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Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990

Thomas Wohlgemuth[1], Peter Kull[2] and Hansjürg Wüthrich[3]

[1] WSL Swiss Federal Research Institute, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. thomas.wohlgemuth@wsl.ch

[2] Amt für Natur- und Landschaftsschutz Kt. Luzern, Murbacherstrasse 23, CH-6002 Luzern, Switzerland. peter.kull@anls.jd.lu.ch

[3] Amt für Wald des Kantons Bern, Effingerstrasse 53, CH-3011 Bern, Switzerland. hansjuerg.wuethrich@vol.be.ch

Abstract

In 1990, the catastrophic storm Vivian created extensive windthrows, particularly in some mountain forests of the Swiss Alps. We have since been observing the vegetation succession and the tree regeneration in uncleared and cleared windthrown stands on four study sites in mountain forests at altitudes of 900 to 1600 m a.s.l. On the study sites, microsites were mapped and, subsequently, 236 permanent quadrats were installed. At two-year intervals, data were collected on plant and moss species between 1992 and 2000. Vegetation dynamics were analysed with respect to the succession of microsites, disturbance types, treatments and years of tree seed germination. Vegetation cover increased in all quadrats observed independent of microsites and types of disturbance. On most of the microsites, *Rubus idaeus* increased in frequency and in cover during the first 10 years after the windthrow. Grasses such as *Calamagrostis villosa*, *Agrostis capillaris* and *Avenella flexuosa* also increased. The most abundant regenerating tree species were *Picea abies*, *Acer pseudoplatanus* and *Sorbus aucuparia*. Seedlings and saplings were small or absent in tall herb communities. Advance regeneration was of predominant importance on all study sites. Post-windthrow regeneration was greatest on disturbed microsites. The regeneration density of the whole study area (projected from the permanent quadrats) ranged between 2000 and 45 000 seedlings and saplings per ha. This indicates considerable differences in recruitment conditions in mountain forests after windthrow. Disturbance to tall herb-dominated gaps in mountain forests favours seedling recruitment during the early succession after the windthrow. Disturbance effects caused by timber harvest after a windthrow resulted in a large density of post-windthrow regeneration that may compensate, at least partly after only 10 years, for the advance regeneration destroyed.

Keywords: windthrow, storm, disturbance, advance and post-windthrow regeneration, tall herb communities, *Picea abies*, *Rubus idaeus*, mountain forest, Switzerland

1 Introduction

Catastrophic storm winds are the most frequent exogenous disturbance agent affecting forest stands in Central Europe (SCHERZINGER 1996). According to the Swiss National Forest Inventories in Switzerland, about two thirds of all unplanned felling in Switzerland were caused by windthrow, and 13% by insect attacks that are usually triggered by wind damage (BUWAL 1997; BRASSEL and BRÄNDLI 1999). Many of these disturbed forests serve a protective function, i.e. they protect people and assets in the European Alps against the impact of natural hazards such as rockfall and snow avalanches (BRANG *et al.* 2001). Against this background, sustainable tree regeneration has been declared a key issue in the management of mountain forests, including both undisturbed or disturbed stands (OTT *et al.* 1997; BRASSEL and BRÄNDLI 1999).

In February 1990, the storm Vivian left 5 million m^3 of windthrown timber in Switzerland, with major centres in the Northern Pre-Alps. A controversial debate on the appropriate management of windthrown stands in protective forests followed (SCHÖNENBERGER *et al.* 1992). Based on the question of elasticity i.e. the "speed of return to the referential state or dynamics after a disturbance" (GRIMM and WISSEL 1997; BRANG 2001), different strategies have since been proposed or applied by foresters (ANGST *et al.* 2000). Even on steep slopes over towns or above main roads, the windthrown timber from Vivian was removed immediately after the wind disturbance, avalanche prevention structures were subsequently built and tree saplings planted. This procedure was aimed at both maintaining avalanche protection and ensuring tree regeneration. On remote steep slopes where the forest served no obvious protective function for people or assets, the timber was often harvested using costly helicopter logging or by mobile cable-cranes, followed partly by tree planting. As a consequence, not only has this "clean" management been questioned but so too has the Swiss government's policy of subsidising it. A preliminary decision support system (BUWAL 2000) raised the crucial question of whether the option "timber harvest" is, when all its effects are considered, superior to the option "leave the timber untouched".

Tree regeneration takes place sooner or later after windthrow. The speed and the density of tree regeneration, however, depend on various conditions. Wind disturbance in forests creates gaps and new microsites e.g. pit-and-mound topography (EVERHAM and BROKAW 1996; CLINTON and BAKER 2000; PALMER *et al.* 2000; ULANOVA 2000). The importance of microsites for tree regeneration has been stressed by many authors (e.g. PETERSON and PICKETT 1990; SIMARD *et al.* 1998; PALMER *et al.* 2000; HARRINGTON and BLUHM 2001). In small, untouched windthrow gaps, changes in the vegetation composition after disturbance are slight (COOPER-ELLIS *et al.* 1999; PALMER *et al.* 2000). In contrast, in larger gaps the plant communities change dramatically (PETERSON and PICKETT 1995). Seed rain quantity declines with increasing distance from the remaining stands (LÄSSIG *et al.* 1995). It has been shown that the regeneration density correspondingly declines (ASSELIN *et al.* 2001) and that gap size affects regeneration density (e.g. GRAY and SPIES 1996; COATES 2000). Timber removal from windthrow areas (harvest disturbance; DIBBLE *et al.* 1999) results in an additional, partly extensive, disturbance to the herbaceous and shrub layer.

In order to compare natural succession of both untouched and harvested windthrown stands, a 10-year time series of 236 permanent quadrats (1 m^2) on four Vivian-disturbed study sites in the Swiss Northern Pre-Alps (LÄSSIG *et al.* 1995; SCHÖNENBERGER *et al.* 1995; WERMELINGER *et al.* 1995; WOHLGEMUTH *et al.* 1995) was analysed with respect to the following questions:

- What types of microsites occur in mountain forests after catastrophic windthrow and how do they change during the first years after the disturbance?
- What factors hinder or favour tree regeneration after catastrophic windthrow?
- Does timber harvest, in comparison to no treatment, change the speed of return to a referential state after wind disturbance (elasticity)?

2 Study sites and methods

2.1 Microsites and permanent quadrats

Four Vivian-damaged forest stands in the Swiss Alps at Schwanden, Disentis, Pfäfers and Zweisimmen served as study sites for multiple research purposes (SCHÖNENBERGER *et al.* 1995; SCHÖNENBERGER 2002b). Basically, three different treatments were distinguished on different areas (variants) within the study sites: T1) "uncleared", i.e. no timber harvest followed by natural regeneration, T2) "cleared", i.e. timber harvest by mobile cable-cranes followed by natural regeneration, T3) "cleared and planted", i.e. timber harvest followed by planting of saplings. In Zweisimmen, no timber was harvested (T1 only). On all study sites, however, the occurrence and the cover of microsites obviously differed. In order to stratify the location of permanent quadrats, the vegetation found on the study sites was first classified according to vegetation cover, species composition, dominant species and soil properties in order to identify and map microsites in 1991 (Table 1; WOHLGEMUTH *et al.* 1995). The resulting maps were digitised and integrated into a Geographical Information System (ArcView©) for spatial analysis. Quadrats of 1x1 m size were installed in 1991 and 1992 using microsite maps and random placement. As a rule, we installed five or more replicates per microsite and treatment (Table 2). The planted variant in Pfäfers and the uncleared variant in Disentis were not considered in the sampling because sites were so steep. Deadwood substrate, such as massive windthrown timber, were not defined as microsites and hence were excluded from all quadrat locations. Quadrats on places where trees had been planted after the windthrow were also avoided.

The following data were collected on the quadrats in all study sites during the years 1992, 1994, 1996, 1998 and 2000: cover of plant and moss species in classes: r = <1%, + = 1–5%, 1 = 5–15%, 2 = 15–25%, 3 = 25–35%, 4 = 35–45%, 5 = 45–55%, 6 = 55–65%, 7 = 65–75%, 8 = 75–85%, 9 = 85–100%, according to LONDO (1975) and Domin-Krajina (MUELLER-DOMBOIS and ELLENBERG 1974); total vegetation cover and maximum height; species, position, height, estimated year of germination and browsing (yes or no) of all tree seedlings/saplings (regeneration). From a total of 236 permanent quadrats installed in 1992, 213 were also found in the year 2000. In the study site of Pfäfers, two landslides destroyed 13 quadrats shortly before the census in 2000. Another 10 plots in the Schwanden and Disentis sites were lost during the study period because of inadequate positioning.

Microsites were grouped according to the most obvious disturbance effects of the windthrow (disturbance types; HUGHES and FAHEY 1991). In many of the microsites, the original forest vegetation after the windthrow was not disturbed but exposed to direct sunlight, i.e. light-climate had improved, resulting in the class "l" for "light-exposed". In addition to this effect, in many microsites the original vegetation was removed by timber harvest and related clearing activities or new microsites were created, e.g. pits and mounds. These microsites were grouped together and defined as class "s" for "soil disturbed and light-exposed". Finally, at some places, the light conditions after the windthrow changed only moderately or not at all, e.g. in forest gaps that had already existed before the windthrow. Disturbance effects in these microsites were small or absent, resulting in the class "n" for "not disturbed".

Table 1. Study sites with information on bedrock, altitude a.s.l., aspect, slope and community, and properties of microsites examined: M = microsite abbreviation; T = treatments with T1 = uncleared, T2 = cleared, T3 = cleared and planted; D = disturbance type with n = not disturbed, l = light exposed, s = soil disturbed and light exposed. Soil terms according to ANONYMOUS (1997).

M	T	D	Site description and dominant species in 1992	Soil	Original name
Schwanden			**Verrucano, 920–1125 m; W, 25–35°;** Fir-Beech forest dominated by **Norway Spruce**		
MO	1,2,3	n	**Mo**ist sites with *Stellaria nemorum, Lysimachia nemorum* and *Impatiens noli-tangere*	Acidic Mull Brown Soil, deep	FU
WE	1	n	**We**t sites with *Juncus effusus, Lysimachia nemorum* and *Carex remota*	Mull Pseudo-Gley	NU
DR	1,2,3	l	Convex **dr**y sites with *Luzula sylvatica* and *Blechnum spicant*	Acidic Moder Brown-Podzol, shallow	TR
ME	1,2,3	l	**Me**sic sites dominated by *Luzula sylvatica*	Acidic Moder Brown Soil, deep	TU
CL	2,3	s	Totally disturbed sites due to **cl**earing activities; new soils due to clearing	Regosol, dry	KO
MD	1	s	**M**oun**d**s	Regosol, dry	WT
PI	1,2,3	s	**Pi**ts	Regosol, moist	WA
Disentis			**Gneiss, Granite and Schists, 1400–1550 m; NW, 35–45°;** Bilberry-Norway Spruce forest dominated by **Norway Spruce**		
THa	2	n	**T**all **h**erbs with *Adenostyles alliariae*	Acidic Mull Brown Soil, deep	B1
THb	2,3	n	**T**all **h**erbs with *Aconitum altissimum*	Acidic Mull Brown Soil, deep and coarsly textured	B2
THc	2,3	n	**T**all **h**erbs with *Milium effusum*	Acidic Mull Brown Soil, deep and coarsly textured	B3
GR	2,3	l	**Gr**ass dominated slopes with *Calamagrostis villosa*	Acidic Iron-Humus Podzol, shallow	E
SCa	3	l	**Sc**rees with *Hieracium sylvaticum*	Acidic Brown Soil	A
SCb	2	l	**Sc**rees with *Vaccinium myrtillus* and *Avenella flexuosa*	Limestone Screes with or with no mor/moder layer, shallow	F
SH	3	l	**Sh**allow soils dominated by *Avenella flexuosa* and *Vaccinium myrtillus*	Acidic Iron-Humus Podzol, shallow	D
ME	3	s	**Me**sic sites with *Melampyrum sylvaticum* and *Prenanthes purpurea*	Acidic Moder Brown-Podzol	C
Pfäfers			**Wildflysch (Schist, Limestone), 1400–1490 m; WNW, 40–45°;** Fir-Beech forest dominated by **Norway Spruce**		
GR	2	n	**Gr**ass-dominated convex sites with *Calamagrostis varia* and *Carex flacca*	Mull Regosol	W
THa	1,2	n	**T**all **h**erbs with originally 100% cover	Mull Brown Soil, deep	HA
MO	1,2	l	**Mo**ist sites dominated by *Carex ferruginea*	Gleyed Mull Brown Soil	HV
THb	1,2	l	**T**all **h**erbs with originally < 50% cover	Acidic Mull Brown Soil	HM
CL	1,2	s	Totally disturbed sites due to **cl**earing activities, or pits	Regosol or Mull Brown Soil; Humus is missing	R
SH	2	s	Tall herbs on **sh**allow soil layer over limestone bedrock	Mull Brown Soil, shallow	HG
Zweisimmen			**Breccia (Limestone), 1475–1590 m; WNW, 15-40°;** Silver Fir-Norway Spruce forest dominated by **Norway Spruce**		
TH	1	n	**T**all **h**erbs dominated by *Petasites albus* and *Tussilago farfara*	Mull Brown Soil	10
CO	1	l	Colluvial slopes with *Aposeris foetida* and *Valeriana tripteris*	Mull Regosol	5
MEa	1	l	**Me**sic sites dominated by *Knautia dispacifolia, Veronica chamaedris* and *Galium odoratum*	Alkaline Moder Brown Soil, coarsly textured	7
MEb	1	l	**Me**sic sites dominated by *Luzula sylvatica*	Moder Regosol	9
SCa	1	l	Slope-**Sc**rees dominated by ferns, concave type	Tangel on Limestone Screes, hollows on slopes	6A
SCb	1	l	Slope-**Sc**rees dominated by mosses, convex type	Lithosols on Limestone Screes, rocks on slopes	6B
SCc	1	l	Horizontal **Sc**rees dominated by mosses	Lithosols on Limestone Screes, tops	8

Table 2. Sample numbers in 1992 and 2000. M = microsite abbreviation; D = disturbance type with n = not disturbed, l = light exposed, s = soil disturbed and light exposed; T1 = uncleared, T2 = cleared, T3 = cleared and planted.

