

Impact of Fencing on the Recovery of the Ground Flora on Heavily Eroded Slopes of a Deciduous Forest

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ABSTRACT / This paper seeks to outline early stages in the recovery of forest ground flora on eroded slopes impacted by recreation activities and to suggest how these data might be applied in the formulation of management policies for forest recreation areas. Based on a fencing experiment in the Sonian Forest near Brussels, we investigated whether, over a 6-year period, the vegetation was able to recover after having been destroyed by recreation use. Short-term trends in overall species composition were already observable during this 6-year

study. Species recovery on eroded hills was related to slope, aspect, and soil type. During the considered time scale, the proportion of hemicryptophytes and the number of ancient forest species increased significantly. A downward trend was detected for Ellenberg's nitrogen and temperature indexes and for the proportion of therophytes and pioneer plants of disturbed places. Changes in species' frequencies suggest six recovery strategies: early, late, expanding, disappearing, transient, and fluctuating species. Aside from seedling reproduction from overstory influences, *Luzula sylvatica* appeared to be the most resilient of the species identified in the study since this species has the highest global frequency in our sampling plots and has increased its cover during the study period. Study results indicate that (1) protection from recreation has initiated the recovery of species in the herb layer, but (2) it may take a long time before vegetation previously present in the ground flora may recover in both density and species composition.

Of all the physical components of the forest ecosystem, soil is generally the hardest to replace once lost (Kimmins 1997). A review of the literature dealing with the concept of recreational impact on vegetation and soil yields many citations related to trampling effects of hikers, bikers, motorcycles, horses, and vehicles on the soil and vegetation. However, only a few of these studies documented the recovery of impacted areas when fencing was used to halt recreational use. These studies of plant resilience after damage (defined as the ability to subsequently recover) often find that recovery takes much time and that a full recovery sometimes never occurs. In a study of vegetation recovery from trampling in a Norwegian rich fen, Arnesen (1999) found that the vegetation did not completely recover 15 years after trampling cessation. Recovery was dependent on which species were present at the outset and which species arrived early. Further development seemed to

depend largely on the species' capacity for rapid increase in cover. This is consistent with the findings of Sun (1992) showing that recovery rate is positively correlated to species growth rate. In a study of vegetation recovery after vehicle track abandonment in England, Charman and Pollard (1995) found that recovery may be rapid in grassland and heathland sites but areas of higher moorland and blanket bog recover more slowly and may never revert to their original vegetation composition on a relevant time scale.

According to Kuss and Hall (1991), recovery of an impacted area may be due to the resilience of members of the original plant stand, by colonization of the impacted areas by opportunistic invaders that replace all or some of the species that occupied the undisturbed space, or a combination of resilience and opportunism. del Moral (1979) observed that factors that increase resilience are moist habitats, a long growing season, and southwesterly aspects. Marshland (1980) points out that if there are no living below-ground remnants of plants that formerly occupied the impacted site, then recovery will be restricted to successful seedling establishment. In their study of the rate of decline and recovery of two alpine communities, Bell and Bliss (1973) reported that some plant communities classified

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as highly sensitive to low trampling intensities recover much more rapidly than those showing moderate to high resistance to trampling. This pattern of recovery is consistent with the findings of Sun (1992) showing that high resistance and high recovery appear to be two mutually exclusive characteristics of some pasture species.

If the vegetation is destroyed but the soil is left intact, recovery can occur very quickly, as fragments of the original plants remaining can sprout again and new plants can also arise from dormant seeds (Bradshaw 1997). If the soil is degraded, plant colonization and ecosystem regeneration are much more difficult, since there will be an almost-complete absence of propagules. Bradshaw (1997) recognized three limitations for vegetation recovery: (1) species immigration, (2) hostile physical conditions, and (3) essential resource deficiencies. According to Coleman (1981), who studied footpath erosion in England, a threshold for soil erosion by trampling occurs at a 12–13° slope and problems increase exponentially above it.

Despite the above-mentioned literature, the knowledge related to plant communities impacted by recreation is incomplete. In the seventies, when seeking to outline the nature of the changes caused by human trampling in the soils and ground vegetation of seminatural areas in Great Britain, Burden and Randerson (1972) stressed the importance of knowing the rates of recovery of certain communities after a period of trampling. Twenty years later, the lack of knowledge concerning the resilience of impacted areas was again pointed out by Kuss and Hall (1991), and recently by Dale and others (2002). When available, those studies commonly address herbaceous ecosystems such as mountain meadows, marshlands, and dunes, mostly outside Europe, while in the United States, studies on recreation impact were carried out for some national parks (Leung and Marion 1999a, b) or high-use recreation areas (Marion 1995; Marion and Cole 1996). Among the scarce studies on resilience of plant communities impacted by recreation, few were conducted in a forest ecosystem. This gap in our knowledge is particularly regrettable, as forests are among the most appreciated areas for hiking and mountain-biking. Furthermore, deciduous forests with sensitive, forb-dominated understories are among the most vulnerable terrestrial habitats to damage by recreational activities (Kuss 1986; Cole 1987, 1995c; Marion and Cole 1996). Additional research is needed, especially in forests used intensively for recreation, to understand better the rate-of-recovery processes in sensitive forest ecosystems.

To evaluate the relevance of fencing without other restoration practices (e.g., revegetation) for the forest

vegetation recovery, we monitored the dynamics of vegetation on soils altered by recreation activities in the Sonian Forest (Brussels, Belgium), which experiences impacts from recreation activities (e.g., hiking and biking). These activities produce disturbance to the upper soil horizons. Using permanent plot sampling, we (1) assessed the variability of temporal dynamics among species recovering on fenced eroded slopes and (2) related the species temporal dynamics to the recovery ability of eroded slopes.

Study Area

The research was conducted in the Sonian Forest, which lies south of Brussels (50°47'30"N, 4°26'30"E). It is a remnant of the extensive forest that covered Western Europe after the last Ice Age. The forest currently covers 4383 ha, 1654 ha of which is situated within the administrative limits of the Brussels Capital Region. The prevailing soils are Typic or Gleyic argillic brown earths (USDA, Hapludalf and Glossudalf; FAO, Luvisols and Podzoluvisols; French classification: Sols lessivés, Sols lessivés, Sols lessivés hydromorphes, and Sols lessivés à pseudogley), developed in calcareous loessic deposits of the Würm age (Herbauts and others 1996). The forest ranges in altitude from 65 to 130 m above sea level. The climate of the area is temperate and humid, with a growing season of 7 months (April–October). Mean annual temperature is 9.9°C; annual precipitation is 835 mm.

Originally, the Sonian Forest was an oak–hornbeam forest (dominated by *Quercus robur* and *Carpinus betulus*). Since the plantation work of the Austrian administration at the end of the 18th century, it is now dominated by beech trees (*Fagus sylvatica*, 85% cover, with few other woody species). Seven percent of the forest is occupied by oak stands (*Quercus robur*), and 8% is represented by introduced conifer stands (*Pinus sylvatica*, *Larix decidua*, *Picea abies*). Continued use of the research area for intensive leisure activities (biking, hiking, scouting) has degraded the soils and vegetation to such an extent that soil erosion has resulted.

A common problem in the periurban Sonian Forest is the tendency of visitors to go off-trail, creating impromptu paths. This impact can vary from a slight disturbance of the forest floor to complete loss of the upper soil horizons. Indeed, in this highly visited forest, damage to soils by recreation activities is not limited to surface disturbance: on steep slopes, the stability of the soil may be reduced to the point at which severe soil erosion occurs, often denuding tree roots. Therefore, restoration practices, such as fencing, have been implemented to minimize the human impact.

