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Liquan Zhang

Vegetation Ecology and Population Biology of *Fritillaria meleagris* L. at the Kungsängen Nature Reserve, Eastern Sweden

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Abstract

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The Kungsängen Nature Reserve is one of the most important sites for the bulbous perennial Liliaceae *Fritillaria meleagris* L. Its occurrence in the wet meadows of this reserve was studied by means of numerical classification and ordination methods, which resulted in the establishment of five main plant community types. These community types were distinguished along an environmental gradient from mesic to wet, and the relationships between the variations in vegetation and in soil-water regimes were outlined. Differences in soil physical and chemical properties for each plant community type were also examined. The peak standing crop of these plant communities amounted to 340–585 g/m^2. The development of the vegetation over 40 years was investigated using Ellenberg's "ecological indicator values" as an aid in the interpretation. Changes in vegetation could be related to changes in the soil-water regime due to water management in the surrounding area and the management practice at the study area.

The population study of *Fritillaria meleagris* included population flux, distribution, phenology and dry matter allocation during the annual cycle, seed production, seed bank in the soil, seed germination characteristics and changes in the distribution of the fritillary population over 40 years in the study area due to changes in the soil-water regime.

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内容提要

張利權，1983. 瑞典东部Kungsängen自然保留地的植被生态学与欧洲贝母(Fritillaria meleagris L.)种群生物学研究

Kungsängen自然保留地是欧洲贝母重要的生长地之一。该植物是百合科具鳞茎的多年生草本。应用数量分类和排序方法，该保留地的湿草甸植被可分为五个主要植物群落类型。这些群落类型与土壤水分状况有密切的联系，是按从中生到潮湿的环境梯度分布的。本文也描述了这些植物群落的土壤物理和化学性质方面的差异。植物群落的生产量达每平方米340-585克。通过永久样地，比较了该保留地四十年前后的植被变化，并应用"生态指示值"给予了解释。其植被变化是与该保留地内土壤水分条件的改变和管理措施有关，而前者主要受周围地区水文条件的影响。

欧洲贝母种群的研究包括种群的消长和分布，物候学观察和年生活周期中的干物质分配，繁殖，土壤中种子的动态变化，种子萌发特征和由于土壤水分条件改变而导致的四十年前后种群分布的变化。

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My study at the Institute of Ecological Botany, Uppsala University began in September 1979. Hugo Sjörs (now emeritus) and Håkan Hytteborn (my supervisor) initiated this investigation and I wish to express my gratitude for their guidance, encouragement and never-failing interest throughout my investigation as well as for the critical scrutiny of the manuscript and many improvements and corrections. I also wish to thank warmly Eddy van der Maarel (head of the institute) and Erik Sjögren for valuable advice and comments during their critical examination of the manuscript.

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I would also like to express my sincere appreciation to my country, The People's Republic of China, and to the Department of Biology, East China Normal University, Shanghai, who enabled me to visit Sweden for further study and, finally, I extend my thanks to my colleagues in China and also to my family. My stay in Sweden would not have been possible without their enthusiastic support.

Institute of Ecological Botany, Uppsala,
September 1983
Liquan Zhang

Contents

1 Introduction

1.1 The study area

1.1.1 Location and size

The study was carried out in the Kungsängen Nature Reserve, which is part of a low-lying plain located 2–3 km south-east of Uppsala city, at a latitude of N 59°50′ and a longitude of E 17°40′. From the phytogeographical point of view, this area lies within the boreo-nemoral zone (Sjörs 1963). The Nature Reserve lies between the River Fyris and the road from the bridge Vindbron to Lilla Ultuna. The river and the road form its western and eastern borders, and agricultural land and pasture adjoin it on its northern and southern borders, respectively (Fig. 1). The total study area, which is fenced, is approximately 14 ha, of which 11 ha belong to the Nature Reserve. This reserve area was established in 1943, according to a proposal by Flodkvist, Sandberg and Sernander. Their objectives were conservation of the semi-natural wet meadow with respect to its slight topographical unevenness and continuous as well as typical zonation, including conservation of the large population of *Fritillaria meleagris* L. (Sernander 1948).

1.1.2 Geology and substrate

When the Quaternary ice sheet retreated northward, the Uppland district was 125–175 meters under the surface of the Yoldia sea. At that time the crustal uplift was quick, with about 3 meters per century, but later became slower. Nowadays, the average uplift in the study area is about 58 cm per century. Sediments deposited in the Baltic waters and later in the formerly much larger Lake Mälaren were gradually laid bare, beginning with glacifluvial gravels and sands, then moraine glacial clays and alluvial clays formed by re-deposition, and finally local lake and river deposits (Högbom 1935, Hofman-Bang 1938). The soil on the Kungsängen area mainly consists of alluvial clay which has formed through the River Fyris overfloodings in relatively late time. From a geological point of view, the soil is very young. The soil types are rather homogeneous and fertile with high humus and nutrient contents (Giöbel 1933). According to Westerberg (1899), the alluvial clay in the Kungsängen area shows the following mechanical composition:

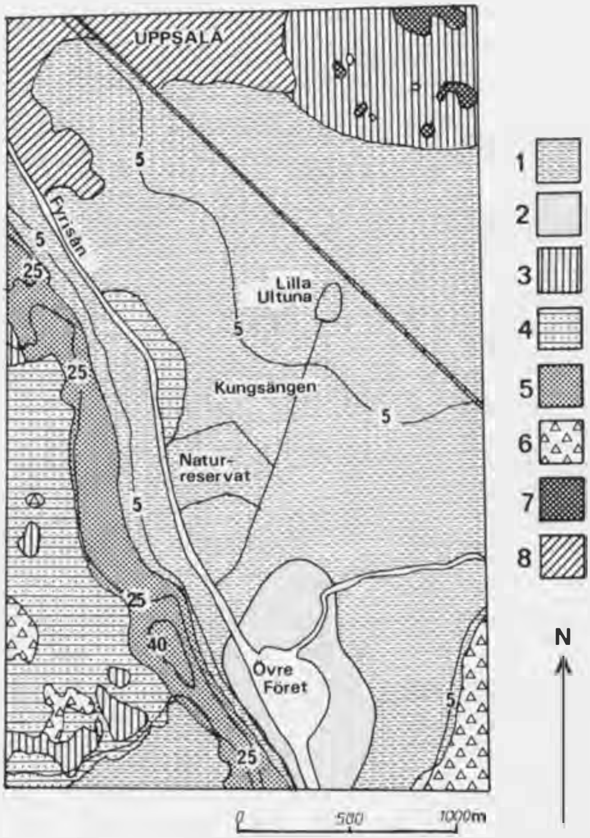


Fig. 1. Map showing the situation and soil type of the study area as well as the surrounding areas. Contour-levels in meters are drawn. Soil types: 1. Heavy clay, 2. Alluvial clay, 3. Glacial varved clay, 4. Sand and fine sand, 5. Glacifluvial gravel and sand, 6. Till (Moraine), 7. Oldest Archean granite, 8. Urban area (Uppsala). Redrawn from SGU's Jordartskarta Ser Ba Nr 15, 1956.

Coarse gravel–coarse sand	0.0%
Sand	11.3%
Fine sand	22.2%
Silt	20.8%
Clay substance	22.9%
Calcium carbonate	0.1%
Loss on ignition	10.7%
Hygroscopic water	4.6%

In the eastern part of the area, the alluvial clay contains much "gyttja" which has an acid reaction owing to its high sulphur content (Giöbel 1933).

Big crack systems occur in the subsoil but cannot be seen on the surface. They play a considerable role in this area. For this reason, most parts of the area are self-drained (Giöbel op. cit.).

1.1.3 Topography

As can be seen from Fig. 2, the topography of the Kungsängen plain is slightly uneven with continuous, typical zonation according to frequency and duration of floods and amount of sedimentation. Of the whole study area, about 11 ha are covered by wet meadow vegetation and about 3 ha by swamp vegetation in the depressions, the latter coinciding approximately with the area below the 1.40 m contour. The levelling of the study area was carried out during the summer of 1981, with levelling point No. 653 (Statens Lantmäteriverk, Topographical map III, Uppsala) in the Swedish precision system of 1970 as a reference. The whole study area is at an altitude of only 0.90–2.40 m above sea level.

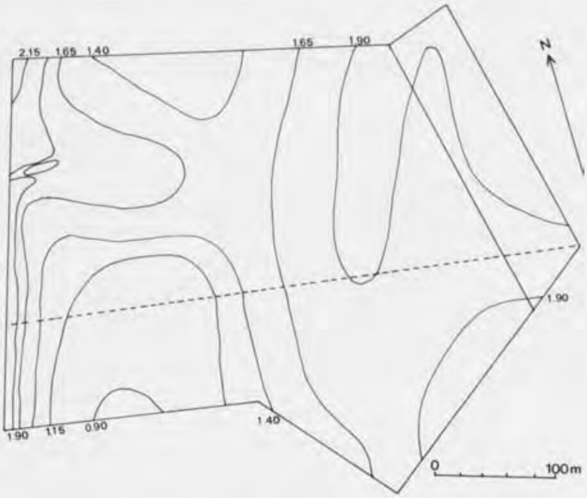


Fig. 2. Topographical map of the Kungsängen Nature Reserve in the Swedish precision levelling system of 1970. Redrawn from Sernander (1948). The dashed line indicates the vegetation transect used by Sernander and Sandberg.

1.1.4 History and management

Before the seventeenth century, most parts of Kungsängen were permanently under water (Rudbeck in the Atlantica's first part, 1679, Nelson's edition 1937, see also Sernander 1948). From the four maps of the 17th, 18th, 19th and 20th centuries a slow development from open water or waterlogged areas to meadows for hay-making or pastures can be seen. Kungsängen (literally meaning The King's meadow) was early used for supplying fodder for the royal stable. At that time, the hay mainly consisted of horsetail (*Equisetum fluviatile*), sedges (*Carex* spp.) and other wetland plants (Hebbe 1936). Through the general uplift, the sedimentation due to the floods and the progressive succession of plant communities, an *Alopecurus-Deschampsia* wet meadow was developed on most of this area, except for some depressions where the swamp vegetation became dominated by *Carex* species and other wetland species. Historical cultural factors are also of importance for the continued existence of these ecosystems. According to Sandberg's investigation (1948), if the mowing and grazing was discontinued, most of the Kungsängen area would develop into forest, mainly of alder (*Alnus glutinosa*), or wetland thicket. So in order to maintain the reserve area and to keep the present plant communities more or less stable, yearly mowing or grazing is necessary.

