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# Soil acidification and vegetation changes in deciduous forest in southern Sweden

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**Summary.** Thirtyfour deciduous forest sites in southern Sweden, originally studied in 1949–1970, were resampled in 1984/85. The average pH change in the humus layer was −0.78 and −0.23 in soils originally studied 30–35 and 15–20 years ago, respectively. Cover changes in the field layer were measured and related to pH changes. The number of species had increased in spite of pH decreases, reaching a maximum at pH 4.0–5.0, while the total cover of the field layer was unchanged.

Two groups of species showed no correlation with pH decreases in the humus layer. A large number of species had increased in cover on a majority of sites over the entire species specific pH interval, including nitrophilic species (*Rubus idaeus, Chamaenerium angustifolium, Aegopodium podagraria, Stellaria nemorum*). A few species had decreased in cover on a majority of sites (*Polygonatum multiflorum, Pulmonaria officinalis, Dentaria bulbifera*). Some species showed a covariation with pH changes, decreasing in cover in sites in the acidic part of the pH interval (*Mercurialis perennis, Lamium galeobdolon, Galium odoratum, Oxalis acetosella, Luzula pilosa*). Without excluding other factors, this paper suggests that the increased nitrogen deposition and the increased acidity in the humus layer might cause some of the cover changes in the presented species.

**Key words:** Soil pH – Acidification history – Nitrogen deposition – Herb vegetation changes

Considerable attention has been paid to effects of acid deposition on trees, much less to herbs. Acidification of soils, either occurring naturally or as an effect of deposition, might influence the occurrence of some species in a negative or positive way. The interest of this study, relating long-term acidification of the humus layer of forest soils to changes in the floristic composition of the field layer, is focused on pH changes in soils. However, other changes are known to occur in the field layer during the development of a forest, even if the tree layer remains constant. They can be ascribed to either tree population demography and regeneration strategy of the field layer plants themselves or to changes in environmental conditions, e.g. shade, soil etc.

The pH of the humus layer and mineral soil studied to a depth of 1 m has decreased in many deciduous forests in South Sweden during the last 15–35 years, especially in sites studied 30–35 years ago (Falkengren-Grerup 1986). It is concluded that the pH decreases are of such magnitude that acid deposition must be a main contributor. The present study relates changes in the field layer to increased soil acidity in the above mentioned sites completed with 12 additional sites.

Soil acidification, measured as an increased hydrogen ion concentration, is associated with other characteristics, e.g. loss of base cations, reduction of cation-exchange capacity, mobilization of aluminium ions, mineral degradation, and impacts on the soil biological activity (Overrein et al. 1980, pp 116). Species might be sensitive to the increased acidity per se, or to poorer nutrient conditions, toxicity of heavy metals or aluminium, podsolization leading to an increased mor layer. Grasses are often favoured in disturbed soils, while species diversity is thought to decrease (Huttunen 1976). Compared to 1935, the number of species 50 years later has decreased markedly in West German forests in *Carpinus-Quercus* and in *Melica-Fagus* forests, while only small changes have occurred in species rich *Fagus* forests and in *Fagus* forests on chalk (Jahn unpublished work).

The wet deposition during the last 15 years in six stations in southern Sweden has been about the same for nitrogen as for sulphur, 5–15 kg $ha^{-1}$ $year^{-1}$. Long-term measurements of deposition are few, but the increase in nitrogen deposition in southern Sweden can be illustrated by one station (Skurup, Scania), having a nitrogen wet deposition of 6 kg $ha^{-1}$ $year^{-1}$ in the middle of the 50ies and 10 kg $ha^{-1}$ $year^{-1}$ in the middle of the 70ies, when the station was closed. The same station showed no changes in sulphur, while pH had decreased somewhat. Mean yearly pH has been 4.2–4.4 during the last 15 years, with monthly pH often lower than 4.0 (European atmospheric chemical network, unpublished work).

The effect of increased nitrogen deposition on the vegetation might be of great importance, increasing nitrophilic and decreasing nitrogen fixing plant species. Nitrophilic species are often of a high and dense growth, reducing competitive power of small and slow-growing species (Fiskesjö and Ingelög 1985). The following three studies of vegetation changes in forests are made in West Germany in soils, which are influenced by immissions and fertilization, however, without measuring changes in soil characteristics. An increased number of acidophilic species according to Ellenberg's index (1979) is found in two studies, analyzing a time period of 7 and 50 years respectively (Wittig et al. 1985; Jahn unpublished work). According to Ellenberg

(1985), the higher nitrogen deposition have caused the decrease of threatened species.

The objectives of this paper is to compare cover changes in single vascular plant species of the field layer with changes in pH of the humus layer. By correlating species cover to the particular ground characteristic, that has been possible to reanalyze, other influencing characteristics are not denied. If, however, pH is correlated to cover changes of a species, the ground characteristics combined with pH might be of greater importance than other factors such as vegetation changes due to succession or changed light conditions.

The present study has some characteristics that enables the above mentioned approach:

- the number of studied sites is large
- the sites are dispersed over a 5.000 $km^2$ area in Scania, southernmost Sweden, equaling the effects of locally large deposition
- the sites have large variations in original pH (3.9–6.9) as well as in pH changes (from +0.85 to −1.65)
- the original studies are made in different years (1949–53, 1965–70) and at different times of the year (May–November), diminishing the effects of inter-year and inter-seasonal variation
- the original studies are performed by different persons, diminishing effects of systematical error in description of vegetation and chemical analysis.

## Materials and methods

Thirtyfour geographically separated sites spread all over Scania, southernmost Sweden, were resampled in 1984 and 1985, using the same methods as in the original studies, performed from 1949 to 1970 (Table 1). All sites had mainly the same tree population as in the first study, although thinning of the stand and the appearance of new tree species had to be accepted to a certain degree. *Fagus sylvatica* was dominant in most sites, representing all vegetation types of beech forests in Sweden (Lindgren 1970). *Carpinus betulus, Tilia cordata, Quercus robur*, and single individuals of other species were also represented (Fig. 1). Descriptions of tree cover, age or other stand factors are not available for all original studies. The age of the beech forests can be estimated to at least 60 years at the first study, while the other tree species probably are somewhat younger.