For the surveyed areas, no information is available about the state of vegetation before recreation impact occurs, but prior to fencing, vegetation relevés were made in 1992–1993 (Roelandt and De Clercq, personal communication) (Table 1). *Fagus sylvatica* was dominant and the most frequent tree layer species. *Sorbus aucuparia* and *Acer pseudoplatanus* had the highest frequency in the shrub layer. Thirty-one species were mentioned in the herb layer, including eight species of tree seedlings.

Methods

The purpose of this study was to determine the effect of protective fencing on species composition of herb-tree seedlings over a 6-year period in a heavily used hiking and biking recreation area. Fencing in the winter of 1994 was followed by summer surveys which were conducted each year from 1995 to 2000, the results of which are presented here.

Within the Sonian Forest, three field sites were used. All of them are nature reserves since 1990 or 1992. In spite of this protection status, these sites have been used intensively for a long time for hiking, scouting, and biking, because of free access for public use. Continued use of these areas for leisure activities has degraded the soils and vegetation to such an extent that soil erosion has resulted. The absolute number of visitors per year was difficult to measure but it was estimated that the study sites were used by 5–50 hikers, bikers, or scouts per day each sunny weekend. To stop this human impact, fencing was installed in 1994 as a restoration practice. Fences were regularly controlled. As no damage were observed, the study sites remained virtually undisturbed during the experiment.

Within the three study sites, concentrated trampling has resulted in the creation of extended areas devoid of vegetation, showing complete removal of litter and with highly compacted soil. In these barren places, 10 permanent plots (1×1 or 2×2 m) were randomly laid out for vegetation sampling. The permanent plots selected within the forest satisfied three criteria: (1) a homogeneous area without any trail in the vicinity, (2) a mature deciduous forest with continuous canopy, and (3) an absence of timber harvesting. Species composition was characterized by classical phytosociological relevés (Braun-Blanquet 1964), which means that the total coverage for each species (vertical projection onto the ground) was estimated visually and recorded within seven cover classes: **r**, 1 or 2 individuals; **+**, a few individuals (< 20) with cover $< 5\%$; **1**, many individuals (20–100) with cover $< 5\%$; **2**, 5–25% cover; **3**, 25–50% cover; **4**, 50–75% cover; **5**, 75–100% cover (presented

as ordinal transformation, i.e., numbers 1 to 7 for original grades of the Braun-Blanquet scale). Plots were sampled in the growing season (June and July) each year, starting in 1995. Initial sampling was conducted 7 months after the fencing action. The names of samples are as, e.g., r95p1, which means “recorded 1995, plot1.”

The entire data set was analyzed using Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980) to examine floristic gradients in the vegetation using the program Canoco 4 for Windows (ter Braak and Šmilauer 1998). In order to characterize the environmental preferences of the species in the plots, mean characteristic Ellenberg indicator values were calculated (N, nitrogen; L, light; F, moisture; R, reaction; T, temperature [Ellenberg and others 1991]). Using these ecological indicator values, we have calculated, for each relevé, averages of environmental variables that most closely fit each of the ordination axes. These averages were weighted by the species' cover. Since Braun-Blanquet cover-abundance values are not suitable for mathematical treatment, raw data were transformed by taking the median of each scale interval: 87.5, 62.5, 37.5, 15, 2.5, 0.5, and 0.2, accounting, respectively, for 5, 4, 3, 2, 1, +, and r (arbitrary values were taken for r, +, and 1). Ellenberg's indicator values have been widely employed and validated for the interpretation of the variation among plant communities in space and time in many northern European countries (e.g., Persson 1981, ter Braak and Gremmen 1987; van der Maarel 1993; Diekmann and Dupré 1997). The method is used to highlight potential changes and restoration in the vegetation. An advantage of the Ellenberg values is that they are predefined and therefore provide an objective benchmark to interpret ordinations in terms of known gradients (Hill and others 1999). The correlation between the axes and the inferred environmental ecological parameters was measured using the Spearman rank correlation coefficient r_s .

The species data were analyzed with canonical correspondence analysis (CCA) (ter Braak 1987) using Canoco 4 for Windows (ter Braak and Šmilauer 1998). Two explanatory variables were dummy variables (1/0) representing the soil type (identified from soil maps) and aspect. One variable was quantitative (i.e., slope). Dummy variables are represented by their centroids, while the quantitative variable is represented by an arrow along with species scores, on ordination biplots. To determine the variation in the species data that is uniquely attributable to this particular set of environmental variables, the time effect was evaluated as a covariate and was used for defining blocks for the Monte Carlo permutation test.

Table 1. Vegetation prior to fencing in the surveyed areas (Roelandt and De Clercq, unpublished)^a

Relevé number (past survey):		17	11	12	58	91	100	101	105		
Corresponding permanent plot (present study)		p1	p2	p3	p5	p4	p8	p7	p9	Frequency (%)	Mean cover (%)
	Layer cover (%)										
	A:	70	80	70	70	70	80	—	70		
	a:	40	50	25	5	15	60	2	70		
	h:	40	1	60	2	2	2	70	5		
A	<i>Fagus sylvatica</i>	4	4	r	3	4	2	.	2	87.5	36.5
	<i>Acer pseudoplatanus</i>	.	r	.	2	.	2	.	3	50.0	16.9
	<i>Quercus robur</i>	.	.	2	.	.	2	.	3	37.5	22.5
	<i>Quercus rubra</i>	.	3	2	+	37.5	17.5
	<i>Quercus petraea</i>	.	.	4	+	25.0	31.3
	<i>Carpinus betulus</i>	.	2	.	2	25.0	15.0
	<i>Castanea sativa</i>	.	.	.	+	.	2	.	.	25.0	7.6
	<i>Robinia pseudoacacia</i>	2	12.5	15.0
	<i>Tilia cordata</i>	.	.	.	+	12.5	0.2
	<i>Sorbus aucuparia</i>	+	.	.	12.5	0.2
	<i>Prunus serotina</i>	.	r	12.5	0.2
	<i>Pinus sylvestris</i>	.	.	r	12.5	0.2
	<i>Betula pendula</i>	.	.	r	12.5	0.2
	<i>Acer platanoides</i>	+	.	.	.	12.5	0.2
	<i>Acer campestre</i>	+	.	.	12.5	0.2
a	<i>Sorbus aucuparia</i>	3	2	2	+	.	+	.	+	75.0	8.9
	<i>Acer pseudoplatanus</i>	r	.	r	.	+	2	+	2	75.0	5.1
	<i>Fagus sylvatica</i>	2	2	2	.	+	.	.	.	50.0	11.3
	<i>Corylus avellana</i>	.	.	.	+	.	2	+	2	50.0	7.6
	<i>Prunus serotina</i>	2	.	r	.	r	.	.	.	37.5	5.1
	<i>Carpinus betulus</i>	.	2	.	+	25.0	7.6
	<i>Castanea sativa</i>	.	.	.	+	12.5	0.2
	<i>Lonicera periclymenum</i>	.	r	12.5	0.2
	<i>Sambucus nigra</i>	r	.	.	.	12.5	0.2
h	<i>Polygonum hydropiper</i>	+	.	.	r	r	+	3	1	75.0	6.5
	<i>Rubus fruticosus</i>	1	.	.	.	r	+	1	1	62.5	0.6
	<i>Athyrium filix-femina</i>	2	.	.	+	.	.	3	1	50.0	13.4
	<i>Luzula sylvatica</i>	2	.	.	r	+	.	1	.	50.0	4.1
	<i>Pteridium aquilinum</i>	.	r	4	.	.	.	+	.	37.5	20.9
	<i>Juncus effusus</i>	+	.	.	.	r	+	.	.	37.5	5.1
	<i>Acer pseudoplatanus</i> (pl.)	+	.	.	+	+	.	.	.	37.5	0.2
	<i>Scrophularia nodosa</i>	+	.	.	.	r	+	.	.	37.5	0.2
	<i>Carex sylvatica</i>	2	.	.	.	1	.	.	.	25.0	8.0
	<i>Dryopteris dilatata</i>	2	+	.	.	25.0	7.6
	<i>Teucrium scorodonia</i>	2	+	25.0	7.6
	<i>Epilobium angustifolium</i>	+	+	25.0	0.2
	<i>Poa annua</i>	+	.	+	.	25.0	0.2
	<i>Prunus serotina</i> (pl.)	r	.	.	r	25.0	0.2
	<i>Viola</i> sp.	+	.	.	.	r	.	.	.	25.0	0.2
	<i>Blechnum spicant</i>	1	.	12.5	1.0
	<i>Ajuga reptans</i>	+	12.5	0.2
	<i>Betula pendula</i> (pl.)	r	12.5	0.2
	<i>Carpinus betulus</i> (pl.)	r	12.5	0.2
	<i>Circaea lutetiana</i>	+	.	.	.	12.5	0.2
	<i>Convallaria majalis</i>	.	+	12.5	0.2
	<i>Crataegus monogyna</i> (pl.)	.	.	.	r	12.5	0.2
	<i>Fagus sylvatica</i> (pl.)	.	.	.	r	12.5	0.2
	<i>Geum urbanum</i>	r	.	.	.	12.5	0.2
	<i>Impatiens parviflora</i>	.	.	.	r	12.5	0.2
	<i>Juncus tenuis</i>	+	.	.	.	12.5	0.2
	<i>Lonicera periclymenum</i>	r	12.5	0.2
	<i>Moerhingia trinervia</i>	+	12.5	0.2
	<i>Sambucus nigra</i> (pl.)	.	.	.	+	12.5	0.2
	<i>Sorbus aucuparia</i> (pl.)	.	.	.	r	12.5	0.2
	<i>Urtica dioica</i>	+	.	12.5	0.2