		T1		T2		T3		Sums	
M	D	92	00	92	00	92	00	92	00
Schwanden									
MO	n	5	3	7	7	5	5	17	15
WE	n	5	4	–	–	–	–	5	4
DR	l	4	4	5	5	6	6	15	15
ME	l	14	12	5	4	5	5	24	21
CL	s	–	–	5	5	4	4	9	9
MD	s	6	6	–	–	–	–	6	6
PI	s	4	4	–	–	–	–	4	4
Disentis									
THa	n	–	–	6	6	–	–	6	6
THb	n	–	–	7	7	1	1	8	8
THc	n	–	–	7	5	1	1	8	6
GR	l	–	–	5	4	4	4	9	8
SCa	l	–	–	–	–	5	5	5	5
SCb	l	–	–	7	7	–	–	7	7
SH	l	–	–	–	–	8	8	8	8
ME	s	–	–	–	–	8	8	8	8
Pfäfers									
GR	n	–	–	3	3	–	–	3	3
THa	n	10	3	5	4	–	–	15	7
MO	l	5	5	5	5	–	–	10	10
THb	l	4	3	5	5	–	–	9	8
CL	s	6	3	5	4	–	–	11	7
SH	s	–	–	5	5	–	–	5	5
Zweisimmen									
TH	n	8	8	–	–	–	–	8	8
CO	l	5	5	–	–	–	–	5	5
MEa	l	8	8	–	–	–	–	8	8
MEb	l	5	5	–	–	–	–	5	5
SCa	l	6	6	–	–	–	–	6	6
SCb	l	5	4	–	–	–	–	5	4
SCc	l	7	7	–	–	–	–	7	7
Sums		107	90	82	76	47	47	236	213
Disturbance types									
n		28	18	35	32	7	7	70	57
l		63	59	32	30	28	28	123	117
s		16	13	15	14	12	12	43	39

2.2 Species composition and species turnover

Based on 1142 year by quadrat records, species covers i.e. means of cover classes were averaged by microsite, treatment and year. Resulting values served as centroid scores for a new data set consisting of 210 centroids of year by microsite combination and 193 species (WILDI and ORLÓCI 1996). Tree species were excluded from the analyses because results were intended to compare the succession of moss and herbaceous vegetation with the natural tree recruitment. Due to their rare occurrence, shrub species were also excluded, as well as species with an overall frequency of two or less. In order to analyse the succession of microsites with respect to species composition and species turnover, we performed an indirect gradient analysis, the Detrended Correspondence

Analysis (HILL and GAUCH 1980) using the software CANOCO 4 (TER BRAAK and SMILAUER 1998) with default options. The method is based on the Correspondence Analysis that represents species and samples – here quadrats – as occurring in a postulated environmental or ordination space. Usually, such a space is displayed as a two-dimensional diagram. A species is located in that location of space (diagram) where it is most abundant. There are two major problems with Correspondence Analysis: the ordination diagram is distorted (arch effect) and the ends of the gradient compressed. These problems are corrected by Detrended Correspondence Analysis (DCA) which involves detrending, i.e. removing the arch effect, and rescaling, i.e. shifting the positions of samples (quadrats) along ordination axes to make the beta diversity constant. The resulting units of the DCA-axes correspond to the average standard deviation of species turnover (SD), i.e. a 50% change in sample composition occurs in about 1 SD (GAUCH 1982). Results from the DCA-runs were ordinated in Systat (1996) and figures were optimised using Adobe Illustrator ® 8.0.

2.3 Regeneration of tree species

In order to generalize despite the diverse regeneration features of the study sites, regenerating trees found on the quadrats were distinguished by the height and by the year of germination. Regeneration was classified either as seedlings (1–20 cm tall) or saplings (trees taller than 20 cm). Trees that had germinated before 1991 were classified as "advance regeneration" (MESSIER *et al.* 1999). Two classes of "post-windthrow germination" were distinguished: germination between 1991 and 1994, and germination after 1994. Because permanent quadrats were excluded from places with planted saplings, only naturally regenerated seedlings and saplings were recorded in variants T3.

The nomenclature for vascular plants follows AESCHIMANN and HEITZ (1996); for bryophytes FRAHM and FREY (1987).

3 Results

3.1 Changes in the study sites and microsites

The species pools in the four study sites differed considerably according to different site conditions (Table 1). Only a few species were common to all study sites, e.g. the trees *Picea abies* and *Sorbus aucuparia* and herbs such as *Rubus idaeus*, *Epilobium montanum*, *Oxalis acetosella*, *Viola biflora*, *Solidago virgaurea*, *Hieracium sylvaticum* (see Appendix). On the study sites Disentis, Pfäfers and Zweisimmen, between 1400 and 1590 m a.s.l., *Rubus idaeus* increased most in frequency and cover between 1992 and 2000 (Table 3). On the lower Schwanden site, *Rubus fruticosus* aggr. became as abundant as *R. idaeus*. On acidic bedrock in Schwanden and Disentis, *Galeopsis tetrahit* was an abundant pioneer species early after the windthrow. On all study sites, the most obvious successors were fern species, such as *Athyrium filix-femina*, *Dryopteris dilatata* and *Gymnocarpium dryopteris;* buttercup species, such as *Ranunculus lanuginosus*, *R. nemorosus*, *R. repens;* rose species, such as *Rubus idaeus* and *R. fruticosus* aggr.; willowherb species, such as *Epilobium angustifolium* and *E. montanum;* daisy species *Solidago virgaurea;* and grasses, such as *Agrostis capillaris*, *Calamagrostis villosa* and *Avenella flexuosa* (Appendix). Moss species were generally more frequent 10 years after the windthrow. Their mean cover increased particularly on the acid substrates in Schwanden and Disentis (Table 3).

Total cover increased on all microsites during the years monitored. The increase was largest in disturbed microsites (Fig. 1). Even in microsites with moderate or no changes in light climate, e.g. tall herb communities with *Adenostyles alliariae*, *Cicerbita alpina*, *Chaerophyllum hirsutum*, and *Aconitum altissimum*, the total cover increased continuously during the first 10 years after the windthrow. In 2000, the total cover of the undisturbed microsites was still larger than that of the light-exposed and soil-disturbed microsites.

With respect to the different quadrats, microsites and disturbance types, changes during the first 10 years after the windthrow varied greatly. The eigenvalues and percentage variances per axes as well as the total inertias resulting from the four DCA-runs indicate that samples from the Schwanden and Disentis sites were more heterogeneous – with a higher total inertia – than those from the Pfäfers and the Zweisimmen sites (Table 4).

Table 3. Distinct positive (+) and negative (–) changes in the frequencies and mean cover quadrat^{-1} (in brackets) of abundant plant species and the moss layer between 1992 and 2000, according to disturbance type.

Schwanden	Not disturbed		Light exposed		Soil disturbed and light exposed	
	92	00	92	00	92	00
+ *Epilobium angustifolium*	3 (3%)	10 (14%)	3 (3%)	20 (8%)	2 (3%)	13 (12%)
+ *Rubus fruticosus* aggr.	6 (4%)	18 (19%)	30 (19%)	34 (37%)	4 (3%)	17 (18%)
+ *Rubus idaeus*	12 (7%)	16 (15%)	26 (17%)	32 (30%)	11 (7%)	18 (15%)
+ *Agrostis capillaris*	4 (6%)	10 (6%)	13 (7%)	26 (24%)	14 (4%)	19 (43%)
+/– All mosses	7 (8%)	18 (11%)	25 (11%)	23 (9%)	9 (3%)	16 (18%)
– *Galeopsis tetrahit*	17 (15%)	5 (2%)	25 (7%)	17 (3%)	10 (7%)	3 (2%)
Disentis	Not disturbed		Light exposed		Soil disturbed and light exposed	
	92	00	92	00	92	00
+ *Rubus idaeus*	10 (7%)	16 (18%)	9 (5%)	16 (18%)	5 (24%)	8 (28%)
+ *Calamagrostis villosa*	2 (10%)	8 (14%)	9 (81%)	16 (44%)	0 (0%)	5 (17%)
+ *Avenella flexuosa*	0 (0%)	1 (3%)	10 (7%)	25 (15%)	0 (0%)	7 (29%)
+ All mosses	9 (16%)	20 (35%)	21 (28%)	26 (45%)	2 (2%)	8 (9%)
– *Galeopsis tetrahit*	6 (6%)	5 (2%)	12 (4%)	7 (1%)	8 (40%)	7 (3%)
Pfäfers	Not disturbed		Light exposed		Soil disturbed and light exposed	
	92	00	92	00	92	00
+ *Rubus idaeus*	3 (17%)	9 (42%)	9 (5%)	17 (22%)	11 (19%)	11 (35%)
+ *Deschampsia cespitosa*	0 (0%)	2 (2%)	6 (10%)	16 (8%)	1 (3%)	7 (14%)
+ *Petasites albus*	8 (30%)	4 (48%)	6 (7%)	7 (11%)	3 (5%)	4 (17%)
+/– All mosses	6 (4%)	7 (3%)	8 (7%)	16 (7%)	2 (5%)	8 (2%)
– *Adenostyles alliariae*	12 (31%)	1 (10%)	11 (5%)	4 (5%)	4 (3%)	0 (0%)
Zweisimmen	Not disturbed		Light exposed		Soil disturbed and light exposed	
	92	00	92	00	92	00
+ *Rubus idaeus*	1 (3%)	7 (71%)	22 (5%)	33 (42%)	–	–
+ *Myosotis sylvatica*	2 (3%)	6 (2%)	4 (3%)	17 (2%)	–	–
+ *Epilobium angustifolium*	0 (0%)	4 (19%)	3 (3%)	23 (20%)	–	–
+/– All mosses	4 (7%)	8 (11%)	29 (39%)	35 (22%)	–	–

Table 4. Eigenvalues of the first to fourth axes from Detrended Correspondence Analyses on microsite per year centroids of the four study sites. Total inertia equals the sum of all eigenvalues, i.e. all axes. Percentage variances of the DCA-axes 1 and 2 are given in brackets.

Study sites	DCA-axis 1	DCA-axis 2	DCA-axis 3	DCA-axis 4	Total inertia
Schwanden	0.516 (13.5%)	0.295 (7.7%)	0.173	0.114	3.825
Disentis	0.592 (15.5%)	0.383 (10.1%)	0.198	0.102	3.810
Pfäfers	0.497 (16.5%)	0.233 (7.8%)	0.153	0.096	3.008
Zweisimmen	0.436 (18.9%)	0.180 (7.8%)	0.100	0.059	2.306

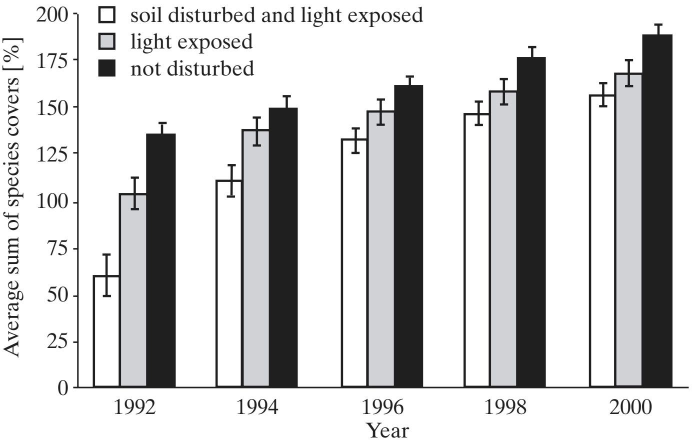


Fig. 1. Mean sum of species covers of vascular plants and mosses per year by quadrat, arranged according to the three disturbance types. For each bar, ±95% confidence levels are indicated.