In the description of vegetation squares of $1 \times 1$ $m^2$, $4 \times 4$ $m^2$, and $10 \times 10$ $m^2$ were used. Six sites were sampled with 6–10 squares of $4 \times 4$ $m^2$. These squares were ten to hundreds of meters apart, and are therefore treated as 51 separate plots, representing their own species composition. These sites might therefore have a large influence on the results, should all data be restricted to one of these. Special attention has been paid to this fact but is only relevant for one of the studied species (*Hepatica nobilis*). Including the subdivision a total of 79 plots have been analyzed.

**Table 1.** Number, source and year of original study of resampled, deciduous forest sites

| No. of sites | Source | Year | Reference |
|---|---|---|---|
| 6 | Linnermark | 1949–50 | (Linnermark 1960) |
| 6 | Andersson | 1953 | (Andersson, unpublished work) |
| 2 | Påhlsson | 1965 | (Påhlsson 1969) |
| 10 | Nihlgård | 1966–67 | (Nihlgård 1970, 1971) |
| 2 | Lindgren | 1966–67 | (Lindgren 1969) |
| 8 | Dept. Plant Ecology | 1969–70 | (Dept Plant Ecol 1969, 1970) |

If previously measured, cover of tree layer was estimated visually. The original studies use different scales to estimate cover of the field layer. The Hult-Sernander-Du Rietz scale is used in studies made by Andersson (unpublished work), Nihlgård (1970, 1971), Lindgren (1969), Påhlsson (1969), and Dept. Plant Ecology (1969, 1970). The scale is logarithmic and has five cover degrees (<1/16, 1/16–1/8, 1/8–1/4, 1/4–1/2, >1/2). Linnermark (1960) uses five cover classes of each 20%, with the lowest class divided into 1–10 and 10–20%.

Comparisons of the cover of a species in the original and the present study can be directly made when $4 \times 4$ $m^2$ squares are compared or otherwise after converting frequency and characteristic cover into mean cover. The scale used by Linnermark was converted into the four upper classes of the Hult-Sernander-Du Rietz scale by using the class middles. 1–10% was re-scaled to <1/8 in the latter scale. When species mean cover is presented, the class middle of the two lowest classes is set to 5%, thereafter to 15%, 35%, and 75%.

Soil sampling in the humus layer was made using cylinders of 5 cm in length (Lindgren 1969; Nihlgård 1971; Påhlsson 1969; Dept. Plant Ecology 1969, 1970), digging to about 5 cm depth (Andersson unpublished work), taking 4 cm wide samples from depths as given in the first study but not deeper than 10 cm (Linnermark 1960), or representing all of the F/H- or $A_1$-horizons, often extending to 10 cm depth (Nihlgård 1970).

The soil samples were sieved as originally (2.0 mm or 0.6 mm) and pH determined in distilled water of different soil:water proportions from 1:1 to 1:15 using a glass electrode. More details of methods and chemical analysis are found in Falkengren-Grerup (1986), where soil characteristics in vertical profiles and other analysis are described.

The species are named according to Lid (1974).

## Results

The pH of deciduous forest soils in southernmost Sweden decreased during the last 15–35 years. The largest pH changes are found in sites measured 30–35 years ago. Looking at the 34 sites, without subdivision into smaller plots, several of these sites (original pH 4.3–6.6) had decreased by more than 1 pH unit, making an average decrease of 0.78 (pH is measured in water extract). In the originally more acid soils from 1965–70 (pH 4.3–5.3), the average pH decrease was 0.23. Both pH decreases are significant at $P < 0.005$. Making the subdivision into smaller plots, 65 out of 79 sites show a pH decrease greater than 0.1, and 45 sites greater than 0.5 pH unit (Fig. 1).

Changes in the vegetation are analyzed with regard to original pH, pH decrease, and final pH interval. The number of species within different pH intervals shows the same pattern in the original as in the present study (Fig. 2A). The largest number of species is found at pH 4.5–5.0 in the present study and at 4.0–5.0 in the original study. The soils within these pH intervals are not identical, as

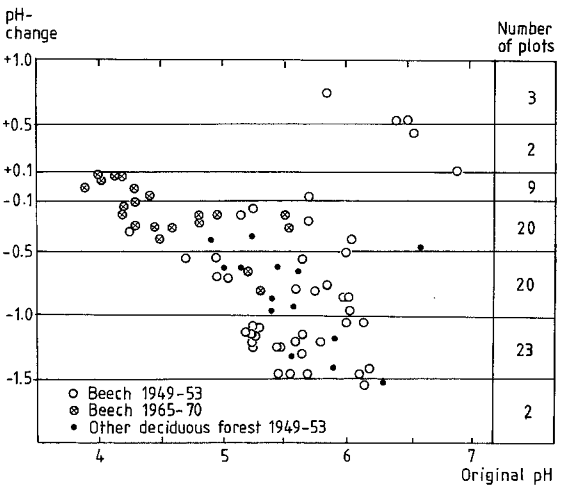


**Fig. 1.** Forest sites with original pH ($H_2O$) in the humus layer related to changes in pH measured 1984/85. Number of sites with different degree of pH changes are given in the right margin. Beech forests are illustrated with open circles (a cross, study performed in 1965–70), and other deciduous forests with a filled circle