^aA, tree layer; a, shrub layer; h, herb layer; r, 1 or 2 individuals; +, few individuals (< 20) with cover < 5%; 1, many individuals (20–100) with cover < 5%; 2, 5–25% cover; 3, 25–50% cover; 4, 50–75% cover; 5, 75–100% cover.

Nomenclature and species life forms are given by Lambinon and others (1998). The highly variable and taxonomically disputed *Rubus fruticosus* was considered a single species. Socioecological groups are determined according to Stieperaere and Franssen (1982). As defined by these authors, different units recognized in this study were as follows.

- 1 Group 1: pioneers from disturbed, artificial, anthropized habitats—road verges, dry wastelands, fields.
- 2 Group 2: pioneers from disturbed seminatural habitats, on open humid soils.
- 3 Group 5: plants from mesotrophic to eutrophic humid to damp grasslands.
- 4 Group 7: plants from heathlands, peat bogs, and alkaline marshlands.
- 5 Group 8: plants from clear-felled areas.
- 6 Group 9: forest plants.

Vegetation recovery was also examined with special reference to ancient-forest plant species, which, for our study area, are given by Honnay and others (1998).

Results

Floristic Composition

Thirty-one vascular plant species were encountered in our permanent plots (Figure 1). The most common species were *Luzula sylvatica* (frequency, 40%) and seedlings of the tree *Acer pseudoplatanus* (60%).

Ordination

The relevé ordination (Figure 2) of the first two axes of the DCA displays a clear pattern. Indicator values for nitrogen (N) and soil moisture (F) have a strong positive correlation with the first axis (respectively, $r_s = 0.65$ and 0.71 ; $P < 0.0001$). The proportion of geophytes also shows a positive correlation with this axis ($r_s = 0.53$, $P < 0.001$). The proportion of plants of the phytosociological order *Quercetalia robori-petraeae* (species from acidophilous oak forests) is negatively correlated with the first axis ($r_s = -0.49$, $P < 0.001$). The second axis reveals a highly significant positive correlation with temperature (T) and proportion of therophytes (respectively, $r_s = 0.68$ and 0.54 ; $P < 0.0001$), while the proportion of plants from the phytosociological class *Quercio-Fagetea* (species from beech forests) is negatively correlated with this axis ($r_s = -0.53$, $P < 0.001$). The arrangement of the third axis is not shown and has to be found as a negative gradient of light (L) ($r_s = -0.38$, $P < 0.01$). The proportion of pioneer plants

from disturbed habitats was also correlated with that axis ($r_s = -0.37$, $P < 0.01$).

Environmental Factors

CCA indicates that the recovery of eroded hills differs according to the slope, aspect, and soil type. Species scores illustrate taxa typical on north-facing slopes in the lower-left quadrant in Figure 3; those most frequent on south-facing slopes, in the lower-right quadrant. *Luzula multiflora*, *Carex pilulifera*, *Teucrium scorodonia*, *Poa annua*, and *Deschampsia cespitosa* show a strong bias for north-facing slopes. *Circaea lutetiana*, *Allium ursinum*, and *Urtica dioica* are more frequent on south-facing slopes. The presence of the alien *Impatiens parviflora* seems to be correlated with eastern slopes. Steep slopes are not problematical for the regeneration of overstorey trees: *Carpinus betulus*, *Fraxinus excelsior*, *Fagus sylvatica*, and *Acer pseudoplatanus* are restricted to the upper part of the ordination diagram in the direction of the slope gradient. The close positioning of *Carex sylvatica* and *Polygonum hydropiper* near the loam centroid indicates that these species have a strong preference for this soil type. For *Betula pendula*, *Luzula sylvatica*, and *Anemone nemorosa*, the preference is for sandy loam.

Species Richness

Species richness ranges between one and nine species per plot. The total number of species increased progressively from 1995 till 1999, with a slight regression in 2000 (Figure 4). Within each plot, the species richness fluctuates greatly, and no overall trend could be shown by the Kruskal–Wallis test ($\chi^2 = 6.22$, $P = 0.2858$).

Plant Functional Groups

The dynamics of life forms, socioecological groups, and ecological indicator values are illustrated in Figure 5. Only the significant trends are shown. A total of four life forms were encountered. Hemicryptophytes ranked first, with 16 species, followed in turn by tree seedlings, i.e., phanerophytes (8 species), therophytes (4 species), and geophytes (3 species). During the monitoring, an upward trend has been shown for hemicryptophytes ($r_s = 0.3851$, $P = 0.0075$). The opposite trend was highlighted for therophytes, as their proportion decreased throughout the years in the permanent plots ($r_s = -0.4569$, $P = 0.0012$). No clear pattern is shown for geophytes ($r_s = 0.0453$, $P = 0.7625$) or phanerophytes ($r_s = -0.0155$, $P = 0.9177$).

