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Survival and flowering of some perennial herbs

II. The behaviour of some orchids on permanent plots

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Observations on permanent plots, each of one m² (in one case 0.25 m²), in a partly wooded meadow in eastern Sweden show population changes in four orchid species over periods of between 14 and 30 years. Three species, *Dactylorhiza sambucina*, *D. incarnata*, and *Orchis mascula* showed decreasing frequencies and decreasing flowering during the observation period, while the fourth species, *Listera ovata*, showed a marked increase in number. The death-rate in these species was not constant over the period, as in some other herbs in the same meadow, with the possible exception of *Listera ovata*, where the death-rate was remarkably low. Marked variations occurred in flowering frequency between different years. Propagation by seedlings does occur, but is apparently a slow process in the studied species when they grow in a closed plant community.

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Наблюдения на постоянных опытных площадках размером в 1 кв.м. (в одном случае 0,25 кв.м.) на лугу, частично заросшем лесом, в восточной Швеции показали, наличие популяционных изменений у 4 видов орхидных растений в течение периодов от 14 до 30 лет. У трех видов *Dactylorhiza Sambucina.*, *D. incarnata* и *Orchis mascula* установлено снижение частоты встречаемости и обилия цветов в течение периода исследований, а численность четвертого вида – *Listera ovata* наоборот, значительно возросла. Показатели смертности у этих видов были непостоянны, как и у других растений на том же лугу, за исключением видимо *Listera ovata* где смертность была относительно низка. Заметные различия в разные годы наблюдаются в обилии цветов. Имеет место размножение отрезками, однако, у исследуемых растений это медленный процесс, если они произрастают в замкнутых растительных ассоциациях.

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1. Introduction

A report of investigations on permanent quadrats was published in an earlier volume of this journal (Tamm 1956). It concerned some perennial forest and meadow herbs studied on plots in eastern Uppland, middle Sweden. The present report deals with the behaviour of some orchids, studied on meadow plots in the same area. Some observations on *Orchis mascula* L. and *Dactylorhiza sambucina* (L.) Vermln. were published in an earlier paper (Tamm 1948), but in the case of *Listera ovata* (L.) R. Br. and *Dactylorhiza incarnata* (L.) Vermln. no such data have been published.

For description of the area, see the previous papers (Tamm 1948 and 1956). The method for the investigation is described in the first paper. The plots have, with some exceptions, been revised annually and all individual plants of a certain species within the plot were mapped with the help of a frame with a grid. The method has worked well for the species chosen for this investigation, but does not entirely exclude mistakes, particularly in the case of species propagating vegetatively by subterranean organs, as in the case of *Listera ovata*. Here doubts can sometimes arise, as to whether an individual is identical with one observed earlier or has grown up since the last revision on the site of a dead one observed earlier. The revisions have been performed rather carefully as regards the established individuals, but seedlings (or other very small individuals) may well be overlooked in one or more years. Very detailed revisions must be considered as a kind of manipulation of the vegetation which should be minimised.

The vegetation of the sample plots was recorded at intervals using the Hult-Sernander-Du Rietz scale. The changes in vegetation will be discussed in a special paper.

2. Results

2.1. *Dactylorhiza incarnata* (coll.)

This species was observed on a wet meadow beside a small lake, the level of which varies with that of the Baltic (Lake Gräsvarpet, see Willén 1962). At the start of the investigation, fertile specimens of the orchids were concentrated to a relatively narrow zone, corresponding to a height of some dm above mean water level. Since the land is rising four to five dm per century, constancy in the number of orchids in a zone with a certain degree of moisture would require colonization of the outer part of the zone and a decrease in the inner part.

With this in mind, three plots were laid out in 1944 in different parts of the zone. Unfortunately, the plots could not be revised until 1948, and the marking sticks of two of the plots could not be found then, probably because of trampling by cows (this area was regularly grazed until 1956, in contrast to the main part of the meadow). Only the innermost plot was rediscovered,

and Fig. 1 shows the behaviour of the individual orchids within it.

