

Vegetation dynamics in canopy gaps of a beech forest on limestone – The influence of the light gradient on species richness

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Synopsis

Species richness of the forest ground layer vegetation increased with increasing light availability in experimentally created canopy gaps for 3 years after impact. After 5 years at least for one gap, a unimodal species richness – light relationship was found, indicating that the number of species dropped in areas of highest light supply. This might be explained with the regeneration of tree saplings, which increasingly compete with the species of the herb layer for light. These findings are compared to current diversity models related to resource and disturbance gradients.

Diversity, species richness, forest gap, disturbance, light availability, beech forest, forest floor vegetation, resource gradient, Allium ursinum, Mercurialis perennis

Diversität, Artenzahl, Schlaglücke, Störung, relativer Lichtgenuß, Buchenwald, Waldbodenvegetation, Ressourcengradient, Allium ursinum, Mercurialis perennis

1 Introduction

Much attention in ecology is paid to the number of species within communities. Species diversity is – beside production, energy flow and nutrient cycling – considered to be one of the key parameters characterizing ecosystems (HUTCHINSON 1959). Accordingly intensive has been the search for explanations for different species numbers and for the factors determining differences in diversity. A strong and widely used approach in this sense is the examination of species richness along environmental gradients. Such studies commonly find unimodal distributions of species numbers along resource gradients with a peak in the area of intermediate resource availability. With an universally accepted explanation for this pattern still under discussion (ROSENZWEIG 1992), partially contradicting explanations are offered at least for land plants, in functional models and hypotheses by GRIME (1973) and TILMAN (1982). According to these hypotheses, inter-specific competition is responsible for a reduction of the number of coexisting species in sites which are especially rich in resources. But this number is not determined alone by the avail-

ability of resources, it also has to be asked whether the ecosystem in question can be considered to be in an – at least transient – equilibrium state or not (SHMIDA & WILSON 1985). According to the 'intermediate disturbance hypothesis' by CONNELL (1978), highest species numbers are to be expected in areas with an intermediate frequency and amplitude of disturbance, a pattern often described in empirical studies. The typical optimum curve of species diversity, initial increase and a following decrease in species number, as it is commonly observed in the course of vegetation regeneration and secondary succession, can be viewed in this context (LOUCKS 1970, MILES 1979, SCHMIDT 1993).

In the past the validation of models and hypotheses concerning species richness and resource gradients has been undertaken chiefly by looking at nutrient gradients (HOUSTON 1979, TILMAN 1982, GOLDBERG & MILLER 1990). The current study aims at the development of diversity (species number and evenness as an indicator of dominance, cf. HAEUPLER 1982) in forest floor vegetation following the creation of canopy gaps. By creating a gap in the forest canopy the limiting resource – light – is changed and the ecosystem is, at least for some time, moved away from its near-equilibrium point. The forest community can be expected to either compensate the effect of disturbance by means of internal buffering mechanisms, or – especially if the intensity of disturbance is exceeding a certain level – a succession leading through different stages results in a newly founded forest stand. The governing factors of this succession are the ones, which control the naturally occurring regrowth of tree saplings and determine the time span needed for the formation of a new forest canopy, which in turn will cause the return of mature forest site conditions. In this study the dependence of diversity in the forest floor vegetation on the changed light regime, on the growth and establishment of tree saplings, and on competition with existing species in the herb layer, is to be investigated.

2 Research area and methods

The research area is located at the eastern edge of the Göttinger Wald, a Triassic limestone plateau at 420m above sea level with a subatlantic low montane

* Dedicated to Prof. Dr. Reinhard Bornkamm on the occasion of his 65th birthday.

