Sweden | 1949/70 → 1984/85 | 34 | pH: ↓ (-0,78 pH-units, in several cases more than -1)<br>no. of species ↑<br>cover degree of nitrogen indicators ↑ |
| Ojcow Nat. Park/ Southern Poland | MEDWECKA-KORNAS & GAWRONSKI 1991 | Pino-Quercetum, Fagus-Var. ("acidophilous mixed forest") | 1958/59 → 1987/88 | 10 | acidophilous species ↓<br>Vaccinium myrt., Luzula lux. ↓<br>abundance of species<br>of deciduous forests ↑<br>mN ↑<br>mR +- constant<br>interpretation: accumulation of nitrogen in the forest environment |
| Holstein/N-Germany | ROST-SIEBERT & JAHN 1988 | Drahtschmielen-Buchenwald + Buchen-Eichenwälder<br><br>Flattergras-Buchenwald<br><br>Perlgras-Buchenwald | <br><br>1935 → 1983/84 | 10<br><br>27<br><br>16 | <br><br>mL ↑<br>no. and quantity of N-indicators ↑<br>no. of species ↓<br>mR +- constant<br>mN +- constant |
| [illegible]/ Germany | RÖDER et al. 1996 | Luzulo-Fagetum | 1950 → 1990 | 54 | mR ↑<br>mN ↑ |
| Kirchheim/Teck/ Germany | BÜCK-FEUCHT 1986 | Asperulo-Fagetum, Luzulo-Fagetum | 1951/53 → 1983/85 | ca. 20 | hypothesis: as a consequence of "acid rain" ground layer vegetation is changing - hypothesis not confirmed |
| Schwäbische Alb/ SW-Germany | WILMANNS 1989 | Elymo-Fagetum | 1953 → 1988 | 6 | species no. ↓<br>tree canopy: became closed<br>accompanying species ↓ (esp. Trifolio-Geranietea-species, N-indicators) |
| Black Forest/ SW-Germany | BÜRGER 1991, 1994 | Luzulo-Fagetum, Eu-Fagenion, Abieti-Fagetum, Aceri-Fagetum | since 1940 → 1985/86 ([illegible]) | | mN ↑<br>mR ↑ (no floristic base on acidification)<br>mL ↑ (in most cases) |
| Kaiserstuhl/ SW-Germany | WILMANNS & BOGENRIEDER 1986 | Carici-/ Asperulo-/ Luzulo-Fagetum | 1942/44 → 1985 (comparison of vegetation types) | | species no. ↓<br>tree canopy: became closed<br>regeneration of beech and further tree species ↑<br>canopy trees (esp. beech) ↓<br>light demanding species ↓<br>interpretation: increasing density of tree layer (regeneration of degraded forests) |
| Virgin forests Rothwald & Neuwald/E-Austria | ZUKRIGL et al. 1993 | Cardamino trifoliae-Fagetum | 1958/65 → 1989/90 | | mN +- constant<br>representativity of N-indicators ↑<br>conclusion: no eventual modification by N-indicators |
| Anhang: | | | | | |
| N- + W-Switzerland | KUHN et al. 1987 | Querco-Betuletum, coppice and standard woodland ("Mittelwald"), no longer used in this way | 1938/39 → 1984 | 19 | importance of beech ↑<br>indicators of acid and nutrient poor sites ↓<br>mN ↑<br>mL ↓ |
| Lorraine Plain (Nancy)/NO-France | THIMONIER et al. 1992 | mixed hardwood forests with beech | 1970/71 → 1990 | 220 | species no. ↑<br>frequency of Fagus ↑<br>mN ↑<br>mR ↑ ([illegible])<br>mL ↓ |

and a “typical subtype” could be distinguished, 1990 a “typical” and “Epilobium-subtype” were found (fig. 7), reflecting the ecological change mentioned above. In Querco-Carpinetum-forests of the Kaiserstuhl/SW-Germany a new classification became necessary on the level of the variant (Wilmanns *et al.* 1986).

