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The behavior and dynamics of some dominant herbaceous plants of Swiss deciduous forests

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ABSTRACT**:** In the late sixties, K. Zarzycki investigated the behavior of some forest herbs in different beech communities near Zürich. In 1994 we examined four of the herbs, *Deschampsia flexuosa* (L.) Trin., *Carex pilosa* Scop., *Mercurialis perennis* L. and *Galim odoratum* (L.) Scop., with respect to their behavior and dynamics. We compared the data obtained, in the context of global warming and "forest decline," with those of K. Zarzycki as well as with data from 1950 –1970 taken from Swiss sources by other authors. The results of these comparisons suggest several conclusions. *(1)* Generally the four forest herbs behaved similarly regarding their trends of major changes and their steadiness; *(2)* In the field the examined species are becoming rarer in terms of both abundance and constancy. Abundance is somewhat lower, but the species generally have not disappeared from those old plots. So far no physiognomic adaptations to the somewhat changing environment have been detected. *(3)* Until now acid rain has been buffered in most soils and acidity indicators have not increased; they have even decreased in many cases (*Luzula*). Nutrient flux has increased due to input by rain, but many indicators have not really responded. *(4)* Changes in terms of species abundance and constancy are probably due to the light factor. Forest cover values have become denser but the crowns are thinner. However, the tendencies are not quite clear. *(5)* All four species follow their typical site preferences, with the exception of *Luzula*. *Mercurialis* is more frequent on nutrient-rich and basic soils, *Galium odoratum* is on more mesic sites, and *Carex pilosa* occurs in more acid conditions. *(6)* There is no special trend regarding gains/losses of the species examined in any of the forest associations. The dynamics of these species are discussed as to the predictability of their fluctuations in the herb layer. The species clearly behave according to the rules of models of chaotic development.

KEY WORDS: species dynamics, forest herbs, plant indicators, environmental changes, nutrient flux, predictability, models of chaos

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INTRODUCTION

In the 1960s, Kazimierz Zarzycki (1968) tried to estimate which of the factors, abiotic or biotic (= competition), play the most important role in determining the species composition of the herb layer in different beech communities. He carried out a field experiment in three different beech communities near Zürich (Baden/AG) using six herb plants. Plants characteristic of one beech association, attached to a given type of soil, were planted in single- and multispecies cultures in two other beech associations growing on different types of soil. His results give some information on the behavior and dynamics of the plants. This paper assesses the present performance of the same species (treated as indicator species), especially in the context of global warming and “forest decline.”

In 1994 we revisited the relevé plots from that time (ca. 1950–1970), established and analyzed by numerous Swiss authors (list in Ellenberg & Klötzli 1972). Then we compared some analyses of these plots, which had not been disturbed or altered by silviculture management, with their current state, assessing their development under changing environmental conditions such as the increasing influence of nutrients, acidity and temperature, probable changes of light intensity in stands of deciduous forests, possible changes in browsing intensity, etc. We evaluated changes of site conditions and the floristic composition of the moss, herb, shrub and tree layers.

Recent work (Carraro *et al.* 1999; Klötzli *et al.* 1996) has shown that trends in the changing herb and moss layers may be correlated to changing environmental factors (nutrient conditions, local climate, etc.), considering the indicator values (e.g., Ellenberg 1950, 1952, 1956; Ellenberg *et al.* 1992) of all plants of the herb and moss layers (compare discussion by Carraro *et al.* 1999 on the dynamics of, e.g., temperature indicators).

Here we assess recent trends in some of the forest herbs examined by Zarzycki, considering their indicator values, especially regarding their behavior under the influence of changes in climate and nutrient conditions.