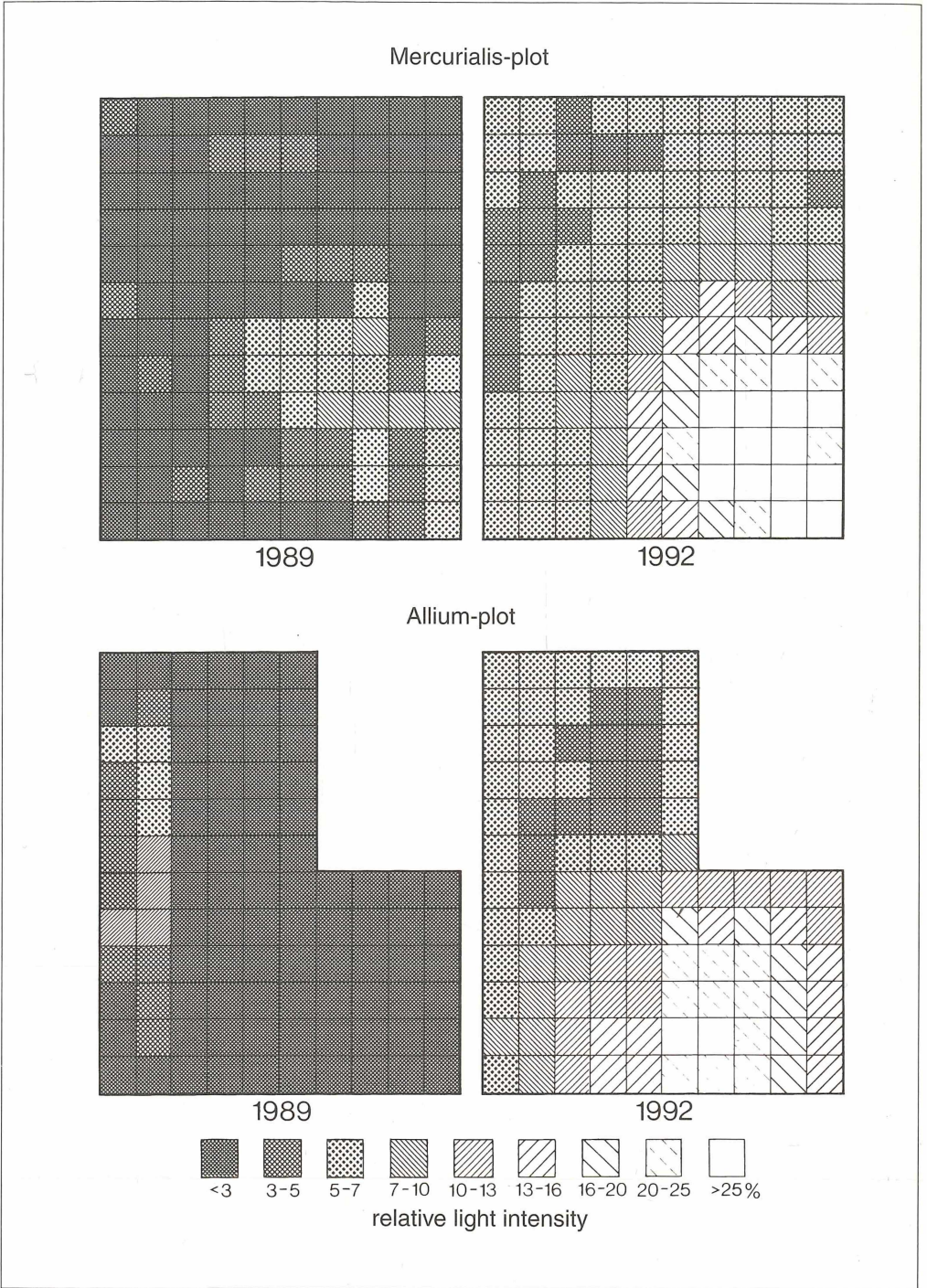


Fig. 1

Distribution of relative light intensity (rL) on investigated plots prior (1989) and after (1992) canopy opening. According to the measurements in 1992 grid squares (5 x 5 m) less than 7% rL were combined to 'forest', between 7 and 16% rL to 'edge' and more than 16% rL to 'gap'.

