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FURTHER OBSERVATIONS ON THE SURVIVAL AND FLOWERING OF SOME PERENNIAL HERBS, I

BY

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The behaviour of individual plants of certain species has been studied on permanent quadrats laid out during the period 1942–1944 in forest and hay-meadow in central Sweden. The results observed during the first four to six years have been published in a preliminary paper (TAMM 1948).

Of several interesting conclusions the most important concerned the rate of replacement of the species, both from seedlings and by branching. The rate of replacement, particularly from seedlings, has hitherto not received due attention. Earlier investigations, and particularly those conducted in Finland, have shown that in many plant communities only a very small percentage of the seedlings ever attain the floral stage (LINKOLA 1935; PERTTULA 1941). The true rate of reproduction is unknown, however, even in the meadow community which Linkola studied so closely. In Sweden, MALMSTRÖM (1949) has pointed out the great difference in the rate and type of reproduction in forest communities for the "mobile" and "equilibrium" stages, but no figures are available for the rate of replacement in these various stages.

In the preliminary paper figures were presented for the death rate and the rate of reproduction by vegetative propagation of certain species. It appears as if the conditions for the seedlings were even more adverse on the plots studies here than in the case of the types of vegetation studied by the Finnish investigators. The rate of renewal from seedlings was found to be almost nil in many cases, and the individual plants of the species studied must have been rather old. The figures presented were preliminary on account of the short period of observation and the difficulty of deciding the extent to which the communities under study were stable or developing towards a climax.

Another observation of ecological interest concerned the rate of flowering of certain species in different years. Annual differences in the number of flowering individuals on the same plot were found not only for orchids (*Orchis mascula* and *sambucina*) but also for *Primula veris* and *Sanicula europaea*. It was concluded that "flowering years" occur for perennial herbs as well as for orchard and forest trees.

These preliminary results encouraged continuation of the records, and most plots have been inspected annually. As the observations collected in this way are numerous they will be reported as a series of papers, of which this is the first. It deals with two plants, *Anemone hepatica* and *Sanicula europaea*, observed on forest plots, the former also on a meadow plot. The observations made on some other meadow plots in the immediate vicinity of the *Anemone* plot are also included in this paper.

The area investigated

The area investigated is situated 100 km northeast of Stockholm, near the Baltic coast.

A brief description of the experimental plots was given in the preliminary paper. Some details have been mentioned in a more recent publication (TAMM 1953). General views of the meadow and forest habitats are shown in Figs. 1 and 2, respectively. The vegetation of the plots is recorded in Table 1. (Taxonomic nomenclature according to HYLANDER 1955.) In many cases plant lists were made in 1943–1944 and in 1955. If large vegetational changes occurred from 1943–1944 to 1945 they will be evident in Table 1; on the other hand no definite conclusions can be drawn from minor differences in the degree of cover, as the vegetational development often differs from year to year, even if the records are made on approximately the same date. It should also be mentioned that the writer had not had much experience of vegetation analyses at the beginning of the present investigation, and some species may on that account have been overlooked at that time.

Nevertheless, comparison of the different counts from the same plots reveals relatively small differences. Among the more conspicuous changes are an increase in *Pteridium aquilinum* on plot 3 and increases in *Vicia silvatica* on plots 2 and 37; in both cases the changes may have been due to the establishment of a few vigorous specimens of these species.

Table 1 deals only with ground vegetation. All the meadow plots are well exposed and outside tree canopy, or on the border of the projection of the tree crowns. A slight increase in shade occurred in most meadow plots during the period, as the trees and hazel shrubs surrounding the clearings containing the plots had grown higher and denser.

In the forest the canopy was rather close for most plots but it was opened up slightly by a cut in the winter of 1950–1951. The felling of a spruce a few metres south of plot 40 on this occasion must have affected the conditions on this plot and on the adjacent plot 39. Yet the disturbing influences were not so strong as to produce major changes in the vegetation. The differences shown in Table 1

Fig. 1. View of the meadow with plots 2, 37, 38 and 47 in the background. Photographed 9.6. 1951.

Fig. 2. View of the forest with plot 4 in the foreground. Photographed 12.7. 1956.

Table 1. List of plants on the quadrats and the degrees of cover (Hult-Sernander scale).

	Forest plots							Meadow plots						
Plot no.	3		4		39		40	2		37		38	47	50
Size in sq. m	1		1		1/4		1/4	1		1/4		1/4	1/4	1/4
Date of inspection	26/4 1943	24/7 1955	26/4 1943	24/7 1955	11/7 1943	22/7 1955	22/7 1955	6/7 1944	23/7 1955	9/7 1943	6/7 1955	6/7 1955	21/7 1955	23/7 1955
Dwarf shrubs														
Helianthemum nummularium	–	–	–	–	–	–	–	–	–	1	1	2	1	–
Vaccinium myrtillus	1	2	–	–	1	–	–	–	–	–	–	–	–	–
– *vitis idaea*	2	2	–	–	–	–	–	–	–	–	–	–	–	–
Herbs														
Achillea millefolium	–	–	–	–	–	–	–	1	–	1	–	–	–	–
Aegopodium podagraria	–	–	–	–	–	–	–	2	3	–	–	–	–	–
Alchemilla sp.	–	–	–	–	–	–	–	2	2	2	3	–	1	2
Anemone hepatica	2	3	3	4	3	3	3	2	4	–	–	4	2	3
– *nemorosa*	2	2	2	3	–	2	2	1	–	+	4	4	–	–
Campanula rotundifolia	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Centaurea jacea	–	–	–	–	–	–	–	2	2	1	–	3	1	–
Convallaria majalis	–	–	–	–	–	–	–	1	1	–	–	–	–	–
Filipendula ulmaria	–	–	–	–	–	–	–	1	–	–	–	–	–	–
– *vulgaris*	–	1	–	–	–	–	–	2	2	2	3	3	1	3
Fragaria vesca	2	2	2	3	1	1	3	1	1	–	–	–	–	–
Galium boreale	–	1	–	–	–	–	–	2	2	1	4	3	1	3
– *verum*	–	–	–	–	–	–	–	1	1	2	2	2	–	1
Geranium silvaticum	–	2	1	1	1	–	2	1	1	1	3	–	2	2
Geum rivale	1	2	–	1	–	–	–	1	1	–	2	–	–	–
Hieracium sp.	–	–	–	–	–	–	–	2	–	–	–	–	–	1
Hypericum maculatum	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Lathyrus vernus	–	1	–	–	–	1	2	–	–	–	–	–	–	–
Listera ovata	–	–	–	–	–	–	–	1	1	–	–	–	–	–
Majanthemum bifolium	2	5	–	3	–	2	3	–	–	–	–	–	–	–
Melampyrum nemorosum	–	–	–	2	–	–	–	2	3	–	3	5	3	2
– *pratense*	–	–	–	–	–	–	–	–	–	1	–	–	–	–
– *silvaticum*	–	–	–	–	–	–	1	–	–	–	–	–	1	–
Oxalis acetosella	2	2	2	3	2	2	2	–	–	–	–	–	–	–
Paris quadrifolia	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Pimpinella saxifraga	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Plantago lanceolata	–	–	–	–	–	–	–	2	–	1	2	–	–	1
Polygonum viviparum	–	–	–	–	–	–	–	1	1	1	2	–	–	2
Potentilla Crantzii	–	–	–	–	–	–	–	1	1	–	1	–	–	–
– *erecta*	–	1	–	–	–	–	–	1	1	1	2	–	3	2
Primula veris	–	–	–	–	–	–	–	2	3	1	3	3	3	1
Pteridium aquilinum	1	4	1	–	2	–	–	–	–	–	–	–	–	–
Pyrola rotundifolia	–	–	–	–	–	–	–	–	2	–	–	–	–	–
Ramischia secunda	2	2	2	3	–	1	–	–	–	–	–	–	–	–