Since the seventeenth century, the development of the area has been well-known due to the plentiful documentation (Hebbe 1936). The reserve area has been used for hay-making only. From the nineteenth century, it has been managed by what now is the Swedish University of Agricultural Sciences. Most of the reserve area, except the swampy parts, is mown yearly around midsummer, i.e. about June 20, but the hay-making may be delayed one or two weeks depending on weather conditions. The variation in the yield of hay during 1877–1929 was estimated at 731–3,828 kg/ha

(Giöbel 1933) and the yield of hay nowadays is about 2,799–3,200 kg/ha per year (Tomas Hedenskog, pers. comm.). About 30–50 head of cattle are put to graze on the "aftermath" for about one or two months from July to September. The reserve area is never fertilized.

For the years of the present investigation, the mowing in 1981 was on June 22, but the hay was collected on July 6, and grazing started on July 8. In 1982, mowing was on June 18, hay was collected on June 24, and grazing began on July 1. In 1983, mowing was on June 16 and hay was collected on June 21.

1.2 Climate

Climatic conditions play an important role for plant and vegetation. A review of such conditions concerning the Kungsängen Nature Reserve is presented below. The nearest meteorological station which records temperature, precipitation, irradiation, humidity and evapotranspiration is the Ultuna Meteorological Station, run by the Department of Plant Husbandry of the Swedish University of Agricultural Sciences, which is located at an altitude of 10–15 m above sea level and 2–3 km south of the study area.

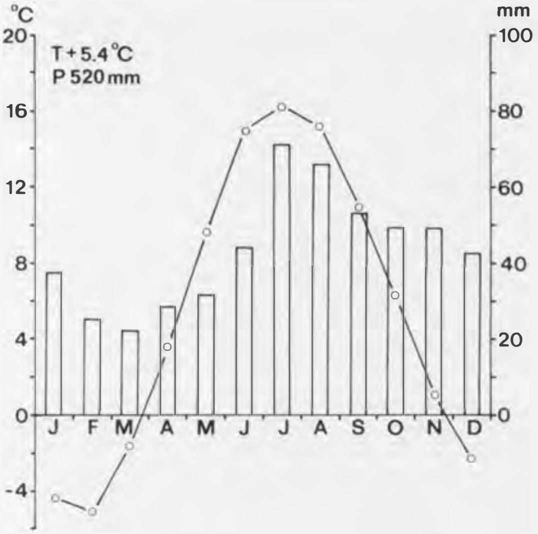


Fig. 3. Mean monthly temperature and precipitation at Ultuna 1951–1980 (from the Ultuna Meteorological Station).

Table 1. Growth period expressed as number of days with mean temperature above certain temperatures and the total solar radiation over the same periods. Mean temperature at Ultuna 1951-1980 and mean radiation at Ultuna 1963-1980.

Criterion	Period	Days	Kcal/cm^2
> 0°C	25 March – 25 November	245	73.1
> +3°C	11 April – 4 November	207	68.0
> +6°C	28 April – 17 October	173	61.9
>+10°C	17 May – 21 September	127	50.2

1.2.1 Temperature

In Fig. 3 some information is given on the general temperature conditions at Ultuna, Uppsala. The mean annual temperature for the period 1951–1980 was +5.4°C; the warmest month was July with +16.3°C and the coldest was February with −5.1°C. The amplitude was, thus, 21.4°C.

1.2.2 Growth period

The number of days with a mean temperature above different temperature criteria is given in Table 1. These temperatures have been considered as suitable temperature limits for the growing period. The frost-free period (number of days with minimum temperature above 0°C) is commonly used. In Sweden the growing period has been defined on an agricultural basis and duration of the period with daily mean temperature above +3°C is used (Atlas över Sverige 1953: 27–28). For the Ultuna area this corresponds to approximately 207 days, coinciding, on average, with the period April 11 – November 4. These dates have been obtained from a graph which was drawn from the mean monthly temperatures for the period 1951–1980, according to Langlet's method (1936).

The mean number of days per year with frost (days with a minimum temperature below 0°C) during the period 1963–1980 amounted to 152 at Ultuna. Thus, 213 days were frost-free, but only the month of July was entirely free from frost throughout the years.

1.2.3 Irradiation

The data on the solar radiation are obtained from the Ultuna Station. The mean monthly values for the period 1963–1980 are given in Fig. 4. The annual total amounted to 81.4 Kcal/cm^2 with the

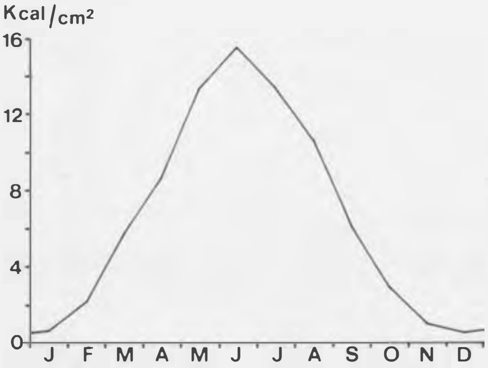


Fig. 4. Mean monthly values of irradiation at Ultuna for the period 1963–1980.

highest monthly value of 15.6 Kcal/cm^2 in June and the lowest value of 0.5 Kcal/cm^2 in December. The irradiation totals measured at Ultuna for the respective growth periods defined by different temperature criteria are presented in Table 1.

1.2.4 Precipitation and snow conditions

The average annual precipitation during the period 1951–1980 amounted to 520 mm at Ultuna. The mean monthly precipitation for the same period is shown in Fig. 3. Late winter and spring were characterized by low precipitation, approximately 30 mm per month, while a precipitation maximum occurred during the months of July and August, with 71 mm and 66 mm respectively. These conditions are typical of most of Sweden.

The mean number of days per year with snow cover (>0 cm) during the period 1963–1980 amounted to 104 at Ultuna. Both precipitation and snow conditions differed considerably from year to year.

1.2.5 Humidity index and evapotranspiration

There are many ways to describe the degree of climatic humidity, i.e. effective surplus of precipitation. According to the Martonne's method (see Hesselman 1932: $H = P/(T + 10)$, where P = annual precipitation in mm, T = annual mean temperature in °C), a humidity index of 34 is obtained, which is fairly low for Swedish conditions.

Surplus of precipitation over evapotranspiration, i.e. run-off, has been suggested as a suitable measure of climatic humidity (Tamm 1959). If run-off is used as a humidity index, according to Tamm's formula 1 (Tamm op. cit.), a value of 164 mm is obtained for the period 1931–1960 for Uppsala, which refers to a mildly humid region with a yearly run-off of 100–200 mm. Wallén (1966) has calculated the potential evapotranspiration (ETP) by applying the Penman formula (Penman 1963) and arrived at a mean value of 541 mm for Uppsala during the period of 1931–1960. According to the value given by Wallén (1966), the yearly theoretical water balance was slightly positive, +13 mm for Uppsala. But from the agricultural point of view, the evapotranspiration during the growing season is of more practical interest. The potential evapotranspiration and precipitation during the period April–October (period 1931–1960) for Uppsala were 516 mm and 365 mm respectively, the theoretical deficit during the main growth period thus being 151 mm on average.

2 Classification and ordination of the vegetation

The vegetation of the Kungsängen Nature Reserve was investigated by means of the Braun-Blanquet approach (Westhoff & van der Maarel 1978). Numerical classification and ordination have been proved to be powerful tools in vegetation ecology (van der Maarel 1979). Such methods were applied in the present studies of the vegetation in this reserve. Classification and ordination are complementary and can be combined in various ways for studying and understanding plant communities and their relationship to the environment. In many cases ordination results can clarify obscure units of classification, identify the important environmental trends and provide deeper insights in the relations between community types and their environment (Whittaker 1978, van der Maarel 1979).

The aims of this investigation were to recognize the major plant community types in terms of their species composition and to relate the observed variations in the distribution and composition of the vegetation to the variations in the environmental factors. Furthermore, on the basis of these identified community types a vegetation map was prepared for further detailed research on vegetation in the study area.

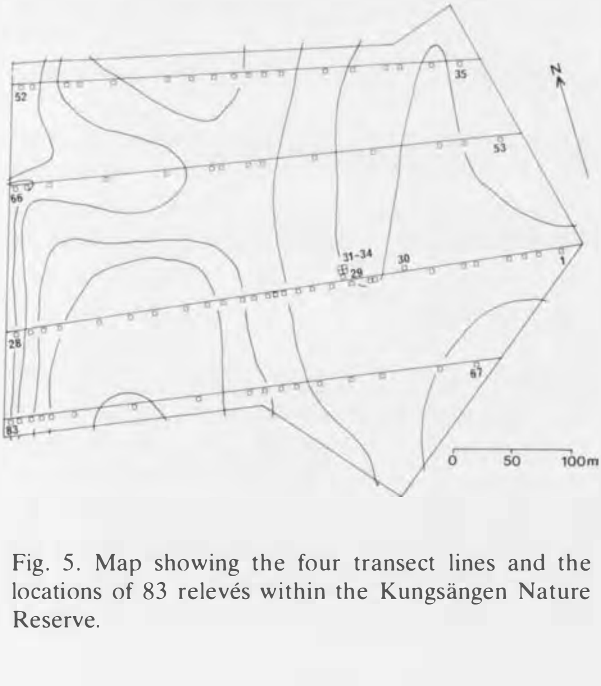


Fig. 5. Map showing the four transect lines and the locations of 83 relevés within the Kungsängen Nature Reserve.

The earlier phytosociological study on this reserve was presented by Sernander (1948) and Sandberg (1948) who gave the first general description of the vegetation by using a transect through the zonation of vegetation in the study area. In this study, the vegetation of the whole area was surveyed on the basis of Braun-Blanquet "typological relevés" (a typological relevé is meant to be used as a basis for a typology, i.e. a classification) (Westhoff & van der Maarel 1978). A more comprehensive analysis of the vegetation was attempted here.

2.1 Methods

2.1.1 Sampling procedure

Sampling was preceded by field reconnaissance and by reviewing the literature as well as a topographical map and an aerial photograph, which all aimed at determining the major trends in the vegetational variation. Four transects were laid out on the reserve area. They were run in parallel from east to west and covered the most representative zones of the vegetation as deduced from field reconnaissance and the topographical map (Fig. 5). A subjective "stratified" sample selection was adopted which, according to Westhoff & van der Maarel (1978), would be desired to effectively represent the variation in the vegetation under study. This sampling approach assumed that by sampling all recognizable habitats and vegetation types, the responses of plants and plant communities to the environment could be represented.