Among the socioecological groups, we found a significant decline in pioneer plants of disturbed places

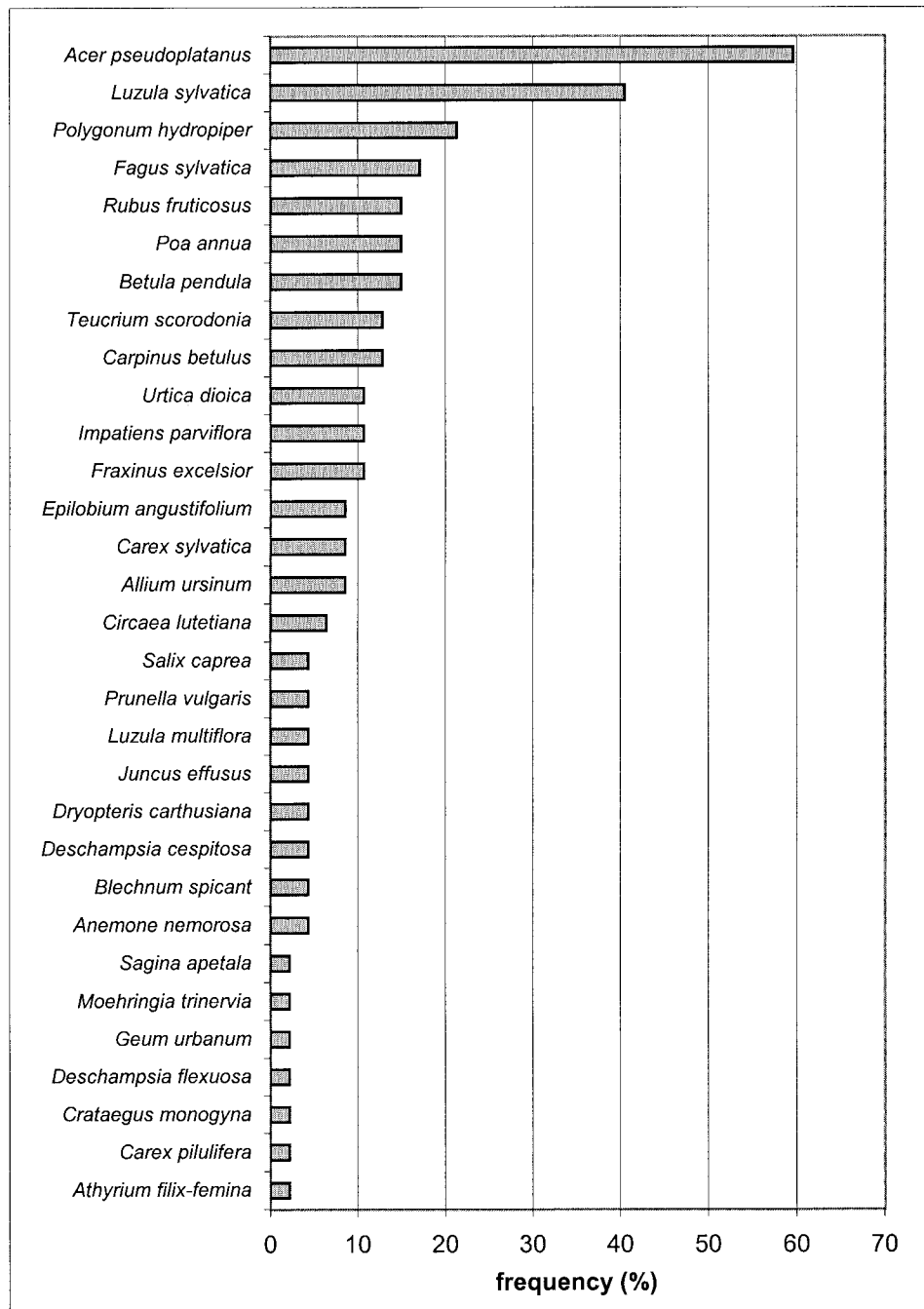


Figure 1. Frequency distribution of the species encountered on eroded slopes (all years taken together).

($r_s = -0.3170$, $P = 0.0299$): *Poa annua*, *Deschampsia cespitosa*, *Juncus effusus*, *Polygonum hydropiper*, and *Sagina apetala*. No significant correlations were found for the other groups, i.e., plants of clear-felled areas ($r_s = -0.0393$, $P = 0.7929$) and forest plants ($r_s = 0.2594$, $P = 0.0783$, for the acidophilous oak forest plants; $r_s = 0.0771$, $P = 0.6063$, for the beech forest plants).

Temporal variations of Ellenberg ecological values show an overall downward trend for nitrogen index (N)

($r_s = -0.3651$, $P = 0.0137$). A marginally significant decrease in temperature index (T) was detected throughout the years ($r_s = -0.3099$, $P = 0.0583$). Soil moisture (F) has also shown a slight downward trend, but this relationship is much less clear-cut, as it is not statistically significant at the 0.05 level ($r_s = -0.2581$, $P = 0.0870$). No significant temporal variation of light ($r_s = -0.1405$, $P = 0.3516$) or reaction ($r_s = -0.0634$, $P = 0.7132$) could be highlighted.

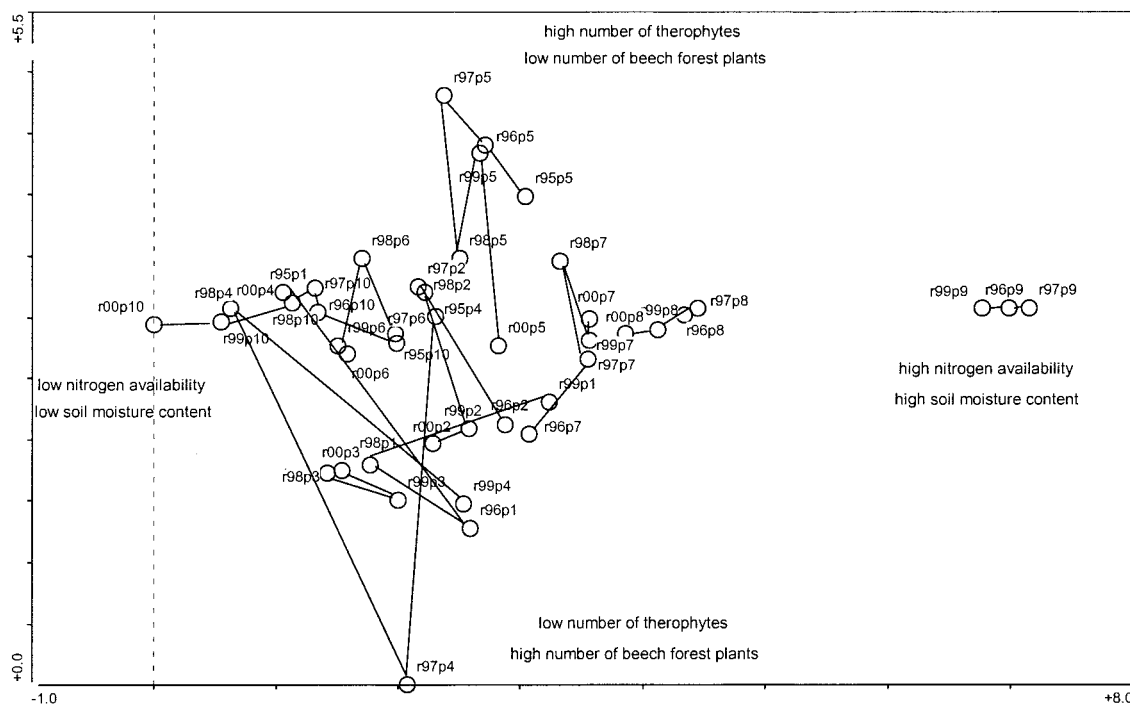


Figure 2. Shifts in plot positions from 1995 to 2000, in the Detrended Correspondence Analysis ordination space (r97p5 means plot 5 recorded in 1997). The axes (1, horizontal; 2, vertical) are scaled in standard deviation units. Along the axes, plots globally shifted to the left-bottom quadrant of the ordination diagram. As an aid for the interpretation, soil nitrogen availability, soil moisture content, and proportions of therophytes (annuals) and plants from beech forests are indicated according to the results of the Spearman rank correlation between the plot ordination scores and the characteristic indicator values in the plots.