Table 1 (continued).

	Forest plots							Meadow plots						
Plot no.	3		4		39		40	2		37		38	47	50
Size in sq. m	1		1		1/4		1/4	1		1/4		1/4	1/4	1/4
Date of inspection	26/4 1943	24/7 1955	26/4 1943	24/7 1955	11/7 1943	22/7 1955	22/7 1955	6/7 1944	23/7 1955	9/7 1943	6/7 1955	6/7 1955	21/7 1955	23/7 1955
Ranunculus acris	–	–	–	–	–	–	–	1	1	–	1	–	–	–
– *auricomus*	–	–	–	–	–	–	–	1	1	–	–	–	–	–
– *cassubicus*	1	1	1	2	1	2	2	–	–	–	–	–	–	–
– *polyanthemus*	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Rubus saxatilis	–	–	–	2	–	2	4	–	–	–	–	–	–	–
Sanicula europaea	–	–	–	1	5	5	4	–	–	–	–	–	–	–
Trientalis europaea	–	–	–	–	1	1	3	–	–	–	–	–	–	–
Trifolium medium	–	–	–	–	–	–	–	1	1	1	–	–	–	–
– *montanum*	–	–	–	–	–	–	–	–		–	1	–	3	–
– *pratense*	–	–	–	–	–	–	–	–	–	–	–	–	1	–
– *repens*	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Veronica chamaedrys	–	1	–	2	–	–	–	–	1	–	2	3	–	1
– *officinalis*	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Vicia cracca	–	–	–	–	–	–	–	–	–	1	–	–	–	–
– *sepium*	1	2	–	1	–	–	–	–	–	–	–	–	–	–
– *silvatica*	–	–	–	–	–	–	–	–	3	–	3	–	–	–
Viola canina	–	–	–	–	–	–	–	1	1	1	2	2	2	2
– *riviniana*	–	2	–	2	1	1	1	1	–	–	–	2	–	–
Grasses														
Agrostis tenuis	–	1	–	–	–	–	1	–	–	1	–	+	–	+
Anthoxanthum odoratum	–	–	–	–	–	–	–	1	2	1	+	+	2	+
Arrhenatarum pratense	–	–	–	–	–	–	–	–	–	1	–	–	–	–
– *pubescens*	–	–	–	–	–	–	–	1	–	–	–	+	1	+
Brachypodium pinnatum	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Briza media	–	–	–	–	–	–	–	2	3	1	–	+	2	–
Calamagrostis arundinacea	–	–	–	–	–	–	–	–	3	–	–	–	–	–
Carex digitata	1	–	1	2	–	2	1	1	2	–	–	–	–	–
– *flacca*	–	–	–	–	–	–	–	–	1	–	+	+	–	–
– *hirta*	–	–	–	–	–	–	–	–	–	–	–	–	1	–
– *pallescens*	–	–	–	–	–	–	–	–	–	1	+	–	–	–
– *panicea*	–	–	–	–	–	–	–	–	–	–	+	–	1	+
Dactylis glomerata	–	–	–	–	–	–	–	2	1	–	+	+	–	+
Deschampsia caespitosa	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Festuca ovina	–	2	–	–	–	–	–	2	2	1	+	+	–	+
– *pratensis*	–	–	–	–	–	–	–	–	3	–	–	–	–	–
Luzula pilosa	1	1	1	1	–	1	1	1	1	–	–	–	1	+
Melica nutans	–	–	–	1	–	–	2	–	1	–	–	–	1	–
Milium effusum	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Sesleria coerulae	–	–	–	–	–	–	–	2	1	1	+	+	–	+

Table 1 (continued).

	Forest plots							Meadow plots						
Plot no.	3		4		39		40	2		37		38	47	50
Size in sq. m	1		1		1/4		1/4	1		1/4		1/4	1/4	1/4
Date of inspection	26/4 1943	24/7 1955	26/4 1943	24/7 1955	11/7 1943	22/7 1955	22/7 1955	6/7 1944	23/7 1955	9/7 1943	6/7 1955	6/7 1955	21/7 1955	23/7 1955
Mosses									*				*	
Cirriphyllum piliferum	–	–	–	–	–	–	–	1		1	2	2		1
Climacium dendroides	–	–	–	–	–	–	–	1		1	–	–		–
Dicranum scoparium	2	–	2	–	–	–	–	–		–	–	–		–
– *undulatum*	1	–	3	–	–	–	–	–		–	–	–		–
Hylocomium splendens	3	5	3	2	1	1	1	1		1	4	2		2
Mnium undulatum	2	1	–	–	–	2	3	–		–	–	–		–
– sp.	1	–	–	–	–	–	–	–		1	1	–		1
Plagiochila asplenioides	2	3	3	4	1	–	–	–		–	–	–		–
Pleurozium Schreberi	3	2	–	–	–	–	–	1		–	–	–		–
Ptilium crista castrensis	–	–	–	–	1	–	–	–		–	–	–		–
Rhodobryum roseum	2	2	–	–	1	–	–	–		–	–	–		–
Rhytidiadelphus squarrosus	–	–	–	–	–	–	–	4		4	5	5		5
– *triquetrus*	4	3	5	5	4	5	5	1		–	2	3		–
Thuidium tamariscinum	–	–	–	–	–	–	–	1		–	3	2		1

* Mosses not recorded in 1955.

for the period 1943–1955 may or may not have been associated with the felling, or with the gradual closing of tree canopy occurring before and after felling.