Schwanden (Fig. 2a)

On the low, rather acidic study site of Schwanden, the species compositions of fresh and wet undisturbed places (microsites MO1–3 and WE1) contrasted with those of all other microsites in that *Rubus idaeus* was not very abundant. On light-exposed microsites (ME1–3, DR1–3), both *Rubus idaeus* and *Rubus fruticosus* aggr. became dominant. Along cable transects resulting from the timber harvest, *Agrostis capillaris* spread out and was still partly dominating the disturbed microsites even 10 years after the windthrow, e.g. at CL2. *Agrostis* also emerged on mounds (MD1). All pits became completely covered by vegetation within five years. The vegetation succession on moist regosols (soil nomenclature: ANONYMOUS 1997) corresponded with the species composition of fresh sites. *Epilobium angustifolium* spread out continuously into all microsites, but without reaching dominance. Species turnover was not only considerable at disturbed sites such as in CL2, CL3 in the cleared and planted variants or on mounds MD1 and in pits PI1, but also at sites without soil disturbance and even at sites with no or only moderate changes in the light climate, e.g. ME1. Many shade-tolerant species such as *Dryopteris filix-mas, Impatiens noli-tangere, Vaccinium myrtillus* or *Hieracium sylvaticum* decreased in frequency between 1992 and 2000 (Appendix). Also, the open-ground species *Galeopsis tetrahit* disappeared from more than 50% of the 52 permanent quadrats where it was present in 1992.

Disentis (Fig. 2b)

Undisturbed microsites of tall herb communities with dominant *Adenostyles alliariae*, *Petasites albus*, *Cicerbita alpina*, *Milium effusum* on acid mull-brown soils covered large areas (THa, THb, THc). Changes in species composition were partly affected by the temporally limited spread of *Rubus idaeus*. Light-exposed microsites on *Calamagrostis villosa*-dominated slopes (acidic iron-humus podzol) either did not change (GR3) or were partly invaded by *Rubus idaeus* (GR2). On the shallow soils of the light-exposed microsites SH3 and SCb2, the vegetation changed only moderately with an increase in the mosses, *Vaccinium myrtillus* and *Avenella flexuosa*. The pioneer species *Galeopsis tetrahit* dominated the disturbed microsite ME3 early after the windthrow, but already in 1994 it had been replaced by *Rubus idaeus* and *Prenanthes purpurea,* and these were still dominant in 2000.

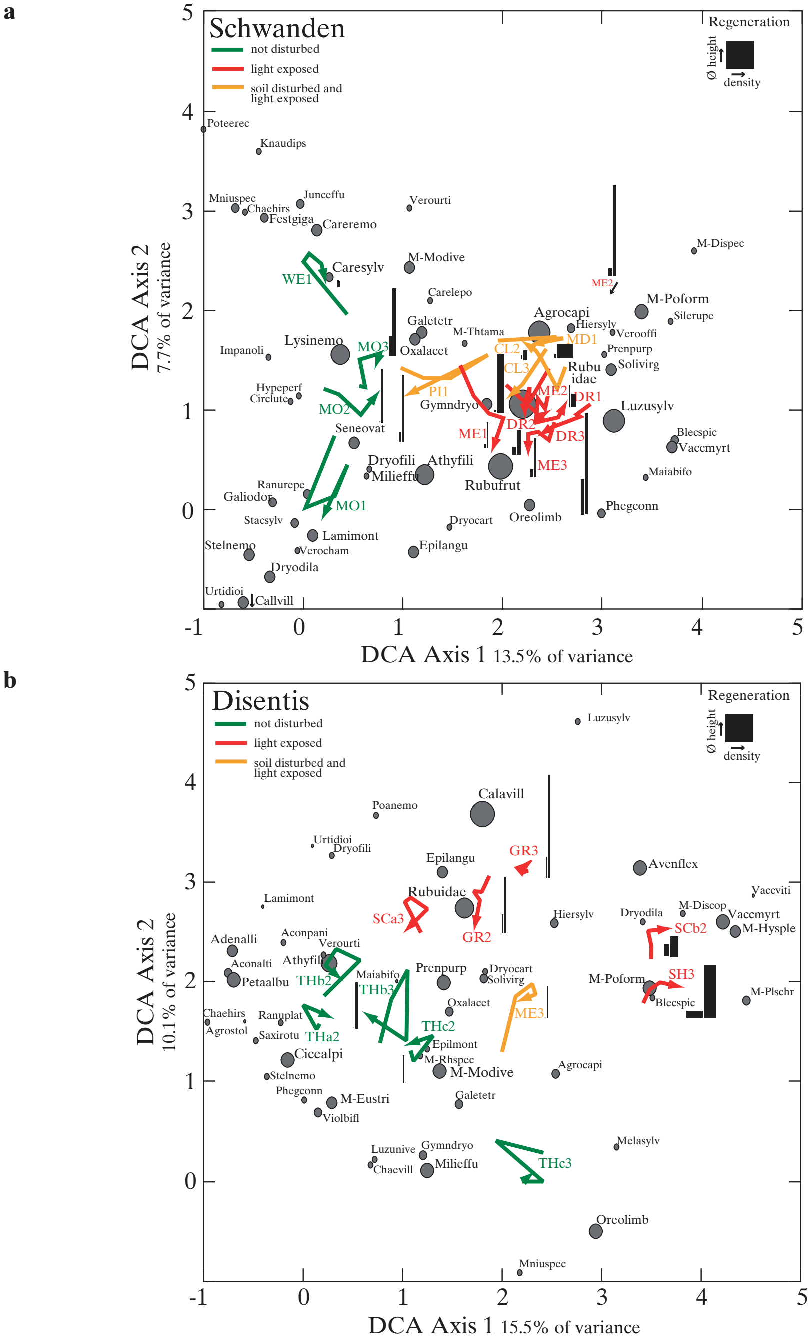
In general, *Calamagrostis villosa*, *Avenella flexuosa* and *Rubus idaeus* accounted for the most obvious increase in both frequency and cover (Table 3). Both grasses increased in most of the quadrats except in those of the light-exposed microsite GR where the species were already dominant.

Pfäfers (Fig. 2c)
On the calcareous substrate, differences in the species composition of microsites were related to the soil depth, i.e. to the influence of the schist bedrock (Wildflysch). Tall herbs, such as *Aconitum altissimum*, *Adenostyles alliariae*, *Chaerophyllum hirsutum*, *Cicerbita alpina*, *Peucedanum ostruthium*, *Petasites albus*, or *Senecio ovatum*, dominated the deep acidic mull-brown soils of the undisturbed microsites THa1 and THa2. Calcicole species (definition see GRIME 1979), such as *Calamagrostis varia*, *Carex flacca* or *Valeriana montana,* were abundant on the grass-dominated microsite GR2 with shallow mull regosol. Light-exposed microsites on acid mull-brown soil (THb1 and THb2) were moderately covered by tall herb species. Changes in vegetation were slight on the moist microsites MO1 and MO2 on gleyed mull-brown soil. Here, *Carex ferruginea* was dominant and *Deschampsia cespitosa* frequent, but *Rubus idaeus* could not establish with any density. Timber harvest led to the disturbed microsites, SH2 and CL2, where calcicole tall herbs on shallow mull-brown soil or on regosol emerged. In the uncleared variant, the disturbed microsite CL1 became dominated early by *Rubus idaeus*. In general, a distinct increase in frequency was observed for the grass *Deschampsia cespitosa*. The tall herb *Adenostyles alliariae* dominated the original forest community and was abundant early after the windthrow in microsites THa and THb. It was continuously replaced by *Petasites albus*. The highest species turnover rates were found on the disturbed or light-exposed microsites CL, SH and THb.

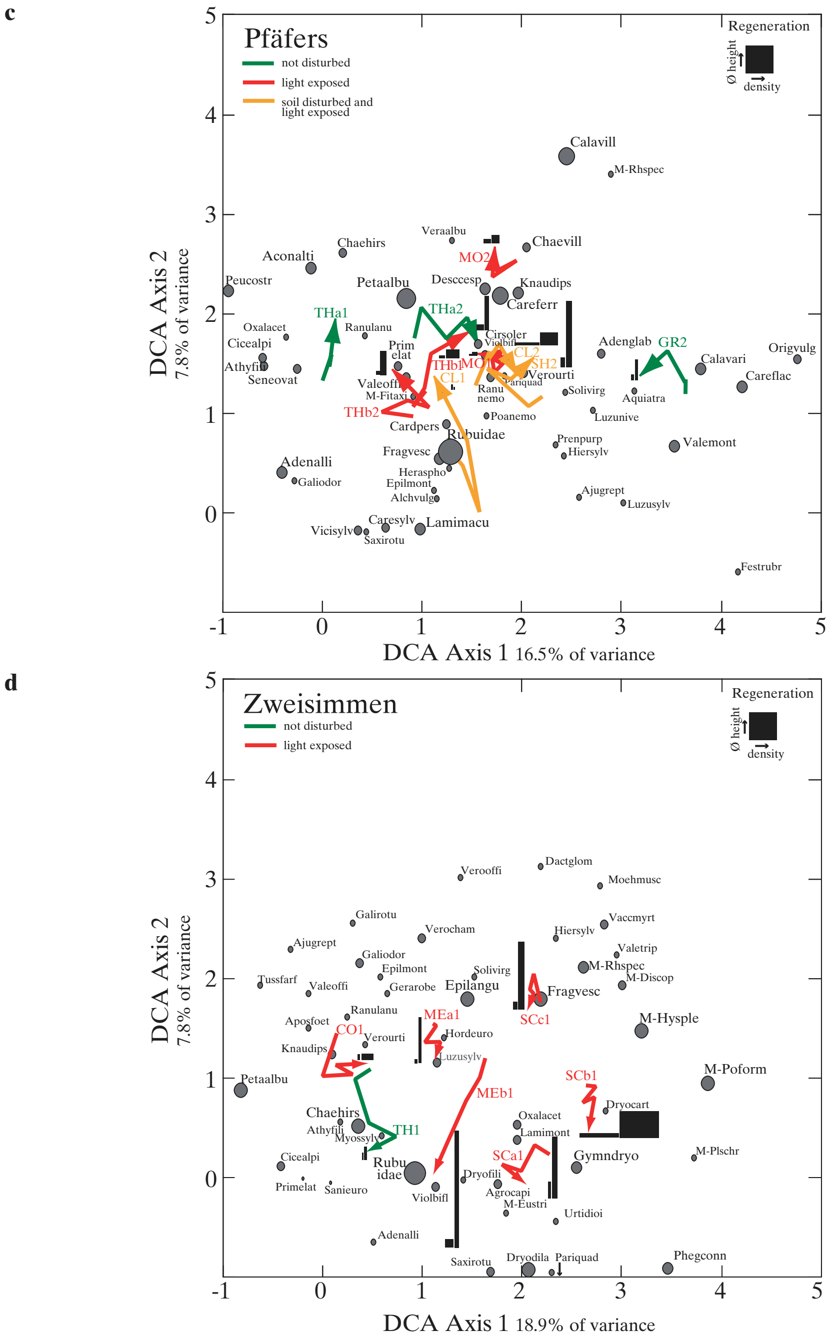
Zweisimmen (Fig. 2d)
Differences between the microsites depended on the influence of limestone bedrock. On the undisturbed microsite TH1 on mull-brown soil *Tussilago farfara* and *Petasites albus* were successively replaced by tall herbs, such as *Cicerbita alpina* and *Chaerophyllum hirsutum* as well as by *Rubus idaeus*. The light-exposed microsite SCc1 on lithosol was continuously covered by mosses and changed only moderately. In contrast, all other light-exposed microsites were invaded by *Rubus idaeus* that often became dominant. *Petasites albus* decreased on colluvial slopes (microsite CO1) and *Luzula sylvatica* decreased in mesic places on moder regosol (microsite MEb1). On the concave scree microsite SCa1, the cover of mosses and ferns did not change but *Rubus idaeus* increased. Similarly, the moss- and fern-dominated, convex scree microsite, SCb1, changed only slightly with a moderate increase in *Rubus*. On alkaline moder brown soil (microsite MEa1), *Rubus* and *Epilobium angustifolium* invaded the original, but did not completely cover the forest floor. In general, *Rubus idaeus* became the most dominant species in 2000. Additionally, both *Myosotis sylvatica* and *Epilobium angustifolium* became frequent in 2000, and the latter species increased also in cover.