MATERIAL AND METHODS

On a 30 km wide transect crossing Switzerland, relevés from the late 1950s, 1960s and 1970s were resurveyed in 1994 with Braun-Blanquet methods (details given in Carraro *et al.* 1999). From this data set, relevés containing the widespread target species [*Luzula nemorosa* (Poll.) E. Mey., *Deschampsia flexuosa* (L.) Trin., *Carex pilosa* Scop., *Mercurialis perennis* L. and *Galium odoratum* (L.) Scop.], which were used in the Zarzycki-experiments (Zarzycki 1968) were selected. The twofold set of old and new relevés was compared to determine the fluctuations of these target species in the time span between the two surveys, considering relative changes in the abundance and constancy of the species. The analyses revealed matrices for each species, with the number of relevés and directional trends of the major changes of every tested species. The changes in these target species were analyzed as to their affiliation to the most common forest associations in the investigation area. Changes in constancy are listed in the tables as gains and losses; they signify that a species has disappeared or is newly occurring in one of the compared relevés.

RESULTS

Species’ preferences and general changes in occurrence

Compiled from Zarzycki’s results (compare Tables 1 & 2), *Mercurialis perennis* shows clear supremacy on nutrient-rich and basic (limestone) soils and is presently gaining and losing constancy and abundance in equal amounts (Table 3a).

Table 1. Conditions of the Zarzycki's field experiment on competition between forest herbs occurring in the herb layer of different beech forests (compiled on the basis of Zarzycki (1968): text & Fig. 1).

Code	Forest community	Herb dominating before beginning of the experiment	Type of soil	NH_4^+ mg per 100g ds	NO_3^- mg per 100g ds	pH (H_2O)	Start of the experiment
A	*Tilio-Fagetum*	*Mercurialis perennis*	Rendzina	0	2–3	7–8	autumn 1964
B	*Galio od.-Fagetum*	*Carex pilosa*	Acid brown	2–6	< 1	5–5.5	autumn 1964
C	*Luzulo-Fagetum*	*Vaccinium myrtillus*	Moder brown	6–30	~0	4.5–5	autumn 1965

Location of the experiment: near Baden (CH), altitude 470–490 m a.s.l., ∅ P ≈ 1000mm/y, ∅ T 8.5°C.

Ecosystem dynamics: + N; pH ± constant (buffered), biotic factors (e.g. browsing roe deer).

Species examined: *Deschampsia flexuosa*, *Carex pilosa*, *Carex alba*, *Mercurialis perennis*, *Luzula nemorosa*, *Galium odoratum*.

Design of the experiment: each pure or single-species culture was started with 84 plants of a species; each species was represented in a mixed or multi-species culture by 28 plants; pure and mixed cultures were grown in 3 different beech communities (coded as **A**, **B** and **C**) on plots on which the natural herb layer was removed; 4 replications were made.

Galium odoratum is dispersed over a wide range, taking a medium position on the acidity gradient, especially in competition with other mesic species (Tables 1 & 2). Gains and losses are not considerable, but decreases in abundance are marked, affecting around 30% of all occurrences (Table 3b).

The last two species obviously compete best under more acid soil conditions (Tables 1 & 2). In the comparison of relevés, *Luzula nemorosa* has lost constancy (40%) and abundance in 26% of all occurrences (Table 3c), whereas *Carex pilosa* is generally increasing its presence in terms of both constancy and abundance (Table 3d).

Specific changes in occurrence (compare Table 3a-d):

Balance. On average all tested species are tending to become rarer, independent of their site conditions, at least quantitatively. Abundance is diminishing nearly everywhere. Of all four species only *Mercurialis perennis* remained in a certain balance.

Gains. *Galium odoratum* increased, considering the occurrence in all relevés, but not quantitatively considering the losses in abundance. *Carex pilosa* also is more on the gain side, with increasing constancy and abundance.

Losses. The only true loser is *Luzula nemorosa* – it has lost in constancy and in abundance, independently of the forest associations it occurs in, including acid sites.

Fluctuations in the number of occurrences (constancy) and in abundance are usual. No species is steady in its occurrence.