The meadow had earlier been used for yielding hay, but it is not known when the mowing ceased. An adjacent part of the meadow was grazed from 1911 to 1943 (TAMM 1956), but the area in question, comprising about one hectare, seems to have lacked permanent fencing partition from the neighbouring fields, which probably means that it was not used regularly as a pasture. Mowing probably continued – more or less regularly – until about 1930 or even later. The area was then left untreated until 1943, when mowing was resumed except on the experimental plots. The disadvantages of leaving the plots unmown soon became apparent, however, (see below) and from 1948 onwards the plots have been mown – as a rule in the second half of July, but sometimes at the beginning of August.

Results

The observations are in most cases presented in diagrams of the same type as in the previous publication. It must be remembered that occasional errors may occur in the counts. The annual inspection should not, of course, be made so

thoroughly as to risk appreciable damage to the plants on the plots. For example, it was sometimes impossible to decide whether a small individual originated from a new seedling or from a small one previously observed on the same spot. New plants may also have been overlooked for a year or more. In the diagrams the marking for the year before the first observation of an individual is usually indicated by a broken line, one exception being where a seedling with cotyledons was observed.

There are minor discrepancies between the accompanying diagrams and those published earlier, most of them relating to specimens for which the observations can be variously interpreted as mentioned above. Specimens growing near the border of the plot have also in some cases been included in these diagrams, but not in the earlier ones.

On most plots one species was studied. In one meadow plot, however, an attempt was made to follow the changes in the entire field vegetation, although in less detail than on the other plots. The results from this plot are presented diagrammatically (see below).

The behaviour of each species is discussed in connection with the associated diagrams, and some concluding remarks are made at the end of this paper.

1. *Anemone hepatica*

This species has been observed on three plots, each comprising one square metre. One was situated in the meadow (No. 2) and two in the forest (Nos. 3 and 4). Originally, one more plot (No. 5) was laid out in the meadow close to plot No. 2, but lack of time for the inspections made it impossible to follow this for more than three years. The forest plots are situated about 30 metres apart in a forest predominantly spruce but with some pine and birch, together with scattered shrubs (*Corylus avellana*, *Lonicera xylosteum*, etc.). The subsoil is a clayey moraine, originally rich in lime, but this has now been leached away from the top soil to a depth of 6 dm or more. The humus layer is mull, both in the forest and in the meadow. The vegetation is detailed in Table 1. The meadow plot has a subsoil similar to that of the forest plots, but the lime content of the top soil is as a rule greater here than in the forest, according to an unpublished investigation by ALMBERGER & MATTSSON MÅRN.

Fig. 3 presents the results from the meadow plot. At the commencement of the study in 1944 (the records from 1943 are not entirely reliable on account of the too early season of the first inspection) 23 vigorous specimens occurred on the plot. Only four of these died during the period. On the other hand many of the remaining ones ramified once or several times. In 1956 34 specimens were recorded, 15 of them new, as four had died. On an average one new individual a year was formed by ramification (about 5 per cent). As the death rate was

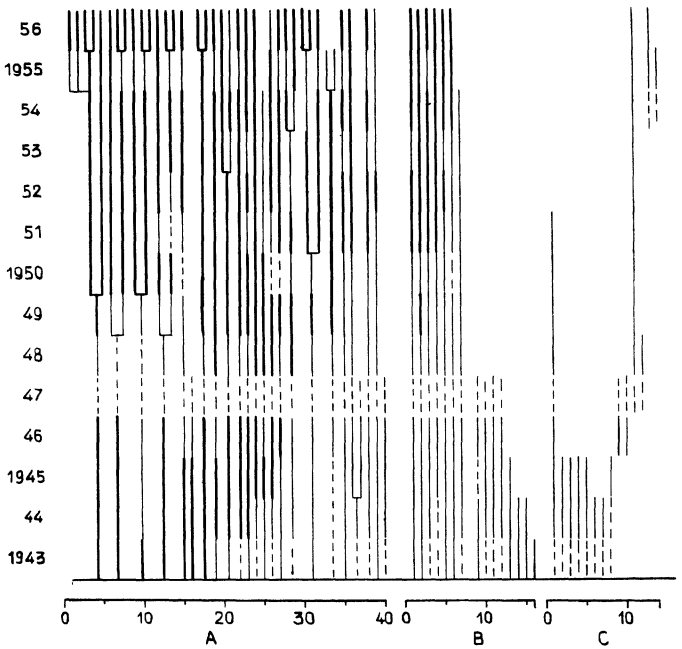

Fig. 3. The behaviour of the *Anemone hepatica* specimens on plot 2 (in the meadow). – Each vertical line represents one individual, straight for unramified ones, and branched where the plant has ramified. The heavier lines are for years when the specimens flowered, and broken lines indicate that the plant was not seen that year. Group A includes specimens of large or intermediate size at the first inspections, group B small or rather small ones, and group C those appearing in 1944 or later, presumably from seedlings. When first observed they were as a rule smaller than those of group B. – On this plot the observations of the flowering are not entirely reliable for some of the years (1946 and 1948 in particular), when the inspections were made in unsuitable seasons (too early or too late).

much lower, there was a considerable increase in the number of specimens originating from those recorded as vigorous at the beginning of the study.

Fifteen specimens were recorded as small in 1943–1944. Six of them survived the full period and attained the flowering stage. The addition of entirely new individuals from seedlings was very small. Although they occurred at a higher frequency than the diagram would indicate, they were as a rule very short-lived.

The rôle of *Anemone hepatica* as a constituent of the vegetation on the meadow plot has increased considerably, according to Fig. 3, even if the total number of specimens is not very different; almost all individuals occurring in 1956 are at the fertile stage, whereas many of these were small and weak at the beginning of the period. In 1943 and 1944 only seven and ten specimens flowered, respectively; 30 flowered in 1954, 16 in 1955 and 37 in 1956.