When the first survey was performed in 1995, only two ancient forest species were recorded: *Teucrium scorodonia* and *Luzula sylvatica*. As shown in Figure 6, the total number of ancient forest species (sum for all the permanent plots) has increased continuously over the considered time scale and reached eight species in 2000: *Carex pilulifera*, *Deschampsia flexuosa*, *D. cespitosa*, *Blechnum spicant*, *Circaea lutetiana*, *Carex sylvatica*, *Teucrium scorodonia*, and *Luzula sylvatica*. Our data fit the linear model very well ($r_s = 0.9856$, $P = 0.0003$).

Recovery Strategies

The evolution of species' frequencies along the years has allowed us to highlight six recovery strategies (Table 2). Some genetically or ecologically variable species can belong to several groups, as individual plants may have different recovery strategies. Early species are species which are already present from the first year of the monitoring: *Acer pseudoplatanus*, *Impatiens parviflora*, *Luzula sylvatica*, *Poa annua*, *Polygonum hydropiper*, and *Teucrium scorodonia*. Late species are those which appeared later and successfully established. They show a more or less rapid recovery. *Epilobium angustifolium* appeared 3 years after fencing. *Blechnum spicant*, *Carex sylvatica*, and

Fraxinus excelsior appeared 4 years after closure, *Deschampsia cespitosa* and *Luzula multiflora* appeared 5 years after fencing, and *Carex pilulifera*, *Deschampsia flexuosa*, *Geum urbanum*, and *Dryopteris carthusiana* appeared 6 years after closure. Expanding species are species whose frequency shows a clear upward trend, such as *Carex sylvatica* and *Luzula sylvatica*. Disappearing species are those whose frequency shows a clear downward trend, i.e., *Polygonum hydropiper*, *Poa annua*, and *Impatiens parviflora*. We called transient the species which appeared once or twice and then disappeared, i.e., species without a clear trend of establishing. Those species are *Athyrium filix-femina*, *Crataegus monogyna*, *Juncus effusus*, *Moehringia trinervia*, *Prunella vulgaris*, *Salix caprea*, and *Sagina apetala*. Fluctuating species are well-established species whose frequency fluctuates a lot throughout the years (*Acer pseudoplatanus*, *Betula pendula*, *Carpinus betulus*, *Circaea lutetiana*, *Fagus sylvatica*, *Rubus fruticosus*, and *Urtica dioica*).

Discussion

Restoration practices such as fencing of eroded slopes in the Sonian Forest have been initiated without

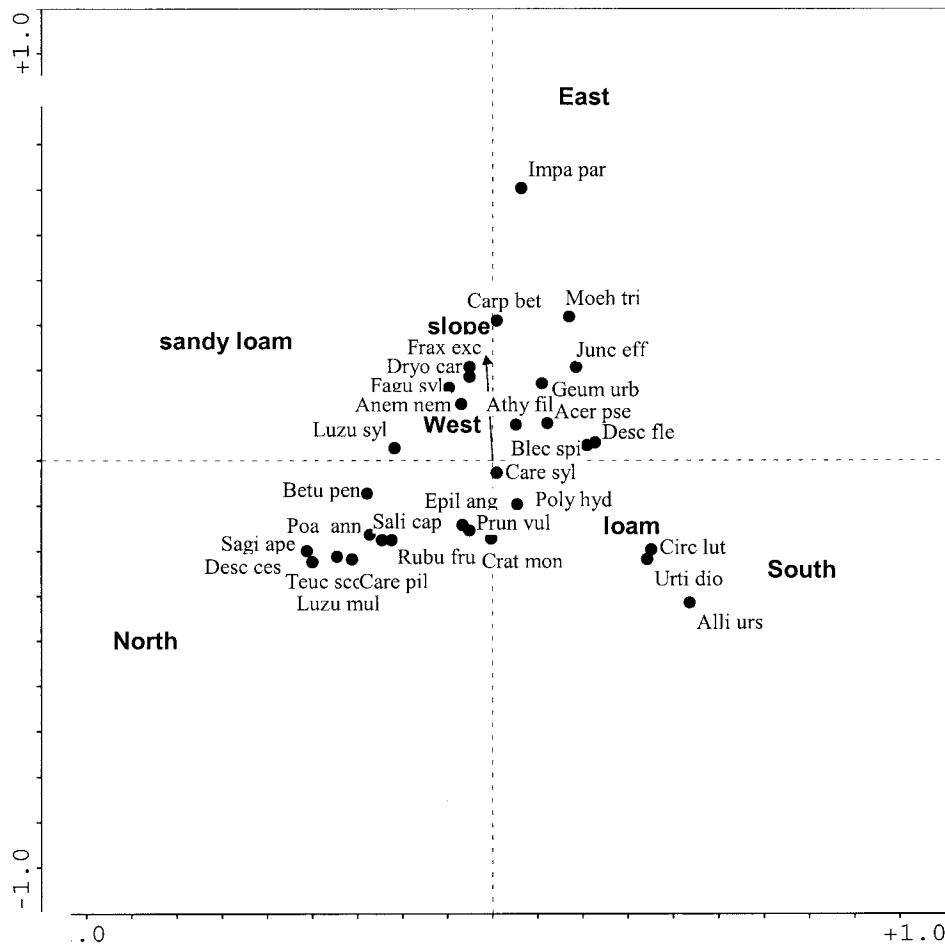


Figure 3. Species ordination diagram based on Canonical Correspondence Analysis with respect to one quantitative variable (slope) represented by the arrow and two nominal variables (soil type and aspect) shown by their centroid. The axes (1, horizontal; 2, vertical) are scaled in standard deviation units. Gradients of axes 1 and 2 are significant ($P = 0.001$) according to a Monte Carlo permutation test. Species abbreviations are based on the first four letters of the genus and the first three letters of the species: *Acer pseudoplatanus*, *Allium ursinum*, *Anemone nemorosa*, *Athyrium filix-femina*, *Betula pendula*, *Blechnum spicant*, *Carex pilulifera*, *Carex sylvatica*, *Carpinus betulus*, *Circaea lutetiana*, *Crataegus monogyna*, *Deschampsia cespitosa*, *Deschampsia flexuosa*, *Dryopteris carthusiana*, *Epilobium angustifolium*, *Fagus sylvatica*, *Fraxinus excelsior*, *Geum urbanum*, *Impatiens parviflora*, *Juncus effusus*, *Luzula multiflora*, *Luzula sylvatica*, *Moehringia trinervia*, *Poa annua*, *Polygonum hydropiper*, *Prunella vulgaris*, *Rubus fruticosus*, *Sagina apetala*, *Salix caprea*, *Teucrium scorodonia*, and *Urtica dioica*.

much information about how this measure would affect the development of the degraded ecosystems. Nevertheless, this decision made by the managers is understandable, as the major aim was to stop erosion as a matter of urgency and to prevent further destruction of vegetation and soil. The purpose of this study was to follow the plant recolonization of surfaces barren of vegetative cover following long-term use. Three principal findings emerged from this study. First, a sudden removing of trampling intensity by fencing enhances, over a relatively short term, vegetation recovery on eroded areas. Second, the recovery time varies with the species. Third, species recovery differs according to the

slope, aspect, and soil type. These findings are discussed below and are followed by considerations about management implications.