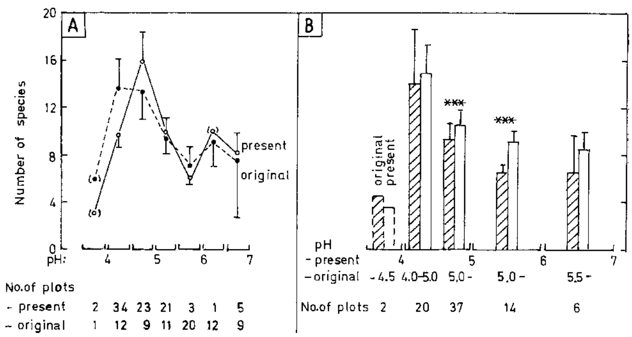


**Fig. 2A, B.** Mean number of species and standard error related to pH classes. Original and/or present number of plots within each pH class is given below the abscissa. Brackets indicate <3 sites.
**A** The mean species number is related to original and present pH. Soils within a given pH class are not identical, since many have moved into lower pH classes.
**B** The mean species number for sites which fall into the same present pH class, originating from the pH given below the abscissa. Within the present pH 4.0–5.0 plots with different degree of pH decreases are illustrated separately, as discussed in the text. Changes in number of species per plot is tested with Student's t-test, *** indicating $P<0.005$

many have pH decreases large enough to get into a lower interval.

The mean number of species in the original and the present study is shown in Fig. 2B. The hypothesis that the sites have not changed in number of species is tested. A significant increase ($P<0.005$) is only found in sites with an original pH of 5.0–6.5, nowadays having a pH of 4.0–6.0. As the number of species is largest at a pH of 4.0–5.0 (Fig. 2A), species development within sites (Fig. 2B) is illustrated such that it does not mingle with a "natural" increase in species number, due to a decrease in soil pH from above 5.0 to a lower pH, with an increase within pH intervals of about the same "natural" number of species. If all sites are calculated together, the mean increase of 1.4 species (9.7 to 11.1 species per site) is highly significant ($P<0.005$).

The total cover of the field layer is similar in the original

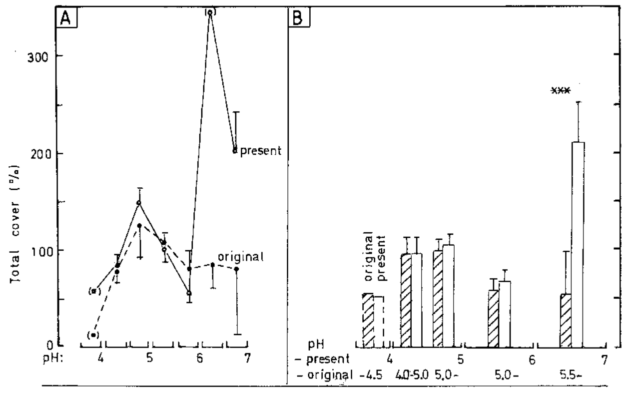


**Fig. 3A, B.** Mean total cover in the field layer and standard error related to pH classes. Original and/or present number of plots within each pH class is identical with the numbers given in figure 2. Brackets indicate <3 sites.
**A** The mean total cover is related to original and present pH. Soils within a given pH class are not identical, since many have moved into lower pH classes.
**B** The mean total cover for sites which fall into the same present pH class, originating from the pH class given below the abscissa. Within the present pH 4.0–5.0 plots with different degree of pH decreases are illustrated separately, as discussed in the text. Changes in number of species per plot is tested with Student's t-test, *** indicating $P<0.005$

and the present study (Fig. 3A) and compared to each other (Fig. 3B). The increase per site is significant ($P<0.005$) only in soils with a present pH>6.0. These soils however, have increased in pH when compared to the first study, and the total cover increase is not caused by the change in the number of species, but to the higher cover of *Aegopodium podagraria* and *Mercurialis perennis* (Table 4). The estimation of cover is rather crude, as small area frequency and class middle of cover interval were used as a substitute for mean cover. As the species number has increased, an increase in cover automatically follows by at least 5%, as this is the lowest class middle. At high covers, the class middle of 75% results in a higher estimate of the mean cover, as more species have a cover closer to 50% than to 100%.

As tree cover is only registered for 19 of the original studies, the light factor cannot be related to changes in vegetation. However, 11 out of the 19 sites are relatively unchanged, as the tree cover has not changed by more than 10%. Three plots have increased and five plots have decreased by more than 10% in tree cover. No tendency in tree cover change can thus be seen.

*Species composition*

As species occur along a pH-gradient of variable length and pH changes are of different magnitude, at least 10 sites holding the species at either or both studied times are required here to get representative data (Table 2). Many species show an increased cover (some increasing from zero) in more than 50% of the sites, while only four species decrease in cover or disappear in a majority of sites. Out of seven species considered as nitrophilic in Central Europe (Ellenberg 1979), five are found among the increasing species. This indicates that higher deposition of nitrogen might contribute to an increased cover of the species showing a general cover increase.

**Table 2.** Species which occur or have occurred in at least 10 out of 79 sites

*A* Proportion (%) and total number (n) of sites where the species in the present study show a decreased (−), unchanged (=) or increased (+) cover compared to the original study. To be considered as a change, the species must fall into different cover classes at the two observation times (Hult-Sernander-Du Rietz or 10–20% cover classes). Colonizing a site is considered as an increased cover, and disappearing from a site a decreased cover

*B* Proportion (%) of sites where the species has disappeared (Out) or has colonized (In). If the proportion of sites with disappearing and colonizing species is greater than two thirds, the species is considered fast reacting (F) ans slow reacting (S), if the proportion is less than one third