The number of flowers per specimen may be taken as a rough measure of the size of fertile plants, and it is therefore of some interest to compare these num-

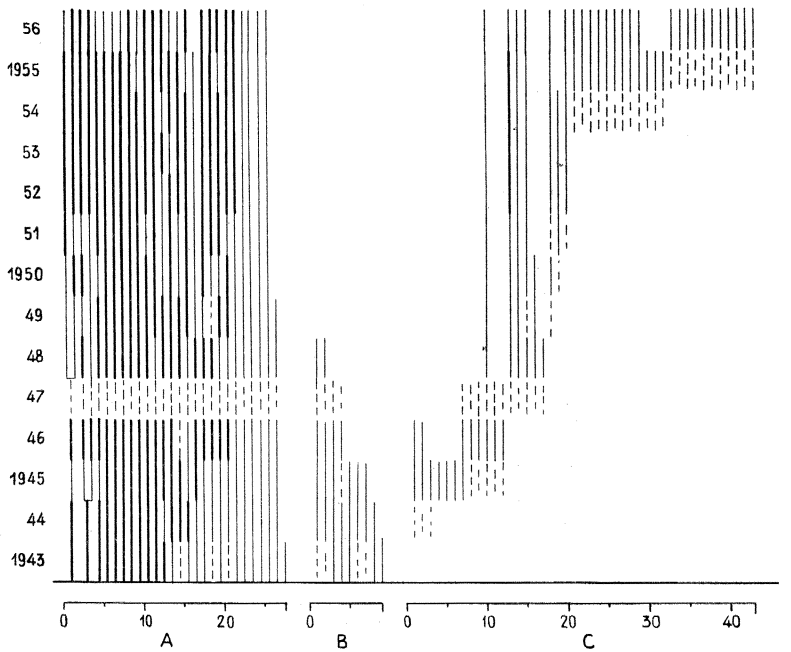

Fig. 4. The behaviour of the *Anemone hepatica* specimens on plot 3 (in the forest). Symbols and other details as in Fig. 3.

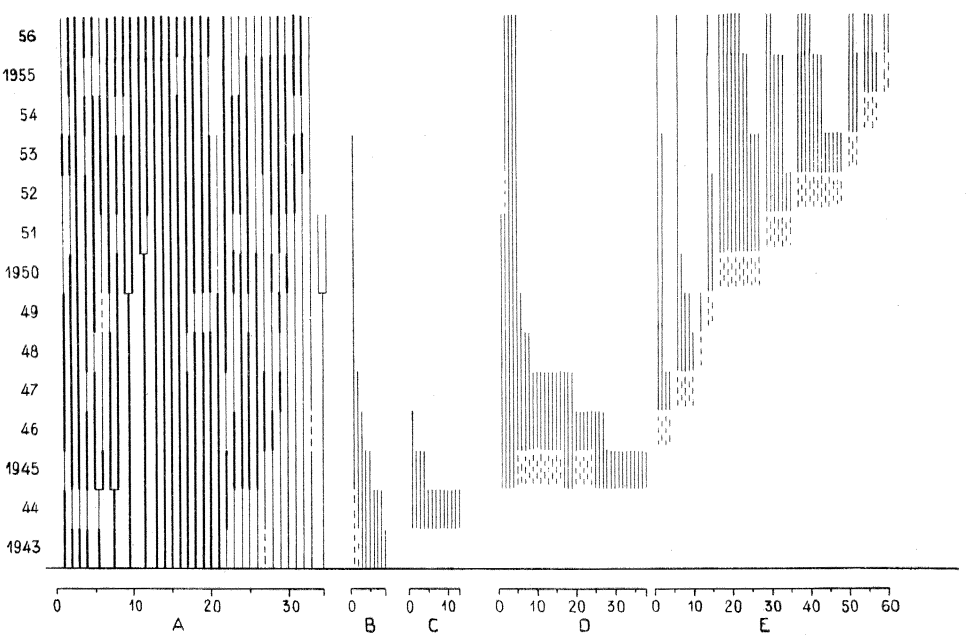

Fig. 5. The behaviour of the *Anemone hepatica* specimens on plot 4 (in the forest). Symbols and other details as in Fig. 3; groups C, D and E include different crops of seedlings.

bers in different years. Yet the counts were not always made at the most suitable date, and the stalks of unfertilized flowers may in some cases have withered completely before the inspection, particularly in 1946 and 1948, when the examinations were made in early summer. The data are thus not suited to detailed statistical analysis. In Fig. 6 (plot 2), however, it is possible to compare the number of flower stalks per individual for 1944–1945 and 1954–1955; daughter plants formed by ramification were considered as parts of the mother plants in this case. The use of two years instead of one at the beginning and end of the period to some extent decreases the random dispersion. Evidently there is a certain regression of the number of flower stalks in 1954–1955 on the corresponding number 10 years previously. Plants flowering profusely on the first occasion tended to flower more profusely on the second occasion than those with few or no flowers in 1944–1945; in other words, the bigger plants maintained their relative positions.

The development of *Anemone hepatica* in the forest plots is shown in Figs. 4 and 5. The differences between the two plots are very small in the case of the specimens well established at the beginning of the investigation: two individuals of 26 had ramified on plot 3, and five of 32 on plot 4. On plots 3 and 4, respectively, two and three individuals died, 22 and 24 surviving the full period. On each plot 9 specimens were noted as small at the first inspection; none of these survived until 1956.

The differences between the two plots are in respect of the new individuals, which are more numerous on plot 4 than on plot 3. On the other hand, one of the new specimens on plot 3 soon reached fertility. It is, however, possible that this one is older than is suggested in the diagram, but was overlooked in the first inspections. When it was first observed it was growing very close to a larger specimen, but it had not sprouted from this, as a later examination showed. As in the meadow plot seedlings were not searched for systematically at all the inspections. In both forest plots most of the seedlings generally died within a few years. The majority of those surviving a longer period remained small.

As in the case of the meadow plot there seems to be a correlation between the number of flowers per plant at the beginning and the end of the period (Fig. 6, plots 3 & 4). The relationship is clearer on plot 4 than on plot 3. Here, too, the larger specimens tend to maintain their position in the community for long periods.