climate type. The limestone catena is characterized by heterogeneous, shallow to medium deep, biological very active soils (rendzina and terra fusca) which have a low water holding capacity but are fairly nutrient-rich. In a nature-like, approximately 120 year old beech forest stand (*Hordelymo-Fagetum lathyretosum*, DIERSCHKE & BRÜNN 1993) two canopy gaps of 30 m diameter were created at the end of 1989. These gaps differed in the their forest floor vegetation, one was dominated by *Mercurialis perennis*, the other by *Allium ursinum*. Additionally, there were differences in developmental stages of tree regeneration (young tree saplings) at the beginning of the experiment. The *Mercurialis*-plot (3,000 m², fig. 1) is situated under an older already closed canopy gap where numerous small tree saplings – stagnating in growth already for some years – had established themselves (fig. 2). The *Allium*-plot (2,400 m², fig. 1) is located in a closed canopy forest stand with scattered sapling regrowth (fig. 2).

Both plots were fenced to prevent herbivory by game in 1989 and a 5 x 5 m grid was marked. The forest floor vegetation was documented in 1989 before the creation of the canopy gap, and in 1990, 1991, 1992, and 1994 during its spring and summer phases. The development of the vegetation from 1989 until 1994 was analyzed using a DCA ordination method (HILL 1974, fig. 3). The data base for this was – as for the determination of species number and evenness – the combination of spring and summer vegetation samples, the respective highest cover values were used. Diversity was expressed using the number of species per grid square (25 m²) and the evenness-index (HAEUPLER 1982) based on the SHANNON-WEAVER-diversity-index (SHANNON 1949).

In July/August of 1989, 1992, and 1994, during the period of full development of leaves in the canopy, light measurements were made in the grid using PPF silca sensors (LI-COR 190 SB). The relative light intensity (compared to the light regime above the forest canopy) at the forest floor was calculated (details of methodology see DIERSCHKE & BRÜNN 1993). The grid squares were combined into three light classes according to the measurements in 1992 (fig. 1): »forest« <7% of relative light intensity (rL), »edge« 7–16% rL, »gap« >16% rL. A few grid squares had to be omitted from the analysis due to experimental manipulations on this squares.

3 Results

3.1 Development of vegetation

The seasonal two-phase development of the herb layer made a consideration of spring and summer aspects necessary (cover of herb layer: fig. 2). There is

no common trend in the seasonal dynamics over the years, which could be assigned to the change in light regime. The *Mercurialis*-plot is characterized in its spring and summer phase by a relatively uni-directional development in all three light classes (forest, edge and gap). Especially noticeable is the low coverage in 1994, and a gradient with decreasing values from closed forest to gap is evident in all years. In the *Allium*-plot the influence of the gap-creation is discernible in the development of vegetation cover in the summer phase. The cover in the gap increased two-and-a-half fold from 1989 to 1994, but the cover values of the herb layer in summer increased also in the light classes »forest« and »edge«.

The development of tree regrowth, including increase of ground cover and height growth, clearly follows the light gradient (fig. 2). The differences between the plots reflect the influence of the pre-impact history on the growth rate of tree saplings. In the *Mercurialis*-plot, tree saplings were more numerous and more developed than in the *Allium*-plot, and after amelioration of the light regime they showed an immediate growth-reaction. In the *Allium*-plot, a distinct increase in height was noticeable only starting from the 3rd year (1992) after gap creation.

Vegetation changes in the permanent plots are depicted as trajectories in an ordination scatter plot in fig. 3. Selected plant species, which showed a clear correlation to site scores, are added to the graph. The following trends are most apparent:

1. The degree of light availability is determining the magnitude of change in the vegetation, as can be seen by the length of trajectories. The change from 1989 until 1994 was largest in the gap and smallest in closed forest.
2. The increase of tree saplings (especially *Fagus sylvatica*, *Fraxinus excelsior* and *Acer pseudoplatanus*) on both gaps occurs on the expense of the herbaceous species which dominated before the canopy opening. This development caused the two initially different plots to become more similar in areas with high light availability (gap).
3. The dominating stands of *Allium ursinum* (*Allium*-plot) and *Mercurialis perennis* (*Mercurialis*-plot) disintegrate and make space for more mixed plant communities rich in tree saplings. The development in the gap of the *Mercurialis*-plot, which had even prior to canopy opening a developed population of tree saplings, appears to be uni-directional. In the *Allium*-plot, a similar directional trend is discernible only in the 5th year.