3.2 Tree regeneration

The densities and height growth of seedlings/saplings quadrat^{-1} varied greatly between microsites (Figs. 2a–d). The most frequent regenerating trees were *Picea abies*, *Acer pseudoplatanus* and *Sorbus aucuparia* (Fig. 3). On the Pfäfers site, *Acer pseudoplatanus* regeneration was most abundant, whereas in Disentis and Zweisimmen, *Picea abies* and *Sorbus aucuparia* regenerated most successfully. On average, quadrats on the Zweisimmen site had the largest total increase in seedling/sapling heights and the fastest growth rates for *Sorbus aucuparia* and *Picea abies*. *Acer pseudoplatanus* grew fast on the Pfäfers site.



Figs. 2a–d. Vegetation dynamics of microsites as positions of plot centroids in Detrended Correspondence Analysis (DCA). Scores of the microsite centroids of 1992, 1994, 1996, 1998 and 2000 are connected and end with an arrow. Abbreviations indicate microsites and treatment according to Table 1: e.g. MO1 indicates the microsite MO in the uncleared area i.e. treatment 1. Scores of the 50 most abundant species per study site are displayed as bubbles with r = sqr(weight) according to the out-



put of DCA-runs. Abbreviations of species names are explained in the Appendix. Regeneration rates per centroids for 1992 (left bar) and 2000 (right bar) are displayed in the neighbourhood of the centroid arrows. The width indicates the number of saplings per centroid. The average sums of the seedlings'/saplings' heights per quadrat correspond with the heights of the bars.

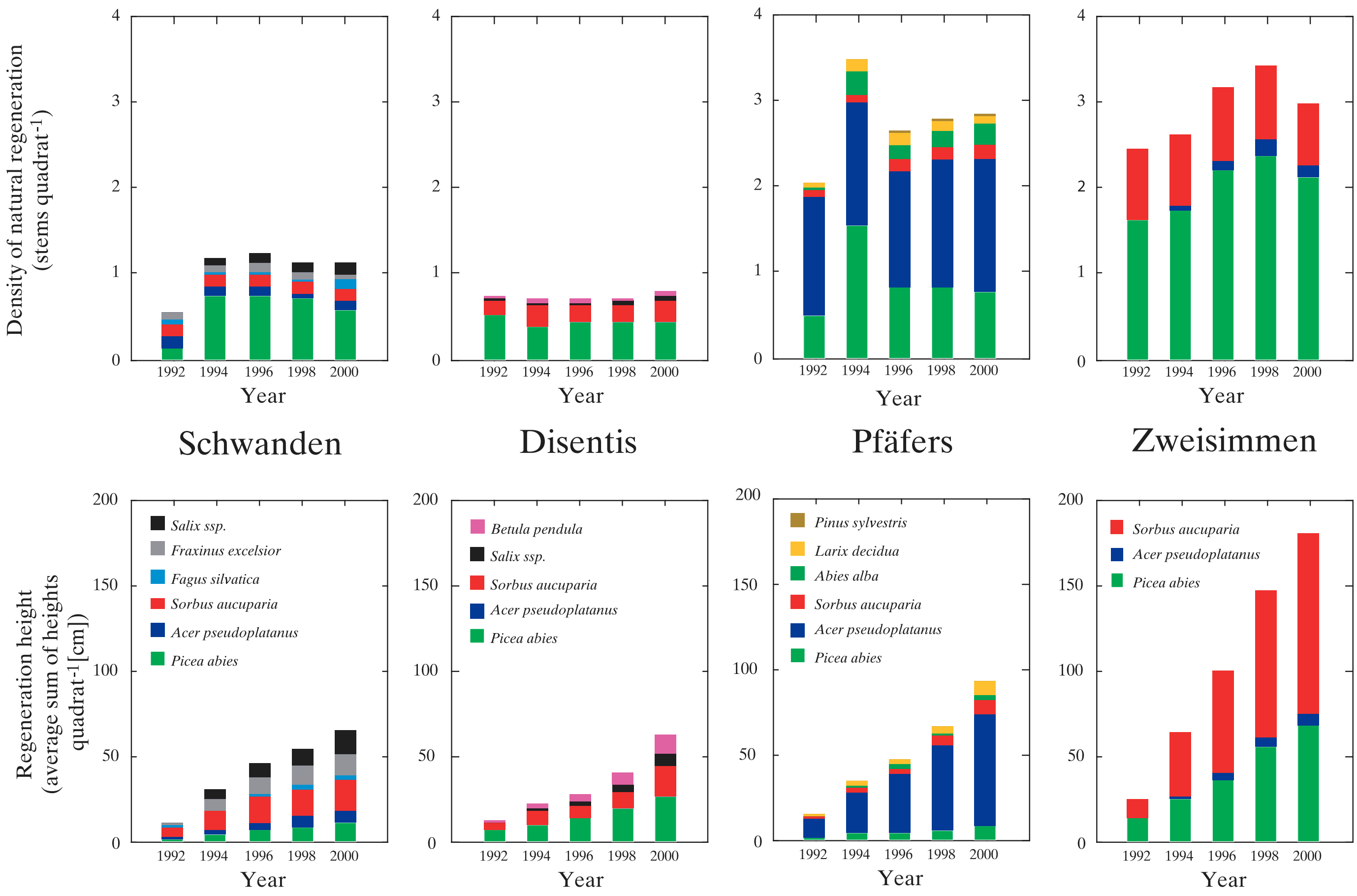


Fig. 3. Regeneration (seedlings and saplings) density and height in quadrats grouped by study sites and tree species.

On the basis of the microsite maps available for all study sites, the regeneration density in the variants were projected from the regeneration densities in each microsite (Fig. 4). The resulting figures reflect only the natural regeneration (but see SCHÖNENBERGER this issue, a). The small and uncleared study site of Zweisimmen had the largest regeneration density in 2000 with 45 400 stems ha^{-1}, in contrast with the large windthrown stand in Disentis where tree regeneration in the year 2000 was low (4700 ha^{-1} in the cleared and 3900 ha^{-1} in the planted variant). Densities on the uncleared variants on the Schwanden and Pfäfers sites, in 2000 were lowest (3600 and 2000 stems ha^{-1} respectively). The cleared and planted variants in the Schwanden site had moderate densities of 10 000 and 13 400 stems ha^{-1}. These are comparable with the density on the cleared variant in the Pfäfers site (12 500 stems ha^{-1}).

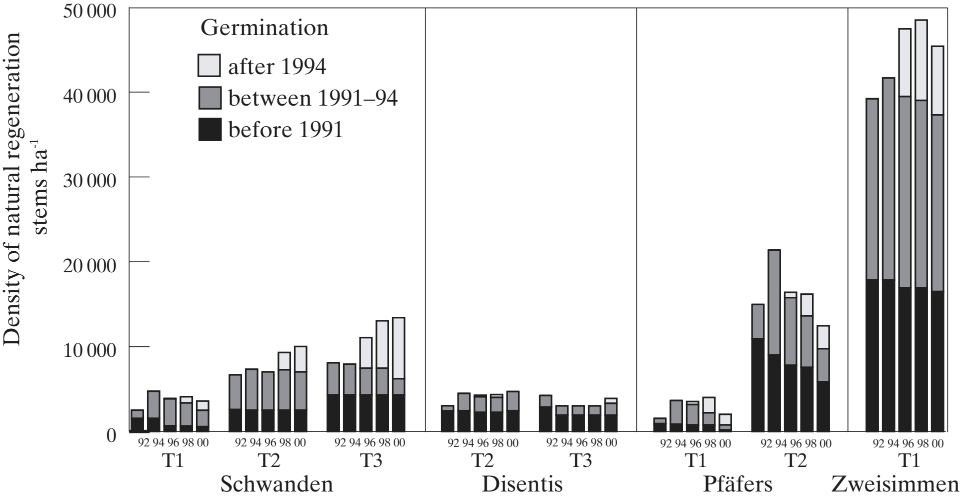


Fig. 4. Projected regeneration (seedlings and saplings) density per study site, treatment (T1 = uncleared, T2 = cleared, T3 = cleared and planted), and year of germination. Microsite maps were used to calculate the area proportion of regeneration.

Quadrats in the undisturbed microsites had the smallest regeneration densities (0.56 stems quadrat^{-1} in 2000). In contrast, light-exposed quadrats and disturbed quadrats had significantly larger densities with 2.15 and 2.41 stems quadrat^{-1} in 2000 (Fig. 5, Table 5). Post-windthrow regeneration in 2000 was most abundant in light-exposed (1.39 quadrat^{-1}) and disturbed quadrats (1.95 quadrat^{-1}) and differed significantly from undisturbed quadrats (0.37 quadrat^{-1}). Advance regeneration, i.e. the density of saplings/seedlings that germinated earlier than 1991, was slight on undisturbed quadrats in 1992 (0.35 quadrat^{-1}) and differed significantly from that on light-exposed quadrats (0.89 quadrat^{-1}).

Advance regeneration accounted for a considerable proportion of total regeneration (Table 6), varying from 49.6% for the cleared and and 52% for the planted variants on the Disentis site, to 15.8% in the uncleared variant of Schwanden and 8.8% in Pfäfers. In absolute numbers however, the uncleared Zweisimmen site had clearly the most dense

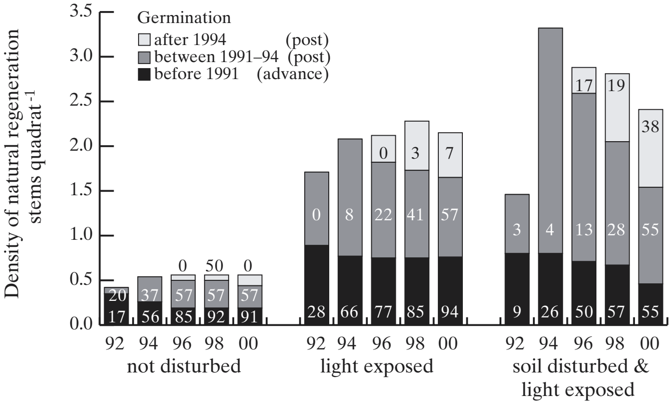


Fig. 5. Regeneration densities (seedlings and saplings) per disturbance types (n = not disturbed, l = light exposed, s = soil disturbed and light exposed) and year of germination. Numbers in bars indicate the proportion of saplings (>20 cm) in %.

advance regeneration with 16 500 stems ha^{-1} (36.3%) in the year 2000, in comparison to Disentis (between 1930 and 2500 stems), Schwanden (between 560 and 4300 stems) and Pfäfers (between 180 and 5850 stems).

Browsing played a small role in all the study sites. It did not cause sapling mortality in any quadrat. Where browsing took place, *Sorbus aucuparia* was the most affected species. The impact of browsing on the regeneration density and height has therefore been ignored in this study (see also SCHÖNENBERGER this issue a; SENN *et al.* this issue).

Table 5. Probabilities generated by Wilcoxon rank sum test for differences in regeneration densities with respect to disturbance types (n = not disturbed, l = light exposed, s = soil disturbed and light exposed). Significant values in bold (p≤0.001) and in normal (p≤0.01).

Year	1992	1994	1996	1998	2000
All regeneration					
l > n	**0.0060**	**0.0006**	0.0020	0.0030	0.0040
s > n	0.0030	**0.0001**	**0.0001**	**0.0001**	**0.0010**
s > l	*0.7850*	*0.9180*	*0.4190*	*0.3400*	*0.6510*
Advance regeneration					
l > n	*0.0510*	*0.0270*	*0.0110*	*0.0110*	0.0080
s > n	0.0070	0.0060	0.0030	0.0170	*0.0910*
s > l	*0.6130*	*0.5400*	*0.8380*	*0.6800*	*0.2780*
Post-windthrow regeneration					
l > n	0.0040	0.0020	*0.0130*	*0.0110*	*0.0130*
s > n	*0.0320*	**0.0003**	**0.0004**	**0.0003**	**0.0010**
s > l	*0.6770*	*0.3590*	*0.4270*	*0.3050*	*0.2390*

Table 6. Advance regeneration as proportions (%) of total regeneration density, and in absolute numbers (# stems ha^{-1}), based on projected regeneration density (seedlings and saplings) displayed in Fig. 4. Treatment T1 = uncleared, T2 = cleared, T3 = cleared and planted.