Eighty-three relevés were spread along these four transects, the vegetation being sampled at 50 m intervals or wherever there were readily apparent changes in its physiognomy, composition or habitat. All potential sampling locations were inspected for homogeneity. The size of samples was 2×2 m, which was earlier considered to be the minimal area with regard to these types of meadow vegetation (Du Rietz 1921, Sandberg 1948). The relevés were made during the middle of June, 1982. The lists of phanerogams (cryptogams were of little importance) were recorded for each relevé and taxa occurring just outside the sample plot were noted in parentheses. The quantitative occurrence of each taxon was estimated as a cover value. The five degree scale of Hult-Sernander-Du Rietz was used. This scale is traditionally used in Sweden and has the following degrees: 5 (100%–50%), 4 (50%–25%), 3 (25%–12.5%), 2 (12.5%–6.25%) and 1 (less than 6.25%). Nomenclature of phanerogams is according to Lid (1974). The vegetation data set for numerical classification and ordination consisted of 83 relevés and 78 taxa.

2.1.2 Classification

The following classification techniques were applied: the TABORD program, which performs agglomerative clustering of relevés and is based on relevé similarity combined with a procedure for obtaining a diagonal structure in the table presenting clusters arrived at (van der Maarel et al. 1978). The resemblance measure used is the similarity ratio (Wishart 1969):

$$S_{X,Y} = \frac{\Sigma X_i Y_i}{\Sigma X_i^2 + \Sigma Y_i^2 - \Sigma X_i Y_i} \quad (i = 1,2, \ldots, n)$$

where X_i and Y_i are the scores of the species i in the relevés X and Y, and n is the number of species.

A polythetic divisive clustering approach was performed with the TWINSPAN program (Hill 1979). It is a Two-Way-Indicator-Species-Analysis program based on Reciprocal Averaging.

2.1.3 Ordination

The ordination of the samples was performed by means of Principal Component Analysis (PCA; Orlóci 1978) and Detrended Correspondence Analysis (DCA; Hill & Gauch 1980). The PCA was performed with the ORDINA program (Roskam 1971) based on Orlóci's method with the square root of the Euclidean Distance (ED) normalized by the number of species as resemblance function. DCA was performed with DECORANA program (Hill 1979). The particular attraction of DCA is that it simultaneously produces ordination results for both species and relevés.

2.2 Results

2.2.1 Stand classification (TABORD)

The final structured table with 83 relevés and 78 taxa as presented in Table 2, was based on an automatic initial array of 10 clusters, with options: threshold value 0, frequency limit 0.50 and fusion limit 0.70. No clusters with less than three members were allowed, which resulted in six clusters. The sequence of clusters in the final table was improved manually according to the PCA-configuration run with the same relevé data set. The sequence of species reflected the diagonal structure in the table. All six terminal clusters showed a high internal homogeneity, with average similarity values over 0.70. Between clusters similarities were relatively low. The next two possible fusions were: cluster 1 and 4 at level 0.66, and cluster 3 and (1+4) at level 0.68. Further fusions were all at much lower levels (less than 0.40) and were not taken into account. These six clusters could be interpreted as subassociations and the four-cluster solution could be interpreted on an association level (van der Maarel 1979). However, because there are few reference tables and working syntaxonomy systems available for Fennoscandia (Tyler 1979), a syntaxonomical assignment of the data was difficult for the moment.

On closer inspection of this final table, five plant community types could be recognized with their own character-species and differential-species combinations. They were also well separated in space and showed certain physiognomical characters.

Plant community type D (Fig. 6) occurs in the depressions within the reserve area. It is characterized by a tussocky vegetation with a dominance of *Carex acuta*. The vegetation is poor in species, with an average of 8 species per relevé. *Lemna minor, L. trisulca, Lysimachia thyrsiflora, Equisetum fluviatile* are presented in more than 50% of the relevés and can be used as the differential species for this community type. The height of the tussocks is

Table 2. Structured table of the Kungsängen Nature Reserve relevés, obtained with TABORD. The resulting 6 clusters are arranged according to the PCA-configuration presented in Fig. 11. An automatic initial array of 10 clusters with options: threshold 0, frequency limit 0.50 and fusion limit 0.70 were applied.

Relevé Number	12222224447777711144456772488111455677000001112233333334455556666666780000233355568
	90123454565678967837890346901345208112567890127901234890115672345789021234856723463
Cluster Number	00000000000000011111111110000000000000000000000000000000000000000000000000000000000
	55555555555555500000000002222333333333444444444444444444444444444444441111111111111
Community type	D C E B A
Equisetum fluviatile	11111------111---
Lemna minor	1111111----111---
Lemna trisulca	1111111----111---
Lysimachia thyrsiflora	-111111----1111------------1---
Carex acuta	5555555455455551121211-121-1---------1---
Polygonum amphibium	1111111111111111111-11-11111-11111111111-----1------1--11--1111---111------11------
Agrostis stolonifera	---------------11-1-11111-1---111-1112------------------1-----------1-----------1--
Lysimachia nummularia	---------------11-1-11111-1--111111111------------------1---1------11-------------1
Potentilla anserina	-------111-----11-1-1--11-----11----11---------------------------------12-------1--
Alopecurus arundinaceus	1------1--1---1-141-1--111-21--
A. pratensis x arundinaceus	-------1-------11-1-1111111-11211111-1--------1----------------------1-------------
Carex caespitosa	------1-------11----111125544-1211-1-1--------2------------------------------------
Carex disticha	1-----111-----15525455535111--1211111--
Carex sp.	---------------11-111111111--------1----------1------------------------------------
Deschampsia caespitosa	---------------11-1-1213111113323133445532223312222331312112212122132123431133-131-
Festuca rubra	---------------21-1--211-11-133212222111121112211111132221223111144331---1--11--1--
Poa pratensis	---------------1--1--1111--11111-11111111111111111111111121111222211114332223224-22
Filipendula ulmaria	------1--11---1111--111112112111111211--1---112----1-11111--12211---12----1--11--11
Galium uliginosum	---------------11-1-11111111111111111-11--11-1111111--11--1111----111--------------
Arrhenatherum pubescens	-------------------------1--1111-1---11133221121211112211221222122112----1-------11
Phalaris arundinacea	21----1---1------1-1----11-11--
Caltha palustris	1-----1---1---1--11------1-1---
Galium boreale	-------------------------1--11---1-------11--11--11--111-111111111---1----1---1--11
Galium palustre	1--1---111-1-------11---1-11---
Taraxacum sp.	---------------------------111---1-------11111-11----2-1-1111211121--12121122212111
Thalictrum flavum	------1---1---1-----1-1--11--
Alopecurus pratensis	---------------------11---1-1211232211222234322453332322342223333343334433544354355
Fritillaria meleagris	-------------------------11-1111-1-11-11111111111111111111111111111111--1111-11--11
Geum rivale	---------------1-----111-11--111111111-1111111111111111111111111111111----1-------1
Lathyrus pratensis	---------------1-----11--11-111111111111111111111111111111111111111111----11111--11
Ranunculus acris	---------------1-----111-11-1111111111111111111111111111111111111111111111111111111
Ranunculus auricomus	---------------1-----111-1111111111111-11111111111111111111111111111111111111111111
Vicia cracca	---------------11---111--111111111111111111111111111111111111111111112111111112-122
Ranunculus repens	----------1------------11-1---1-11-1-1----------------------------111--1121-1---1--
Cardamine pratensis	---------------------1111-1--111--1111--111-11-----1--11-111111--111---------------
Trifolium pratense	------------------------------111----11--11111111111--1111121-111111111-----1---11-
Trifolium repens	---------------1------1------1111-1-111111111111122--2111211-1113222111111-111-121-
Alchemilla sp.	---111--111111-11--1-1-11111---1----1------11
Galium verum	---1111--1-11-1-1--1-1111111---1----1---1--11
Glechoma hederacea	--------------------------------------111--1---11111111---11---1-1111---11-1---1---
Rumex acetosa	----------------------------11---1-1--111121111111111111-122-221122111----1--1----1
Veronica chamaedrys	---1111--11111111--111-1111111-1-------111-11
Festuca pratensis	---------------------------------------1-11111-11111111111111--11111-1--111--111111
Phleum pratense	-------------------------------------1-111111--121221111111121111111111111211121121
Poa trivialis	-----------------------1---1-------11-11111111111111111111111-11112111-1111--1--1-1
Achillea millefolium	--------------------------------------1111111--111111111-111---1131--11111111111-11
Anthriscus sylvestris	---111----111-111--111--1111---111--12--23-21
Cerastium caespitosum	-------------------------------------11--11111--1111--211-11111-111111-1111111-11--
Stellaria graminea	---------------------------------------1111111--11111111---11----1111-1111-111-11--
Agropyron repens	--1-----------------11---13211321-22132
Capsella bursa-pastoris	--111111---11--
Matricaria inodora	--11-1-111-11--
Plantago major	--------------------------------------1--------------1----------------1111--11-11--
Equisetum sp.	--1----
Iris pseudacorus	------------------------1--
Urtica dioica	--11--11-11
Veronica sp.	---1---------1----11-------11---11---1--1--
Stellaria palustris	---------------------------------1-------------------111----------1111-111---1-11--
Saxifraga sp.	---11--11---1-----1--------
Ranunculus sceleratus	1---------1------1---------1---
Ranunculus polyanthemus	1---------1------1-----1---
Potentilla reptans	--1----------------1-
Polygonum aviculare	--1-11--11--1--
Oenanthe aquatica	11--------11---
Matricaria matricarioides	---1----------------111----1-11--
Lotus corniculatus	---11---------1--------
Leontodon autumnalis	---1----------------11--11--1--
Heracleum sphondylium	---1------1---------1---1--12
Galeopsis sp.	---1-1---1---
Cirsium vulgare	--1-11-----1----11---111--1---1--11
Carum carvi	---111---1111111---1---11--------------------
Arctium sp.	---2---
Alisma plantago-aquatica	1--
Scirpus palustris	--------11-------------1-------------------------------------1---------------------
Poa annua	---1----1--1-11--1---
Glyceria maxima	-1--------311--
Dactylis glomerata	---11--1-1---111--------11--12-21
Briza media	--1----------------1-

Fig. 6. View of the *Carex acuta* plant community in the Kungsängen Nature Reserve. —Photo. Author. June 1982.

20–50 cm as measured from the soil surface between the tussocks up to the top of the aerial rhizome trunk of the tussock. The size of these tussocks is 20–40 cm in diameter. The distance between them is 30–60 cm. The surface of the interspaces is almost inundated for most of the year. However, the sites with the *Carex acuta* community lack a bryophyte layer and do not contain peat (highly organic material accumulated under anaerobic conditions). These sites would be called wetland instead of more specifically fen (Sjörs 1971). When the vegetation is fully developed (June–July), the height of the sedge is 70–100 cm, the vegetation cover is more than 75% and the interspaces are almost completely shaded by the overhanging sedge leaves. It is a tall-sedge community. Associated with the tussocks are the species: *Galium palustre*, *Potentilla anserina* and *Polygonum amphibium*. In the interspaces there is a rich growth of floating-leaved water plants, e.g. *Lemna minor* and *L. trisulca*. On a few places (not covered by the relevés), *Glyceria maxima* occurs

Fig. 7. View of the *Carex disticha* plant community in the Kungsängen Nature Reserve. —Photo. Author. June 1982.