3.2 Light gradient and diversity

The species diversity structure of both plots was clearly different before gap creation. While the *Mer-*

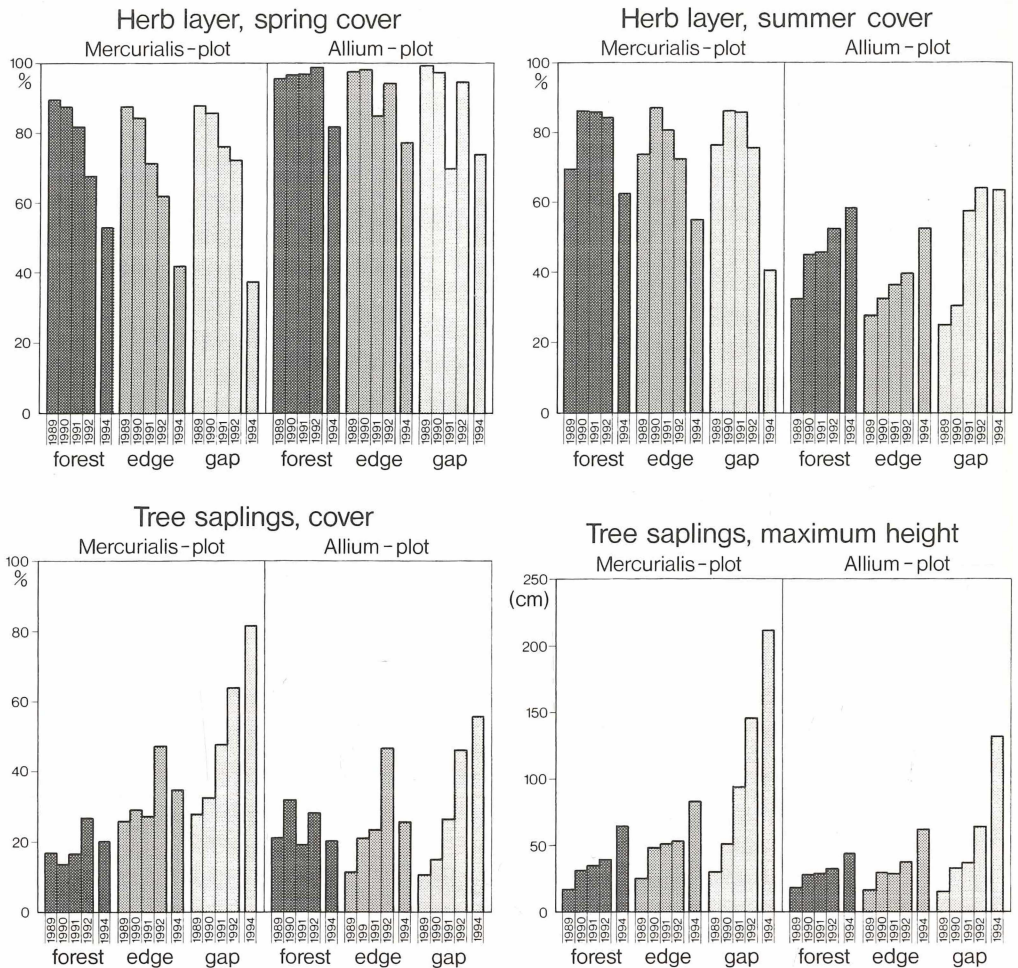


Fig. 2

Change of structural parameters (ground cover and height) in the forest floor vegetation of the two plots before (1989) and after canopy opening (1989 until 1994). Grid squares are lumped according to three classes of light availability in 1992 (see methods and fig. 1).