*C* Original and present pH intervals for the species. Intervals in brackets are based on less than five sites

| | *A* | | | | *B* | | | *C* | |
|---|---|---|---|---|---|---|---|---|---|
| | − | = | + | n | Out | In | F/S | Original | Present |
| *Increasing* | | | | | | | | | |
| Rubus idaeus[a] | 11 | 4 | 86 | 28 | 7 | 64 | F | 4.0–5.5 | 4.0–7.0 |
| Lactuca muralis | 8 | 15 | 77 | 13 | 8 | 77 | F | (4.0–5.5) | 4.0–5.5 |
| Dryopteris filix-mas | 13 | 13 | 73 | 15 | 13 | 73 | F | (4.0–6.5) | 4.0–5.0 |
| Chamaenerium angustifolium[a] | 27 | 0 | 73 | 11 | 27 | 73 | F | (4.0–6.0) | 4.0–5.0 |
| Carex sylvatica | 15 | 15 | 69 | 13 | 15 | 69 | F | (5.0–6.0) | 4.0–6.0 |
| Stellaria holostea | 14 | 19 | 67 | 21 | 10 | 38 | | 4.0–6.0 | 4.0–5.5 |
| Aegopodium podagraria[a] | 29 | 5 | 67 | 21 | 14 | 24 | | 4.0–7.0 | 4.0–7.0 |
| Melica uniflora | 17 | 20 | 63 | 35 | 9 | 40 | | 4.0–7.0 | 4.0–5.5 |
| Stellaria nemorum[a] | 23 | 16 | 61 | 31 | 6 | 48 | | 4.0–7.0 | 4.0–6.5 |
| *Increasing to unchanged* | | | | | | | | | |
| Deschampsia flexuosa | 7 | 36 | 57 | 14 | 7 | 43 | | 4.0–5.0 | 3.5–5.0 |
| Milium effusum | 18 | 25 | 57 | 28 | 18 | 46 | | 4.0–6.5 | 4.0–5.5 |
| Hepatica nobilis | 8 | 46 | 46 | 13 | 8 | 0 | S | 5.0–7.0 | 4.0–6.5 |
| *Increasing > unchanged* | | | | | | | | | |
| Urtica dioica[a] | 31 | 15 | 54 | 13 | 31 | 54 | F | 4.0–6.5 | 4.0–5.5 |
| Convallaria majalis | 31 | 15 | 54 | 13 | 23 | 46 | F | 4.0–6.0 | 4.0–5.5 |
| Lamium galeobdolon | 28 | 24 | 49 | 68 | 15 | 4 | [b] | 4.0–7.0 | 3.5–7.0 |
| Deschampsia caespitosa | 36 | 18 | 45 | 11 | 36 | 36 | F | 4.0–5.5 | 4.0–5.0 |
| Poa nemoralis | 22 | 38 | 41 | 32 | 22 | 34 | | 3.5–6.5 | 4.0–5.5 |
| Mercurialis perennis[a] | 36 | 21 | 42 | 33 | 33 | 3 | | 4.0–7.0 | 4.0–7.0 |
| *Decreasing > increasing* | | | | | | | | | |
| Maianthemum bifolium | 33 | 42 | 25 | 24 | 29 | 17 | | 4.0–6.5 | 3.5–5.5 |
| Athyrium filix-femina | 40 | 30 | 30 | 10 | 40 | 30 | F | 4.0–5.5 | 4.0–5.0 |
| Luzula pilosa | 44 | 28 | 28 | 18 | 44 | 18 | | 3.5–5.5 | 4.0–5.5 |
| Oxalis acetosella[a] | 49 | 19 | 32 | 63 | 11 | 21 | [b] | 3.5–7.0 | 4.0–6.5 |
| *Decreasing* | | | | | | | | | |
| Pulmonaria officinalis | 63 | 13 | 25 | 24 | 63 | 25 | F | 4.0–7.0 | 4.5–7.0 |
| Galium odoratum | 63 | 15 | 22 | 46 | 15 | 20 | | 4.0–7.0 | 4.0–7.0 |
| Dentaria bulbifera | 69 | 25 | 6 | 16 | 69 | 6 | F | 5.0–7.0 | 4.0–5.0 |
| Polygonatum multiflorum | 73 | 9 | 18 | 11 | 73 | 18 | F | 4.0–7.0 | (4.0–5.0) |

[a] Nitrophilic species (Ellenberg 1979) with indicator values ≥ 7
[b] As the species occurs in a great proportion of sites in the first study few sites remain to colonize. The definition "slow reacting" is therefore not meaningful in this case

The pH interval of the species is given by the two extremes of sites. The sites might thus be clustered in a smaller part of the interval. Most species have not changed their pH interval of occurrence between the two studies by more than 0.5 unit. Some species show changes totaling to at least 1.0 pH unit at one or both sides of the pH interval. *Rubus idaeus* has widened its interval into less acid soils, and *Hepatica nobilis* into more acid soils. Smaller intervals than originally are found for *Melica uniflora, Urtica dioica, Poa nemoralis, Maianthemum bifolium,* and *Dentaria bulbifera.*

Species which in two thirds of the plots have either appeared or disappeared are considered as fast reacting (F). Fast reacting species are generally of two kinds, either colonizing new plots and thus belonging to the increasing species, or disappearing from the original plots, and therefore a decreasing species. Four species colonize and disappear from sites in the same proportion, namely *Urtica dioica, Convallaria majalis, Deschampsia caespitosa,* and *Athyrium filix-femina.* Only one slow reacting species (S), with appearance or disappearance in less than one third of the plots, is found. *Hepatica nobilis* has not appeared in any new plot and it only disappeared from one plot.