Table 2. Results of Zarzycki's field experiment: growth and development of some forest herbs under competitive conditions (compiled on the basis of Zarzycki 1968: text & Figs 4–6). **A** – *Tilio-Fagetum*; **B** – *Galio odorati-Fagetum*; **C** – *Luzulo-Fagetum*; **s** – acidity indicator; (**s**) – weak acidity indicator; **b** – base indicator; **m** – mesic species.

Characteristic examined	Culture	1964* (1965)	**A**	**B**	**C**	**A**	**B**	**C**
			Species examined in 1966					
			Deschampsia flexuosa **s**			*Carex pilosa* (**s**)		
Survival of planted individuals (%)	pure	100	35	75	90	10	70	95
	mixed	100	55	60	>95	0	70	95
Assimilating surface per individual (cm^2)	pure	30	25	30	25	5	55	30
	mixed	30	25	40	30	<5	60	30
Assimilating surface per 1 m^2 (cm^2)	pure	1400	400	1100	1100	100	1400	1700
	mixed	1400	800	1200	1400	0	1800	1600
Number of shoots (%)	pure	100	50	>100	120	<5	115	135
	mixed	100	80	>100	150	0	105	125
			Carex alba **b**			*Mercurialis perennis* **b**		
Survival of planted individuals (%)	pure	100	Not included1)			122	55	50
	mixed	100				336	50	20
Assimilating surface per individual (cm^2)	pure	120				60	40	40
	mixed	120				50	35	20
Assimilating surface per 1 m^2 (cm^2)	pure	5620				3335	950	250
	mixed	5620				8163	800	150
			Luzula nemorosa **s**			*Galium odoratum* **m**		
Survival of planted individuals (%)	pure	100	30	60	95	75	65	90
	mixed	100	30	60	90	80	85	75
Number of shoots (%)	pure	50/100*	20	50	75	80	50	50
	mixed	50/100	15	90	70	<110	115	80

1964* – a value of the characteristic examined at the start of the experiment in 1964 (or in 1965 in the case of beech community **C**).

50/100* – a value of the characteristic calculated for *Luzula nemorosa*/ a value of the characteristic calculated for *Galium odoratum*.

1) *Carex alba* is a test-species in Zarzycki (1968) but not constant enough to consider an analysis of its dynamics.

Dynamics

Steadiness. Seen in terms of all the aforementioned results there is a certain steadiness. Species fluctuate, they disappear from certain places, reappear in others, appear newly in an area or, more often, shift in from nearby; on average, however, most test species are tending to become rarer – they occur with less abundance.

Adaptation. Considering the average changes in the upper soil horizon, slight acidification, eutrophication, probably more regular desiccation processes due to higher summer temperatures coupled with drought periods, there is no change in the plants' physiognomy; for example, *Galium odoratum* groups are not less dense or less high or with less vitality (as on dry acid sites). However, any genetically fixed adaptations would have to be investigated.

Table 3a. Comparisons of given pairs of relevés from the two surveys (1950–1970 and 1994): changes in the presence (= constancy and abundance) of *Mercurialis perennis* L.

		Losses					Persistent						Gains				
Old values ⇒ **New values ⇒**		**4** ↓ **Ř**	**3** ↓ **Ř**	**2** ↓ **Ř**	**1** ↓ **Ř**	**+** ↓ **Ř**	+	**1**	**2**	**3**	**4**	**5**	**Ř** ↓ +	**Ř** ↓ **1**	**Ř** ↓ **2**	**Ř** ↓ **3**	(Survey 1950-70) (Survey 1994)
# losses		2		3	3	3											
# gains													5	6	1	1	
Decrease in abundances (steps)*	*-1*								2	2	1						
	-2									2	1	1					
	-3										1						
	-4																
	-5																
Indifferent							3	1	1	1	2						
Increase in abundances (steps)*	*+1*						1	1	2	1							
	+2						2	1									
	+3																
	+4																
	+5																

Species		
Total occurrence	**50**	[%]
Total Gains	**13**	26
Total Losses	**11**	22
Persistent	**26**	52
↑ ↑ ↑	↑	↑
Decreasing abundancy	10	20
Increasing abundancy	8	16
Same abundancy	8	16

*steps +/1/2/3/4/5 abundancy sensu Braun-Blanquet, to be calculated from the basis values given in the persistent column.