curialis-plot was relatively rich in species and showed a rather even dominance distribution (tab. 1), the *Allium*-plot in 1989 was largely characterized by a stand of a single species, *Allium ursinum* (tab. 2). After canopy opening, different developments occurred in the two plots along the newly created light gradients. The number of species increased in the first three years after impact in the *Mercurialis*-plot, paralleling the light gradient. In the 5th year, a slight but statistically significant decrease of species number was seen in the highest light class (gap, > 16% rL, tab. 1a). Light availability did not effect evenness prior to, and in the first year after, gap creation. Most of all evenness decreased in the first year after impact on all grid squares, but this

change was statistically not supported (probably due to high variation). After the first year, a general increase of evenness was observed. This trend was significant only in areas with the highest light availability. A decrease of values in the 5th year, as it was found for species number, was not (yet?) present for evenness (tab. 1b).

Similar trends are discernible for the *Allium*-plot, which had comparably lower species numbers and lower evenness values, especially an increase of species number with increasing light availability (tab. 2a). An important difference concerns the number of species: no decrease (yet?) is found in the *Allium*-plot in the 5th year after impact. Remarkable was the reaction in the first year after impact, where a slight decrease in

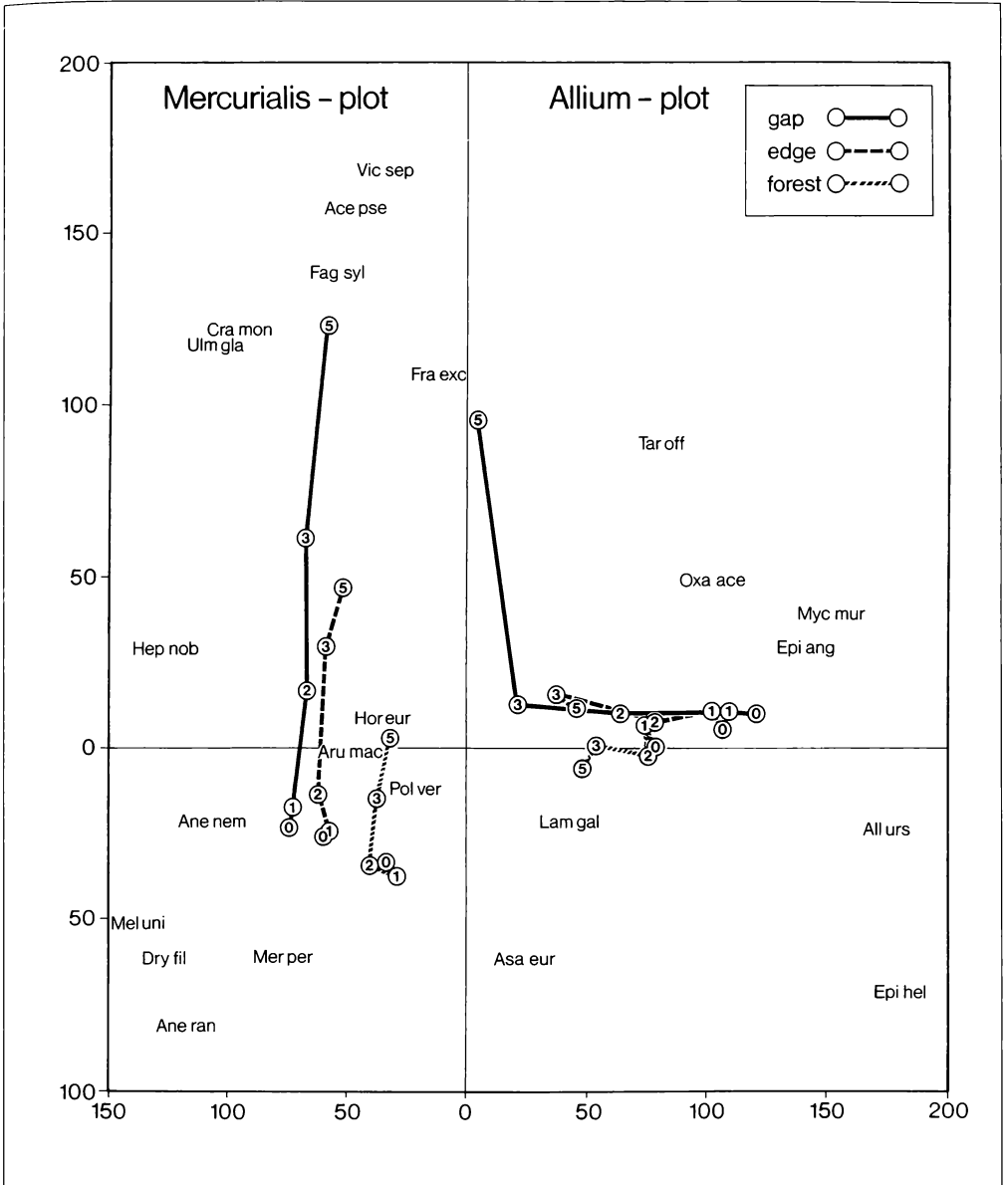


Fig. 3
 Development of forest floor vegetation on the two plots. This ordination scatter plot (DCA) contains site scores (0 – year before canopy opening: 1989, 5 – fifth year after impact: 1994, the remaining dots stand for the intermediate years: 1 – 1990, 2 – 1991, 3 – 1992, in 1993 no data were collected) which are linked to form trajectories, separated for three light classes (see methods and fig. 1). Scores for selected plant species are included with abbreviations (3 letters of genus and species name):