A comparison between the meadow (Fig. 3) and the forest diagrams (Figs. 4 and 5) seems to show that *Anemone hepatica* is living under more stable conditions on the forest plots than in the meadow. However, in the meadow vegetation, which seems to be slowly changing in composition, the annual rate of replacement of the *Anemone* individuals is also low – of the order of a few per

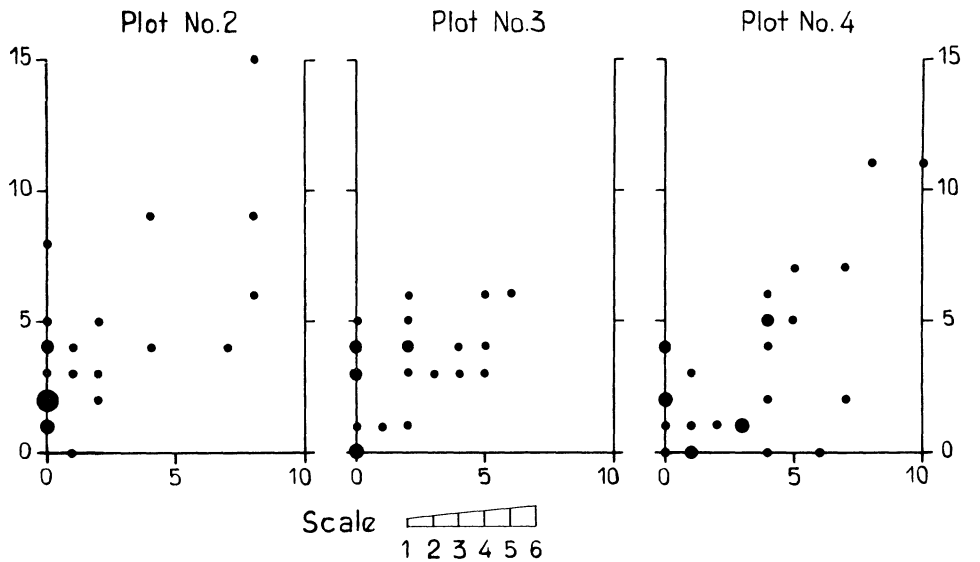

Fig. 6. The number of flowers per specimen in 1944–1945 (vertical axis) plotted against the corresponding number in the same specimens in 1954–1955 (horizontal axis) in the three *Anemone* quadrats. – Only specimens belonging to group A in Figs. 3–5 are included; daughter plants formed by ramification are considered as part of the mother plant. The size of each dot corresponds to the number of cases with the given number of flowers on the two occasions (see scale).

cent of the number of plants at the fertile stage. Moreover, this replacement is taking place mainly by vegetative propagation, and is thus from a genetic viewpoint not a renewal.

2. *Centaurea jacea*

This species was observed from 1944 to 1956 on a 1/4 sq. metre plot close to the *Anemone* meadow plot and the *Filipendula* plots described below. As mentioned in the previous publication the number of *Centaurea* specimens diminished considerably from 1944 to 1947. This decrease continued from 1947 onwards (Fig. 7). Since 1954 there has been only one *Centaurea* on the plot (of 51 in 1944). None of the specimens had flowered since 1947. The early phase of the decrease in number and fertility of *Centaurea* was believed to be due to the activity of voles seeking shelter on the plot when the rest of the meadow had been mown. From 1948, however, the quadrats also were mown, but the decrease of *Centaurea* persisted. There are thus also other, and possibly more important, factors than the voles, to which the decrease must be ascribed. The death of *Centaurea* seems to be a very local phenomenon, however, as fertile *Centaurea* still occurs in the neighbourhood of the plot.

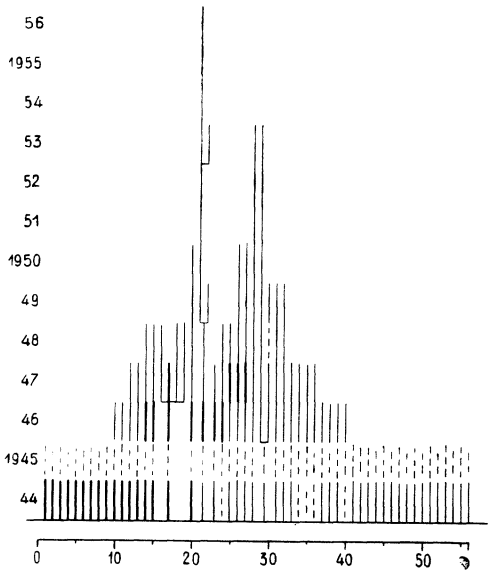

Fig. 7. The behaviour of the *Centaurea jacea* specimens on plot 47. Symbols as in Fig. 3.

3. *Filipendula vulgaris*

The observations on *Filipendula vulgaris* were made on two 1/4 sq. metre quadrats close to the *Centaurea* plot and with rather similar vegetation. Hazel shrubs occur in the neighbourhood of all three plots and extended considerably during the period of observation. Although the plots lack any tree or shrub canopy, the shade from the hazels had increased somewhat from 1943 to 1955 for all the plots, and least for the one with *Centaurea*. The development of the *Filipendula* specimens was closely similar on both plots, and they are therefore treated together (Fig. 8).

Filipendula vulgaris, as *Centaurea*, ceased to flower in 1948. The total number of individuals on the plots increased from 33 to 40 in the period from 1943 to 1946, but the average size probably decreased at the same time. Most of the new specimens were doubtlessly tillers, to judge from observations on root systems (TAMM 1948). Seedlings were rare, small and short-lived.

Now and then specimens noted as absent in one year reappeared in the following year. This was probably due in most cases to damage by animals (larvae or snails), which cut off the leaves. The plants in question were often small. Yet it is possible that some of the specimens noted as reappearing were in fact new ones, and that the old specimens growing on the same sites were dead.

As mentioned in the previous publication, in 1947 the vegetation on the *Filipendula* plots appeared more luxuriant than outside them, where the meadow

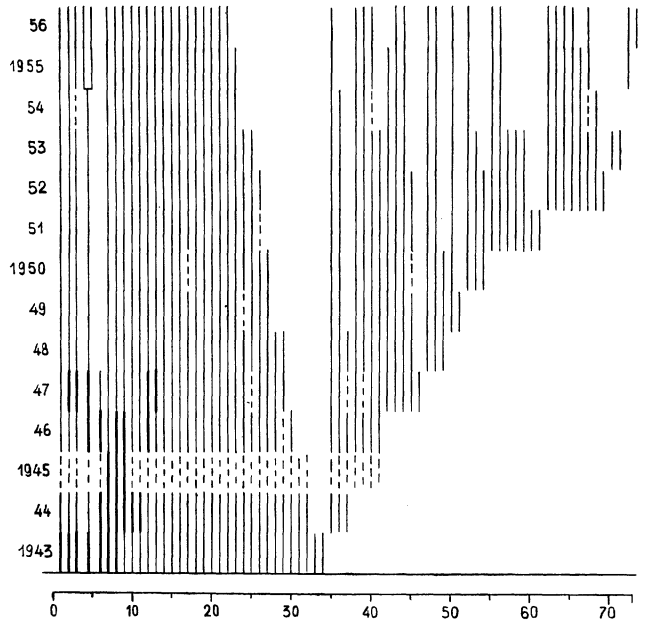

Fig. 8. The behaviour of the *Filipendula vulgaris* specimens on plots 37 and 38. Symbols as in Fig. 3.

had been mown for some years. This difference has subsequently dwindled; the plots are now mown each year just as the adjoining land. It is difficult to believe that mowing was responsible for the decreasing fertility of *Filipendula vulgaris* during the latter years. Mowing at the end of July is not likely to cause serious damage to a plant such as *Filipendula vulgaris*, which occurs and flowers abundantly also in other parts of the meadow, mown as well as unmown.