Sociological distribution of occurrences

Forest association [vegetation unit n° according to Ellenberg &Klötzli (1972)]		Number of occurrences	% of total number	Total losses	Total gains
Galio odorati-Fagetum typicum	[7]	8	16	3	1
Milio-Fagetum	[8]	2			2
Pulmonario-Fagetum typicum	[9]	2			
Pulmonario-Fagetum melittetosum	[10]	1			1
Aro-Fagetum	[11]	10	20	2	
Cardamino-Fagetum typicum	[12]	1			
Cardamino-Fagetum tilietosum	[13]	1			1
Carici albae-Fagetum caricetosum montanae	[15]	9	18	4	4
Seslerio-Fagetum	[16]	1			1
Taxo-Fagetum	[17]	4		1	
Asperulo taurinae-Tilietum	[25]	2			
Aceri-Fraxinetum	[26]	6		1	1
Ulmo-Fraxinetum listeretosum	[29]	2			1
Galio silvatici-Carpinetum	[35]	1			1
	Total	**50**		**11**	**13**

Effects of site factors

Acidity. Judging from the behavior of *Luzula nemorosa*, a reliable acidity indicator, and of *Mercurialis perennis* a baseness indicator, there are no direct signs of promotion of acidity indicators due to acid rains. On the contrary, *Luzula* has decreased and *Mercurialis* has remained stable.

Nutrients. Judging the physiognomy and size of plants normally reacting to more nutrient input, there is apparently no promotion of plants such as *Mercurialis*, whose abundance is favored by nutrient inputs. However, there is a slight tendency to spread centrifugally from the site of the old plots.

Table 3b. Comparisons of given pairs of relevés from the two surveys (1950–1970 and 1994): changes in the presence (= constancy and abundance) of *Galium odoratum* (L.) Scop.

		Losses					Persistent						Gains				
Old values ⇒ **New values ⇒**		4 ↓ Ř	3 ↓ Ř	2 ↓ Ř	1 ↓ Ř	+ ↓ Ř	+	1	2	3	4	5	Ř ↓ +	Ř ↓ 1	Ř ↓ 2	Ř ↓ 3	(Survey 1950-70) (Survey 1994)
# losses				2	3	5											
# gains													7	9	4	1	
Decrease in abundances (steps)*	*-1*							6	29	1							
	-2								6	6							
	-3									1							
	-4																
	-5																
Indifferent							8	25	10								
Increase in abundances (steps)*	*+1*						10	15									
	+2						3	1									
	+3																
	+4																
	+5																

Species		
Total occurrence	**152**	[%]
Total Gains	**21**	14
Total Losses	**10**	7
Persistent	**121**	79
↑ ↑ ↑	↑	↑
Decreasing abundancy	49	32
Increasing abundancy	29	19
Same abundancy	43	28

*steps +/1/2/3/4/5 abundancy sensu Braun-Blanquet, to be calculated from the basis values given in the persistent column.