- | | | | |
|------------------------------|--------------------------------|-----------------------------|----------------------------------|
| <i>Acer pseudoplatanus</i> | <i>Crataegus monogyna</i> | <i>Hepatica nobilis</i> | <i>Oxalis acetosella</i> |
| <i>Allium ursinum</i> | <i>Dryopteris filix-mas</i> | <i>Hordelymus europaeus</i> | <i>Polygonatum verticillatum</i> |
| <i>Anemone nemorosa</i> | <i>Epilobium angustifolium</i> | <i>Lamium galeobdolon</i> | <i>Taraxacum officinale</i> |
| <i>Anemone ranunculoides</i> | <i>Epipactis helleborine</i> | <i>Melica uniflora</i> | <i>Ulmus glabra</i> |
| <i>Arum maculatum</i> | <i>Fagus sylvatica</i> | <i>Mercurialis perennis</i> | <i>Vicia sepium</i> |
| <i>Asarum europaeum</i> | <i>Fraxinus excelsior</i> | <i>Mycelis muralis</i> | |

Tab. 1

Change of diversity parameters in relation to light availability on the *Mercurialis*-plot. Mean values are given separated for three light intensity classes based on light measurements in 1992 (see fig 1: relative light intensity in percent = % rL, n = number of grid square per light class). Different small letters represent significant differences between years, while different numbers indicate significant differences between light classes (Scheffé-test, data log transformed, $p < 0.05$).

a) number of species per grid square (25 m²)

| years after canopy opening | | | | | | | | | | | | | | | | |
|----------------------------|----|-----------|---|---|-----------|----|---|-----------|----|---|-----------|----|---|-----------|----|---|
| light class | | 0. (1989) | | | 1. (1990) | | | 2. (1991) | | | 3. (1992) | | | 5. (1994) | | |
| (% rL) n | | | | | | | | | | | | | | | | |
| < 7 | 64 | 16.8 | a | 1 | 17.9 | ab | 1 | 17.2 | ab | 1 | 18.2 | b | 1 | 18.1 | b | 1 |
| 7–16 | 27 | 18.8 | a | 2 | 19.7 | ab | 2 | 19.6 | ab | 2 | 20.6 | ab | 2 | 21.2 | b | 2 |
| > 16 | 23 | 18.7 | a | 2 | 20.0 | ab | 2 | 20.7 | ab | 2 | 22.2 | b | 2 | 19.8 | ab | 2 |

b) evenness per grid square (25 m²)