Fig. 8. View of the *Carex caespitosa* plant community in the Kungsängen Nature Reserve. —Photo. Author. June 1982.

with relatively high cover values; for example in relevé 75 this species has a cover value of 3. On the edges of these community sites, the following species are found: *Alopecurus arundinaceus, Phalaris arundinacea, Thalictrum flavum, Ranunculus sceleratus, Oenanthe aquatica, Caltha palustris, Carex caespitosa, Carex disticha, Scirpus palustris* and *Filipendula ulmaria*, etc., all with low frequencies and cover values.

Plant community type C (Fig. 7) mainly occurs around the depressions. The boundary between plant communities C and D is rather sharp and within a few meters the vegetation changes. This community type is characterized by the dominance of *Carex disticha*. The height of the vegetation is 30–50 cm when fully developed. It is a low-sedge community. The average number of species per relevé is 16. *Alopecurus arundinaceus, Deschampsia caespitosa, Festuca rubra* and *Carex acuta* are frequent in this community. *Agrostis stolonifera, Alopecurus pratensis × arundinaceus, Poa pratensis, Galium uliginosum* and *Lysimachia nummularia* are frequent species and may be usable as differentiators for the *Carex disticha* community in relation to community D.

Plant community type E (Fig. 8) is based on only four relevés. This community occurs mainly around the western part of the depressions with a similar topographical position as the *Carex disticha* community type. It is, however, characterized by a tussocky sedge vegetation with the dominance of *Carex caespitosa* and abundance of *Filipendula ulmaria*. The height of the tussocks is 15–30 cm and their size is 20–40 cm in diameter. The tussocks are rather widely separated, ranging from 30 to 100 cm. The vegetation cover in the interspaces is very low and during the winter and early spring the soil surfaces are flooded and covered with dead plant material. The average number of species per relevé is 20. The problem encountered with the description of the tussocky vegetation has been the fact that the habitat conditions are completely different between the tussocks and the interspaces and their species composition differs considerably (cf. Andersson 1970 a, Regnell 1980). The tussocks are relatively rich in species. Associated with the tussocks are: *Polygonum amphibium, Geum rivale, Fritillaria meleagris, Lathyrus pratensis, Ranunculus acris, R. auricomus* and *Vicia cracca*, all with a low cover value. The interspaces are characterized by *Filipendula ulmaria, Alopecurus arundinaceus, A. pratensis × arundinaceus, Phalaris arundinacea* and, less frequently, *Caltha palustris* and *Thalictrum flavum*.

Plant community type B (Fig. 9) is composed of clusters 3 and 4. This community type occupies the largest part of the reserve area and is at a relatively high topographical position. It is characterized by the abundant species *Alopecurus pratensis, Deschampsia caespitosa, Arrhenatherum pubescens,*

Fig. 9. View of the *Arrhenatherum pubescens—Alopecurus pratensis* plant community in the Kungsängen Nature Reserve. —Photo. Author. June 1982.

Poa pratensis and *Festuca rubra*. The height of the vegetation is 40–100 cm when fully developed. The number of species per relevé, on the average, reaches 26 and the vegetation is rich in species especially herbs. *Lathyrus pratensis, Geum rivale, Ranunculus acris, R. auricomus, Vicia cracca, Rumex acetosa, Fritillaria meleagris, Trifolium pratense, T. repens* and *Galium uliginosum* are frequent. *Arrhenatherum pubescens, Fritillaria meleagris, Rumex acetosa, Geum rivale* and *Trifolium pratense* may be usable as differentiators for this plant community in relation to communities A or C and D.

Cluster 3 in this community represents a transition towards the *Carex disticha* community type, which shares many species with clusters 4 and 10. As clusters 3 and 4 share the same character species such as *Alopecurus pratensis, Deschampsia caespitosa, Arrhenatherum pubescens, Poa pratensis* and *Festuca rubra* and at a level yielding four clusters, cluster 3 is at once fused with cluster 4. It is, thus, reasonable to group them into community type B.

Fig. 10. View of the *Poa pratensis—Alopecurus pratensis* plant community in the Kungsängen Nature Reserve.—Photo. Author. June 1982.

Plant community type A (Fig. 10) follows from cluster 1. This community occurs on the eastern and western borders of the reserve area with the highest topography. It is characterized by the dominance of *Poa pratensis, Alopecurus pratensis, Deschampsia caespitosa, Agropyron repens* and *Taraxacum* sp. The vegetation is dense and high, 70–110 cm, when fully developed. It is a tall-grass community. The mean number of species per relevé is 25. *Phleum pratense, Anthriscus sylvestris* and *Vicia cracca* have high frequencies, while *Arrhenatherum pubescens* and *Festuca rubra* are less frequent. Several species such as *Agropyron repens, Capsella bursa-pastoris, Matricaria inodora, M. matricarioides, Poa annua, Plantago major, Urtica dioica, Galeopsis* sp., *Polygonum aviculare* and *Leontodon autumnalis* are restricted to this community and may be usable as differentiators.

The result of TWINSPAN classification of the relevés was not shown since it did not yield a result as satisfactory as the TABORD classification, and some misclassifications have been found. The TABORD result, compared with the TWINSPAN result, shows a clearer and more interpretable scheme of clusters.

2.2.2 Stand ordination (PCA, DCA)

The result of the PCA ordination is shown in Fig. 11, which presents the position of eighty-three relevés along the first two components. The variances accounted for by the first four components were 0.394, 0.152, 0.087 and 0.066, respec-

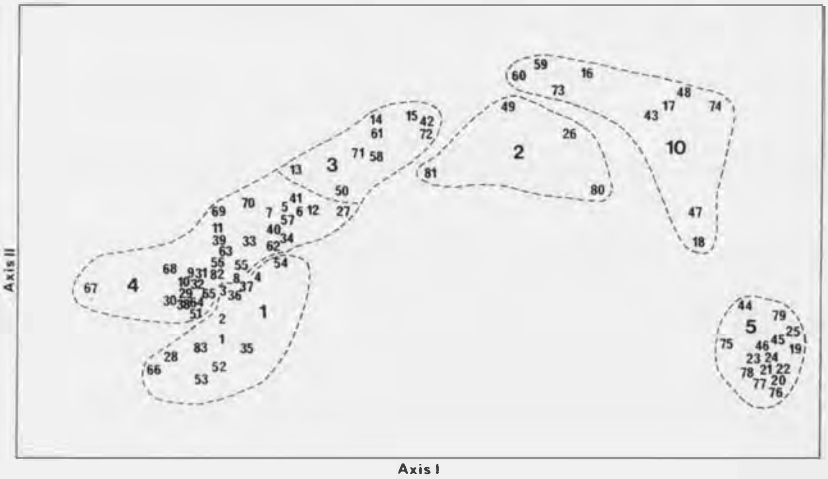


Fig. 11. PCA ordination of the Kungsängen Nature Reserve vegetation data with the TABORD classification clusters superimposed, principal components 1 and 2. Small figures are relevé numbers, large figures represent cluster numbers.

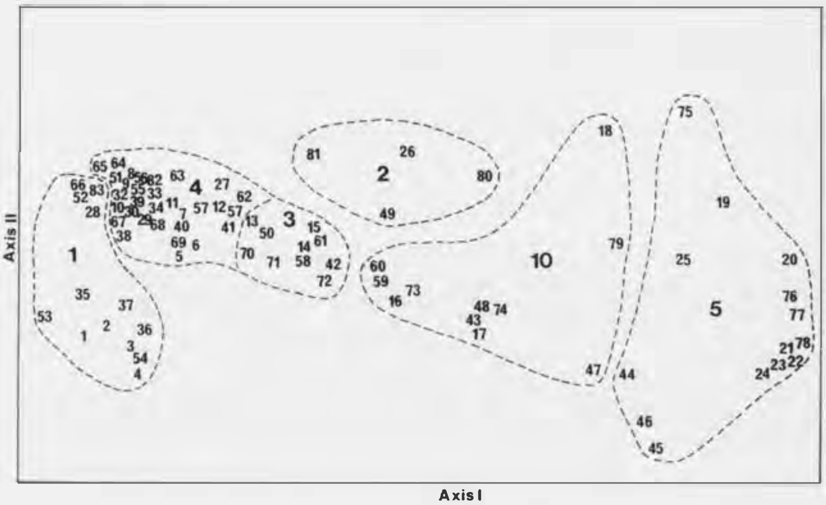


Fig. 12. DCA of the Kungsängen Nature Reserve vegetation data with the TABORD classification clusters superimposed, first and second axes. Small figures are relevé numbers, large figures represent cluster numbers.

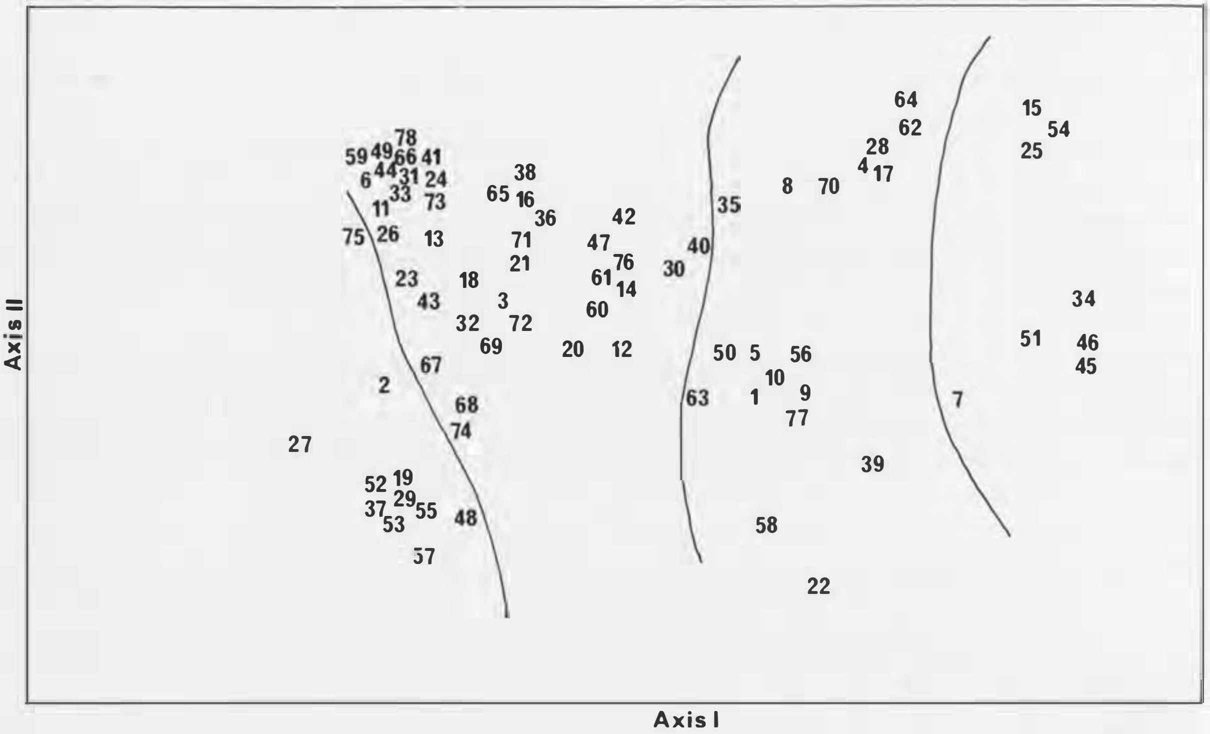


Fig. 13. DCA of species ordination (Axes I and II) of the Kungsängen Nature Reserve vegetation data (83 relevés and 78 species). The four groups of species are shown by the lines.