	1992		1994		1996		1998		2000	
	%	#	%	#	%	#	%	#	%	#
Schwanden-T1	**61.1**	1536	**32.4**	1536	**17.3**	673	**15.8**	647	**15.8**	566
Schwanden-T2	**38.7**	2582	**34.3**	2516	**35.8**	2516	**27.0**	2516	**25.1**	2516
Schwanden-T3	**53.2**	4309	**54.3**	4309	**39.0**	4309	**33.0**	4309	**32.1**	4309
Disentis-T2	**80.2**	2428	**54.6**	2428	**52.9**	2260	**52.0**	2260	**52.0**	2448
Disentis-T3	**68.0**	2881	**64.0**	1931	**64.0**	1931	**64.0**	1931	**49.6**	1931
Pfäfers-T1	**59.9**	924	**23.7**	864	**22.0**	777	**19.4**	777	**8.8**	179
Pfäfers-T2	**73.1**	10941	**42.2**	9023	**47.6**	7810	**46.7**	7550	**47.0**	5851
Zweisimmen-T1	**45.6**	17876	**42.9**	17858	**35.7**	16948	**35.0**	16948	**36.3**	16494

4 Discussion

4.1 Windthrow disturbance and vegetation dynamics in mountain forests

A general feature on all study sites was the increase in *Rubus idaeus* after windthrow. At low altitudes it was also found in combination with *Rubus fruticosus* aggr. (Schwanden). The dominant role of *Rubus idaeus* in the first decade after windthrow has been reported for many northern temperate, northern hardwood and boreal forests (FISCHER 1992; BROWN 1994; PETERSON and PICKET 1995; COOPER-ELLIS *et al.* 1999; PALMER *et al.* 2000; FISCHER *et al.* 2002). Its invasion into most of the microsites in this study may be due to both the presence of propagules (PETERSON and CARSON 1996) and by the “release” of existing plants (PALMER *et al.* 2000). However, *Rubus idaeus* does not appear to be able to establish on all microsites after windthrow. It was found to be limited in growth on wet and moist microsites, i.e. on MO and WE in Schwanden and on MO in Pfäfers, as well as on microsites with shallow and dry soils such as SH and SCb in Disentis, SCc in Zweisimmen and mounds MD in Schwanden. Additionally, on undisturbed mesic places where tall herbs dominate, *Rubus* is less competitive than the plants already present (in accordance with FISCHER 1998 and FISCHER *et al.* 2002). Our results imply that *Rubus* becomes dominant on mesic places, whether they are light-exposed, disturbed or both.

Gaps in Swiss mountain forests are often colonized by tall herb communities, by dense *Calamagrostis villosa* stands or by dwarf shrub communities with *Rhododendron ferrugineum* and *Vaccinium myrtillus* (OTT *et al.* 1997). Such communities delay forest regrowth for decades (MICHIELS 1993). On the study sites of Disentis, Pfäfers and Zweisimmen tall herbs had already covered large areas before the windthrow. The species compositions of these communities changed only moderately after the windthrow, but the total species cover increased. Such increases may be caused by moderate changes in the light climate (COLLINS *et al.* 1985), but it may also be related to an increase in the maximum temperatures on windthrow areas, in contrast to the more even climate in the closed forest before windthrow (DEFREITAS and ENRIGHT 1995). Analogous microclimatic differences are also reported between pit and mounds (SCHMIDT *et al.* 1998). Moreover, a cleared windthrow area without complete vegetation cover in a German deciduous forest showed higher minimum and maximum temperatures in comparison to an uncleared and completely covered windthrow patch (BOGENRIEDER *et al.* 1998).

In Disentis, dense *Calamagrostis villosa* stands were found to have covered the upper parts of the study site. The expansion of *Calamagrostis* grass species into disturbed or cleared mountain forest is a well-known phenomenon and has been much discussed in relation to its negative influence on tree recruitment (LIEFFERS and STADT 1994; PYSEK 1994; LEPS *et al*. 2000). *Rubus idaeus* has also partly established on these *Calamagrostis* stands, as part of its general expansion into disturbed places, and may reduce the dominance of the persistent grass.

Forest species generally declined in abundance and were gradually replaced by shade-intolerant species. In the first three years after the windthrow, early colonizers such as *Galeopsis tetrahit* grew rapidly, especially on the study sites of Schwanden and Disentis, but they disappeared in the following years. In contrast, *Epilobium angustifolium* spread out slowly and reached its highest frequency 10 years after the windthrow. We found distinct differences between the four study sites in the frequency and abundance of early colonizers (Appendix). These differences reflect differences in disturbance types, soil properties and species pools (WOHLGEMUTH *et al.* 1995).

4.2 Microsites favourable and adverse to tree seedlings

Mountain forests offer different conditions for tree regeneration from those in lowland forests (OTT 1989). In mountain forests lower temperatures, snow accumulation and, as a consequence, shorter vegetation periods are growth-limiting factors during the recruitment phase (MAYER and OTT 1991; OTT *et al.* 1997; KÖRNER 1998; BRANG *et al.* 2001). The Black Snow Mould *Herpotrichia juniperi* is related to snow accumulation and accounts for high mortality rates of *Picea abies* seedlings (IMBECK and OTT 1987; BRANG 1998). Based on the first Swiss National Forest Inventory (EAFV and BFL 1988), sapling densities ha^{-1} (all tree species) are lower in the subalpine zone than in the upper montane zone (BRÄNDLI 1995). The majority of mountain forests grow on steep slopes (59% on slopes steeper than 40%, 27% on slopes steeper than 60%; BRASSEL and BRÄNDLI 1999), where topographic factors such as altitude, aspect and slope lead to very local differences in thermal regime. Sites therefore vary greatly from an ecological point of view. This means that choosing appropriate places for tree regeneration is crucial for the forest life cycle (BISCHOFF 1987; HALPERN *et al.* 1990; WASSER and FREHNER 1996; KRÄUCHI *et al.* 2000; HARRINGTON and BLUHM 2001).

The microsites found on the four study sites reflect site conditions on N-, NW- and W-exposed slopes. On all study sites, the original forest canopy did not cover the whole area. In many of the canopy gaps, different tall herbs, e.g. tall, exuberant, perennial forbs with rhizomes, had assembled to form a dense vegetation cover. In Swiss mountain forests, such tall herb communities whether in forests (KELLER *et al*. 1998) or in tree-free eutrophic communities in the subalpine or lower alpine zone (Betulo-Adenostyletea; ELLENBERG 1996), are widespread regardless of the substrate (HELLER-KELLENBERGER *et al*. 1997). As long as the supply of water and nutrients is guaranteed, these tall herb communities are limited particularly by light (LANDOLT 1977). They are said to hamper the growth of tree seedlings and saplings by producing shading effects (BAVIER 1910; TREPP 1955; IMBECK and OTT 1987; OTT 1989). Deadwood may serve as an important natural recruitment substrate in those communities (EICHRODT 1970; IMBECK and OTT 1987; OTT 1989). We observed (but did not document) initial *Picea abies* seedling recruitment on nurse logs only seven years after the windthrow. This corresponds to similar findings on windthrow sites in Baden-Württemberg, Germany (FISCHER 1998). Our results from monitoring undisturbed tall herb communities, undisturbed fresh and wet places and undisturbed grass-dominated microsites (Figs. 2a–b; Table 1: MO and WE in Schwanden, THa–c and GR in Disentis, THa and GR in Pfäfers, TH in Zweisimmen) confirm that such communities are regeneration adverse (BELL *et al*. 2000). Regeneration is almost completely hindered on the shady ground under the closed vegetation layer, and the density of regenerating trees here is very small. However, *Fraxinus excelsior* could regenerate even in dense vegetation on fresh sites in Schwanden, and *Sorbus aucuparia* could establish on similar sites in Disentis.

Tree seeds germinated and developed on many undisturbed but light-exposed quadrats, after the windthrow. On deep and active soils, the sudden light exposure resulted in the rapid establishment of *Rubus idaeus* and of tall herb species. Such microsites are only favourable to regeneration soon after a windthrow as long as the floor has not been completely covered by vegetation. The success of the subsequent regeneration depends largely on the competitive abilitiy of the tree species germinated. The seedlings of *Acer pseudoplatanus*, *Sorbus aucuparia*, *Betula pendula*, *Alnus incana*, *Larix decidua* and *Salix* species were able to compete with tall herbs. On shallow soils, moss species often dominated the original vegetation, e.g. on the microsites SH and SCb in Disentis and SCa–c in Zweisimmen (Table 1; Figs. 2a–b), where tall herbs have not established because of the limited availability of water and nutrients. Here *Picea abies* seeds were able to germinate instead without having their subsequent seedling growth hampered by fast-growing and shade-producing species. Our findings demonstrate that moss-dominated microsites are favorable places for *Picea abies* seedling recruitment after windthrow (FOWELLS 1965; MOTTA *et al*. 1994; SIMARD *et al*. 1998; LAUTENSCHLAGER 1999).

In most of the study site areas water and nutrient conditions would be suitable for tall herb communities. However, as long as the forest canopy is sufficiently closed, these species remain small in frequency and cover. After a windthrow, places with soil disturbance and vegetation disruption will be highly receptive to any tree seeds. On untreated windthrow areas, such places are particularly restricted to pits and mounds. In Schwanden where we distinguished these microsites (PI and MD), *Picea abies* was able to establish in great density on mounds. Other herbaceous species have not outcompeted the slow growing *Picea* seedlings here because of the poor soil conditions on dry regosols. In contrast, pits on moist regosol were overgrown in the course of four years. Despite the fact that the pit quadrats were located next to the mound quadrats and seed rain must have been similar if not larger, very few *Picea* seedlings germinated in the pits. It is possible that the seeds in pits were more likely to decay under the moist conditions (BRANG 1996) or even be removed by animals (e.g. ants), but we did not investigate these questions.

On cleared windthrow areas, the timber was removed using mobile cable cranes. The timber harvest resulted in a severe disturbance of both vegetation and soils, especially along cable transects, and left large areas of bare soil. In Schwanden and Pfäfers, seedlings were able to germinate and grow on such places because competition was temporally lacking (CL, SH), but in Disentis we did not observe such post-windthrow regeneration on comparable microsites. The difference between the findings from Schwanden and Pfäfers and those from Disentis is probably due to the small amount of seed rain in Disentis (see below).

4.3 Advance regeneration and post-windthrow regeneration

The hypothesis that regeneration rates in mountain forests are low could be confirmed for the study sites in Schwanden, Disentis and Pfäfers. The rates here differed considerably from those found in studies of regeneration at lower altitudes (SCHMID-SCHÜTZ and HUSS 1998; MOTSCHALOW and LÄSSIG 1999). The study site in Disentis had both small densities of regeneration quadrat^{-1} as well as small projected densities ha^{-1} (Figs. 3 and 4). Not only were the densities small (4700 stems ha^{-1} in uncleared and 3900 stems ha^{-1} in cleared sites in the year 2000), but also the proportion of advance regeneration in 2000 was high (52% in uncleared sites and 49.6% in cleared sites; Table 6). The findings are not surprising because of the characteristics of the windthrow area. In Disentis, a neighbouring forest area of 100 ha was completely windthrown. The nearest edges of remnant stands are several hundred meters away from the study site in Disentis. As LÄSSIG *et al.* (1995) demonstrated, seed rain of *Picea abies* decreased to 10% at a distance of 200 m to the nearest stand compared to seed rain within the stand. Correspondingly, ASSELIN *et al.* (2001) found the distance from a remnant stand to be the most important variable in explaining spatial distribution of regeneration when compared to other microsite variables. Similar results with small spruce densities in the centre of forest gaps have been reported by VELTSISTAS (1980), MOSANDL (1984) and IMBECK and OTT (1987) for mountain forests in the Alps. Our results confirm that the extent of advance regeneration is of primary importance in influencing the density and rate of regeneration in extensive windthrow areas where the potential for post-windthrow regeneration is small.

On smaller windthrow gaps where the distances to site edges of remnant stands are shorter, regeneration densities were higher. Both the uncleared variant of Zweisimmen and the cleared one in Pfäfers are close to remnant stands. In both variants, the post-windthrow regeneration was denser than in all the other study sites and variants (Fig. 4). In addition, the advance regeneration was also large with about 16 500 stems ha^{-1} at Zweisimmen (36% of the total regeneration in 2000) and 5850 stems ha^{-1} at Pfäfers (47% of the total regeneration in 2000; Table 6).

The differences in microsites with respect to disturbance types underpins the importance of advance regeneration (Fig. 5). On light-exposed microsites without disturbance, the density of post-windthrow regeneration in 2000 was larger than the density of advance regeneration but the latter included more saplings (stems >20 cm). On disturbed places, however, the proportion of saplings of the advance regeneration in 2000 equalled that of the post-windthrow regeneration. This indicates that some of the advance regeneration on disturbed sites may have been destroyed, e.g. by clearing activities. However, the proportion of post-windthrow regeneration on these sites was larger than on all other quadrats, which corresponds to findings from other studies (e.g. ROBERTS and DONG 1993). The extent of regeneration, in particular seedling densities, corresponded with the vegetation covers of the three disturbance types and resulted in small densities on undisturbed and densely covered microsites. In contrast, seedling densities were high on disturbed microsites with incomplete vegetation cover early after the windthrow (Fig. 1; NGUYEN-XUAN *et al.* 2000).