The *Filipendula* observations thus yield results similar to those of the *Anemone* plot in the meadow. There was a certain annual rate of replacement by vegetative propagation, but this amounted to not more than a few per cent of the number for the well established specimens. It seems clear that, in this habitat, the old and vigorous plants maintain their places in the community for a considerable time.

4. *Sanicula europaea*

Sanicula europaea was observed in two closely situated quadrats, each of 1/4 sq. metre, in forest of essentially the same type as that of the *Anemone* plots (Figs. 9 and 10). On the two *Sanicula* plots nine of 69 fertile specimens died between 1943 and 1956 – that is to say, less than one per cent per annum. Three individuals ramified, but in two cases one of the daughter plants soon died. Of the 23 specimens noted as "small" in 1943 and 1944 only eight survived until 1956, two of them having by then attained the fertile stage. In 1943 and 1944 39

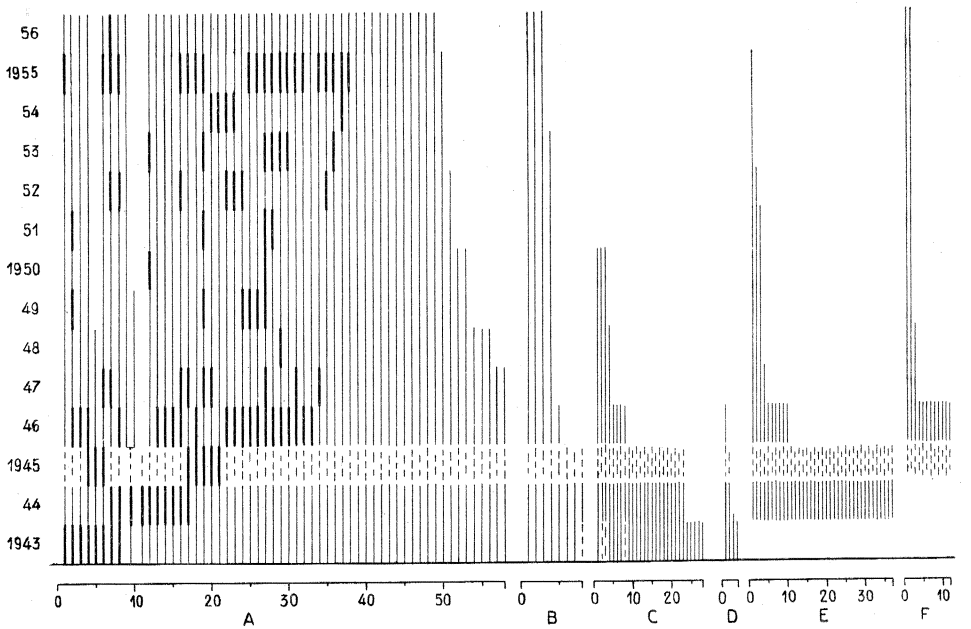

Fig. 9. The behaviour of the *Sanicula europaea* specimens on plot 39. Symbols as in Fig. 3. – Group A includes specimens that were large or intermediate in size at the first inspections, group B rather small ones, group C very small ones, and groups D to F different crops of seedlings.

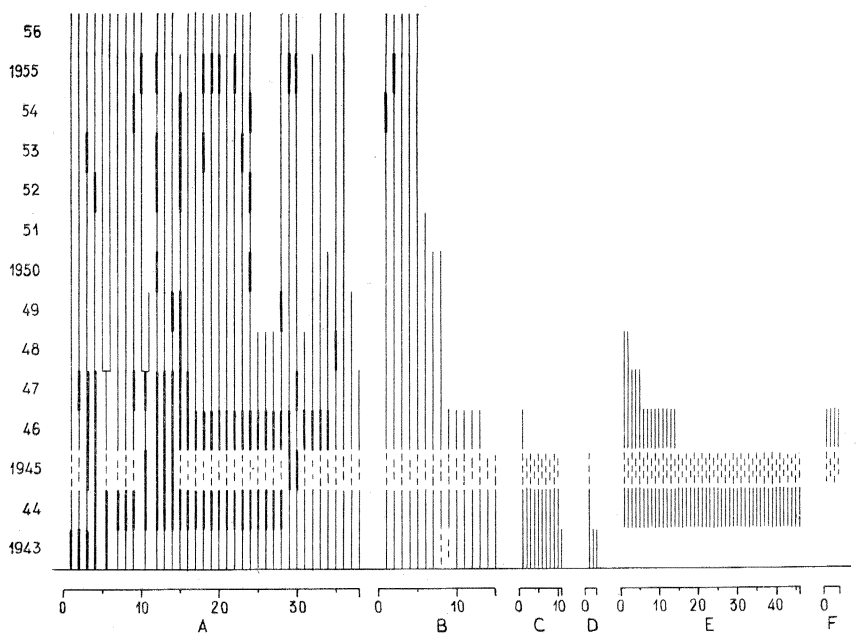

Fig. 10. The behaviour of the *Sanicula europaea* specimens on plot 40. Symbols as in Fig. 3. Grouping as in Fig. 9.

specimens were noted as "very small"; none of them survived 1950. The diagrams also indicate the development of three crops of seedlings from 1943, 1944 and 1945 (in the last case only the seedlings still living in 1946 were observed). The mortality of the seedlings was very high, only two of all of them surviving until 1956.

The two *Sanicula* diagrams are very similar, not only to each other, but also to those depicting the behaviour of *Anemone hepatica* on a similar site (Figs. 4 and 5). The main difference is the striking irregularity of the flowering of *Sanicula*.