1 *Agrostis stolonifera*
2 *Agropyron repens*
3 *Alopecurus pratensis*
4 *Alopecurus arundinaceus*
5 *A. pratensis* x *arundinaceus*
6 *Briza media*
7 *Carex acuta*
8 *Carex caespitosa*
9 *Carex disticha*
10 *Carex* sp.
11 *Dactylis glomerata*
12 *Deschampsia caespitosa*
13 *Festuca pratensis*
14 *Festuca rubra*
15 *Glyceria maxima*
16 *Arrhenatherum pubescens*
17 *Phalaris arundinacea*
18 *Phleum pratense*
19 *Poa annua*
20 *Poa pratensis*
21 *Poa trivialis*
22 *Scirpus palustris*
23 *Achillea millefolium*
24 *Alchemilla* sp.
25 *Alisma plantago-aquatica*
26 *Anthriscus sylvestris*
27 *Arctium* sp.
28 *Caltha palustris*
29 *Capsella bursa-pastoris*
30 *Cardamine pratensis*
31 *Carum carvi*
32 *Cerastium caespitosum*
33 *Cirsium vulgare*
34 *Equisetum fluviatile*
35 *Filipendula ulmaria*
36 *Fritillaria meleagris*
37 *Galeopsis* sp.
38 *Galium boreale*
39 *Galium palustre*
40 *Galium uliginosum*
41 *Galium verum*
42 *Geum rivale*
43 *Glechoma hederacea*
44 *Heracleum sphondylium*
45 *Lemna minor*
46 *Lemna trisulca*
47 *Lathyrus pratensis*
48 *Leontodon autumnalis*
49 *Lotus corniculatus*
50 *Lysimachia nummularia*
51 *Lysimachia thyrsiflora*
52 *Matricaria matricarioides*
53 *Matricaria inodora*
54 *Oenanthe aquatica*
55 *Plantago major*
56 *Polygonum amphibium*
57 *Polygonum aviculare*
58 *Potentilla anserina*
59 *Potentilla reptans*
60 *Ranunculus acris*
61 *Ranunculus auricomus*
62 *Ranunculus polyanthemus*
63 *Ranunculus repens*
64 *Ranunculus sceleratus*
65 *Rumex acetosa*
66 *Saxifraga* sp.
67 *Stellaria graminea*
68 *Stellaria palustris*
69 *Taraxacum* sp.
70 *Thalictrum flavum*
71 *Trifolium pratense*
72 *Trifolium repens*
73 *Veronica chamaedrys*
74 *Veronica* sp.
75 *Urtica dioica*
76 *Vicia cracca*
77 *Iris pseudacorus*
78 *Equisetum* sp.

tively. The clusters indicated in the TABORD classification table were apparent on the diagram of the PCA's first and second axes. It is significant that the six clusters established could be drawn as discrete entities and there was no marked overlapping of the clusters. This suggests that the resulting six clusters are reasonable and appear fairly homogeneous. A clear "horseshoe" pattern is shown in the scatter diagram. The non-linear species response to one environmental factor complex is believed to result in a horseshoe-shaped pattern of PCA ordination (Noy-Meir & Austin 1970, Noy-Meir & Whittaker 1977).

The diagram of the first two axes of the DCA stand ordination is shown in Fig. 12. The first four eigen-values for the DCA ordination were 0.782, 0.199, 0.111 and 0.093, respectively. The clusters indicated in the TABORD classification table are also apparent and the sequence of the clusters along the first axis is the same as that of PCA ordination. The DCA ordination eliminated the horseshoe-shaped pattern presented in the PCA ordination and therefore may separate the independent direction of variation on the ordination axes (Hill & Gauch 1980).

The sequence of the clusters in the TABORD classification appears essentially to be related to the first axis of the PCA and DCA ordinations, although in the PCA ordination diagram it is along the well-known "horseshoe" pattern. Both PCA and DCA ordinations show that the eighty-three relevés represent a vegetational gradient from plant community A which occurs on the border area to plant community D which, in turn, occurs in the depressions in the reserve area (see also Fig. 21).

2.2.3 Species ordination (DCA)

The first two axes of the DCA species ordination are shown in Fig. 13. Four species groups can be identified (synecological indications according to Ellenberg 1974).

1. A group of species occurring on the border is presented in the lower left of the ordination diagram: *Arctium* sp., *Matricaria matricarioides, M. inodora, Galeopsis* sp., *Agropyron repens, Urtica dioica, Poa annua, Capsella bursa-pastoris, Polygonum aviculare* and *Leontodon autumnalis*. Among them, several species are typical ruderal ones.

2. A group of mesic meadow species is situated on the upper left of the diagram which includes *Alopecurus pratensis, Festuca pratensis, Arrhenatherum pubescens, Phleum pratense, Poa pratensis, Poa trivialis, Achillea millefolium, Cerastium caespitosum, Fritillaria meleagris, Galium verum, Geum rivale, Lathyrus pratensis, Ranunculus acris, R. auricomus, Rumex acetosa, Stellaria graminea, Taraxacum* sp., *Trifolium pratense, T. repens, Veronica chamaedrys* and *Vicia cracca.*

3. A group of relatively wet site species is in the centre of the diagram, which includes *Agrostis stolonifera, Alopecurus pratensis* × *arundinaceus, A. arundinaceus, Carex disticha, C. caespitosa, Scirpus palustris, Filipendula ulmaria, Galium palustre, Lysimachia nummularia, Polygonum amphibium, Potentilla anserina, Ranunculus repens, Thalictrum flavum, Ranunculus sceleratus* and *Iris pseudacorus.*

4. A distinct group on the right side of the diagram is composed of species characteristic of the wet site which is often inundated. *Carex acuta, Glyceria maxima, Alisma plantago-aquatica, Equisetum fluviatile, Lemna minor, L. trisulca, Lysimachia thyrsiflora* and *Oenanthe aquatica* occur there.

The results of both species and stand ordinations for the first two axes produced by the DCA program are similar and the first axis of both ordinations may suggest a strong relationship to the variation in the hydrotopography within the study area (see next chapter).

2.2.4 Species richness

Species richness, one of the community-level attributes, is normally calculated from the number of species per relevé. A clear trend has been shown in the plant communities at the study area. The highest number of species was found in the mesic sites (plant communities A and B) with a strong decline towards the wettest sites (plant community D). This may suggest that the soil moisture condition is also an important factor to determine the species richness of the vegetation at the study area.

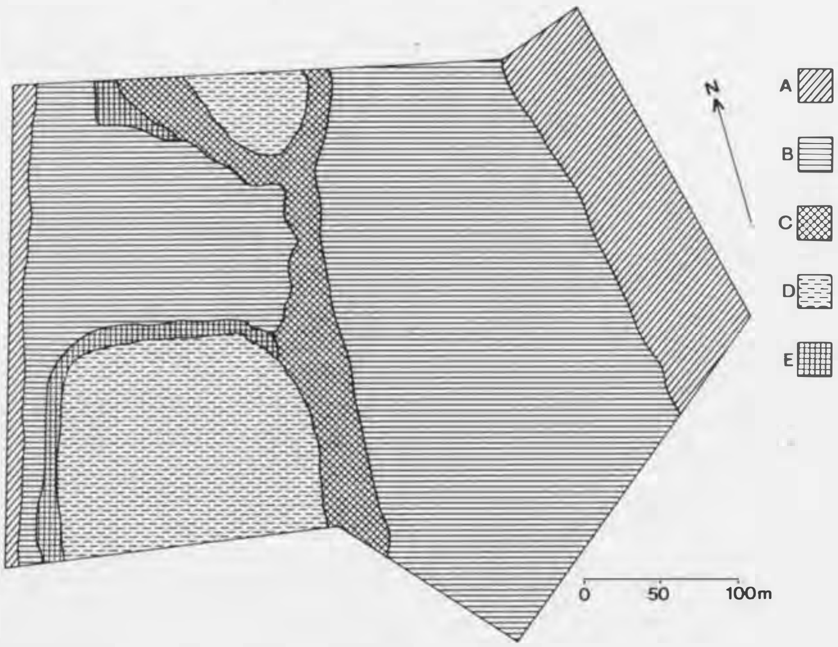


Fig. 14. Vegetation map of the Kungsängen Nature Reserve. Keys: A. *Poa pratensis–Alopecurus pratensis* community, B. *Arrhenatherum pubescens—Alopecurus pratensis* community, C. *Carex disticha* community, D. *Carex acuta* community and E. *Carex caespitosa* community.

2.2.5 Vegetation map

On the basis of these typological relevés and the community types derived from the numerical classification and ordination, together with consulting of the aerial photograph and field reconnaissance, a vegetation map was made by plotting the community types on the location of each relevé (Fig. 14). The distribution of the community types within the study area demonstrated a clear zonation appearance. This evidence confirms that these five main community types can be regarded as distinct ones. This vegetation map could serve as a basis for a detailed knowledge of the differentiation of the vegetation within the study area and in the future it could be also used for further studies of vegetation in relation to management and environmental effects.

2.3 Discussion

This study has examined the vegetation at the Kungsängen Nature Reserve by the combined application of numerical classification and ordination and these two approaches agree on the constitution of the five main plant community types.