Floristic Composition

Eleven species from our study were not mentioned in the survey of 1992–1993: *Allium ursinum*, *Anemone nemorosa*, *Carex pilulifera*, *Deschampsia cespitosa*, *D. flexuosa*, *Dryopteris carthusiana*, *Fraxinus excelsior*, *Luzula multiflora*, *Prunella vulgaris*, *Sagina apetala*, and *Salix caprea*. These species may have come either from activation of the seed bank, from dispersal into the quadrats, or

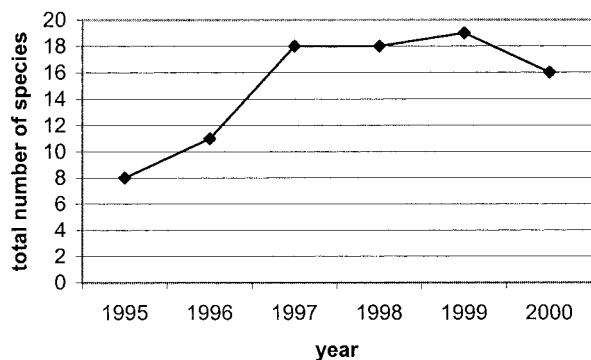


Figure 4. Change in the total number of species along the 6-year monitoring.

from surviving underground organs. It is difficult to determine whether these species have merely survived (from populations that could have been present before recreation degraded the site) or have newly colonized these sites. The seed bank of eroded soils is small as a result of the topsoil having been totally removed during the erosion process (Magnússon 1997). Therefore, we may suppose that the seed bank effect on the vegetation recovery of our eroded sites is limited. Establishment from seed dispersal is also uncertain, as forest plant species are known for their poor mobility and colonization ability, particularly if the sites are distant from existing populations (Grime and others 1988; Bossuyt and others 1999; Ehrlén and Eriksson 2000). Because these two modes of establishment are less probable, we speculate that species recovery was due mainly to the presence of residual propagative structures in the soil (tubers, corms, bulb, rhizome, etc.).

Eleven species that were present in the herb layer in 1992–1993 are completely lacking in our permanent plots and therefore did not recover in 6 years: *Ajuga reptans*, *Convallaria majalis*, *Dryopteris dilatata*, *Juncus tenuis*, *Lonicera periclymenum*, *Prunus serotina*, *Pteridium aquilinum*, *Sambucus nigra*, *Scrophularia nodosa*, *Sorbus aucuparia*, and *Viola* sp. Those species seem not to be able—at least on the considered time scale—to recover on eroded slopes after having been destroyed by recreation activities. For some of them, these findings differ from what might have been expected, as they are well known for their high colonization capacity, such as *Prunus serotina* (Van den Meersschaut and Lust 1997), for their rapid recovery from trampling, such as *Pteridium aquilinum* (Burden and Randerson 1972), or for their ability to grow on compacted soils, such as *Juncus tenuis*.

Slope, Aspect, and Soil Type

For some species, we found a strong affinity for either north- or south-facing slopes. Compared to

north-facing slopes, the south-facing forest floor dries more easily in summer, which renders seedlings susceptible to drought injury or death, while higher and prolonged moisture levels associated with north- to northeastern-facing slopes tend to reduce the rate of desiccation of plants (Kuss 1986).

The behaviors of *Luzula multiflora*, *Carex pilulifera*, *Deschampsia cespitosa* (which occurred more abundantly on north-facing slopes), and *Allium ursinum* (more abundant on south-facing slopes) observed in this study are similar to those found by Grime and others (1988), while for *Teucrium scorodonia* and *Circaea lutetiana*, another pattern emerged when comparing our results with those of Grime and others (1988). The correlation of *Impatiens parviflora* with eastern slopes suggests that this species may be sensitive to the cold western winds which dominate in the study area.

For four tree seedlings, a particular association with sloping grounds has been detected. This is easily understandable for *Carpinus betulus* and *Fagus sylvatica*, as they are the main components of sloping forests. The linking of *Fraxinus excelsior* and *Acer pseudoplatanus* to sloping sites contrasts with the findings of Grime and others (1988) showing that juveniles are distributed along a wide slope range.

A preference for a particular soil texture (loam or sandy loam) also has been highlighted for some species. Loam as a textural class has a different microporosity and retains water and nutrients much better than sandy loam. This result suggests that *Carex sylvatica* and *Polygonum hydropiper* (more abundant on loamy soils) need more water or more nutrients to grow than *Betula pendula*, *Luzula sylvatica*, and *Anemone nemorosa* (related to sandy loams).

Species and Functional Ecological Group Dynamics

This study has shown that plant recovery on heavily eroded forest soils is possible but rather slow. As the total number of species has increased continuously from 1995 until 1999, with a slight decrease in 2000, no significant changes could be shown for the time scale of observation when considering the temporal variation of the species number within sampling plots. This means that the establishment of some species is accompanied by the disappearance of other species (turnover), corresponding to the well-known succession process, which is nothing more than immigration and extinction of species, coupled with changes in the relative abundance of different species (Clements 1916; MacArthur and Connell 1966; West and others 1981; Oliver and Larson 1996; Crawley 1997). This pattern could be due to the fact that eroded sites have an environment of relatively high stress and disturbance