Flowering was relatively uncommon during the period 1948 to 1952, but most of the individuals survived. After 1952, however, many of them disappeared. In some cases a plant not seen on one occasion was found again later. In the years after 1958, superficial examination of the plot revealed no living specimens, until detailed revisions were made in 1965 and 1967. Two specimens were found on the site of old ones; most probably they were identical with those observed earlier. A number of small new individuals also appeared, one in 1965, nine in 1967. Most of these new individuals soon disappeared. It is difficult to draw more definite conclusions from Fig. 1. The two most marked changes were the death of several individuals between the 1952 and 1953 revisions, and the appearance of a number of new individuals in 1967 (or 1966). Neither of these changes coincides with the change in land-use (grazing discontinued after 1956). In recent years, no *Dactylorhiza incarnata* has flowered within the plot, but flowering specimens have been observed in the neighbourhood.

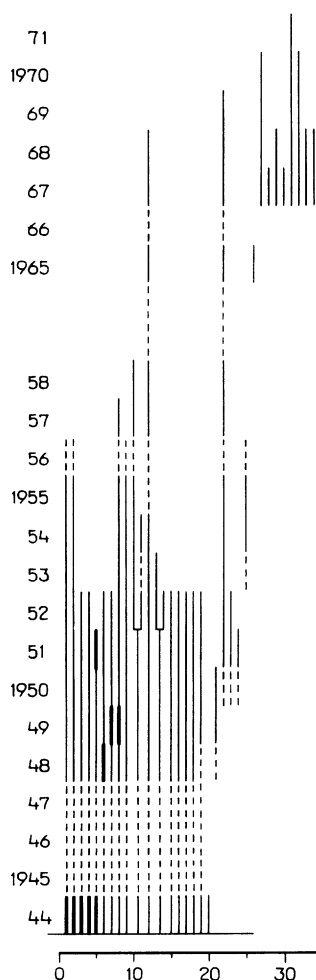


Fig. 1. The behaviour of *Dactylorhiza incarnata* on plot 46 (wet meadow). Each vertical line represents one individual, straight for unramified ones, and branched where the plants appear to have branched. Heavy lines mark years when the plants have flowered, and broken lines indicate that the plant was not observed in that year.

2.2. *Dactylorhiza sambucina*

Dactylorhiza sambucina was the first species studied in this investigation, and has been followed in one plot (No. 17) from 1942 onwards. During this period, the environment of the plot changed considerably, owing to the growth of a small pine just N of the plot. The vegetation of the plot remained, however, relatively little affected by this development from 1942 to 1955 but later several species have disappeared from the plot (*Achillea millefolium* (L.), *Antennaria dioeca* (L.) Gaertn., *Helianthemum nummularium* (L.) Mill., *Lotus corniculatus* L., *Plantago lanceolata* L., *Polygala vulgaris* L., a.o.). New invaders are less numerous, but include *Anemone hepatica* L. and *Lathyrus montanus* Bernh. Plot No. 17 is situated on shallow soil, and the field layer has probably never been very luxuriant.

The number of *Dactylorhiza sambucina* was slightly lower in 1963 than in 1942. Of the original 52, 20 died during this period; on the other hand, 20 new specimens became established between 1945 and 1956. Nine of these were still present in 1963 and five in 1971. After 1963 there was a steady decline in the number of individuals, affecting both original specimens and newly established ones to the same extent. The few cases of branching marked in Fig. 2 are not necessarily true branchings; there may be an independent specimen appearing close to an old one. Such uncertainties can hardly be avoided with the present method.

The flowering of *Dactylorhiza sambucina* has been extremely irregular in plot No. 17. The proportion of flowering individuals varies between zero in 1964–1966 and 40 out of 45 in 1945. No clear trend can be seen in the diagram, except that the period 1943 to 1947 was a rich flowering period and the periods 1948 to 1952 and 1964 to 1971 were poor ones. Flowering shoots have occasionally been picked from the plot, but as a rule the individuals have survived this treatment.