An examination of the ordination results and the vegetation map of the study area reveals that the zonation of vegetation (viz. spatial sequences), is mainly found in the different development of vegetation at various topographical levels. The sequence of vegetation zones seems related to the hydrotopography (see chapter 3). Sandberg (1948) prepared a comparison of the vegetation zonation in the Kungsängen Nature Reserve and around Lake Mälaren, which revealed that the vegetation zones at Kungsängen also occur around Lake Mälaren. The fen series and meadow series in Uppland province have been described by Almquist (1929). Comparisons can be made with these series. The vegetation zones in the study area could be described as an expression for the proposed fen-meadow gradient.

In the study area this gradient begins with the *Carex acuta* community in the depressions, which corresponds to the *Carex acuta* association without a bryophyte layer described by Almquist (op. cit.). Since this type of vegetation lacks some characteristic features of real fens, Almquist considered it as a part of the wet meadow series. He mentioned that this community was an important constituent of shore vegetation along the lakes and rivers in Uppland.

The *Carex disticha* and *Carex caespitosa* community types seem to form a transition within the fen-meadow gradient. They belong, according to

Almquist (op. cit.), to the *Carex disticha* fen-meadow and the *Carex caespitosa* fen-meadow, respectively. The *Carex disticha* community occurs also around Lake Mälaren. This type of vegetation has many meadow species in its species composition and it has, thus, been assigned to the wet meadow series by Almquist. He described the *Carex caespitosa* community as a tussocky fen vegetation and emphasized its dependence on grazing activities. Sjörs (1950) also mentions *Carex caespitosa* as a fen species. However, a detailed description of this community is not given by Almquist. Comparison can also be made with the *Carex caespitosa* community from Linnebjer, southern Sweden (Andersson 1970 a). The community types at Kungsängen and Linnebjer show rather close resemblance, although the community type at Linnebjer shows a richer flora than that in the Kungsängen Nature Reserve.

The *Arrhenatherum pubescens—Alopecurus pratensis* community and the *Poa pratensis—Alopecurus pratensis* community types in the study area can be assigned to the tall-grass meadow category described by Almquist (1929). There are, however, no more closely corresponding meadow types in his description. The *Arrhenatherum pubescens—Alopecurus pratensis* community type is probably close to the *Deschampsia caespitosa* meadow type described there, but there is a considerable variation in the species composition. The *Poa pratensis—Alopecurus pratensis* community type may belong to the *Alopecurus pratensis* meadow type mentioned by Almquist (op. cit.), but he made no detailed analysis of the species composition for this type of vegetation. He emphasized that the *Alopecurus pratensis* meadow is an important and good-quality hay meadow, usually species-rich and with highly variable species composition due to the human influence (hay-making or grazing).

Sandberg (1948) made a comparison of the *Deschampsia caespitosa—Alopecurus pratensis* community type in the Kungsängen Nature Reserve with the *Alopecurus pratensis* community type in Central and Eastern Europe, showing the affinity of the *Alopecurus pratensis—Deschampsia caespitosa* community to that in Central and Eastern Europe.

3 Ground water and soil moisture

In vegetation science much attention has been paid to the water relations of wet meadows. Many ecologists in Sweden as well as elsewhere in Europe have investigated the relation between plant communities and ground water regimes. Among them Sjörs (1954), Malmer (1962), Andersson (1970 a) and Tyler (1971) in Sweden, and Ellenberg (1939), Tüxen (1954), Klötzli (1969), Niemann (1973), Boedeltje & Bakker (1980), Grootjans & ten Klooster (1980) and others in Central or West Europe may be mentioned. In wet sites, the hydrological conditions appear to be correlated with important ecological conditions and processes such as aeration of the soil, mineralization of organic substances and supply of nutrients to plant roots.

The ecological relationships between plants and environment can be grouped into operational, conditional and positional ones. The environmental factors of direct importance to the performance of plants are operational. Factors that regulate the growth conditions are conditional, whereas plants may be positionally connected to the surrounding environment (cf. Spomer 1973, vanWirdum 1979). These relationships can be studied with regard to soil-water conditions and vegetation (Grootjans 1980). For detailed analysis of the relationships between vegetation and hydrological factors long-term regular measurements of both ground water table and soil moisture are necessary, because these factors are usually highly variable over the year.

This investigation has focused on yearly fluctuations of ground water level, including inundation level, and the yearly variation of soil moisture. The aim was to present a detailed picture of correlation between some quantitative aspects of soil-water regimes and the occurrence of the plant communities in the study area. These soil-water data are also considered useful to explain the vegetation dynamics in general (Chapter 6) and in particular the dynamics of *Fritillaria meleagris* L. in the Kungsängen Nature Reserve area.

3.1 Methods

3.1.1 Ground water measurement

The ground water conditions within the study area are mainly governed by the local rainfall, the topography and the water level of the River Fyris (Giöbel 1933). The water level was measured inside a series of ground water tubes along a transect with a recognizable topographical gradient. The water level of the River Fyris was recorded at the same time. Fifteen plastic tubes were arranged representatively along this transect, from the eastern end to the river side. The criteria for placing the tubes were linked to topography and vegetational zones.

community type	A	B	C	D	E
number of tubes	3	6	2	3	1

The tubes were 1–1.5 m long, 2 cm in diameter, and fitted with small seepage holes in two directions for every 2 cm. The water level inside the tubes always fluctuated with the ground water table. To maintain satisfactory drainage in the tubes, they were rinsed when necessary. The measurements were made by lowering a plummet into the tubes and the distance between the water table and the soil surface was recorded. In cases of inundation, the water level above the soil surface was recorded. From these water levels related to the levelled soil surface around each tube, the absolute water level could be calculated, which made comparison between sites possible. The accuracy of the measurements was estimated to ±2.0 cm or better. Observations were carried out from October 1980 to December 1982, at weekly intervals during the growing season, and irregularly for the rest of the year. Freezing conditions and snow made water observations inaccurate and difficult, except at the end of the period which was exceptionally mild.

The fluctuation of water level in the River Fyris was recorded at the river side close to the transect.

All measurements could be converted to absolute water level, i.e. meters above sea level in the system of 1970. This facilitates an analysis of the relation between the water levels of the River Fyris and the study area.

Most interpretations of the ground water level measurements are based on the analysis of the water level curves during the study period and the "duration line" of ground water level during the growing season. From the course of the yearly ground water level and the inundation level the extreme values, fluctuating range and the mean value, as well as the times of rising and subsiding of the water table are clearly shown. These characteristics have usually been used for description of the ground water regime. However, from an ecological point of view an analysis of the duration of different water levels gives, as many ecologists have suggested, more appropriate information. For example, a long duration of high or low water level regulates the biological activity of plants in a drastic way. From the "duration lines" the range, median and mathematical means are easily obtained. Furthermore, a statistical treatment of such "duration lines" is possible.

Therefore, the measured data have been transformed to cumulative frequency diagrams (i.e. duration lines). A duration line presents an approximation of the period, in days, that a certain water level is reached or exceeded. The duration analysis was based on the spring, summer and autumn in 1981 and 1982. This main growing period had daily temperature above 0°C and corresponded for the actual years to the period from April 1 to November 1 (altogether 214 days).

Duration lines have long been used for analyses of hydrological conditions. Niemann (1973) used the ratio of the mathematical mean ($\bar{x}$) to the median (M) of the ground water levels to describe the ground water regime. The indices $\bar{x}/M$ should be calculated from the ground water levels below the soil surface and all the water levels at or above the soil surface are given a value of 0. If $\bar{x}/M>1$, ground water tables higher than the mean are more frequent than lower ones and the duration line has a convex shape. If $\bar{x}/M<1$, lower ground water tables are more frequent than higher ones and the duration line has a concave shape. According to Andersson (1970 a) and Grootjans & ten Klooster (1980) convex-shaped duration lines are associated with continuous supply of surface water, especially during the wet seasons, and concave-shaped duration lines are usually associated with infiltration of water or peak floods in wet seasons, followed by a rapid decrease in level. However, if there is an influence from a river or lake (or sea), or if thresholds exist, the situation is more complicated, and the duration line could also be sigmoid-shaped.

Duration frequencies were calculated for each fifth cm in the soil profile. In order to characterize the ground water regime for different vegetation types, the duration lines of closely related stands have been lumped. The index $\bar{x}/M$ has been calculated from the mean values of each bundle for the same vegetation type. The median value (M) corresponds to a water level with as many days above as below the level in question. This can be derived graphically or calculated.

3.1.2 Soil moisture measurement

Soil moisture content is generally defined as the water content that can be driven off by heating a sample at 105°C. Sampling and gravimetric analysis is the simplest method of measuring soil moisture and provides the standard reference technique for calibrating other methods. It can be expressed in terms of dry weight of soil or volume. The great differences in bulk density give incommensurable soil moisture values when these are expressed in terms of weight. Therefore it is often considered more meaningful to determine moisture content on a soil volume basis. It could also be calculated as the percentage of the porosity taken up by water.

Soil sampling was done by using a 23 mm diameter auger. Separate samples were taken from the main plant communities. The samples were nearly systematically distributed along the vegetation transect, i.e. from sites with different vegetation type. Each sample consisted of four replicate samples and cores were collected adjacent to the transect and taken sufficiently far apart from each other to avoid disturbance. Samples were taken once a month during the growing season of 1981 (from April to November) with the exception of the sites with *Carex acuta* vegetation (D), most of which was inundated almost the year round, so in this case only one sample was taken. All samples

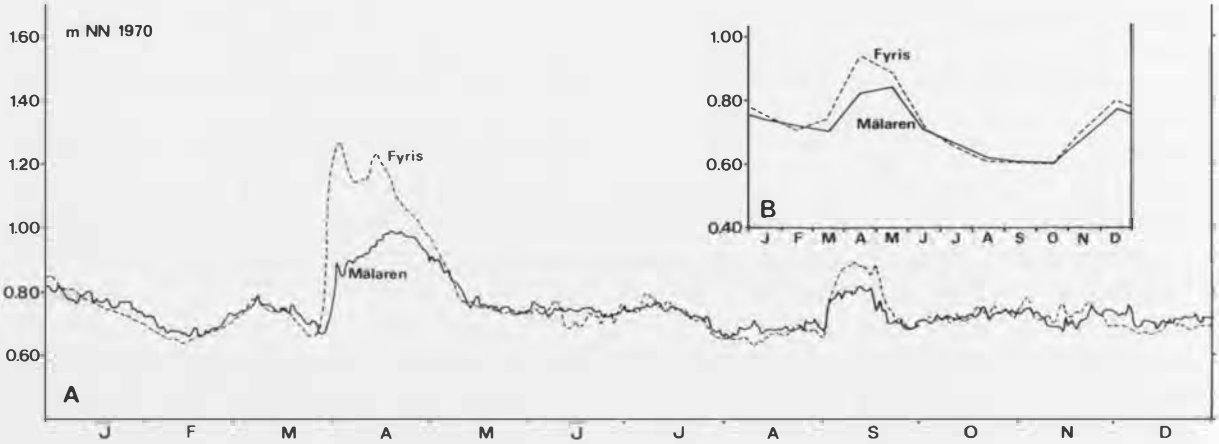


Fig. 15. The daily water levels (A) for 1978 and the monthly mean water levels (B) for the period of 1968–1980 in the River Fyris at Ultuna and in Lake Mälaren (mean value recorded at KJ. Slussen, Södert. Slussen and Västerås Hamn). The water level is expressed in m above sea level in system 1970. The data for the River Fyris obtained from Anders Bjerketorp (unpublished) and for Lake Mälaren from SMHI. Redrawn by the author.

were from the humus layer (0–10 cm) and used to study the yearly variation of soil moisture content in the upper rhizosphere.