Sociological distribution of occurrences

Forest association [vegetation unit n° according to Ellenberg &Klötzli (1972)]	Number of occurrences	% of total number	Total losses	Total gains
Luzulo silvaticae-Fagetum typicum [1]	2			2
Galio odorati-Fagetum luzuletosum [6]	2			1
Galio odorati-Fagetum typicum [7]	90	59	6	9
Milio-Fagetum [8]	12	8		1
Pulmonario-Fagetum typicum [9]	1			
Pulmonario-Fagetum melittetosum [10]	4			
Aro-Fagetum [11]	15	10		2
Cardamino-Fagetum typicum [12]	1		1	
Cardamino-Fagetum tilietosum [13]	1		1	
Carici albae-Fagetum caricetosum montanae [15]	9	6	2	3
Taxo-Fagetum [17]	1			
Abieti-Fagetum luzuletosum [19]	1			1
Asperulo taurinae-Tilietum [25]	1			
Aceri-Fraxinetum [26]	6	4		2
Carici remotae-Fraxinetum [27]	1			
Ulmo-Fraxinetum listeretosum [29]	2			
Galio silvatici-Carpinetum [35]	2			
Cephalanthero-Pinetum silvestris [62]	1			1
Total	**152**		**10**	**21**

Light. Due to a recent development at our forest sites, known as forest decline or more recently called new forest damage, there is no doubt that the crowns have become less dense. Due to changing management conditions, however, the forests as such have become more dense, the forest floor is darker, and light-demanding species have therefore declined. On the other hand, the heliophilous *Carex pilosa*, a species that grows in a wide range of light conditions, has clearly gained. The other three species are clearly shade-tolerant but have not reacted appropriately.

Table 3c. Comparisons of given pairs of relevés from the two surveys (1950–1970 and 1994): changes in the presence (= constancy and abundance) of *Luzula nemorosa* (Poll.) E. Mey.

		Losses					Persistent						Gains				
Old values ⇒ **New values ⇒**		**4** ↓ **Ř**	**3** ↓ **Ř**	**2** ↓ **Ř**	**1** ↓ **Ř**	+ ↓ **Ř**	+	**1**	**2**	**3**	**4**	**5**	**Ř** ↓ +	**Ř** ↓ **1**	**Ř** ↓ **2**	**Ř** ↓ **3**	(Survey 1950-70) (Survey 1994)
# losses				2	7	9											
# gains													1	2			
Decrease in abundances (steps)*	*-1*							7	2								
	-2								2								
	-3									1							
	-4																
	-5																
Indifferent							3	6									
Increase in abundances (steps)*	*+1*						3										
	+2																
	+3																
	+4																
	+5																

Species		
Total occurrence	**45**	[%]
Total Gains	**3**	7
Total Losses	**18**	40
Persistent	**24**	53
↑ ↑ ↑	↑	↑
Decreasing abundancy	12	26
Increasing abundancy	3	7
Same abundancy	9	20

*steps +/1/2/3/4/5 abundancy sensu Braun-Blanquet, to be calculated from the basis values given in the persistent column.

Sociological distribution of occurrences

Forest association [vegetation unit n° according to Ellenberg &Klötzli (1972)]		Number of occurrences	% of total number	Total losses	Total gains
Luzulo silvaticae-Fagetum typicum	[1]	3		1	
Galio odorati-Fagetum luzuletosum	[6]	3			
Galio odorati-Fagetum typicum	[7]	33	73	12	3
Milio-Fagetum	[8]	1		1	
Pulmonario-Fagetum melittetosum	[10]	2		2	
Carici albae-Fagetum caricetosum montanae	[15]	1		1	
Galio silvatici-Carpinetum	[35]	2		1	
Total		**45**		**18**	**3**

Forest associations

In the most widespread forest associations (vegetation units 7, 11, 15, according to Ellenberg and Klötzli 1972, i.e., *Galio odorati-Fagetum*, *Aro-Fagetum*, *Carici-Fagetum*) losses and gains in constancy, not considering changed abundances, are more or less in equilibrium (cf. Table 4).

DISCUSSION

The dynamics of dominant species have been investigated in chronosequences by quite a number of authors. Dierschke and Brünn (1993) in particular showed fluctuations in the herb layer of beech forests, with special attention to *Mercurialis perennis*, *Allium ursinum* and *Galium odoratum*. Further results were presented by Runge (1994, 1995) and others.