5. *Special studies on a meadow quadrat*

The results so far reported relate only to plants of a particular life form: perennial herbs forming a rosette. Although this life form is quantitatively important in many meadow and forest communities, it is by no means the only one of importance. The method used here is not very suitable for the study of tussock-forming grasses or of plants migrating by subterranean tillers; at least it is not possible to decide the origin of new plants observed, as in the case of *Filipendula vulgaris*. Moreover, it was soon found that an annual inspection of many different plants on the same plot was likely to incur damage to the vegetation, in particular if the various species were examined at different seasons. In order to ascertain the extent to which observations for a single species were representative of the whole meadow vegetation a 1/4 sq. metre plot (No. 50) was laid out in 1944 fairly close to the *Anemone* plot (just below the lower right corner of Fig. 1). Three species occurring in sufficient abundance were mapped in the usual way, and the entire field vegetation was recorded, though in less detail. The frame used for the mapping had an iron wire grid with a one decimetre mesh; record was made of all the plants, except seedlings, rooted within each such sub-plot. In order to measure the abundance of the various species within the sub-plots an attempt was made to use the Hult-Sernander scale, but it was soon found necessary to adopt a special scale. Four degrees were distinguished: (1) one or more very small specimens; (2) one or more small specimens (covering only a small part of the sub-plot); (3) one or more vigorous individuals (covering less than 0.5 sq. decimetre); and (4) one or more vigorous individuals covering most of the sub-plot, and sometimes also parts of the adjacent sub-plots). Estimates near the boundaries of the scale were highly subjective.

Individual plants of *Alchemilla* sp., *Plantago lanceolata*, and *Polygonum viviparum* were mapped in 1944 and then annually from 1948. The results of these inspections are presented in Fig. 11. The diagrams, which bear rather a close similarity to that for *Centaurea* (Fig. 7), show a marked decrease in the number of specimens of all three species from 1944 to 1948. During this period

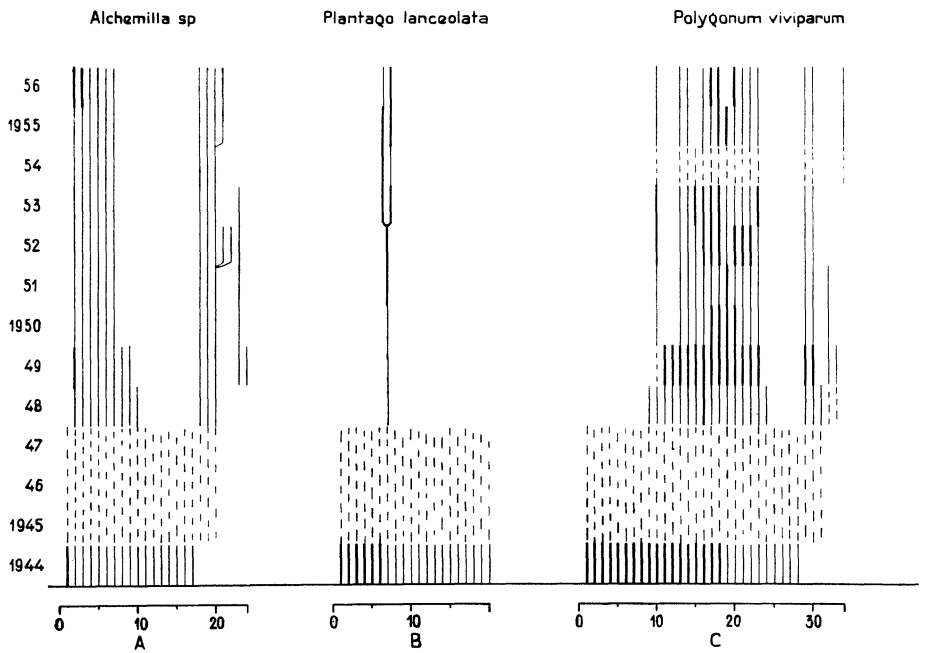

Fig. 11. The behaviour of the specimens of *Alchemilla* sp.[1]), *Plantago lanceolata*, and *Polygonum viviparum* on plot 50. Symbols as in Fig. 3.

the plot was left unmown while the surrounding land was mown. From 1948 onwards these species displayed relatively small changes. As for most of the species reported in this paper, the number of new specimens was small. It is probable that some of the specimens first observed in 1948 were either overlooked in 1944 or had been formed by branching of older plants between 1944 and 1948.

The flowering of *Polygonum viviparum* is evidently very irregular, as already shown in the case of *Sanicula europaea* (Figs. 9 and 10) and *Orchis sambucina* (TAMM 1948).

A new study of the entire field vegetation was performed in July 1956, according to the same procedure as for July 1944. It is evident that the quantitative data for these occasions should not be compared in detail; the scale employed gives only a very rough and rather subjective measure of the abundance of the plants. The frame may also have changed its position by some millimetres, or even more, as a result of the action of repeated freezing and thawing on the iron rods at the corners of the quadrat; this effect may have been so large that some specimens were assigned to different sub-plots in the two

[1]) *Alchemilla glaucescens* occurs close to the plot (two specimens have been determined by Dr. E. ASPLUND, Stockholm).