The moisture content was determined gravimetrically and the samples were oven-dried to constant weight at 105°C (72 hours). The results obtained in percentage by weight were multiplied by the dry bulk density (*Yt*) to convert them to percentage by volume (Andersson & Ericson 1963).

Since the weather conditions are important for the interpretation of the measurements, the monthly temperature and precipitation during the observation period are also given.

3.2 Regime of the River Fyris

The River Fyris is short, draining a low-level area with few lakes. It therefore fluctuates greatly in terms of discharge. Since, however, the study area is fairly near the river's mouth in Lake Ekoln (a bay of Lake Mälaren) and since there are no rapids downstream, the water levels in the river are equalized and much dependent on those in Lake Mälaren (Fig. 15) (Hans Kvarnäs pers. comm.). The latter are regulated to some extent by a threshold at Stockholm. The minimum level of Lake Mälaren is only about 0.3 m above sea level, but both the Baltic Sea and the lake do fluctuate a

Fig. 16. View of the Kungsängen Nature Reserve close to the River Fyris (in the foreground) with an aspect of early spring flooding.—Photo. Author.
April 1982.

good deal, with high levels in the lake after snowmelt, and some years also in autumn. The River Fyris discharge fluctuates in the same way, but much more abruptly and with an earlier spring maximum. Therefore the lower part of the study area is inundated quite frequently, although it is separated from the river and shielded from inflow by a levée (Fig. 16). The in- and outlet is at a depression a short distance downstream (to the south) of the study area, but there is a certain threshold effect, prolonging the inundation of the lowest part (sites with *Carex acuta* vegetation).

3.3 Results

3.3.1 Yearly variation of ground water level, including inundation level

The water level curves of some representative sites and the River Fyris are presented in Fig. 17. The variation of water level curves between years is considerable. The curve ranges of 1981 are smaller than those of 1982. The interpretation of the yearly course and the variation has to be made in relation to weather conditions. In Fig. 17 the monthly temperatures and precipitation for the observation years 1980–82 are given with additional information from the nearby meteorological station at Ultuna, Uppsala.

The yearly mean temperature in 1980 was lower than the average, November was colder. The precipitation exceeded the average (1951–80) by ca 160 mm, the autumn was wetter than average.

The winter of 1980/1981 was poor in snow with periods of bare ground. The precipitation in 1981 exceeded the average by ca 120 mm with low figures for January, February, April, May, July and September, and high figures for March, June and December, and much higher figures for August, October and November. The yearly mean temperature was slightly lower than the average (1951–1980), with lower temperature than usual especially during December.

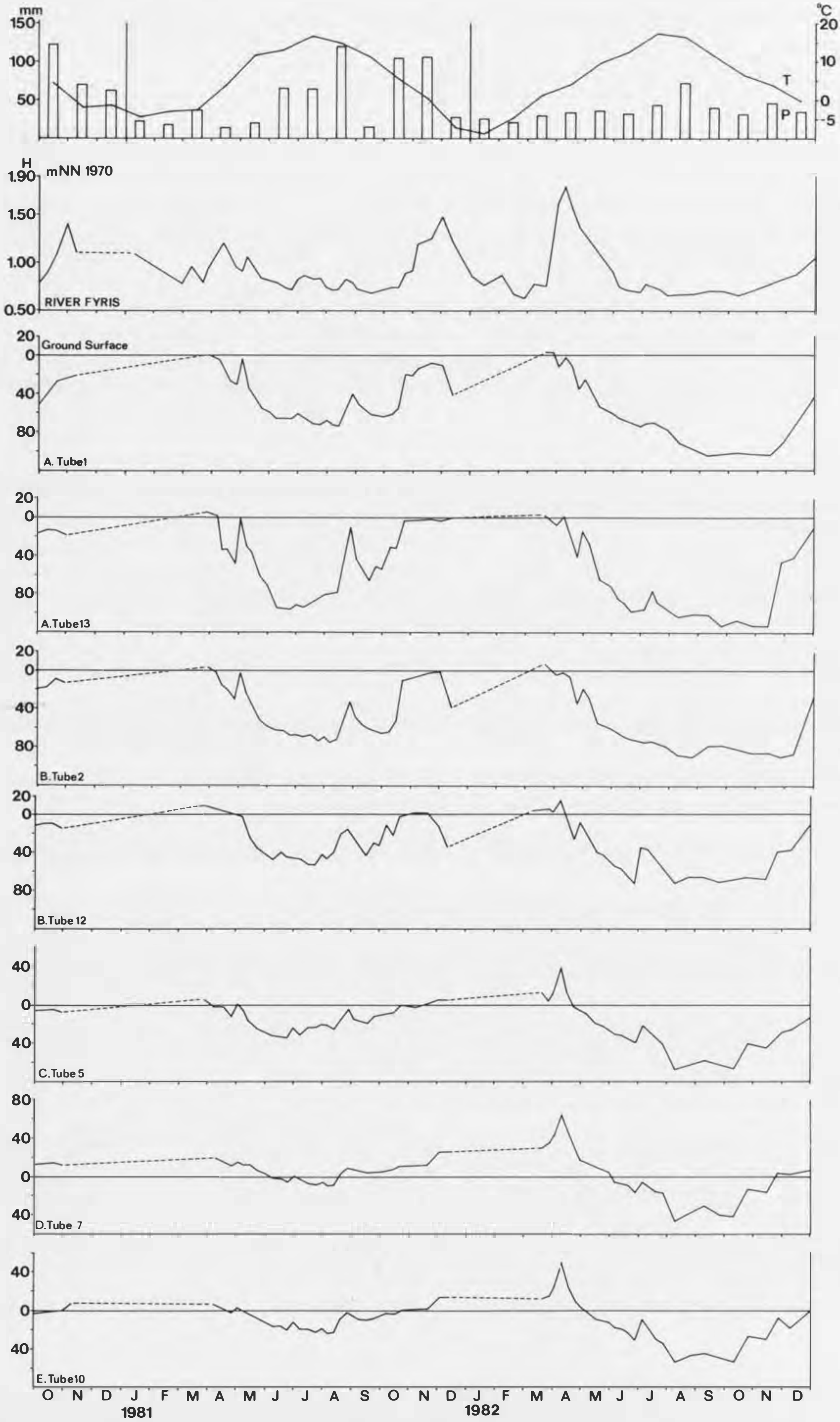
The winter of 1981/82 was rich in snow and during January and February the average snow-depth was 25–26 cm, much deeper in upstream areas. January was very cold, March and April were warmer than usual. June was colder while July–December were warmer. The yearly mean temperature in 1982 was 0.5°C higher than the average. This year the precipitation was 67.5 mm less than the long-term average, especially with less precipitation than usual during June, July, September–December.

The yearly course of the ground water level curves shows lower summer values in the warmer and drier year of 1982. The water level was generally low during summer and high during autumn and early spring. Small fluctuations during summer could be related to precipitation. The maximum level was reached at the same time for all sites each year. It coincided with the melting of snow in the early spring. Another high level was reached during autumn when precipitation was high and temperature was low. Those fluctuation patterns could be explained by the beginning and ending of the period with intensive evapotranspiration due to the temperature, precipitation and radiation conditions.

The variation of the water level curves between years can partly be explained by the weather conditions. During the winter of 1980/81 the snow layer was rather thin but in 1981/82 it was much deeper in the whole catchment area of the river, which produced a considerable flood in April. The year 1981 had a mean temperature 0.3°C lower than the average and the total precipitation exceeded the average, while the year 1982 had a mean temperature 0.5°C higher than the average, combined with a relatively lower precipitation during the summer and autumn, which gave the considerable differences in the fluctuation range.

Comparing the fluctuation patterns of the River Fyris with those of water level in the study area, especially during the growing season, it is quite clear that there is a close correlation between the ground water level in the study area and the water level in the River Fyris. The study area represents a low situation and except at dry periods in summer, its hydrology is predominantly governed by the water level of the River Fyris. This can be seen more clearly from the comparison of the maximum and minimum water levels of the observation sites in the study area and the water levels of the River Fyris at the same time (Fig. 18). The water levels including the flooding water level of the study area, the lower-situated sites in particular, followed the fluctuation of the water level of the River Fyris, although, except in flooding conditions, there was a time lag.

There were also considerable differences be-


mm
150
100
50
°C
20
10
0
-5
T
P
H
mNN 1970
1.90
1.50
1.00
0.50
RIVER FYRIS
20
0
40
80
Ground Surface
A. Tube1
20
0
40
80
A.Tube13
20
0
40
80
B.Tube2
20
0
40
80
B.Tube 12
40
0
40
C.Tube 5
80
40
0
40
D.Tube 7
40
0
40
E.Tube10
O N D J F M A M J J A S O N D J F M A M J J A S O N D
1981
1982

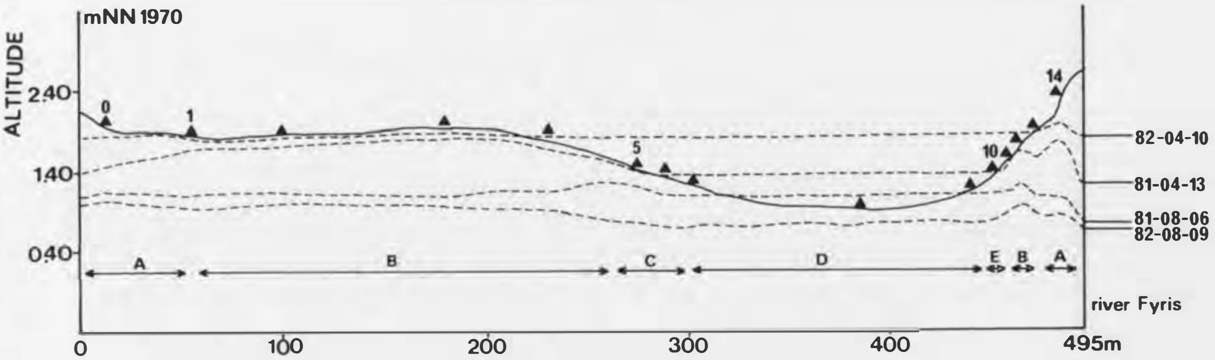


Fig. 18. The maximum and minimum water levels in relation to the soil surface and the River Fyris for the growing seasons of 1981 and 1982 ▲ is measuring tube. A–E are different community types.

tween the observation sites, notably with regard to the extreme values, the fluctuation range and the mean values.