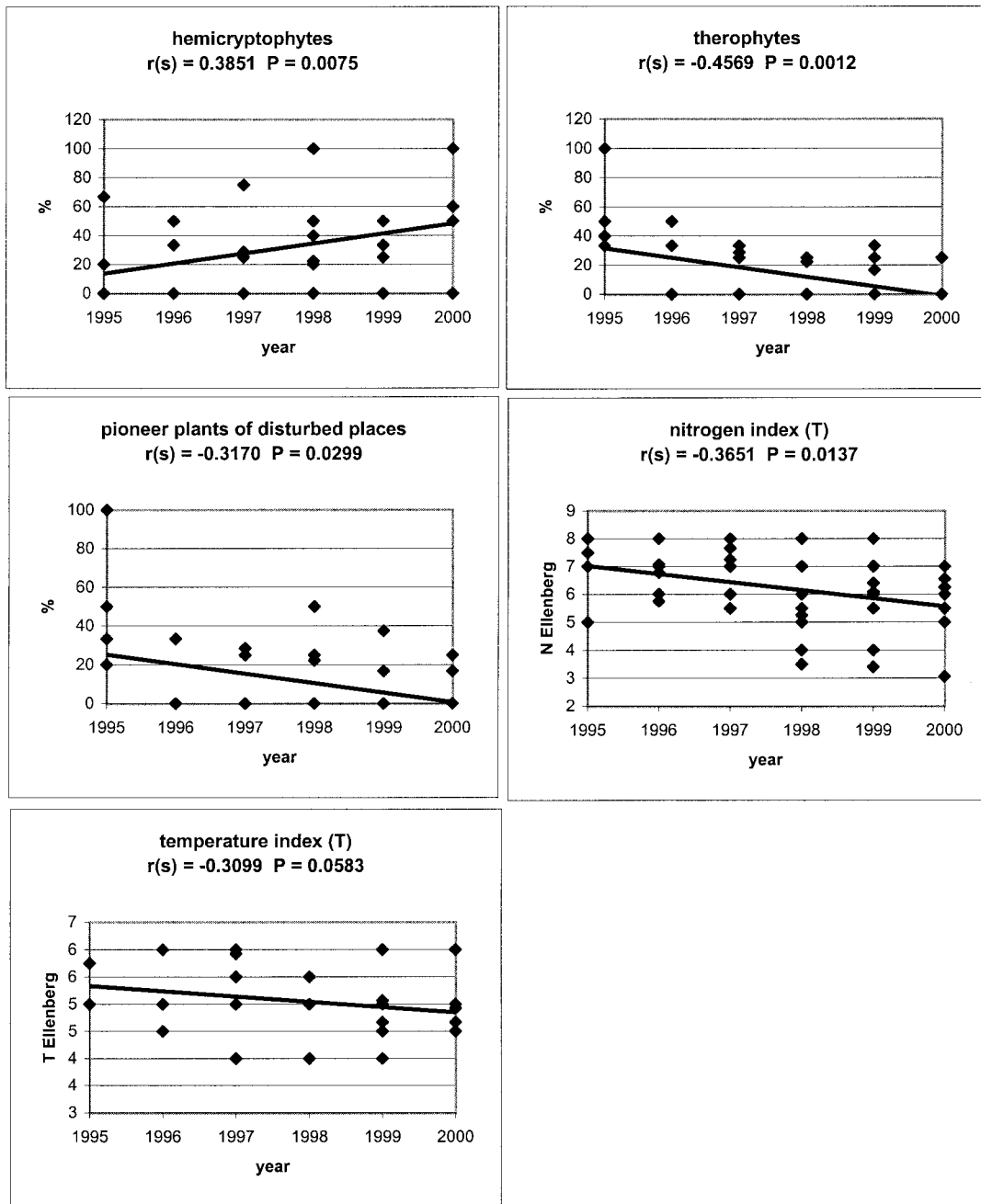


Figure 5. Change in the proportion of the different life forms, socioecological groups, and ecological indexes over the years.

(Magnússon 1997). Soil compaction, for example, may be a major problem, as it creates adverse conditions for plant survival and regeneration by impairing vital root-associated processes such as nutrient uptake and translocation (Kuss 1986). Several studies have shown that compacted soils can restrict root elongation and impede the germination of buried seeds, because many plant roots and seed hypocotyls are unable to penetrate

the compacted soils (Harpers and others 1965; Kirkegaard and others 1992).

Erosion of only the surface few centimeters may also be accompanied by significant reductions in plant growth, because the productive potential of a site is vested in a relatively thin surface layer of soil. Klock (1982) has demonstrated the importance of upper layers of soil for site fertility and growth of tree seedlings.

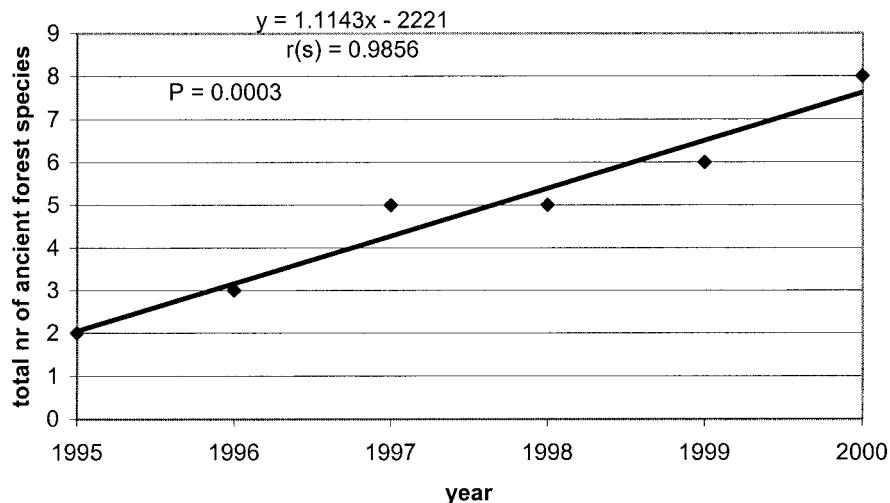


Figure 6. Change in the total number of ancient-forest species along the years.

The studied areas are under a seed-producing overstory of hardwoods. This initiated recovery, but the seedling mortality rate may also be high due to external factors such as drought and rabbit grazing pressure, which may strongly influence the successional process as already highlighted by Grime (2001).

Among life forms, we found the hemicryptophytes to be the most frequent, followed by phanerophytes (juveniles in the herb layer), therophytes, and geophytes. The importance of the hemicryptophytes is probably due to the presence of graminoids among them, which, according to Yorks and others (1997), have the highest mean resilience. The proportion of hemicryptophytes increased in our sample plots along the 6 years of succession, while that of therophytes decreased. These results suggest that annuals are more resilient just after disturbances than perennials, which argues with the study by Yorks and others (1997).

Pioneer plants of disturbed places showed a decline during the study. This result suggests that the disturbance level of the soil progressively decreases. Hence, fencing seems to protect the area from disturbance and to enhance soil restoration. Observations on nonfenced eroded slopes in the same area confirmed this pattern, as *Poa annua* and *Deschampsia cespitosa* were the most frequent species on slopes which are not yet closed to public use.

The temporal variation of Ellenberg ecological values found in this study may suggest a slight evolution of particular ecological parameters. An overall downward trend was detected for nitrogen (N). Nitrogen and phosphorus are the most limiting nutrients on eroded soils (Bradshaw 1983). Since bacteria which convert NH_4^+ to NO_3^- are obligate aerobes, changes in soil structure and aeration such as occur under heavy soil

compaction will adversely affect the availability of nitrate to plants (Kuss 1986). According to this, it might be expected that plants which need a lot of nitrate should normally decline during the compaction process and increase during the restoration process. Our results contrast with this assumption, as a decrease in indicators of soil fertility remained detectable 6 years after closure to human pressure. These findings suggest that perhaps soil changes due to trampling have an effect on vegetation in the longer term and that this effect is still present after banning this damaging action, which is consistent with the results of Kuss and Hall (1991), showing, for a forest in New Hampshire, that trampling effects remain detectable 5 years after removal from human disturbance.

The linear increase in the number of ancient-forest plant species confirms that fencing has a positive effect on the restoration of the forest vegetation. Those species are highly desirable because they are well-known indicators of the ecological value of forests (Honnay and others 1998) and are extinction-prone (Terborgh 1974). As they are considered to have a low colonization capacity and are normally part of ecosystems withstanding a very low degree of recreational use (Honnay and others 1998), their recovery and increasing cover on eroded sites are very encouraging for the restoration process in these areas.

Recovery Strategies

Our observations have led us to recognize six categories of plants reflecting distinctive life history patterns and behaviors in the investigated communities. This classification scheme differs in several respects from the one suggested by Grime and others (1988), who distinguished five regenerative strategies, i.e., veg-

Table 2. Species' recovery strategy as identified on the basis of their yearly frequency^a