Table 3d. Comparisons of given pairs of relevés from the two surveys (1950–1970 and 1994): changes in the presence (= constancy and abundance) of *Carex pilosa* Scop.

		Losses					Persistent						Gains				
Old values ⇒ **New values ⇒**		**4 ↓ Ř**	**3 ↓ Ř**	**2 ↓ Ř**	**1 ↓ Ř**	**+ ↓ Ř**	**+**	**1**	**2**	**3**	**4**	**5**	**Ř ↓ +**	**Ř ↓ 1**	**Ř ↓ 2**	**Ř ↓ 3**	(Survey 1950-70) (Survey 1994)
# losses																	
# gains													2	3		2	
Decrease in abundances (steps)*	*-1*									3							
	-2																
	-3																
	-4																
	-5																
Indifferent								1	1	3							
Increase in abundances (steps)*	*+1*								7								
	+2							1									
	+3																
	+4																
	+5																

<u>Species</u>		
Total occurrence	**23**	[%]
Total Gains	**7**	30
Total Losses	**0**	0
Persistent	**16**	70
↑ ↑ ↑	↑	↑
Decreasing abundancy	3	13
Increasing abundancy	8	35
Same abundancy	5	22

*steps +/1/2/3/4/5 abundancy sensu Braun-Blanquet, to be calculated from the basis values given in the persistent column.

Sociological distribution of occurrences

Forest association [vegetation unit n° according to Ellenberg &Klötzli (1972)]		Number of occurrences	% of total number	Total losses	Total gains
Galio odorati-Fagetum typicum	[7]	22	96	0	6
Pulmonario-Fagetum melittetosum	[10]	1		0	1
Total		**23**		**0**	**7**

We have tried to detect the influence of changing environmental factors on the presence of forest herbs, that is, their constancy and abundance. These reactions of common, often dominant species of the herb layer were compared with Zarzycki's (1968) findings for *Mercurialis perennis*, *Galium odoratum*, *Carex pilosa* and *Luzula nemorosa*.

It is difficult or nearly impossible to predict such dynamic processes. A 40–120-year forecast using cellular automata is feasible (Gassmann *et al.* 2000). Carraro *et al.* (1999) addressed the influence of global change with regard to the increase of winter (and to some extent summer) temperatures. Such an analysis has been done on the basis of the behavior of a number of indicator species in large sets of vegetation relevés, detecting shifts in temperature indicators (cf. Klötzli & Walther 1999; Walther 2001). For northern Switzerland, clear shifts are detectable: both gains of thermophilous species, and losses of montane species in lowland areas, which are tending to shift up the slopes (Walther 1997).

These tendencies make it clear that a combination of other site factors or one site factor may play a decisive role. As presented in Klötzli *et al.* (1996) with the help of Principal Coordinate Analysis, light conditions have also changed. Although crowns have become thinner on many trees (forest decline), stands as a whole are closer compared to stands from the 1950–1970 period. Some target species on the forest floor are therefore suppressed (*Luzula*, *Galium*, *Mercurialis*), and the only species benefitting due to its wider shade tolerance is doubtlessly *Carex pilosa*, also deriving advantages from its capacity to overcome drought periods in summer and from nutrient enrichment. Its occurrence and high presence in subcontinental deciduous forests also indicates its resistance to drought and its adaptation to warmer summers.

Considering that precipitation has become more acid and enriched in nutrients (details in Klötzli 1993) there are a number of discrepancies in the behavior of the tested forest herbs according to Table 3a–d. *Luzula nemorosa*, for example, a typical acidity indicator on drier sites, has lost both abundance and constancy even on acid sites.

Forest associations

Looking at the species distribution in the different forest associations, gains and losses are irregularly distributed among the different units (according to Ellenberg & Klötzli 1972). There are specific trends only in certain associations (Table 4).

Table 4. Balance for the most widespread vegetation units (for nos. see Table 3).