| years after canopy opening | | | | | | | | | | | | | | | | |
|----------------------------|----|-----------|----|---|-----------|---|---|-----------|---|----|-----------|---|----|-----------|---|---|
| light class | | 0. (1989) | | | 1. (1990) | | | 2. (1991) | | | 3. (1992) | | | 5. (1994) | | |
| (% rL) n | | | | | | | | | | | | | | | | |
| < 7 | 64 | 0.780 | a | 1 | 0.761 | a | 1 | 0.765 | a | 1 | 0.776 | a | 2 | 0.761 | a | 1 |
| 7–16 | 27 | 0.800 | a | 1 | 0.782 | a | 1 | 0.796 | a | 12 | 0.813 | a | 1 | 0.824 | a | 2 |
| > 16 | 23 | 0.784 | ab | 1 | 0.768 | a | 1 | 0.811 | b | 2 | 0.804 | b | 12 | 0.815 | b | 2 |

Tab. 2

Change of diversity parameters in relation to light availability on the *Allium*-plot. Mean values are given separated for three light intensity classes based on light measurements in 1992 (see fig 1: relative light intensity in percent = % rL, n = number of grid square per light class). Different small letters represent significant differences between years, while different numbers indicate significant differences between light classes (Scheffé-test, data log transformed, $p < 0.05$).

a) number of species per grid square (25 m²)

| years after canopy opening | | | | | | | | | | | | | | | | |
|----------------------------|----|-----------|---|---|-----------|----|---|-----------|-----|---|-----------|----|---|-----------|---|---|
| light class | | 0. (1989) | | | 1. (1990) | | | 2. (1991) | | | 3. (1992) | | | 5. (1994) | | |
| (% rL) n | | | | | | | | | | | | | | | | |
| < 7 | 42 | 11.3 | a | 1 | 11.3 | a | 1 | 11.5 | a | 1 | 12.5 | ab | 1 | 13.7 | b | 1 |
| 7–16 | 32 | 11.3 | a | 1 | 12.7 | ab | 1 | 13.5 | abc | 2 | 14.5 | bc | 2 | 15.5 | c | 1 |
| > 16 | 16 | 12.1 | a | 1 | 12.7 | ab | 1 | 14.9 | bc | 2 | 17.3 | cd | 2 | 19.2 | d | 2 |

b) evenness per grid square (25 m²)

| years after canopy opening | | | | | | | | | | | | | | | | |
|----------------------------|----|-----------|---|---|-----------|----|---|-----------|----|----|-----------|---|---|-----------|----|---|
| light class | | 0. (1989) | | | 1. (1990) | | | 2. (1991) | | | 3. (1992) | | | 5. (1994) | | |
| (% rL) n | | | | | | | | | | | | | | | | |
| < 7 | 42 | 0.620 | a | 2 | 0.643 | ab | 2 | 0.638 | ab | 1 | 0.691 | b | 1 | 0.615 | a | 1 |
| 7–16 | 32 | 0.574 | a | 1 | 0.588 | a | 1 | 0.665 | b | 12 | 0.743 | c | 2 | 0.676 | b | 1 |
| > 16 | 16 | 0.525 | a | 1 | 0.566 | ab | 1 | 0.715 | bc | 2 | 0.789 | c | 2 | 0.719 | bc | 1 |

number of species with increasing light availability was coupled with a prominent decrease in evenness (tab. 2b). This means that the vegetation was dominated by fewer species in the higher light classes. In the following years, evenness values increased paralleling number of species and light availability. Therefore the increase of the number of species along the light gradient was, as in the *Mercurialis*-plot, connected to an increasing evenness in species composition.

4 Discussion

The development of diversity in the forest floor vegetation after canopy opening was dependent on preexisting conditions, light availability, and time elapsed after impact.