Dactylorhiza sambucina has also been observed in another type of vegetation, a "Sesleria meadow" about one m above sea level. Five plots were laid out here. The results of the observations are presented in Fig. 3. Plots No. 18, 19, and 20 lie close together. For a long period almost all individuals survived (those marked as dying in Plot No. 19 all occurred in a cluster of large and small specimens, where it was difficult to ascertain the identity of each individual).

Towards the end of the observation period, there was a decrease in both the number of individuals and the flowering frequency of the species. It was not possible to revise the plots regularly after 1957, but the flowering frequency was low in the years 1958, 1959 and 1961. In 1963, only three individuals survived in plot No. 18 and none in the others (the marking sticks of plot No. 22 were, however, lost and plot No. 21 had suffered considerable damage from trampling). One flowering individual of *Orchis mascula* was observed within plot No. 19 in 1968 and 1969.

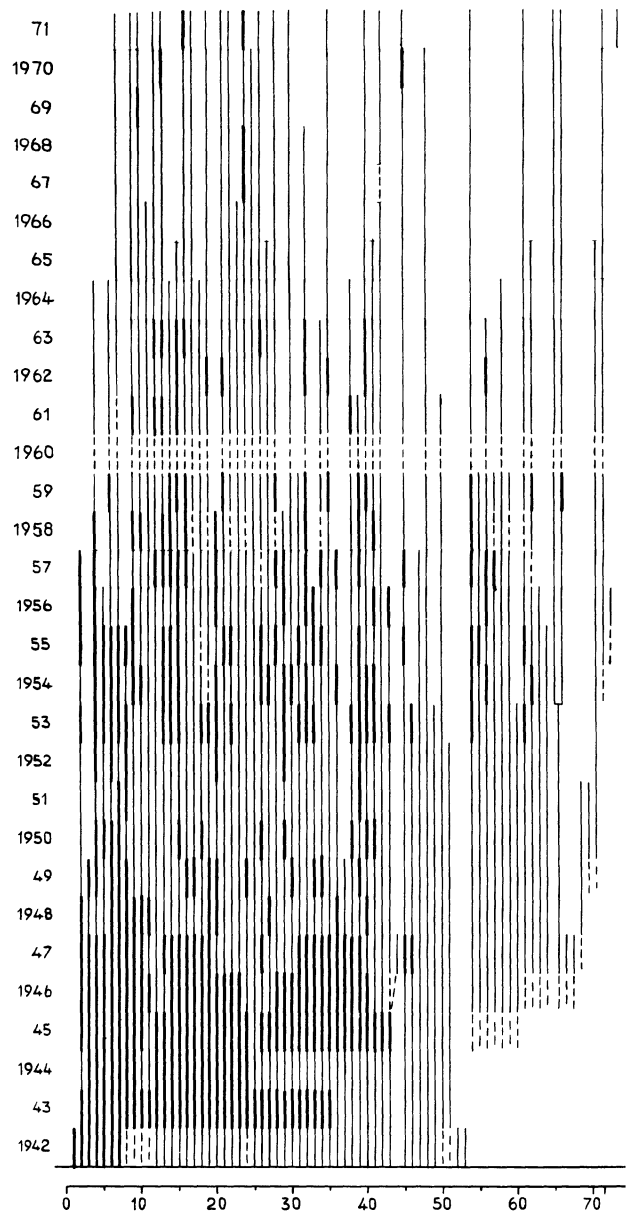


Fig. 2. The behaviour of *Dactylorhiza sambucina* on plot 17 (dry wooded meadow). Symbols as in Fig. 1.

It appears that the environment has now become less favourable for *Dactylorhiza sambucina*, and the most likely explanation is that the competing vegetation has increased successively; the area was originally a hay meadow (Tamm 1956), then grazed until 1943, left without treatment until 1948 and then again mowed until 1956. After this year haymaking could not be continued, and the field layer is growing denser, except where the shade has become too intense.