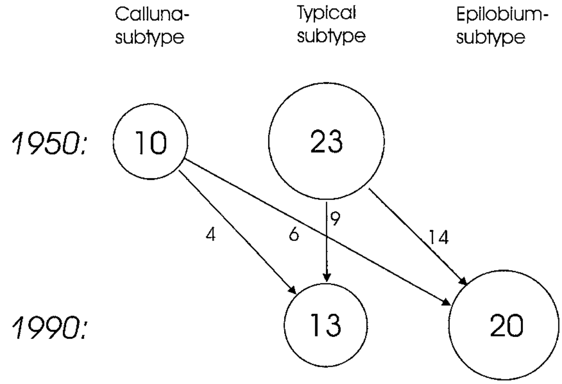



Fig. 7 - Subtypes of Luzulo-Fagetum in the Rhön/Germany in 1950 and 1990 based on 33 quasi-permanent plots. Figures: numbers of phytosociological releves. (Röder et al. 1996, modified).

Apart from immissions a second factor causes floristic change in European (beech) forests at present: regeneration following former devastating land use practices. For example, according to Wilmanns and Bogenrieder (1986) the floristical and structural change in the beech forests of the Kaisterstuhl/SW-Germany is caused mainly by increasing crown density as a consequence of regenerating tree layer following the abandonment of forestry practices like “Niederwald” und “Mittelwald” (coppicing; coppice and standards). The first steps of this developmental process are shown by Kuhn *et al.* (1987), where in secondary oak forests beech is just in the process of gaining dominance.

## FORESTS AND GLOBAL CHANGE

The term “global change” summarizes the climatic changes triggered off by anthropogenic input of so-called “greenhouse gases” into the atmosphere. This is not the place to discuss global change in detail; only a few aspects of general importance shall be stated (see IPCC 1990, 1992, 1996 a, 1996 b, Enquete-Kommission, 1990, 1991):

(1) $CO_2$-content of the atmosphere has been rapidly increasing for decades, from 280 ppm in the pre-industrial period (~ 1750) to more than 350 ppm at present (1994: 358 ppm, IPCC 1995 p.15).

(2) Mean near-surface air temparature is calculated to increase by 1 K at minimum up to 3.5 K in maximum within the next century. All recent scenarios and models project substantial warming within the next century. Especially winter temperatures are expected to increase, and on the northern hemisphere areas far from the equator will be more affected than areas close to the equator.

(3) It is expected that in some parts of the world precipitation will increase, in other parts decrease. In general the southern part of the beech forest area may become

drier, the northern one wetter (see Thomasius, 1991, from Brouwer and Falkenberg, 1989); but our knowlede on this topic is poorly developed up to now.

(4) Atmosperic structure will become more unstable (higher frequency of more violent storms).

As a consequence from (2) and (3) temperature and precipitation appear to increase at a faster rate in the northern part of the *Fagus sylvatica* distribution area than in its southern parts.

Reviews on the effects of global change regarding European forest ecosystems have been published by Kräuchi (1993), Kriebitsch (1991), Thomasius (1991), Ulrich and Puhe (1993), IPCC (1996 b). Some of the most importand predictions regarding European beech forests are the following:

(1) The distribution area of *Fagus sylvatica* will shift northwards, and *Fagus* will reach to higher altitudes in the mountains.

(2) On most of the sites suitable for beech at present, *Fagus* is likely to persist as a forest species of highest productivity, as has been shown by Felbermeier (1993), using an extensive set of height increment data from Bavaria. On the other hand there are suggestions that in some cases the dominance of Fagus will be broken. Roloff (1992) for example documented a sharp break-down of height increment of beech during years with reduced precipitation; that means that beech tends to retreat in landscapes where the summer time will become drier in future. Bugmann and Fischlin (see IPCC 1996 b) simulated the transient response in species composition at a site in Switzerland (1) under current climatic conditions and (2) under a scenario of climate change following doubling of $CO_2$-content. The change of the species composition of the tree layer was impressive; but up to now the model works on the basis of annual mean air temperatures only and therefore is of limited ecological relevance.

(3) The influence of increasing $CO_2$ content of the atmospere on the growth behaviour of plants is under controversial discussion. Recent studies seem to give evidence that with increasing $CO_2$-content the increase of biomass of beech stands is higher than the increase of transpiration of the stands (Stille *et al.* 1996). In a $CO_2$-enriched environment water supply of beech therefore seems less limited than expected so far.