Species, which occur in less than 10 sites, show the same pattern as the more common species (Table 3). Four out of 10 species have increased in cover in most sites, and

**Table 3.** Species which occur or have occurred in at least 4–9 out of 79 sites.

*A* Total number (n) and number of sites where the species in the present study show a decreased (−), unchanged (=) or increased (+) cover compared to the original study. To be considered as a change the species must fall into different cover classes at the two observation times (Hult-Sernander-Du Rietz or 10–20% cover classes). Colonizing a site is considered as an increased cover and disappearing from a site as a decreased cover

*B* Number of sites where the species has disappeared (Out) or has colonized (In). If the proportion of sites with disappearing and colonizing species is greater than two thirds, the species is considered fast reacting (F) and slow reacting (S), if the proportion is less than one third

*C* Original and present pH intervals for the species. Intervals in brackets are based on less than five sites

| | *A* | | | | *B* | | | *C* | |
|---|---|---|---|---|---|---|---|---|---|
| | − | = | + | n | Out | In | F/S | Original | Present |
| *Increasing* | | | | | | | | | |
| Campanula latifolia[a] | 0 | 1 | 3 | 4 | 0 | 3 | F | (5.5–7.0) | (4.5–6.5) |
| *Increasing to unchanged* | | | | | | | | | |
| Polygonatum odoratum | 1 | 1 | 3 | 5 | 1 | 3 | F | (6.0–6.5) | (4.5–5.5) |
| Veronica officinalis | 1 | 2 | 4 | 7 | 1 | 4 | F | (4.0–5.5) | 4.0–5.0 |
| *Decreasing to increasing* | | | | | | | | | |
| Carex remota | 2 | 2 | 2 | 6 | 2 | 2 | F | (4.0–5.5) | (4.0–5.0) |
| Geum urbanum[a] | 3 | 2 | 4 | 9 | 3 | 4 | | 5.0–7.0 | 4.5–6.5 |
| Polygonatum verticillatum | 2 | 0 | 2 | 4 | 2 | 2 | F | (4.0–6.0) | (4.5–5.0) |
| Dryopteris carthusiana | 4 | 2 | 2 | 8 | 4 | 0 | | 4.0–5.5 | 4.0–4.5 |
| *Decreasing* | | | | | | | | | |
| Carex pilulifera | 5 | 3 | 1 | 9 | 5 | 1 | F | 3.5–5.5 | (4.0–5.0) |
| Vicia sepium | 6 | 0 | 0 | 6 | 6 | 0 | F | 5.0–7.0 | — |

[a] Nitrophilic species with indicator values $\geq 7$ (Ellenberg 1979)

four species are increasing and decreasing in about the same proportion of sites. *Carex pilulifera* and *Vicia sepium* decrease in cover in most plots. *V. sepium* is no longer found in any of the original plots and it did not appear in any plots.

### *Floristic changes related to pH interval*

So far, we have only considered the overall changes in cover. However, species are likely to react differently when approaching their pH limits than when being in their intermediate range. If soil pH is considered important for a species, the total number of sites of different pH can be said to reflect how the species thrive in a soil of specified acidity. However, a time might elapse between changes in soil characteristics and a change in cover of a slow reacting species. The number of sites with cover changes reflect species reaction related to the specific pH interval. The reaction might be directly caused by the pH change. It might also depend on changes in floristic composition, a greater total vegetation cover, or other changes in the soil, which might or might not be correlated to pH changes. The change in vegetation is here related to the final pH interval of the site. In general, sites acidified to the same final pH interval show a similar change in cover. If not so, comments are given for each species.

### *Generally increasing species*

Species with a cover increase tendency in most plots (Table 2) show a more varied picture when their occurrence is distributed on pH intervals (Fig. 4A–D). Increasing evenly (or colonizing a plot) over the entire pH interval are *Carex sylvatica, Lactuca muralis, Dryopteris filix-mas, Chamaenerium angustifolium,* and *Deschampsia flexuosa* (Fig. 4A). As seen from the mean cover and number of sites in the original and present study (Table 4) these species are more frequent in deciduous forests today than 15 to 35 years ago. *Deschampsia flexuosa* has a high mean cover in the most acid soils in both studies, while the other species have a low cover.

Some of the species increasing in cover in a majority of sites (Table 2) show a tendency to decrease in cover in the more acid interval, namely *Rubus idaeus, Stellaria nemorum, S. holostea, Aegopodium podagraria,* and *Milium effusum* (Fig. 4B). However, a greater number of sites with increased cover is found even in the more acid interval. Except for *A. podagraria*, the number of sites is greater in the present study, as the species have colonized many new sites (Table 4). The mean cover of the species is about the same in both studies, but in the most acid soils *Stellaria nemorum* and *S. holostea* seem to decrease in cover. The increase of *A. podagraria* has mainly occurred in the original sites. The increase has been large in sites with an increased pH, today having a pH > 6.5.

### *Generally decreasing species*

Of the decreasing species (Table 2) *Polygonatum multiflorum, Dentaria bulbifera,* and *Pulmonaria officinalis* disappeared from sites within the respective pH interval (Fig. 4C). *P. officinalis* decreased proportionally more in the most acid soils, while it colonized neutral soils with a pH increase. All species have a low cover in both studies, so the decrease is due to fewer sites in the present study.