4.4 Elasticity and treatments

The question of how long it takes for a windthrown mountain forest stand to regain its protective effect against natural hazards, such as snow avalanches, is crucial for people living in Alpine regions (BRANG 2001; BRANG *et al.* 2001). It is not crucial, however, for the life cycle of a mountain forest. Even with the small regeneration rates observed in the uncleared variant of the Pfäfers site or on the study sites of Disentis, the succession towards dense mountain forests is only a matter of time, despite the variable mortality rates among seedlings (LÄSSIG *et al.* 1995; SCHÖNENBERGER this issue a). Given the constant risk of both rockfall and snow avalanches affecting people, property and infrastructures in valleys and given that the timber left lying in uncleared windthrow areas presumably provides protection (FREY and THEE this issue), we consider the speed of regeneration of most windthrown stands in mountain regions insufficient to adequately replace the protective function of remnant forests within a period of 20 to 30 years. It may be appropriate to plant trees to replace windthrown stands on steep slopes to accelerate reforestation in addition to building temporary avalanche barriers (SCHÖNENBERGER and WASEM 1997; SCHÖNENBERGER this issue a).

Timber harvest after windthrow causes extensive disturbance to the vegetation and to some of the soil. In tall herb communities present in many mountain forests, such a disturbance is a rare opportunity for tree seeds to germinate in great numbers. Our results support this fact for treatment comparisons in Schwanden and Pfäfers where regeneration densities in cleared study areas exceeded those of uncleared areas. Although the original advance regeneration may be destroyed by clearing activities the post-windthrow regeneration on disturbed sites compensate for much of the presumably destroyed advance regeneration (Figs. 4 and 5). Disturbance effects in mountain forests, such as reduction in the dominance of the tree layer (WOHLGEMUTH *et al.* 2002) or disturbance of the vegetation and soils by timber harvest may have a positive effect on tree regeneration especially in communities dominated by tall herbs. However, the question of resistance and elasticity in relation to appropriate treatments is anthropocentric and hence must be answered individually as each case arises (OTT *et al.* 1997).

5 Conclusion

In the four case studies of the regeneration of windthrown stands in the Swiss Alps, the dynamics of the vegetation in relation to both changes in the light climate and disturbances of the soil surface are of predominant importance. Grasses, tall herbs and *Rubus* species tend to dominate extensive areas after windthrow and reduce the chances of tree seed germination and seedling growth. The marked reduction in the dominance of the tree layer generally increases the availability of light in most sites, which benefits advance regeneration. Both natural disturbances, such as the creation of pits and mounds from falling trees, as well as disturbances caused by timber harvesting and related clearing activities positively influence the germination of tree seeds after a windthrow. The resulting regeneration can compensate for the loss of advance regeneration within a period of 10 years. In large windthrow areas, however, regeneration may be considerably reduced due to the lack of seeds, so that regeneration, including advance regeneration, is very slow.

More information is needed to compare the regeneration rates of mountain forests with those of lowland forests. Further monitoring activities must include nurse log regeneration, which becomes increasingly important in tall herb communities during the second decade after a windthrow.

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Appendix. Frequency of all species found in the study sites of Schwanden, Pfäfers, Disentis and Zweisimmen.

		Presence in quadrats										Presence in percentage										
		S		D		P		Z		all sites		S		D		P		Z		all sites		
year		92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	Δ 92-00
nr of quadrats		81	74	59	56	53	40	43	43	236	213	81	74	59	56	53	40	43	43	236	213	
Latin name	Abbr.																					
Pteridophyta																						
Athyrium filix-femina	Athyfili	28	30	18	20	3	3	9	12	58	65	35	41	31	36	6	8	21	28	25	31	**6**
Dryopteris dilatata	Dryodila	.	7	7	8	.	.	13	13	20	28	0	9	12	14	0	0	30	30	8	13	**5**
Gymnocarpium dryopteris	Gymndryo	11	10	14	16	.	.	16	20	41	46	14	14	24	29	0	0	37	47	17	22	**4**
Oreopteris limbosperma	Oreolimb	5	7	4	6	2	2	.	.	11	15	6	9	7	11	4	5	0	0	5	7	**2**
Polystichum aculeatum	Polyacul	.	.	.	.	.	.	.	2	.	2	0	0	0	0	0	0	0	5	0	1	**1**
Dryopteris affinis	Dryoaffi	4	5	.	.	.	.	.	.	4	5	5	7	0	0	0	0	0	0	2	2	**1**
Cystopteris fragilis	Cystfrag	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Blechnum spicant	Blecspic	11	11	4	3	.	.	.	.	15	14	14	15	7	5	0	0	0	0	6	7	**0**
Equisetum silvaticum	Equisilv	3	3	.	.	.	.	.	.	3	3	4	4	0	0	0	0	0	0	1	1	**0**
Asplenium viride	Asplviri	.	.	.	.	.	.	1	1	1	1	0	0	0	0	0	0	2	2	0	0	**0**
Phegopteris connectilis	Phegconn	4	3	4	3	.	.	8	8	16	14	5	4	7	5	0	0	19	19	7	7	**0**
Equisetum arvense	Equiarve	2	1	.	.	.	.	.	.	2	1	2	1	0	0	0	0	0	0	1	0	**0**
Lycopodium annotinum	Lycoanno	3	2	1	.	.	.	.	.	4	2	4	3	2	0	0	0	0	0	2	1	**-1**
Dryopteris carthusiana	Dryocart	6	6	14	6	.	.	8	9	28	21	7	8	24	11	0	0	19	21	12	10	**-2**
Dryopteris filix-mas	Dryofili	15	2	4	4	.	.	1	3	20	9	19	3	7	7	0	0	2	7	8	4	**-4**
Coniferopsida																						
Picea abies (shrub)	S-Piabie	.	.	.	6	.	.	6	9	6	15	0	0	0	11	0	0	14	21	3	7	**4**
Abies alba	Abiealba	.	.	.	.	2	6	.	.	2	6	0	0	0	0	4	15	0	0	1	3	**2**
Picea abies	Piceabie	10	11	8	7	9	6	9	12	36	36	12	15	14	13	17	15	21	28	15	17	**2**
Larix decidua (shrub)	S-Ladeci	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Pinus sylvestris	Pinusylv	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Larix decidua	Larideci	.	.	.	.	3	2	.	.	3	2	0	0	0	0	6	5	0	0	1	1	**0**
Polycarpicae																						
Ranunculus lanuginosus	Ranulanu	2	3	.	3	8	14	8	8	18	28	2	4	0	5	15	35	19	19	8	13	**6**
Ranunculus nemorosus aggr.	Ranunemo	.	.	4	4	25	30	6	8	35	42	0	0	7	7	47	75	14	19	15	20	**5**
Ranunculus repens	Ranurepe	8	10	1	2	.	1	.	.	9	13	10	14	2	4	0	3	0	0	4	6	**2**
Aconitum variegatum spp. *paniculatum*	Aconpani	.	.	10	13	.	.	.	.	10	13	0	0	17	23	0	0	0	0	4	6	**2**

Aquilegia atrata	Aquiatra	.	.	.	.	5	7	.	.	5	7	0	0	0	0	9	18	0	0	2	3	**1**
Aconitum altissimum	Aconalti	.	.	1	5	17	13	.	.	18	18	0	0	2	9	32	33	0	0	8	8	**1**
Trollius europaeus	Troleuro	.	.	.	.	6	7	.	.	6	7	0	0	0	0	11	18	0	0	3	3	**1**
Thalictrum aquilegiifolium	Thalaqui	.	.	.	.	2	3	.	.	2	3	0	0	0	0	4	8	0	0	1	1	**1**
Caltha palustris	Caltpalu	1	2	.	.	.	.	.	.	1	2	1	3	0	0	0	0	0	0	0	1	**1**
Aconitum napellus aggr.	Aconnape	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Ranunculus platanifolius	Ranuplat	.	.	12	9	.	1	.	.	12	10	0	0	20	16	0	3	0	0	5	5	**0**
Ranunculus bulbosus	Ranubulb	1	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	0	0	**0**
Hamamelididae																						
Betula pendula (shrub)	S-Bepend	.	2	.	7	.	.	.	.	.	9	0	3	0	13	0	0	0	0	0	4	**4**
Urtica dioica	Urtidioi	1	2	.	2	.	.	3	7	4	11	1	3	0	4	0	0	7	16	2	5	**3**
Alnus incana (shrub)	S-Alinca	.	4	.	.	.	.	.	.	.	4	0	5	0	0	0	0	0	0	0	2	**2**
Fagus sylvatica	Fagusylv	3	4	.	.	.	.	.	.	3	4	4	5	0	0	0	0	0	0	1	2	**1**
Alnus incana	Alnuinca	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Corylus avellana	Coryavel	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Fagus sylvatica (shrub)	S-Fasylv	.	1	.	.	.	.	.	.	.	1	0	1	0	0	0	0	0	0	0	0	**0**
Betula pendula	Betupend	1	2	2	1	.	.	.	.	3	3	1	3	3	2	0	0	0	0	1	1	**0**
Rosidae																						
Epilobium angustifolium	Epilangu	8	43	2	20	.	1	3	27	13	91	10	58	3	36	0	3	7	63	6	43	**37**
Rubus idaeus	Rubuidae	49	66	24	40	23	37	23	40	119	183	60	89	41	71	43	93	53	93	50	86	**35**
Rubus fruticosus aggr.	Rubufrut	40	69	.	.	.	.	.	.	40	69	49	93	0	0	0	0	0	0	17	32	**15**
Epilobium montanum	Epilmont	5	8	4	23	13	5	9	15	31	51	6	11	7	41	25	13	21	35	13	24	**11**
Chaerophyllum hirsutum	Chaehirs	5	6	.	7	16	16	21	27	42	56	6	8	0	13	30	40	49	63	18	26	**8**
Chrysosplenium alternifolium	Chryalte	.	7	.	3	.	.	.	7	.	17	0	9	0	5	0	0	0	16	0	8	**8**
Fragaria vesca	Fragvesc	8	12	.	.	15	19	20	23	43	54	10	#	0	0	28	#	47	#	18	25	**7**
Geranium robertianum	Gerarobe	13	9	2	3	5	6	12	25	32	43	16	12	3	5	9	15	28	58	14	20	**7**
Sorbus aucuparia (shrub)	S-Soaucu	3	4	2	2	.	1	4	13	9	2	4	5	3	4	0	3	9	30	4	9	**6**
Circaea alpina	Circalpi	2	11	.	.	.	.	.	.	2	11	2	15	0	0	0	0	0	0	1	5	**4**
Chaerophyllum villarsii	Chaevill	.	.	9	9	6	12	.	.	15	21	0	0	15	16	11	30	0	0	6	10	**4**
Geranium sylvaticum	Gerasylv	.	.	.	3	3	7	.	.	3	1	0	0	0	5	6	18	0	0	1	5	**3**
Acer pseudoplatanus (shrub)	S-Acpseu	.	3	.	.	.	.	.	2	.	5	0	4	0	0	0	0	0	5	0	2	**2**
Sanicula europaea	Sanieuro	.	.	.	.	.	.	2	6	2	6	0	0	0	0	0	0	5	14	1	3	**2**
Saxifraga cuneifolia	Saxicune	.	.	1	5	.	.	.	.	1	5	0	0	2	9	0	0	0	0	0	2	**2**
Potentilla erecta	Poteerec	.	1	1	1	1	2	.	.	2	4	0	1	2	2	2	5	0	0	1	2	**1**
Acer pseudoplatanus	Acerpseu	10	4	.	.	21	18	.	8	31	3	12	5	0	0	40	45	0	19	13	14	**1**
Geum urbanum	Geumurba	.	1	.	.	.	.	.	1	.	2	0	1	0	0	0	0	0	2	0	1	**1**

Appendix continued.