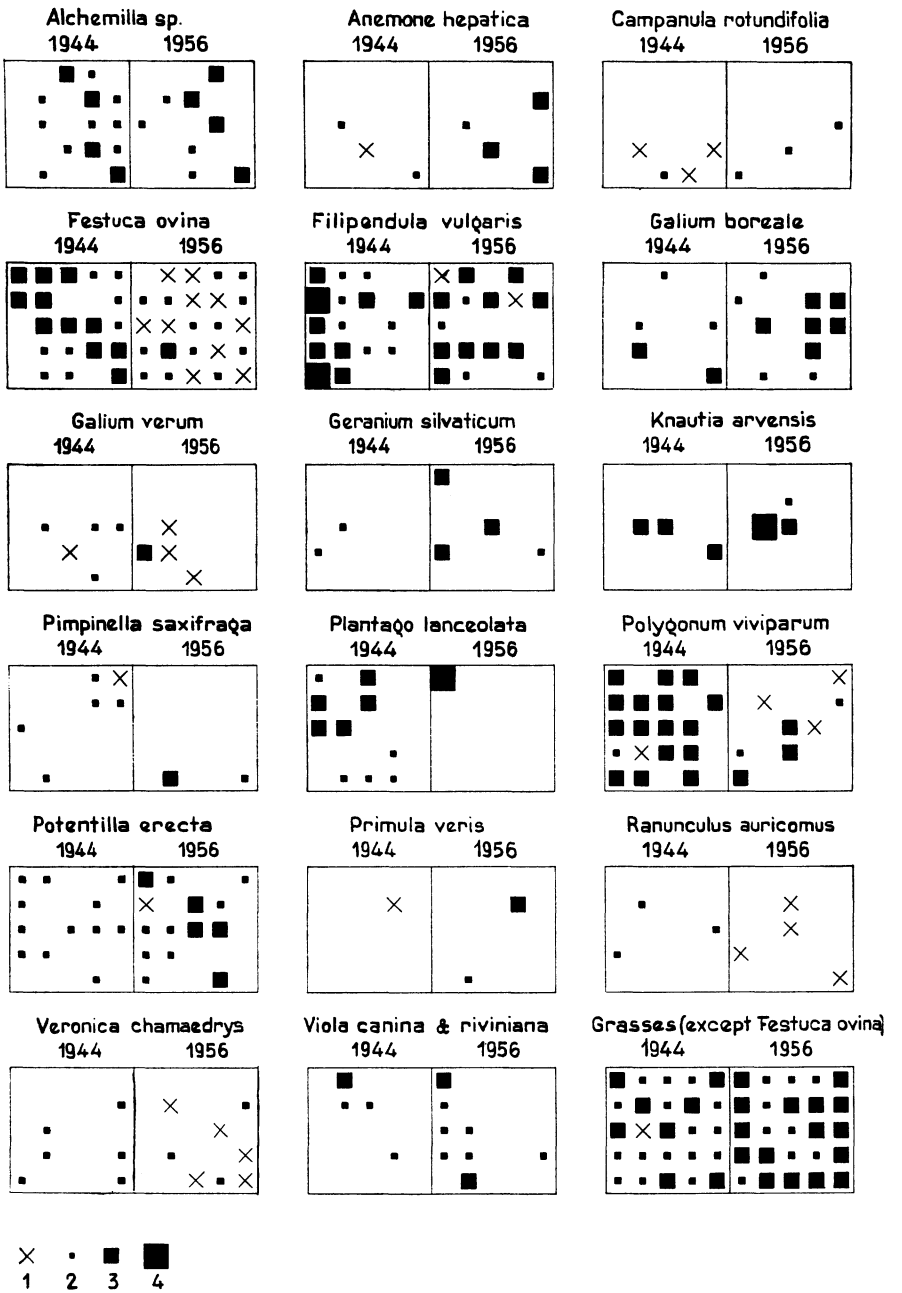

Fig. 12. Distribution of 18 species on plot 50 on July 8, 1944 and July 14, 1956. – The occurrence of each species was observed on the 25 sub-plots one decimetre square on the 1/4 sq. metre quadrat, and their abundance (according to a four-degree scale, see text) on the sub-plots is marked on the maps.

Table 2.
Species occurring on plot 50 in addition to those mentioned in Figs. 11 and 12. Symbols as in Fig. 12; each symbol represents the occurrence within a sub-plot of one square decimetre.

Species	1944	1956
Anemone nemorosa (*partly withered*)	▪	▪▪
Hieracium pilosella	■	–
– sp. (cf. *murorum*)	–	■
Melampyrum nemorosum	▪	–
Ranunculus acris	▪▪	–
Rumex acetosa	–	×
Trifolium sp. (*medium* or *montanum*)	×	–

inspections. Moreover, many plants changed their places during the course of time by rhizome growth.

The results of both mappings are presented in Fig. 12 (for the 18 most abundant species within the quadrat) and in Table 2 (for some species occurring more sparsely).

In Fig. 12 there is very often a certain similarity in the distributional pattern of the same species in 1944 and in 1956. Such is the case for *Anemone hepatica*, *Filipendula vulgaris*, *Knautia arvensis*, *Potentilla erecta*, *Primula veris*, *Veronica chamaedrys*, and others. Marked decrease in abundance is found for *Alchemilla* sp., *Festuca ovina*, *Pimpinella saxifraga*, *Plantago lanceolata*, and *Polygonum viviparum*. On the other hand, *Galium boreale*, *Viola* spp., and the grasses other than *Festuca ovina* increased. Specimens of other species than those enumerated here have also both appeared and disappeared. It should be borne in mind, however, that immigration or emigration of plant individuals may take place – especially in the marginal sub-plots.

From the diagram in Fig. 11, however, we know that most of the individuals of *Alchemilla* and *Polygonum* present in 1956 existed already in 1944. In species where the agreement between the 1944 and 1956 maps is better than for *Alchemilla* and *Polygonum*, there seems to be little doubt that most of the plant individuals were identical on both occasions. In such cases diagrams similar to Figs. 3, 7, 8 and 11 would be obtained if individuals of these species were followed in permanent quadrats.

Concluding remarks

The present investigation deals with two different types of vegetation: (a) forest which is predominantly spruce, with abundant herbs, and (b) openings in a wooded meadow. The four quadrats studied in the forest are all examples

of extremely stable conditions as regards the species observed, while the meadow quadrats had all changed in one way or another.

The observations on the forest plots bear out the opinion expressed by MALMSTRÖM (1949), based on investigations by himself, Hesselman, Romell, and others; viz, that reproduction by seedlings (of trees in particular, but also of most species of ground vegetation) is not very important in many forest types except when their equilibrium is disturbed in some way (by fire, wind-fall, or human agency). In the preliminary paper the difference was pointed out between the reproductive phase of a forest community and the long phase with mainly vegetative reproduction which sets in when a new stand is established. It is an interesting observation on the *Anemone* and *Sanicula* quadrats that vegetative reproduction by ramification is also rare; from a theoretical viewpoint this would be expected under climax conditions.

The observations from the meadow plots described here present a picture of a plant community that is slowly changing its composition, chiefly by vegetative reproduction of some plants at the expense of others. Yet it is difficult to decide what the final results of the development will be if the trees are not allowed to close over the open areas in the wooded meadow. During the 14-year period studied there was hardly any change in the general character of the vegetation, although it is difficult to decide whether there was a shift in the balance between herbs and grasses.

The predominance of the vegetative propagation does not exclude the possibility of some species reproducing themselves by means of seedlings, and that this form of reproduction may be important also for other species on certain occasions – for instance, after local disturbances due to animal activity. Annuals were rare in the meadow with the exception of *Melampyrum* species, but other hapaxanths such as *Linum catharticum* occurred occasionally. Tree seedlings also occurred but were removed from the plots. The abundance and distribution of *Melampyrum nemorosum* changes much from year to year; it is not known whether its parasitism affects the survival of the host plants. As *Melampyrum* often constitutes a considerable part of the meadow vegetation, changes in its distribution may to some extent influence the rest of the vegetation.

Further discussion of the stability and changeability of the meadow vegetation would be premature. Subsequent reports of observations from the permanent quadrats will present data on various other components of the meadow vegetation, together with a discussion of the irregularity in the flowering of certain species.

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