It should be mentioned that no very thorough search has been made for new plants, except at plot No. 17, where some of the revisions have been rather detailed.

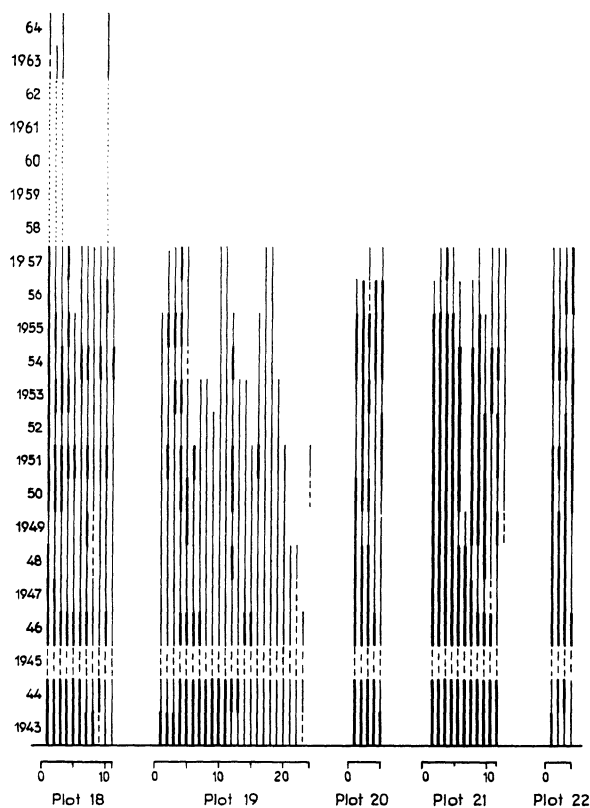


Fig. 3. The behaviour of *Dactylorhiza sambucina* on plots 18–22 (mesic wooded meadow). Symbols as in Fig. 1. Plots 21 and 22 were damaged and not studied after 1957.

2.3. *Orchis mascula*

As mentioned earlier (Tamm 1948), this species has shown a very irregular flowering in the area, with “new” specimens flowering in places where no individuals had been observed for several years, and then disappearing completely after one or more years. This irregular behaviour was confirmed, as regards flowering, by the earlier observations on a permanent plot, but most of the specimens observed survived the first period of observation (1943–1947). From 1948 onwards, however, there was a continuous decrease both in number of individuals and in flowering frequency (Fig. 4). In 1956 only seven specimens were observed, and at later examinations none of these were observed; thus the plot now appears to be devoid of *Orchis mascula*, although the species still occurs and flowers in the neighbourhood, irregularly as before.

The vegetational changes in this plot appear moderate from 1943 to 1958, but the shade from the surrounding ashes and alders has increased during the period.

2.4. *Listera ovata*

Listera ovata has been followed on a plot (No. 48) close to plot No. 24 with *Orchis mascula*, and rather similar

to it. The shade of ashes and alders is more intense on plot No. 48, and has increased during the observation period.

The morphology of *Listera ovata* differs from that of the other orchids studied. As mentioned before, there can be doubt about the identity of certain specimens, which may be either those recorded one or more years before, or new ones, budding from rhizomes. In most cases, however, the position and size of the specimens make identification possible (or unlikely). A few of the new individuals may originate from seedlings, but according to the observations, the normal propagation is vegetative.

Listera ovata is apparently a species favoured by the conditions prevailing on plot No. 48, including the increasing shade (Fig. 5). The number of individuals in 1944 was 22, of which 12 were flowering. In 1969, 25 flowering and 28 sterile individuals were counted. The flowering frequency varied from one out of 35 in 1956, to 25 out of 34 in 1958. Some of the years with high, or low, flowering frequency in *Listera* were also high, or low, in *Dactylorhiza sambucina* (Fig. 2), but the agreement is by no means complete.