		Presence in quadrats										Presence in percentage										
		S		D		P		Z		all sites		S		D		P		Z		all sites		
year		92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	Δ 92-00
nr of quadrats		81	74	59	56	53	40	43	43	236	213	81	74	59	56	53	40	43	43	236	213	
Latin name	Abbr.																					
Rosidae																						
Rosa canina	Rosacani	.	.	.	.	.	.	.	2	.	2	0	0	0	0	0	0	0	5	0	1	**1**
Circaea lutetiana	Circlute	7	8	.	.	.	.	.	.	7	8	9	11	0	0	0	0	0	0	3	4	**1**
Epilobium collinum	Epilcoll	1	2	.	.	.	.	.	.	1	2	1	3	0	0	0	0	0	0	0	1	**1**
Rubus saxatilis	Rubusaxa	.	.	.	.	1	2	.	.	1	2	0	0	0	0	2	5	0	0	0	1	**1**
Geum montanum	Geummont	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Lathyrus pratensis	Lathprat	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Medicago lupulina	Medilupu	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Pimpinella major	Pimpmajo	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Rosa pendulina	Rosapend	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Vicia sylvatica	Vicisylv	.	.	.	.	6	6	.	.	6	6	0	0	0	0	11	15	0	0	3	3	**0**
Lotus corniculatus	Lotucorn	.	.	.	.	2	2	.	.	2	2	0	0	0	0	4	5	0	0	1	1	**0**
Alchemilla conjuncta aggr.	Alchconj	.	.	.	.	1	1	.	.	1	1	0	0	0	0	2	3	0	0	0	0	**0**
Alchemilla vulgaris aggr.	Alchvulg	3	1	.	.	7	8	.	.	10	9	4	1	0	0	13	20	0	0	4	4	**0**
Oxalis acetosella	Oxalacet	52	43	49	46	17	15	34	33	152	137	64	58	83	82	32	38	79	77	64	64	**0**
Heracleum sphondylium	Heraspho	.	.	.	.	3	2	.	.	3	2	0	0	0	0	6	5	0	0	1	1	**0**
Rosa arvensis	Rosaarve	.	.	.	.	2	1	.	.	2	1	0	0	0	0	4	3	0	0	1	0	**0**
Epilobium palustre	Epilpalu	1	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	0	0	**0**
Epilobium parviflorum	Epilparv	.	.	1	.	.	.	.	.	1	.	0	0	2	0	0	0	0	0	0	0	**0**
Potentilla reptans	Poterept	1	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	0	0	**0**
Peucedanum ostruthium	Peucostr	1	1	4	3	3	2	.	.	8	6	1	1	7	5	6	5	0	0	3	3	**-1**
Geum rivale	Geumriva	1	.	.	.	3	2	.	.	4	2	1	0	0	0	6	5	0	0	2	1	**-1**
Saxifraga rotundifolia	Saxirotu	4	2	10	11	14	7	15	17	43	37	5	3	17	20	26	18	35	40	18	17	**-1**
Sorbus aucuparia	Sorbaucu	6	4	4	4	4	3	7	5	21	16	7	5	7	7	8	8	16	12	9	8	**-1**
Impatiens noli-tangere	Impanoli	16	6	.	.	.	.	.	.	16	6	20	8	0	0	0	0	0	0	7	3	**-4**
Dilleniidae																						
Viola biflora	Violbifl	7	13	24	21	27	28	22	28	80	90	9	18	41	38	51	70	51	65	34	42	**8**
Viola reichenbachiana	Violreic	6	13	.	2	3	5	5	6	14	26	7	18	0	4	6	13	12	14	6	12	**6**
Salix caprea (shrub)	S-Sacapr	.	6	.	1	.	.	1	1	1	8	0	8	0	2	0	0	2	2	0	4	**3**
Salix caprea	Salicapr	2	4	1	.	.	.	1	5	4	9	2	5	2	0	0	0	2	12	2	4	**3**

Cardamine flexuosa	Cardflex	3	6	.	.	.	.	.	2	3	8	4	8	0	0	0	0	0	5	1	4	**2**
Hypericum perforatum	Hypeperf	.	5	.	.	.	.	.	.	.	5	0	7	0	0	0	0	0	0	0	2	**2**
Primula elatior	Primelat	.	.	.	.	34	32	2	5	36	37	0	0	0	0	64	80	5	12	15	17	**2**
Lysimachia nemorum	Lysinemo	33	33	.	.	1	1	.	.	34	34	41	45	0	0	2	3	0	0	14	16	**2**
Vaccinium vitis-idaea	Vaccviti	.	.	2	3	.	.	1	1	3	4	0	0	3	5	0	0	2	2	1	2	**1**
Salix appendiculata	Saliappe	.	1	.	.	.	.	.	.	.	1	0	1	0	0	0	0	0	0	0	0	**0**
Salix appendiculata (shrub)	S-Saappe	.	.	.	1	.	.	.	.	.	1	0	0	0	2	0	0	0	0	0	0	**0**
Hypericum humifusum	Hypehumi	1	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	0	0	**0**
Cardamine impatiens	Cardimpa	.	.	.	.	2	.	.	.	2	.	0	0	0	0	4	0	0	0	1	0	**-1**
Soldanella alpina	Soldalpi	.	.	.	.	8	2	.	.	8	2	0	0	0	0	15	5	0	0	3	1	**-2**
Vaccinium myrtillus	Vaccmyrt	31	21	19	17	.	.	14	14	64	52	38	28	32	30	0	0	33	33	27	24	**-3**
Caryophyllidae																						
Rumex alpestris	Rumealpe	.	.	.	7	.	.	.	.	.	7	0	0	0	13	0	0	0	0	0	3	**3**
Moehringia trinervia	Moehtrin	4	3	3	1	.	1	1	5	8	10	5	4	5	2	0	3	2	12	3	5	**1**
Silene vulgaris	Silevulg	.	.	.	.	2	1	1	1	3	2	0	0	0	0	4	3	2	2	1	1	**0**
Stellaria nemorum	Stelnemo	10	9	7	5	1	.	.	1	18	15	12	12	12	9	2	0	0	2	8	7	**-1**
Silene dioica	Siledioi	2	.	.	.	1	.	2	2	5	2	2	0	0	0	2	0	5	5	2	1	**-1**
Moehringia muscosa	Moehmusc	.	.	.	.	.	.	8	4	8	4	0	0	0	0	0	0	19	9	3	2	**-2**
Silene rupestris	Silerupe	10	3	.	.	.	.	.	.	10	3	12	4	0	0	0	0	0	0	4	1	**-3**
Asteridae																						
Solidago virgaurea	Solivirg	17	34	11	20	17	15	5	10	50	79	21	46	19	36	32	38	12	23	21	37	**16**
Myosotis sylvatica	Myossylv	.	.	4	6	.	.	6	23	10	29	0	0	7	11	0	0	14	53	4	14	**9**
Cirsium oleraceum	Cirsoler	.	.	.	.	3	20	.	.	3	20	0	0	0	0	6	50	0	0	1	9	**8**
Valeriana officinalis	Valeoffi	.	.	.	.	11	23	1	4	12	27	0	0	0	0	21	58	2	9	5	13	**8**
Knautia dipsacifolia	Knaudips	1	3	4	4	10	18	16	16	31	41	1	4	7	7	19	45	37	37	13	19	**6**
Prenanthes purpurea	Prenpurp	17	21	24	24	10	9	1	3	52	57	21	28	41	43	19	23	2	7	22	27	**5**
Sambucus racemosa (shrub)	S-Sarace	.	6	.	.	.	.	.	4	.	10	0	8	0	0	0	0	0	9	0	5	**5**
Melampyrum sylvaticum	Melasylv	.	.	13	21	4	4	.	.	17	25	0	0	22	38	8	10	0	0	7	12	**5**
Valeriana tripteris	Valetrip	.	.	2	3	.	1	1	8	3	12	0	0	3	5	0	3	2	19	1	6	**4**
Veronica chamaedrys	Verocham	3	4	.	2	2	1	18	22	23	29	4	5	0	4	4	3	42	51	10	14	**4**
Adoxa moschatellina	Adoxmosc	1	1	.	2	.	.	.	4	1	7	1	1	0	4	0	0	0	9	0	3	**3**
Crepis paludosa	Creppalu	.	3	.	.	5	5	.	1	5	9	0	4	0	0	9	13	0	2	2	4	**2**
Lamium galeobdolon ssp. *montanum*	Lamimont	20	17	8	9	24	17	22	28	74	71	25	23	14	16	45	43	51	65	31	33	**2**
Cicerbita alpina	Cicealpi	.	.	19	20	6	6	1	1	26	27	0	0	32	36	11	15	2	2	11	13	**2**
Petasites albus	Petaalbu	.	.	14	15	17	15	5	6	36	36	0	0	24	27	32	38	12	14	15	17	**2**
Gnaphalium sylvaticum	Gnapsylv	3	6	.	.	.	.	.	.	3	6	4	8	0	0	0	0	0	0	1	3	**2**

Appendix continued.

		Presence in quadrats										Presence in percentage										
		S		D		P		Z		all sites		S		D		P		Z		all sites		
year		92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	Δ 92-00
nr of quadrats		81	74	59	56	53	40	43	43	236	213	81	74	59	56	53	40	43	43	236	213	
Latin name	Abbr.																					
Asteridae																						
Cirsium palustre	Cirspalu	.	3	.	.	.	.	.	.	.	3	0	4	0	0	0	0	0	0	0	1	**1**
Phyteuma ovatum	Phytovat	.	.	.	.	5	7	.	.	5	7	0	0	0	0	9	18	0	0	2	3	**1**
Tussilago farfara	Tussfarf	1	.	.	.	1	3	3	4	5	7	1	0	0	0	2	8	7	9	2	3	**1**
Senecio ovatus	Seneovat	4	7	.	.	9	7	.	.	13	14	5	9	0	0	17	18	0	0	6	7	**1**
Cirsium vulgare	Cirsvulg	.	.	.	.	.	.	1	3	1	3	0	0	0	0	0	0	2	7	0	1	**1**
Leucanthemum vulgare	Leucvulg	.	.	.	.	1	2	.	1	1	3	0	0	0	0	2	5	0	2	0	1	**1**
Adenostyles glabra	Adenglab	.	.	.	.	8	12	3	.	11	12	0	0	0	0	15	30	7	0	5	6	**1**
Clinopodium vulgare	Clinvulg	.	.	.	.	.	.	.	2	.	2	0	0	0	0	0	0	0	5	0	1	**1**
Campanula rotundifolia	Camprotu	.	.	.	.	4	5	.	.	4	5	0	0	0	0	8	13	0	0	2	2	**1**
Campanula cochleariifolia	Campcoch	.	.	.	.	.	.	3	4	3	4	0	0	0	0	0	0	7	9	1	2	**1**
Carduus defloratus	Carddefl	.	.	.	.	3	2	.	2	3	4	0	0	0	0	6	5	0	5	1	2	**1**
Galium odoratum	Galiodor	18	14	1	1	5	2	20	24	44	41	22	19	2	2	9	5	47	56	19	19	**1**
Digitalis lutea	Digilute	1	1	.	1	.	.	.	.	1	2	1	1	0	2	0	0	0	0	0	1	**1**
Gentiana asclepiadea	Gentascl	.	.	.	.	1	2	.	.	1	2	0	0	0	0	2	5	0	0	0	1	**1**
Lamium maculatum	Lamimacu	.	1	.	.	1	1	.	.	1	2	0	1	0	0	2	3	0	0	0	1	**1**
Leontodon hispidus	Leonhisp	.	.	.	.	1	1	.	1	1	2	0	0	0	0	2	3	0	2	0	1	**1**
Lonicera alpigena	Lonialpi	.	.	.	.	1	2	.	.	1	2	0	0	0	0	2	5	0	0	0	1	**1**
Lonicera nigra (shrub)	S-Lonigr	.	.	1	1	.	.	.	1	1	2	0	0	2	2	0	0	0	2	0	1	**1**
Fraxinus excelsior (shrub)	S-Frexce	.	1	.	.	.	.	.	.	.	1	0	1	0	0	0	0	0	0	0	0	**0**
Galium anisophyllum	Galianis	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Helianthemum nummularium	Helinumm	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Lonicera caerulea	Lonicaer	.	.	.	1	.	.	.	.	.	1	0	0	0	2	0	0	0	0	0	0	**0**
Lonicera caerulea (shrub)	S-Locaer	.	.	.	1	.	.	.	.	.	1	0	0	0	2	0	0	0	0	0	0	**0**
Prunella grandiflora	Prungran	.	1	.	.	.	.	.	.	.	1	0	1	0	0	0	0	0	0	0	0	**0**
Prunella vulgaris	Prunvulg	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Senecio viscosus	Senevisc	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Solanum dulcamara	Soladulc	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Teucrium chamaedrys	Teuccham	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**