The decrease of number of species on the *Mercurialis*-plot towards the end of the investigated period is correlated with the growth of young forest trees and probably will in the future also occur on the *Allium*-plot. Tree saplings are increasingly competing for light with herbaceous plants of the forest floor. A number of light-demanding plants, which as typical woodland-clearing species appear for short periods after canopy opening (e.g. *Epilobium angustifolium*, *Taraxacum officinale*), are being driven out by the densely closing canopy of regrowing trees. The transient appearance of such seral plant species in forests (HABECK 1968, AUCLAIR & GOFF 1971, PEET 1978, SCHMIDT 1991) and other communities as well account for a temporary increase in species richness in the course of regeneration and secondary succession (LOUCKS 1970, HORN 1974, BAZZAZ 1975, SCHMIDT 1991, 1993). In the *Allium*-plot, species richness increased over a period of 5 years, indicating that competition for light with tree saplings has not yet had a negative impact on the presence of most herbaceous species. The *Mercurialis*-plot had a high number of growth-suppressed tree saplings, which were stuck in growth due to the lack of light before the gap creation and these saplings started to grow soon after canopy opening. The increase of cover and height of woody species everywhere on the plots, including the closed forests, might be explained by the protection from roe deers herbivory by fencing (SCHMIDT 1991). In the comparison of the plots it has been considered that the investigated limestone beech forest (*Hordelymo-Fagetum lathyretosum*) typically shows strong fluctuations in the cover of *Mercurialis perennis* stands and relatively small changes for *Allium ursinum* stands (LINDQUIST 1931, ELLENBERG 1986). The abundance of *Mercurialis perennis* is commonly strongly reduced after dry and hot summers, as they occurred since 1989 several times, and after especially moist springs and early summers

which favor fungus infections, but population recovery can be rather quick (SCHMIDT 1988).

A pure dependency of plant diversity on light availability has to our knowledge never been described. In most cases, light is investigated in connection with other environmental factors, as did TILMAN (1986) when comparing the importance of light and nutrients in old-field succession. The observed peak of species diversity in areas with intermediate light regimes agrees well with an above mentioned hypothesis about the unimodal relationship between diversity and resource availability (ROSENZWEIG 1971, TILMAN 1982). A seemingly contradicting negative correlation between light availability and species richness is reported by PAUSAS (1994) for pine forests in the Pyrenees. In those forests, an inverse coupling of light and water availability is typical, causing a reduction in the number of species due to increasing aridity. The decrease of species richness (but not of evenness) noted on the *Mercurialis*-plot in the area with highest relative light intensity in the 5th year after canopy opening also agrees with another diversity hypothesis. Here, a saturation of species richness is predicted for disturbed communities for a certain time period after impact. The following decrease is due to biotic interactions – namely competition for light. This appears to be a typical phenomenon of secondary succession or regeneration, i.e. gap dynamics in forests (PEET et al. 1983).

Observing the example of diversity change in an artificially created forest gap, it becomes evident that patterns of species richness can be investigated in their dependency from resource gradients and as being dependent from different stages of succession as well. Therefore, the dynamic of diversity of forest floor vegetation can be described in terms of equilibrium models (e.g. resource gradient) or non-equilibrium models (succession). It appears to be legitimate – and even needed – to apply simultaneously these seemingly contradicting concepts in the present case of diversity dynamics. This is especially true since not only the optimal phase of forest ecosystems, but also regeneration phases are concerned. Following HOBBIÉ et al. (1993) the question is to be raised, whether this is valid also for other vegetation types and whether more universally applicable concepts need to be developed.

Acknowledgments

Thanks to Jochen Schenk (Santa Barbara) for a thorough linguistic revision of the text and for important comments on the manuscript.

Financial support was received from the BMFT (Ministry of Research and Technology, Germany); projects 6.3.5.2 and B2-Z-b of the Forschungszentrum Waldökosysteme, University of Göttingen.

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Zeitschrift/Journal: [Verhandlungen der Gesellschaft für Ökologie](#)

Jahr/Year: 1996

Band/Volume: [25_1996](#)

Autor(en)/Author(s): Schmidt Wolfgang, Holzapfel Claus, Weitemeier Mathias

Artikel/Article: [Vegetation dynamics in canopy gaps of a beech forest on limestone - The influence of the light gradient on species richness 253-260](#)