3. Discussion

The observations reported here confirm the impression obtained from the observations on other meadow plants in the previous publication (Tamm 1956). The vegetation of the meadows seems to be slowly changing, due to changes in land use. In spite of this instability of the vegetation, there seems to be little opportunity for propagation by seed, at least in the species studied. The individual specimens, especially if they are vigorous, have often a marked ability to survive for a long time.

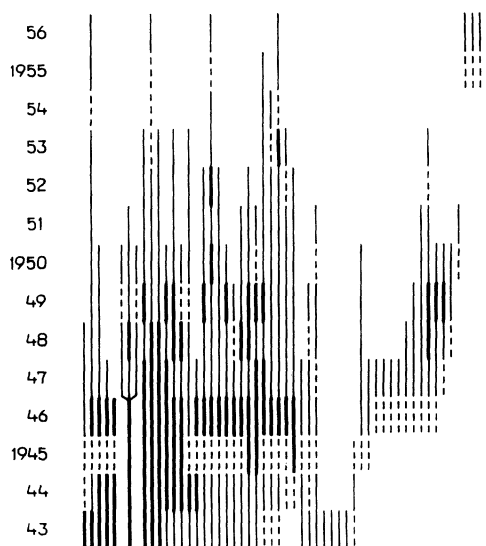


Fig. 4. The behaviour of *Orchis mascula* on plot 24 (mesic wooded meadow). Symbols as in Fig. 1.

It is not uncommon that an individual is recorded as lacking in one year, and then reappears in the next year. The writer attributes much of the irregularity to the activity of snails (or other animals), which preferentially consume orchid leaves. Another possibility is that the orchids may go back to a subterranean life for one or more years (see Wells 1967). It is well known that many orchids have a juvenile stage with mycorrhiza but without green leaves. It is possible that snail activity also is responsible for the relatively rapid decrease in e.g. *Orchis mascula* occurrences within plot No. 24.

The remarkable stability of some of the forest vegetation reported in the previous publication has not been confirmed for the meadow orchids dealt with here. The highest degree of stability was found in the dry meadow plot No. 17, where *Dactylorhiza sambucina* showed only small changes during most of the observation period. Harper (1967) has made an interesting analysis of some of my earlier data (Tamm 1956), using a simple mathematical method. The logarithms of the numbers of individuals surviving in different years were plotted in a diagram, and Harper found straight-line relationships, meaning a constant death-rate, in the case of *Sanicula europaea* L., *Filipendula vulgaris* Moench., and *Centaurea jacea* L. The half-life was > 50 years in *Sanicula*, 18.4 years in *Filipendula*, and 1.9 years in *Centaurea*.

Figs. 6 to 8 present the data from Figs. 1 to 5 in the same way as in Harper's diagram, viz. logarithmic numbers of survivors plotted against time. It is evident from the diagrams that the orchids studied here show more irregular occurrences than the herbs mentioned above. *Listera ovata* is a possible exception, with a very long half-life (Fig. 8). A minor disturbing factor in all the diagrams is the previously mentioned reappearance of individuals observed earlier but absent for one or two years.

A feature common to Figs. 6 to 8 is a long or short period having small changes in numbers of survivors, followed by a period of more rapid decrease. Fig. 6 is of particular interest, as it shows a rapid decrease of the original population of *Dactylorhiza incarnata* from 1952 to 1957, followed by a new colonization in 1966–1967; the new population then decreased at least as fast as the old one (half-life ca. 2 years).

As the decrease in orchids on most plots must be ascribed to environmental changes, presumably associated with the changes in land use, it is by no means surprising that the decrease in number does not exactly follow a mathematical formula like radioactive decay.