Verbascum thapsus	Verbthap	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Aposeris foetida	Aposfoet	.	.	.	.	.	.	7	7	7	7	0	0	0	0	0	0	16	16	3	3	**0**
Centaurea montana	Centmont	.	.	.	.	6	6	.	.	6	6	0	0	0	0	11	15	0	0	3	3	**0**
Phyteuma betonicifolium	Phytbeto	.	2	6	4	.	.	.	.	6	6	0	3	10	7	0	0	0	0	3	3	**0**
Taraxacum officinale	Taraoffi	.	.	.	.	3	1	.	2	3	3	0	0	0	0	6	3	0	5	1	1	**0**
Fraxinus excelsior	Fraxexce	2	2	.	.	.	.	.	.	2	2	2	3	0	0	0	0	0	0	1	1	**0**
Valeriana montana	Valemont	.	.	.	.	12	11	.	.	12	11	0	0	0	0	23	28	0	0	5	5	**0**
Galium album	Galialbu	.	.	.	.	.	.	1	1	1	1	0	0	0	0	0	0	2	2	0	0	**0**
Origanum vulgare	Origvulg	.	.	.	.	1	1	.	.	1	1	0	0	0	0	2	3	0	0	0	0	**0**
Mycelis muralis	Mycemura	2	3	4	.	5	4	9	11	20	18	2	4	7	0	9	10	21	26	8	8	**0**
Veronica officinalis	Verooffi	9	8	.	2	1	1	9	6	19	17	11	11	0	4	2	3	21	14	8	8	**0**
Ajuga reptans	Ajugrept	.	3	.	.	6	6	10	5	16	14	0	4	0	0	11	15	23	12	7	7	**0**
Homogyne alpina	Homoalpi	.	.	1	.	1	1	2	2	4	3	0	0	2	0	2	3	5	5	2	1	**0**
Scrophularia nodosa	Scronodo	2	2	2	1	.	.	.	.	4	3	2	3	3	2	0	0	0	0	2	1	**0**
Aster bellidiastrum	Astebell	.	.	.	.	2	1	.	.	2	1	0	0	0	0	4	3	0	0	1	0	**0**
Lonicera nigra	Loninigr	.	.	2	1	.	.	.	.	2	1	0	0	3	2	0	0	0	0	1	0	**0**
Cirsium arvense	Cirsarve	.	.	.	.	.	.	1	.	1	.	0	0	0	0	0	0	2	0	0	0	**0**
Plantago major	Planmajo	.	.	.	.	1	.	.	.	1	.	0	0	0	0	2	0	0	0	0	0	**0**
Veronica montana	Veromont	.	.	1	.	.	.	.	.	1	.	0	0	2	0	0	0	0	0	0	0	**0**
Stachys sylvatica	Stacsylv	8	6	.	.	.	.	.	.	8	6	10	8	0	0	0	0	0	0	3	3	**-1**
Phyteuma spicatum	Phytspic	1	1	.	.	.	.	3	.	4	1	1	1	0	0	0	0	7	0	2	0	**-1**
Carduus personata	Cardpers	.	.	.	.	17	10	.	.	17	10	0	0	0	0	32	25	0	0	7	5	**-3**
Sambucus racemosa	Sambrace	10	5	3	4	2	.	2	1	17	10	12	7	5	7	4	0	5	2	7	5	**-3**
Hieracium prenanthoides	Hierpren	.	.	13	4	1	3	.	.	14	7	0	0	22	7	2	8	0	0	6	3	**-3**
Adenostyles alliariae	Adenalli	.	.	3	5	27	5	.	6	30	16	0	0	5	9	51	13	0	14	13	8	**-5**
Galium rotundifolium	Galirotu	8	2	.	.	1	2	18	7	27	11	10	3	0	0	2	5	42	16	11	5	**-6**
Veronica urticifolia	Verourti	12	7	12	12	43	30	18	12	85	61	15	9	20	21	81	75	42	28	36	29	**-7**
Galeopsis tetrahit	Galetetr	52	25	26	19	5	2	.	10	83	56	64	34	44	34	9	5	0	23	35	26	**-9**
Hieracium sylvaticum	Hiersylv	34	23	33	29	22	15	22	11	111	78	42	31	56	52	42	38	51	26	47	37	**-10**
Monocotyledonia																						
Agrostis capillaris	Agrocapi	31	55	5	13	5	2	7	11	48	81	38	74	8	23	9	5	16	26	20	38	**18**
Calamagrostis villosa	Calavill	.	2	11	29	9	16	.	.	20	47	0	3	19	52	17	40	0	0	8	22	**14**
Avenella flexuosa	Avenflex	2	2	10	33	.	1	.	.	12	36	2	3	17	59	0	3	0	0	5	17	**12**
Agropyron caninum	Agrocani	1	.	.	.	.	11	.	10	1	21	1	0	0	0	0	28	0	23	0	10	**9**
Deschampsia cespitosa	Desccesp	.	.	.	.	7	25	.	.	7	25	0	0	0	0	13	63	0	0	3	12	**9**
Milium effusum	Milieffu	6	8	17	29	.	.	2	2	25	39	7	11	29	52	0	0	5	5	11	18	**8**

Appendix continued.

		Presence in quadrats										Presence in percentage										
		S		D		P		Z		all sites		S		D		P		Z		all sites		
year		92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	92	00	Δ 92-00
nr of quadrats		81	74	59	56	53	40	43	43	236	213	81	74	59	56	53	40	43	43	236	213	
Latin name	Abbr.																					
Monocotyledonia																						
Calamagrostis varia	Calavari	.	.	.	.	4	15	.	2	4	17	0	0	0	0	8	38	0	5	2	8	**6**
Festuca gigantea	Festgiga	3	13	.	.	.	.	.	.	3	13	4	18	0	0	0	0	0	0	1	6	**5**
Poa nemoralis	Poanemo	.	.	.	1	1	5	.	5	1	11	0	0	0	2	2	13	0	12	0	5	**5**
Dactylis glomerata	Dactglom	.	.	.	1	2	2	.	8	2	11	0	0	0	2	4	5	0	19	1	5	**4**
Luzula sylvatica	Luzusylv	35	37	4	3	6	8	12	12	57	60	43	50	7	5	11	20	28	28	24	28	**4**
Luzula nivea	Luzunive	.	.	1	3	9	14	.	.	10	17	0	0	2	5	17	35	0	0	4	8	**4**
Hordelymus europaeus	Hordeuro	.	.	.	.	1	1	2	9	3	10	0	0	0	0	2	3	5	21	1	5	**3**
Carex sylvatica	Caresylv	20	21	.	.	2	5	1	1	23	27	25	28	0	0	4	13	2	2	10	13	**3**
Juncus effusus	Junceffu	12	17	.	.	.	.	.	.	12	17	15	23	0	0	0	0	0	0	5	8	**3**
Carex ferruginea	Careferr	.	1	.	.	21	24	.	.	21	25	0	1	0	0	40	60	0	0	9	12	**3**
Carex flacca	Careflac	.	.	.	.	5	10	.	.	5	10	0	0	0	0	9	25	0	0	2	5	**3**
Veratrum album	Veraalbu	.	.	.	.	4	8	.	.	4	8	0	0	0	0	8	20	0	0	2	4	**2**
Luzula luzulina	Luzuluzu	.	.	.	3	.	.	.	1	.	4	0	0	0	5	0	0	0	2	0	2	**2**
Paris quadrifolia	Pariquad	.	.	.	1	2	1	7	10	9	12	0	0	0	2	4	3	16	23	4	6	**2**
Polygonatum verticillatum	Polyvert	.	.	1	1	.	1	1	3	2	5	0	0	2	2	0	3	2	7	1	2	**1**
Agrostis stolonifera	Agrostol	1	2	.	1	.	1	.	.	1	4	1	3	0	2	0	3	0	0	0	2	**1**
Festuca rubra	Festrubr	.	.	.	.	1	1	.	3	1	4	0	0	0	0	2	3	0	7	0	2	**1**
Carex pallescens	Carepall	2	6	.	.	2	.	.	.	4	6	2	8	0	0	4	0	0	0	2	3	**1**
Brachypodium sylvaticum	Bracsylv	.	3	.	.	.	.	2	1	2	4	0	4	0	0	0	0	5	2	1	2	**1**
Dactylorhiza maculata	Dactmacu	.	.	.	.	1	2	1	2	2	4	0	0	0	0	2	5	2	5	1	2	**1**
Anthoxanthum odoratum	Anthodor	.	.	.	2	.	.	1	1	1	3	0	0	0	4	0	0	2	2	0	1	**1**
Carex digitata	Caredigi	.	.	.	.	1	1	.	2	1	3	0	0	0	0	2	3	0	5	0	1	**1**
Festuca altissima	Festalti	.	1	.	.	.	1	.	.	.	2	0	1	0	0	0	3	0	0	0	1	**1**
Holcus lanatus	Holclana	.	2	.	.	.	.	.	.	.	2	0	3	0	0	0	0	0	0	0	1	**1**
Maianthemum bifolium	Maiabifo	8	7	5	6	.	1	5	4	18	18	10	9	8	11	0	3	12	9	8	8	**1**
Carex remota	Careremo	15	15	.	.	.	.	.	.	15	15	19	20	0	0	0	0	0	0	6	7	**1**
Melica nutans	Melinuta	.	.	.	.	2	3	.	.	2	3	0	0	0	0	4	8	0	0	1	1	**1**

Luzula pilosa	Luzupilo	1	1	.	.	.	.	.	1	1	2	1	1	0	0	0	0	0	2	0	1	**1**
Carex montana	Caremont	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Listera ovata	Listovat	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Poa pratensis	Poaprat	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Sesleria caerulea	Seslcaer	.	.	.	.	.	1	.	.	.	1	0	0	0	0	0	3	0	0	0	0	**0**
Carex leporina	Carelepo	11	10	1	1	.	.	.	.	12	11	14	14	2	2	0	0	0	0	5	5	**0**
Carex pilulifera	Carepilu	6	3	1	3	.	.	.	.	7	6	7	4	2	5	0	0	0	0	3	3	**0**
Phleum pratense	Phleprat	.	.	.	.	.	.	1	.	1	.	0	0	0	0	0	0	2	0	0	0	**0**
Festuca heterophylla	Festhete	.	.	7	5	.	.	.	.	7	5	0	0	12	9	0	0	0	0	3	2	**-1**
Lilium martagon	Lilimart	.	.	.	.	4	2	.	.	4	2	0	0	0	0	8	5	0	0	2	1	**-1**
Allium ursinum	Alliursi	.	.	.	.	2	.	.	.	2	.	0	0	0	0	4	0	0	0	1	0	**-1**
Carex flava	Careflav	3	.	.	.	.	.	.	.	3	.	4	0	0	0	0	0	0	0	1	0	**-1**
Luzula multiflora	Luzumult	1	2	8	2	.	.	.	.	9	4	1	3	14	4	0	0	0	0	4	2	**-2**
Bryophyta																						
Eurhynchium striatum	M-Eustri	.	.	3	23	1	6	10	25	14	54	0	0	5	41	2	15	23	58	6	25	**19**
Mosses not identified	M-Modive	41	35	15	40	.	11	3	6	59	92	51	47	25	71	0	28	7	14	25	43	**18**
Mnium spec	M-Mnspec	.	14	.	5	.	1	2	14	2	34	0	19	0	9	0	3	5	33	1	16	**15**
Rhytidiadelphus spec.	M-Rhspec	.	.	.	12	8	10	16	27	24	49	0	0	0	21	15	25	37	63	10	23	**13**
Fissidens taxifolius	M-Fitaxi	.	.	.	.	3	20	.	9	3	29	0	0	0	0	6	50	0	21	1	14	**12**
Plagiochila asplenioides	M-Plaspl	.	3	.	15	3	4	2	6	5	28	0	4	0	27	6	10	5	14	2	13	**11**
Thuidium tamariscinum	M-Thtama	.	20	.	.	1	.	.	.	1	20	0	27	0	0	2	0	0	0	0	9	**9**
Hylocomium splendens	M-Hysple	.	1	7	15	2	4	21	21	30	41	0	1	12	27	4	10	49	49	13	19	**7**
Atrichum undulatum	M-Atundu	.	9	.	.	2	1	2	4	4	14	0	12	0	0	4	3	5	9	2	7	**5**
Polytrichum formosum	M-Poform	24	24	14	20	3	3	10	8	51	55	30	32	24	36	6	8	23	19	22	26	**4**
Ctenidium molluscum	M-Ctmoll	.	.	.	.	.	.	.	6	.	6	0	0	0	0	0	0	0	14	0	3	**3**
Dicranella spec.	M-Dispec	.	1	.	.	.	.	6	10	6	11	0	1	0	0	0	0	14	23	3	5	**3**
Rhodobryum roseum	M-Rhrose	.	.	.	.	.	1	.	4	.	5	0	0	0	0	0	3	0	9	0	2	**2**
Dicranum scoparium	M-Discop	.	5	10	17	3	.	21	13	34	35	0	7	17	30	6	0	49	30	14	16	**2**
Ptilium crista-castrensis	M-Ptcris	.	.	.	.	.	.	2	4	2	4	0	0	0	0	0	0	5	9	1	2	**1**
Hypnum cupressiforme	M-Hycupr	.	2	.	.	.	.	.	.	.	2	0	3	0	0	0	0	0	0	0	1	**1**
Hepaticae spec.	M-Hepati	.	1	.	.	.	1	.	.	.	2	0	1	0	0	0	3	0	0	0	1	**1**
Pellia spec.	M-Pespec	.	.	.	.	.	.	.	2	.	2	0	0	0	0	0	0	0	5	0	1	**1**
Rhizomnium punctatum	M-Rhpunc	.	.	.	.	.	.	.	1	.	1	0	0	0	0	0	0	0	2	0	0	**0**
Pleurozium schreberi	M-Plschr	.	.	6	5	3	.	3	5	12	10	0	0	10	9	6	0	7	12	5	5	**0**
Sphagnum spec.	M-Spspec	.	.	1	.	.	.	.	.	1	.	0	0	2	0	0	0	0	0	0	0	**0**