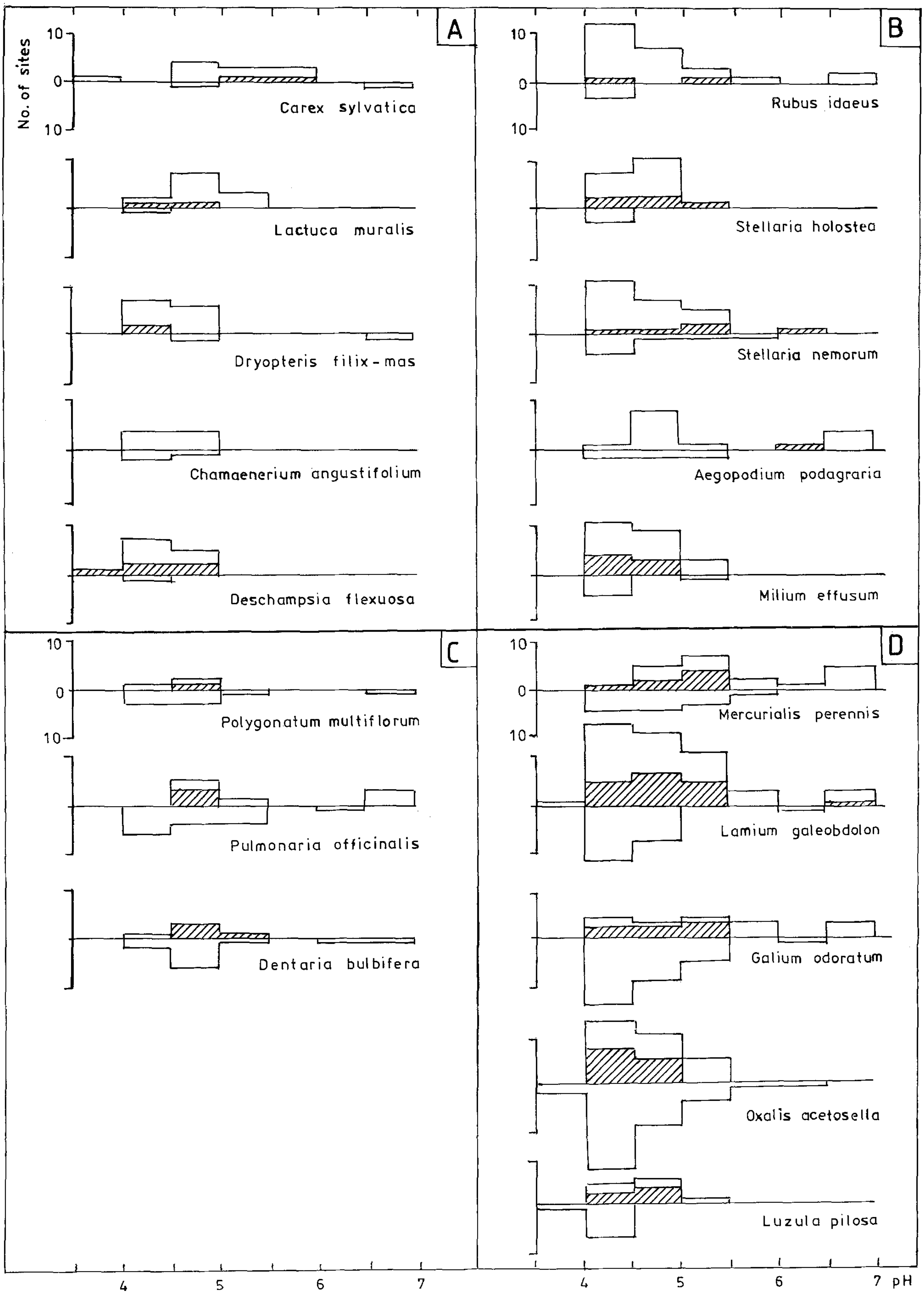
A
B
C
D
No. of sites
10
0
10
Carex sylvatica
Lactuca muralis
Dryopteris filix-mas
Chamaenerium angustifolium
Deschampsia flexuosa
Rubus idaeus
Stellaria holostea
Stellaria nemorum
Aegopodium podagraria
Milium effusum
Polygonatum multiflorum
Pulmonaria officinalis
Dentaria bulbifera
Mercurialis perennis
Lamium galeobdolon
Galium odoratum
Oxalis acetosella
Luzula pilosa
4
5
6
7
7 pH

**Table 4.** Mean cover degree within original (first line) and present (second line) pH intervals. The cover classes are: 1–2, 3, 4 and 5, which represent 1–12%, 13–25%, 25–50%, and >50% respectively. Number of sites are given in brackets within each pH class

| pH | 3.5 | 4.0 | | 5.0 | | 6.0 | 7.0 | |
|---|---|---|---|---|---|---|---|---|
| No. of sites at | | | | | | | | Total site No. |
| original study | 1 | 12 | 9 | 21 | 20 | 12 | 4 | 79 |
| present study | 2 | 34 | 23 | 11 | 3 | 1 | 5 | 79 |
| Aegopodium podagraria | | 1–2 (1) | | 1–2 (4) | 1–2 (5) | 4 (2) | 3 (4) | 16 |
| | | 1–2 (1) | 3 (9) | 1–2 (3) | | 4 (1) | 5 (4) | 18 |
| Carex sylvatica | | | | 1–2 (1) | 1–2 (3) | | | 4 |
| | 1–2 (1) | | 1–2 (4) | 1–2 (3) | 1–2 (3) | | | 11 |
| Chamaenerium angustifolium | | 1–2 (1) | 1–2 (1) | | | 1–2 (1) | | 3 |
| | | 1–2 (4) | 1–2 (4) | | | | | 8 |
| Dentaria bulbifera | | | | 1–2 (5) | 1–2 (4) | 1–2 (5) | 1–2 (1) | 15 |
| | | 1–2 (1) | 1–2 (3) | 1–2 (1) | | | | 5 |
| Deschampsia flexuosa | | 4 (7) | 1–2 (1) | 1–2 (1) | | | | 9 |
| | 5 (1) | 4 (7) | 1–2 (5) | | | | | 13 |
| Dryopteris filix-mas | | 1–2 (2) | | | 1–2 (1) | | 1–2 (1) | 4 |
| | | 1–2 (7) | 1–2 (6) | | | | | 13 |
| Galium odoratum | | 1–2 (4) | 3 (3) | 3 (14) | 3 (7) | 5 (8) | 3 (1) | 37 |
| | | 1–2 (13) | 1–2 (10) | 1–2 (9) | 1–2 (3) | 1–2 (1) | 1–2 (3) | 39 |
| Lactuca muralis | | 1–2 (1) | 1–2 (1) | 1–2 (1) | | | | 3 |
| | | 1–2 (2) | 1–2 (7) | 1–2 (3) | | | | 12 |
| Lamium galeobdolon | | 1–2 (7) | 1–2 (5) | 1–2 (21) | 1–2 (19) | 1–2 (12) | 1–2 (2) | 66 |
| | 1–2 (1) | 3 (28) | 3 (22) | 1–2 (11) | 1–2 (3) | | 3 (3) | 69 |
| Luzula pilosa | 1–2 (1) | 1–2 (7) | 1–2 (4) | 1–2 (1) | | | | 13 |
| | | 1–2 (4) | 1–2 (5) | 1–2 (1) | | | | 10 |
| Mercurialis perennis | | 1–2 (3) | 1–2 (2) | | 3 (11) | 1–2 (12) | 1–2 (4) | 32 |
| | | 1–2 (1) | 4 (5) | 4 (7) | 1–2 (3) | 5 (1) | 5 (5) | 22 |
| Milium effusum | | 1–2 (4) | 1–2 (2) | 1–2 (7) | 1–2 (2) | | | 15 |
| | | 1–2 (11) | 1–2 (9) | 3 (3) | | | | 23 |
| Oxalis acetosella | 1–2 (1) | 1–2 (12) | 3 (7) | 4 (19) | 4 (18) | 1–2 (2) | 1–2 (1) | 50 |
| | | 1–2 (29) | 3 (18) | 3 (9) | | | | 56 |
| Polygonatum multiflorum | | 1–2 (2) | 1–2 (1) | | 1–2 (2) | 1–2 (3) | 1–2 (1) | 9 |
| | | 1–2 (1) | 1–2 (2) | | | | | 3 |
| Pulmonaria officinalis | | 1–2 (1) | 1–2 (3) | 1–2 (3) | 1–2 (4) | 1–2 (6) | 1–2 (1) | 18 |
| | | | 1–2 (5) | 1–2 (1) | | | 1–2 (3) | 9 |
| Rubus idaeus | | 1–2 (6) | 1–2 (1) | 1–2 (2) | 1–2 (1) | | | 10 |
| | | 3 (13) | 1–2 (5) | 1–2 (3) | 1–2 (1) | | 1–2 (1) | 23 |
| Stellaria holostea | | 4 (3) | | 1–2 (6) | 1–2 (4) | | | 13 |
| | | 1–2 (8) | 1–2 (10) | 3 (1) | | | | 19 |
| Stellaria nemorum | | 3 (4) | 3 (3) | 1–2 (3) | 1–2 (2) | 1–2 (3) | 1–2 (1) | 16 |
| | | 1–2 (15) | 3 (8) | 1–2 (5) | | 1–2 (1) | | 29 |