The irregularity of the flowering of all the species studied in this paper is striking, although some plots with *Dactylorhiza sambucina* (No. 20 and 21) showed a high flowering frequency as long as the individuals survived. The causes of the variations in flowering are unknown, and can hardly be discussed on the basis of the present data. It seems probable that variations in weather conditions have an influence, although both direct and indirect effects (e.g. on degree of competition

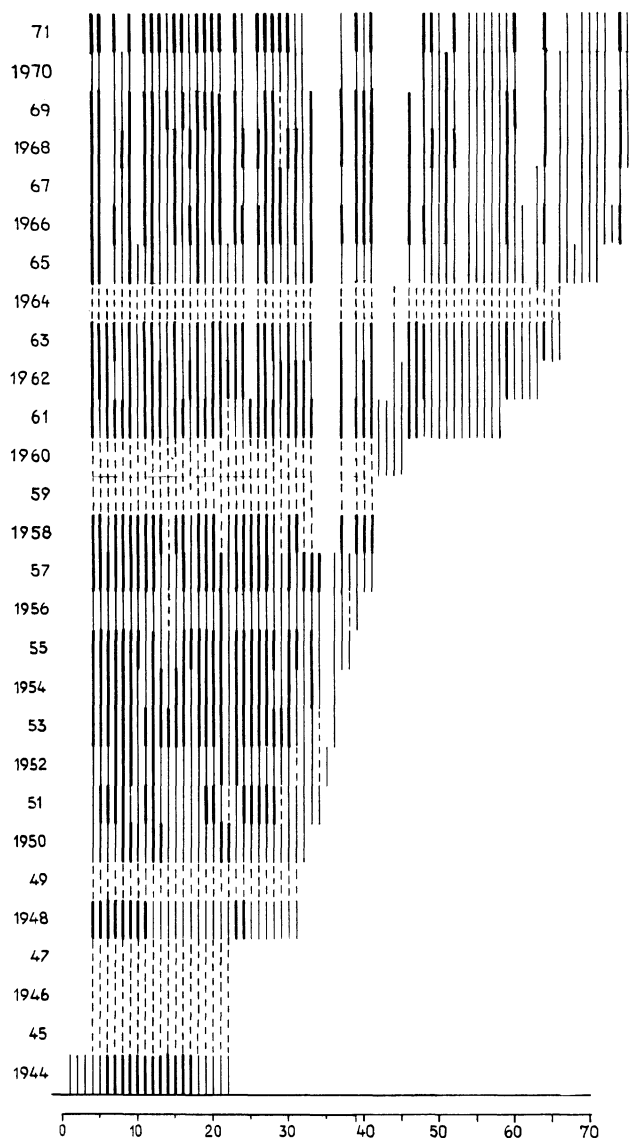


Fig. 5. The behaviour of *Listera ovata* on plot 48 (0.5 m × 0.5 m, mesic wooded meadow with almost closed canopy). Symbols as in Fig. 1.

or on mycorrhiza) are possible. Similar changes in flowering frequency of orchids have been described by Curtis and Greene (1953) and Wells (1967). The stability in the orchid population, described in a previous paper (Tamm 1948), was apparently a transient phenomenon, requiring a relatively constant environment. A statement which holds true is that reproduction by seed seems to be a slow process in closed communities, and that individual herb species may attain a considerable age. Observed maximum ages were 30 years in *Dactylorhiza sambucina*, 28 years in *Listera ovata*, 25 years in *Dactylorhiza incarnata*, and 14 years in *Orchis mascula*. To these figures should be added an unknown number of years before the observations started.