Species	1995	1996	1997	1998	1999	2000
Early						
<i>Acer pseudoplatanus</i>	50.0	62.5	62.5	44.4	70.0	62.5
<i>Polygonum hydropiper</i>	50.0	25.0	37.5	22.2	0.0	12.5
<i>Poa annua</i>	50.0	12.5	12.5	11.1	20.0	0.0
<i>Luzula sylvatica</i>	25.0	25.0	37.5	44.4	50.0	50.0
<i>Impatiens parviflora</i>	25.0	12.5	12.5	11.1	10.0	0.0
<i>Teucrium scorodonia</i>	25.0	12.5	12.5	11.1	10.0	12.5
Late						
<i>Carex pilulifera</i>	0.0	0.0	0.0	0.0	0.0	12.5
<i>Deschampsia flexuosa</i>	0.0	0.0	0.0	0.0	0.0	12.5
<i>Geum urbanum</i>	0.0	0.0	0.0	0.0	0.0	12.5
<i>Dryopteris carthusiana</i>	0.0	0.0	0.0	0.0	0.0	25.0
<i>Deschampsia cespitosa</i>	0.0	0.0	0.0	0.0	10.0	12.5
<i>Luzula multiflora</i>	0.0	0.0	0.0	0.0	10.0	12.5
<i>Blechnum spicant</i>	0.0	0.0	0.0	11.1	0.0	12.5
<i>Carex sylvatica</i>	0.0	0.0	0.0	11.0	10.0	25.0
<i>Fraxinus excelsior</i>	0.0	0.0	0.0	22.2	10.0	25.0
<i>Epilobium angustifolium</i>	0.0	0.0	12.5	11.1	10.0	12.5
Expanding						
<i>Carex sylvatica</i>	0.0	0.0	0.0	11.1	10.0	25.0
<i>Luzula sylvatica</i>	25.0	25.0	37.5	44.4	50.0	50.0
Disappearing						
<i>Polygonum hydropiper</i>	50.0	25.0	37.5	22.2	0.0	12.5
<i>Poa annua</i>	50.0	12.5	12.5	11.1	20.0	0.0
<i>Impatiens parviflora</i>	25.0	12.5	12.5	11.1	10.0	0.0
Transient						
<i>Moehringia trinervia</i>	25.0	0.0	0.0	0.0	0.0	0.0
<i>Athyrium filix-femina</i>	0.0	0.0	12.5	0.0	0.0	0.0
<i>Prunella vulgaris</i>	0.0	0.0	12.5	11.1	0.0	0.0
<i>Salix caprea</i>	0.0	0.0	12.5	11.1	0.0	0.0
<i>Juncus effusus</i>	0.0	0.0	0.0	22.2	0.0	0.0
<i>Crataegus monogyna</i>	0.0	0.0	0.0	11.1	0.0	0.0
<i>Sagina apetala</i>	0.0	0.0	0.0	0.0	10.0	0.0
Fluctuating						
<i>Acer pseudoplatanus</i>	50.0	62.5	62.5	44.4	70.0	62.5
<i>Carpinus betulus</i>	25.0	0.0	25.0	22.2	10.0	0.0
<i>Fagus sylvatica</i>	0.0	50.0	12.5	0.0	30.0	0.0
<i>Urtica dioica</i>	0.0	25.0	12.5	0.0	20.0	0.0
<i>Betula pendula</i>	0.0	12.5	25.0	33.3	10.0	0.0
<i>Rubus fruticosus</i>	0.0	12.5	12.5	22.2	20.0	12.5
<i>Circaea lutetiana</i>	0.0	0.0	12.5	0.0	10.0	12.5

^aSome genetically or ecologically variable species can belong to several groups, as individual plants may have different recovery strategies.

etative expansion, seasonal regeneration, persistent seed or spore bank, numerous widely dispersed seeds or spores, and persistent juveniles. This difference is explained, however, by the fact that the aim of Grime and others (1988) was to recognize mechanisms of regeneration in functional terms by considering the size, number, dispersal, dormancy, and degree of independence of the offspring and the conditions affecting its establishment. In the present study, we identified recovery strategies in temporal terms by examining the species turnover during the monitoring. For this reason, in each of our categories, we may find species with different regenerative strategies according to these authors. Gross (1990) proposed an-

other classification scheme with regenerators, fugitives, and persistors, which is, in a certain way, closer to our system but provides less information, as he defined only three categories. Our classification argues that there are six recovery strategies in our study area, because we found six major types of behaviors according to the temporal trends observed in the species frequency. In some cases, we ascribed two categories to one species, because genetically and ecologically variable species may show a range of positions. Such cases have also been highlighted by Grime and others (1988), who found some difficulties in distinguishing different regenerative strategies and, thus, assigned two strategies to most of the species.

Early species were mostly short-lived, fast-growing colonists. Groups of late species and expanding species were dominated by longer-lived perennial species, some of which have the ability to reproduce vegetatively (clonal growth). This shift in dominance from annuals to short-lived and, finally, to long-lived perennials is a well-known and commonly described mechanism of succession. The persistence of some species in succession may be due to their competitive ability, their ability to inhibit the growth of other species, their longevity (Connell and Slatyer 1977), or simply the long time. But under severe conditions such as those occurring at our experimental sites, abiotic factors such as the structure of the soil, the availability of specific nutrients, and mycorrhizal associations may also be of overriding importance in determining the time, course, and pattern of succession and recovery. For example, the capability to become established in highly compacted soils may be one of the causes for the variation of the recovery time with the species (Kuss and Hall 1991). Vegetation recovery may also be altered by the reduction and simplification of the mycorrhizal community on eroded soils (Miller 1979) and the recovery rate depends in part on the rate of reinvasion by mycorrhizal fungi (Reeves and others 1979).

Management Implications

Of special interest here is the relationship that might be developed between experimental ecology in natural successional communities and ecologically oriented restoration projects. Knowledge of species dynamics may help in choosing the adequate management and restoration experiments. Our results partly support Cole's (1995b) suggestion that deciduous forest understorey plants have a high resilience when the recreational activity is not continuous. In our study, this was true for a large number of species, and even for ancient-forest species, which are known to have a low colonization capacity. This means that, despite long-term concentrated use, our denuded areas did not lose their ability to buffer trampling and so they recovered, but the recovery was slow. However, when examining the species' recovery strategy, we found only a few number of well-established species, many of them being transient, fluctuating, or disappearing. We also regularly observed tree seedling mortality after each summer. As the soil biology and structure change, a certain percentage of seedlings is unable to form roots and gather resources quickly enough to become established before the summer drought arrives. A vicious cycle may ensue in which loss of soil integrity inhibits seedling establishment and the lack of regeneration leads to further loss of soil integrity (Perry and others 1989).

The evidence suggests that it is the water relations of the seed and seedling which are important. This interpretation implies that the seedling germination on a raw substrate is very much exposed to the vicissitudes of weather conditions. There will be little stress if conditions remain permanently wet, but fluctuating wetness can cause great difficulties. Organic matter is particularly important because its own available water capacity can be three or four times that of a mineral fraction (Bradshaw 1997). The aforementioned reasons suggest that projecting full recovery of the ground vegetation of such highly eroded areas would be speculative. Because of the slow species recovery rate in trampled areas like those studied in the Sonian Forest, a "rest/rotation" management option is impractical for this vegetation type. We speculate that if these areas were reopened for public use, only a few months of trampling would revert the flora and soil characteristics to levels found in 1994. These areas should permanently be preserved from recreational use, which is not really a problem in the study area, because the manager has left some other nonfenced trampled areas outside the nature reserves, which can still be used for recreation. We advise visitors to use exclusively those existing places rather than create new barren areas in pristine sites. In this way, the total area of severely impacted soils can be kept from increasing. For hastening the recovery rate of our fenced areas in future years, probably the most important aspect is a rapid stabilization of the soil ecosystem, including nutrients, physical structure, and food webs (Magnússon 1997; Perry and Amaranthus 1997). Surface stabilization can be accomplished by laying dead branches horizontally to the soil, perpendicularly to the slope. This dead wood can influence system recovery in several ways: (1) it reduces erosion by acting as a physical barrier to soil movement; (2) it is a center of biological activity, including not only decay organisms, but also mycorrhizal hyphae, nitrogen-fixing bacteria, amphibians, and small mammals; (3) it may provide cover for small mammals that disseminate mycorrhizal spores from intact area into the disturbed site; and (4) it mitigates environmental extremes within disturbed areas by shading and preventing excessive heat loss at night. Managers of the Sonian Forest recently used such a restoration practice to improve the vegetation recovery obtained by fencing alone. In the near future, a field study will concentrate upon this technique in order to evaluate its effectiveness at restoration.

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