Species	Unit n°	Nr. of relevés	Gains	Losses	Gains [%]	Losses[%]
Mercurialis perennis	7	8	1	3		
Galium odoratum	7	90	9	6		
Luzula nemorosa	7	33	3	12		
Carex pilosa	7	22	6	0		
Total		**153**	**19**	**21**	**12**	**14**
Mercurialis perennis	11	10	0	2		
Galium odoratum	11	15	2	0		
Total		**25**	**2**	**2**	**8**	**8**
Mercurialis perennis	15	9	4	4		
Galium odoratum	15	9	3	2		
Total		**18**	**7**	**6**	**39**	**33**

Our findings are mostly in accordance with the earlier results of Kuhn *et al.* (1987) for two warmer and less humid regions [Schaffhausen (SH), Geneva (GE)] of the Swiss lowlands. Forty or fifty years separate the two sets of relevés [SH (1935–)1938–1984 & GE (1942–)1947–1985]. Their later values for occurrence and abundance are all around 65% of the former values. In the northern region (SH) the frequency of acidity indicators (*Deschampsia flexuosa*, *Luzula nemorosa*) has declined, and the mesic species *Galium odoratum* has kept its balance. *Mercurialis perennis* and *Carex pilosa* have newly appeared in a forest association of dry/acid sites (“*Querco-Betuletum*“, unit 1, now called *Luzulo-Fagetum* in the Swiss lowlands). There is a certain trend at least in this association to more basic and nutrient-rich sites with less light intensity in the stands.

Near Geneva the situation is similar, investigated in stands of *Galio-Carpinetum*, unit

35 (Ellenberg & Klötzli 1972), at the time called *Querco-Carpinetum molinietosum*. Although *Deschampsia flexuosa* is a newcomer in that association, the general tendency is – as in the first example – towards more basic and nutrient-rich sites. Furthermore, acidity indicators have been partially lost, the light conditions remaining more or less constant. From our own results and experience we may conclude that with some restrictions these findings, showing clear tendencies in some forest associations and in some regions, are valid for most regions in Switzerland and for most sites, probably becoming more pronounced each year.

The situation is unclear regarding indicators of changes in average light conditions. No doubt they are all tolerant and able to support conditions of deep shade, but the most light-demanding species have gained even though the cover value in the tree layer has increased. Finally, reactions to pathogens or to distinct changes due to differences in the intensity of browsing or pasturing of forest animals are not known.

Obviously, all changes are accompanied by open questions; most likely the plants' behavior is giving us signs we do not fully understand (cf. also van der Maarel 1996; Agnew *et al.* 1993). Is it a sign due to changing climatic conditions? Clearly there are shifts that are new to us, and we the lack experience to fully analyze such a new situation.

Conclusions

Regarding Tables 1 & 2, depicting behavior in terms of competitive ability, and Table 3a–d, showing the behavior of the four species examined, some general conclusions may be drawn from both investigations:

– acidifying precipitation is still being absorbed by the high buffering capacity of rendzina and often base-rich brown soils;

– nutrient enrichment favors many tall forbs and other nutrient indicators, which partly shade less vigorous species;

– higher temperatures and fewer traumatic events (less late frost, deep winter frost, etc.) are producing shifts in the groups at distinct elevations;

– the change in average light conditions in forest stands is a result of management techniques, the vitality of trees, the effects of nutrient input and leaf development. It influences the composition of the herb layer, and is probably the most general and most operative factor in our changing stands and subsequently modifying the herb layer (cf. Klötzli *et al.* 1996).

To conclude, changes in the composition of the herb layer should be approached with appropriate experiments. As recent evaluations have shown, most indicator plants are good tools – and so far often the only ones due to the lack of old permanent plots – to assess at least the tendencies in the changing environment of the last few decades. For the future, more intensive monitoring on old plots or the establishment of more permanent plots (Schmidt 1974) should be considered.

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