**Fig. 4A–D.** Number of sites where species show a decreased, unchanged or increased cover related to the present pH in the humus layer. To be considered as a changed cover the species must fall into different cover classes at the two observation times (Hult-Sernander-Du Rietz or 10–20% cover classes). Colonizing a site is considered as an increased cover, and disappearing from a site a decreased cover. Number of sites with decreased cover is illustrated below the abscissa. Number of sites with unchanged (screened) and increased cover is illustrated above the abscissa.
**A** Increasing species. **B** Increasing species, showing a tendency of decreasing cover in the more acid pH interval. **C** Decreasing species. **D** Negatively affected species in the more acid part of the pH interval

*Species decreasing in acidified soils*

Five species seem to be negatively affected in soils in the more acidic part of the pH range (Fig. 4D). *Mercurialis perennis, Lamium galeobdolon, Galium odoratum,* and *Oxalis acetosella* have wide pH intervals, and sites with decreasing cover are found in greater proportions the more acid the soils are. *L. galeobdolon* has, however, a relative large proportion of sites with increasing cover in acid soils too. As all the sites with decreasing cover are found in acid sites, it might be considered negatively affected in acid soils. *Luzula pilosa* has a smaller pH interval and the sites with decreasing cover are mainly found in soils nowadays more acid than 4.0.

All the cover decrease of *Mercurialis perennis* in soils with a pH$<$5.5 is identical with disappearance from the sites. As *M. perennis* has only colonized one site, the number of sites is smaller. The mean cover in the present study is higher at pH$>$4.5, except for pH 5.5–6.0, where the mean cover as well as the number of sites are greater in the original study.

*Lamium galeobdolon, Galium odoratum, Oxalis acetosella,* and *Luzula pilosa* occur in about the same number of sites at both studied times. *Lamium galeobdolon* has a larger mean cover in the present study, especially in soils of pH 4.0–5.0, and these soils represent the majority of sites. *Galium odoratum* has decreased markedly in mean cover. Original cover was relatively high in soils with a pH$>$4.5. *Oxalis acetosella* has a mean cover of 1–2 (class middle 5%) in half of the sites today, as opposed to 4 (class middle 35%) in the original study. However, it has also disappeared from soils with a present pH$>$5.5. *Luzula pilosa* is always low in cover, and it has disappeared from most of the acid soils.

*Other species*

*Melica uniflora* is increasing in cover on a majority of sites, especially where large pH decreases have taken place (Table 2). The following three species have an increased to unchanged cover in most sites. *Poa nemoralis* is mainly occurring in soils with pH 4.0–5.0, where it is rather stable in cover. Sites with increased cover are somewhat more numerous than those with decreased. *Deschampsia caespitosa* is found only at a present pH of 4.0–5.0, and all decreasing sites are found within pH 4.0–4.5. *Urtica dioica* shows no covariation with pH decreases. It is concentrated to pH 4.0–5.0 where most sites with decreasing cover are found.

*Athyrium filix-femina, Convallaria majalis,* and *Maianthemum bifolium* are mainly found in sites with a pH of 4.0–5.0. No relationship is found between changes in pH and in cover. *Hepatica nobilis*, mainly found at pH 4.0–5.0, has disappeared from one site only, either increasing or unchanged in cover otherwise. The results from 9 of the 13 studied plots are, however, derived from $4 \times 4$ m$^2$ plots of one geographical area.

## Discussion

The humus layer of deciduous forests in southern Sweden has become more acid during the last 15 to 35 years. 82% of the resampled plots showed a decrease $>$0.1 in pH (measured in water extract) and only 6% showed an increase $>$0.1. The mean pH change during 15–20 years and 30–35 years was $-0.2$ and $-0.8$ pH units, respectively.