Although the global environment is changing rapidly according to present knowledge beech forests will remain the most important natural forests in Europe during the next century. But there is little knowledge on the details of the floristic structure of the future beech forest communities.

## PROSPECTS

The aim of this review on vegetation dynamics in European beech forests was to focus on the variability of the beech forest ecosystems in the spatial dimension (local to global), in time (few vegetation periods to centuries) and depending on both the quality and quantity of the impact of man. On the one hand trends of dynamic processes are subject to general patterns, but on the other hand to a high degree the specific floristic composition and structure of (forest) vegetation stands depend on chance.

The European beech forests are nowaday changing all over Europe owing to fundamental changes of the environmental conditions. Nevertheless the main characteristics of the European beech forests are likely to persist in the near future.

## ZUSAMENFASSUNG

Dynamische Prozesse lasssen sich nach dem Verhalten der Vegetationsbestände im Zeitverlauf, nach der Flächengröße, den beobachteten Elementen und nach dem Ausmaß des menschlichen Eingriffes klassifizieren. Hinsichtlich dieser Kriterien werden in diesem Übersichtsartikel die Regeneration der Baumschicht der europäischen Buchenwälder, die Regeneration ihrer Krautschicht sowie gerichtete Veränderungen von überregionaler Bedeutung als Folge von Immissionen und Klimaänderung behandelt.

Natürliche Buchenwälder stellen ein Mosaik von Kleinbeständen unterschiedlicher Struktur dar, die Entwicklungsabschnitte in einem Regenerationszyklus der Baumschicht repräsentieren. In unbeeinflußten Buchenwäldern findet diese Regeneration der Baumschicht i.d.R. unmittelbar mit den Schlußbaumarten selbst statt; lichtbedürftige Pioniergehölze scheinen bei anthropogen unbeeinflußter Bestandesentwicklung auf kleine Sonderstandorte (Störstellen wie aufgeklappte Wurzelteller) während kurzer Phasen im Entwicklungsgang beschränkt zu sein. Dagegen ist die Abfolge Schlagflur - Pioniergehölz - Schlußwald ein Merkmal des bewirtschafteten (Buchen-) Waldes: Folge von Störungen, die im Zuge der Fäll und räumungsarbeiten am Boden gesetzt werden.

Während des Entwicklungsganges der Baumschicht bleibt auch die floristische Zusammensetzung der Bodenvegetation in den Grundzügen gleich. Die generative Regeneration vieler Waldbodenpflanzen ist an Kleinstörungen (Maulwurf- und Schwarzwildtätigkeit, Aufklappen von Wurzeltellern bei Windwurf) gebunden. Dagegen sind Bodenstörungen auf forstlichen Räumungsflächen großflächig vorhanden; zusammen mit den geänderten Beleuchtungs- und Mineralisationsbedingungen bilden sie die Grundlage für die Entwicklung von Schlagflurvegetation und Pioniergehölz auf Räumungsflächen.

Seit einigen Jahrzehnten laufen in Buchenwäldern floristische Änderungen als Folge von Immissionen (besonders N-Einträge) ab. Die rasch- und üppigwachsenden Pflanzen mit hohen Stickstoffbedarf verdrängen, wenn genügend Stickstoff verfügbar, die meist schwachwüchsigeren Säurezeiger, so daß - obwohl vielerorts eine pH-Absenkung in Waldböden nachgewiesen wurde - die Bedeutung der Säurezeiger (mit wenigen Ausnahmen) rückläufig ist! Syntaxonomisch wirken sich diese floristischen Änderungen mittlerweile bereits aus, bisher aber im wesentlichen erst auf Niveaus unterhalb der Assoziation. - Zusätzlich ergeben sich in Buchenwäldern floristische Änderungen als Folge einer noch laufenden Regeneration von Waldbeständen nach zurückliegenden devastierenden Nutzungen.

Als Folge prognostizierter Klimaänderungen ist mit floristischen Änderungen in den Buchen(misch) wäldern Europas zu rechnen. Nach heutigem Kenntnisstand werden Buchenwälder aber auch im 21. Jahrhundert die dominierende natürliche Vegetationseinheit in weiten Teilen Mitteleuropas sein; welche floristische Zusammensetzung diese Wälder haben werden ist heute aber nicht abschätzbar.

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