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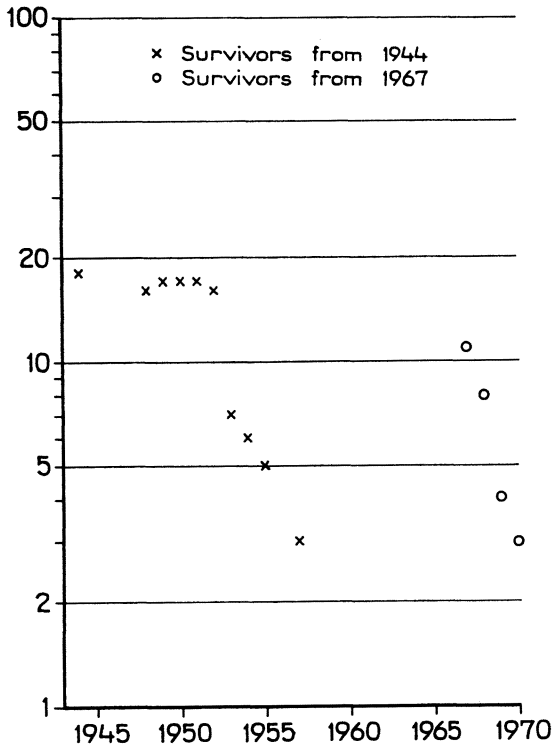
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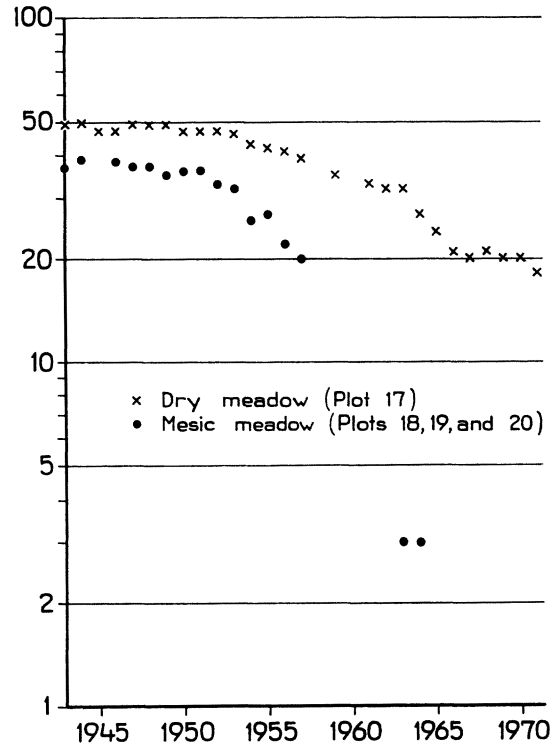
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Dactylorhiza incarnata



Dactylorhiza sambucina, survivors from 1943-44



• *Listera ovata*, survivors from 1948
 x *Orchis mascula*, survivors from 1943-44

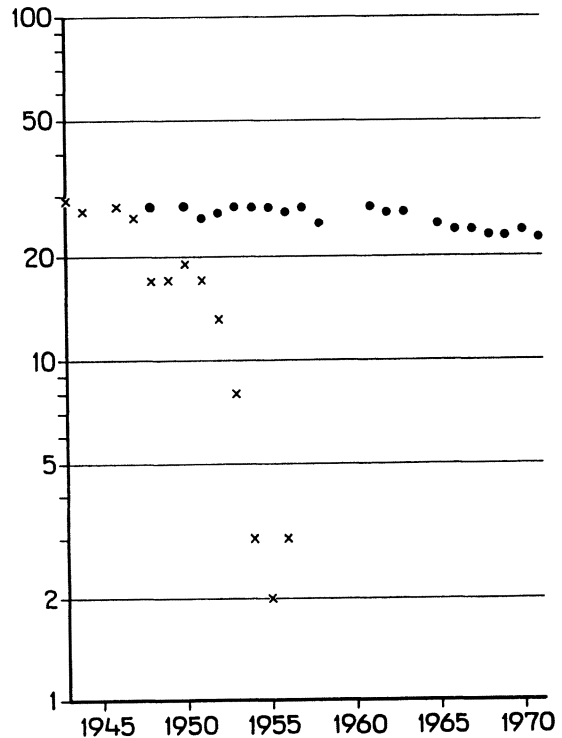


Fig. 6-8. Numbers of individuals surviving in different years on the various plots. Note logarithmic scale, according to which a constant death-rate would correspond to a straight-line decline. (Fig. 6: *Dactylorhiza incarnata*; Fig. 7: *D. sambucina*; Fig. 8: *Listera ovata* and *Orchis mascula*).