In the present study only pH has been available for reanalysis. Other characteristics related to acidification may, however, be more important for the vegetation. Data from top soil of deciduous forest in South Sweden (Tyler et al. 1986) show that macronutrients (K, Ca, Mg) are ca. 50% less in soils with 0.7 units lower pH. Extractable aluminium increases sharply at about pH$<$4.5, and cadmium and other heavy metals also have specific pH limits for solubility. A spacial acidification studied as a pH gradient caused by stemwater in beech forest show that Ca and Mg may be ten times lower at the stem base than 2.5 m away (Falkengren-Grerup unpublished work).

When soils become more acid the number of species is thought to decline (Huttunen 1976). However, the pH intervals of the studied soils must be considered, as the maximum number of species may not occur in the least acid soils. The maximum number of species in this study is found at pH 4.0–5.0, decreasing towards the more extreme pH intervals. In another study, 95 beech soils in southern Sweden show an increasing number of species in a pH (KCl) range of 2.7–4.5, increasing from 1.6 to 7.9 species (Falkengren-Grerup unpublished work). A pH (KCl) of 4.5 equals about 5.0–5.5 in pH ($H_2O$), thus the species number is highest in the same pH interval as in the present study. The great reduction in species number found by Jahn (unpublished work). in only some of the studied soils might be explained if related to actual species number of the area and changes in acidity of the soils. However, the present study rather shows an increased number of species in acidified soils. This increase is only partly explained by soils decreasing in pH into a species richer pH interval. Whether the increased nitrogen deposition in southern Sweden might contribute to the species number increase can be discussed. Studies in Germany show increases in the number of acid and in nitrogen indicating species in soils which are influenced by deposition (Ellenberg 1985; Wittig et al. 1985; Jahn unpublished work).

Many species in the present study show no relationship with decreasing pH in the humus layer. Cover changes for such species are independent of soil acidity and the degree of pH decrease within the species specific pH interval. Among the species, which have increased in cover in most sites, are those having high demands on nitrogen according to Ellenberg (1979). *Chamaenerium angustifolium, Rubus idaeus, Stellaria nemorum,* and *Aegopodium podagraria* have a mean nitrogen index of 7.75 (9 being maximum value for all indices), relatively high demands on light (6.0), and intermediate demands on soil reaction (5.0). This is in accordance with a study, comparing oak forests of different acid and nitrogen deposition in souther Sweden. The nitrophilic species are more frequent where the nitrogen deposition is larger (Rühling and Tyler 1986).

Other increasing species are *Carex sylvatica, Lactuca muralis, Dryopteris filix-mas, Deschampsia flexuosa, Stellaria holostea,* and *Milium effusum.* They all show cover increase in most sites within their respective pH interval. Ellenberg's index is, as a mean for all species, intermediate for light, soil reaction and nitrogen (4.0, 5.0, 5.0).

An increase in cover is not necessarily a sign of good performance. By definition, cover is only an approximation of biomass. Unless the individuals are fertile and produce easily dispersable seeds, the species may have a reduced long-term survival possibility. *Hepatica nobilis* could be such an example. It seems unaffected in this study, as it has disappeared from only one site, having unchanged or increased cover in other sites. *H. nobilis* has, however, not appeared in any new site, and is characterized as a slow reacting species. As *H. nobilis* can reach ages of more than 100 years and seedlings are sparse (Inghe and Tamm 1985), possible effects of acidification are prone to appear late.

Species disappearing from a majority of sites, where they were found 15–35 years ago, are *Pulmonaria officinalis, Dentaria bulbifera,* and *Polygonatum multiflorum.* They were originally most common in soils above pH 5, soils which probably have become too acid. The species have not colonized any of the few soils still having a pH above 5. For these species, Ellenberg's index of soil reaction is 7.0, showing preference for better soils. The nitrogen index is intermediate (5.3) and the light index low (3.3) – especially *Dentaria bulbifera* and *Polygonatum multiflorum* prefer shade.

Some species seem to be negatively affected by a more acid environment, decreasing in cover in soils only in the lower pH interval. One explanation might be the pH decrease itself or other factors depending on a low pH, e.g. higher availability of aluminium and heavy metals or by a changed species competition. *Mercurialis perennis* is increasing in cover in soils of higher pH, while it is disappearing from many sites, which have a pH of 4.0–5.5. The opinion, that *M. perennis* is increasing in Sweden (Fiskesjö and Ingelög 1985), might therefore be true for better soils but not for soils reaching lower pH.

Four other species are negatively affected in acid soils: *Luzula pilosa, Lamium galeobdolon, Galium odoratum* and *Oxalis acetosella.* The latter two have decreased markedly in cover in a majority of soils. *L. galeobdolon* has, however, increased in mean cover in soils of pH 4.0–5.0, and these soils represent the majority of sites. *L. galeobdolon* is mainly increasing by vegetative growth of established plants and possible acidification effects on fertility, seeds and seedlings are not considered. As a cover decrease was found in the most acid soils, it could be a sign of conditions getting unfavourable for the species. Ellenberg's index is less interesting for species showing different reaction in different parts of the pH interval. The reaction and nitrogen indices for the five species above are intermediate (5.8, 5.6), while the light index is low (2.0).

Grasses can take advantage of disturbed soils (Fiskesjö and Ingelög 1985) and the changes in cover of *Melica uniflora* and possibly *Milium effusum* may partly be explained in this way. Whether the disturbance is caused by very large pH decreases or other factors is outside the scope of this study.

As most of the resampled sites showed a lower pH, only species negatively affected in acidified soils could be detected. However, some of the species showing an increased cover throughout the whole pH interval might be species favourably affected by acidification. If some soils in the upper part of a species pH interval had increased in pH, and the species had reacted with a decreased cover, then a species favoured in acidified soils had been found.

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