In the relatively dry sites with plant community A, the water level started to subside in April–May, soon after the maximum level had been reached in the early spring (Fig. 17, curve 1,13). The range was considerable and both maximum and minimum levels were low; on average, 17.5–101.3 cm in 1981, 11.3–117.5 cm in 1982, below the soil surface.

The curves for the mesic sites with plant community B (curves 2,12) had a similar pattern of subsiding and rising times as the sites with plant community A. They differed, however, regarding the fluctuation range; for the sites with plant community B it was, on average, +2–68 cm in 1981, +12–93 cm in 1982 (+ is used for a water level above the soil surface).

The curves for the sites with plant communities C and E were similar (curves 5,10) both regarding the fluctuation ranges and the extreme levels. The fluctuation ranges were rather small with higher extreme levels: on average for C and E +3.3–26.7 cm in 1981 and +46.6–58.3 cm in 1982.

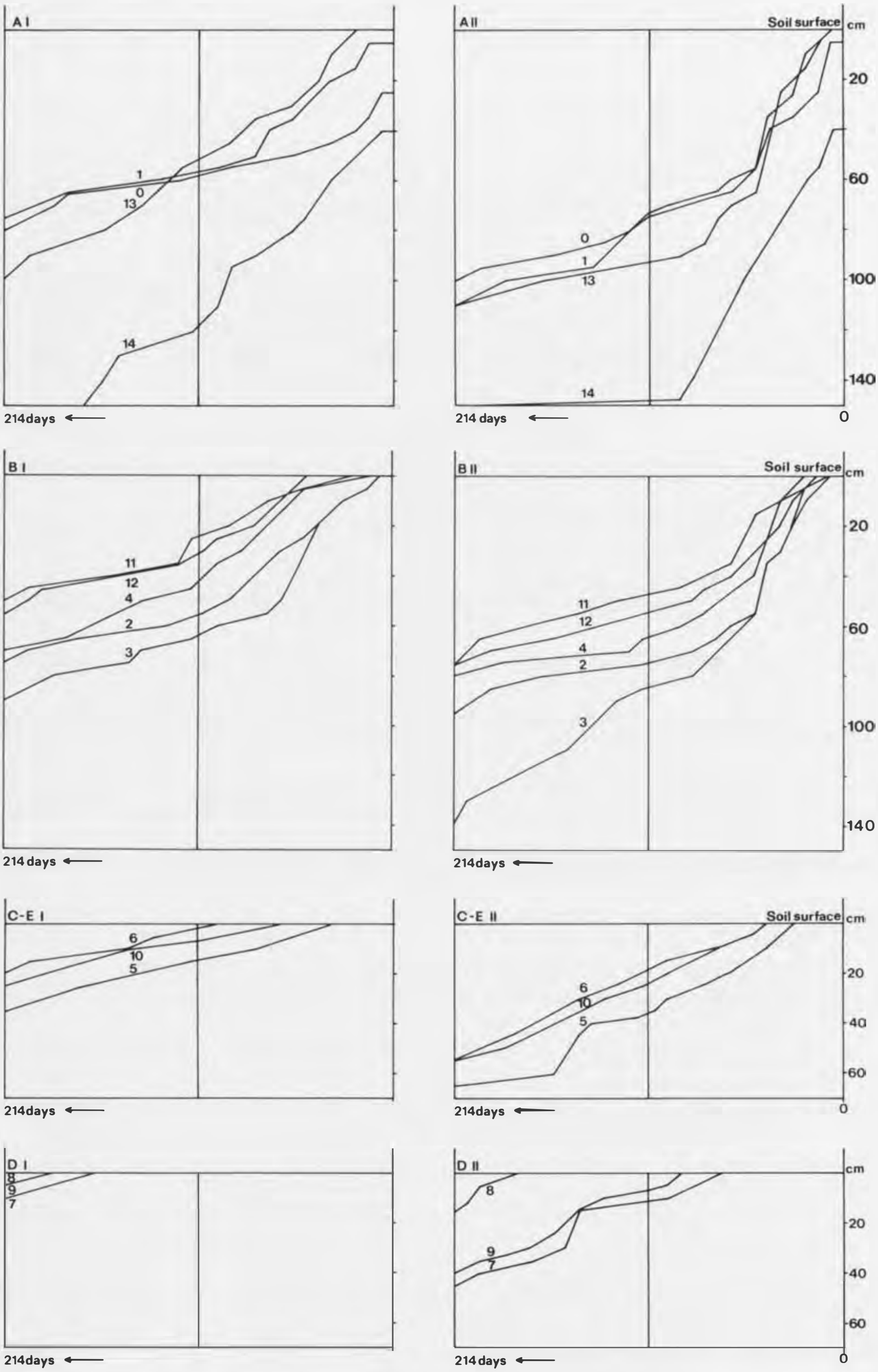
The wettest sites with plant community D had a quite distinct curve (curve 7). Subsiding of the water level below the soil surface occurred only for short periods during summer. The ground water table was never far below the soil surface (never more than 45 cm) and the average fluctuation range was +31.7–+1.7 cm in 1981 and +78–33.3 cm in 1982. For the greater part of the year these sites were inundated.

3.3.2 Characterization of duration lines

The duration lines derived from individual water level curves have been combined for each type of plant community. Thus four groups (group A, group B, group C+E and group D) of duration lines both for 1981 and 1982 are presented in Fig. 19. The indices $\bar{x}/M$ for each group for 1982 are shown in Table 3 by calculating the mean values of a bundle of individual duration lines derived from the sites with the same vegetation. The indices $\bar{x}/M$ for communities A and B, 0.54 and 0.72 respectively, are less than 1, which suggests a diminishing influence of surface flow. The indices $\bar{x}/M$ for communities C+E and D are 1.15 and 2.78 respectively, which suggests a prolonged influence of surface flow and free water table (inundation).

The characteristic duration lines of four groups have been constructed by calculating the mean values of a bundle (Fig. 20). To describe ground water characteristics of wet meadows, the height of the water table above the soil surface (flooding level or free water table) has been considered as an important factor in determining the occurrence of plant communities. The means of the highest level,

◀ Fig. 17. Yearly variation of water levels at seven sites representing plant communities A–E (explanation see text) and in the River Fyris from October 1980 to December 1982. Dashed lines indicate freezing conditions (ice). The soil surface is marked with a horizontal line. The mean monthly temperature and precipitation conditions during the study period are given (Data from the Ultuna Meteorological Station).


A I
1
0
13
14
214days
A II
Soil surface
cm
20
60
100
140
0
1
13
14
214 days
0
B I
11
12
4
2
3
214days
B II
Soil surface
cm
20
60
100
140
11
12
4
2
3
214days
C-E I
6
10
5
214days
C-E II
Soil surface
cm
20
40
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6
10
5
214days
0
D I
8
9
7
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D II
cm
20
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0

Table 3. Median (M) and mean ($\bar{x}$) ground water levels (cm below soil surface), and the indices $\bar{x}$/M of four groups of duration lines for the growing season 1982.

	M	$\bar{x}$	$\bar{x}$/M
Community A	97.5	53.1	0.54
Community B	64.8	46.5	0.72
Communities C + E	25.3	29.2	1.15
Community D	6.0	16.7	2.78

Table 4. Comparison of the means of characteristic duration levels of four groups for the data from 1982 (t-test). x = significant difference at $t_{0.1}$ level, xx = at $t_{0.05}$ level, xxx = at $t_{0.01}$ level, N.S = no significant differences.

Compared plant communities	A-B	A-C+E	A-D	B-C+E	B-D	C+E-D
Maximum level	x	xxx	xxx	xxx	xxx	xx
Intermediate level	x	xx	xxx	xxx	xxx	x
Minimum level	N.S	xxx	xxx	x	xx	x

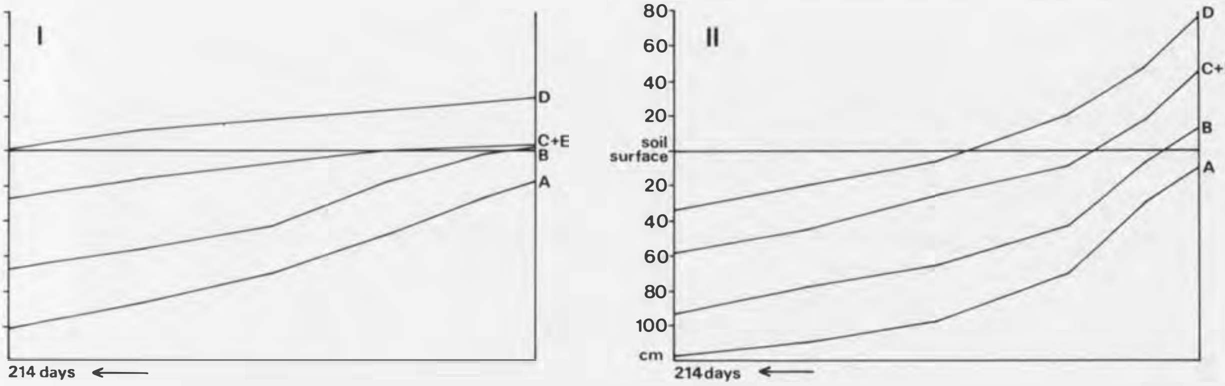


Fig. 20. Characteristic duration line of plant communities A, B, C+E and D, during the growing seasons of 1981 (I) and 1982 (II).

whether above or below the soil surface, were adopted here as the maximum level. A statistical analysis was made for the observation results in 1982 to establish the probability of significant differences in characteristic duration lines at maximum, intermediate and minimum levels. The duration lines, bundles of four groups, have been compared two by two. The results of the t-test analysis for data from 1982 are given in Table 4.

The average water table of the sites with plant community A was 71 cm in 1981 and 97 cm in 1982 below the soil surface during half of the growing season. The differences in duration lines between communities A and C+E, and A and D respectively, were significant (at the t 0.05 and 0.01 levels) not only in maximum water levels but also in intermediate and minimum water levels. However, the duration lines of plant community A differed only from those of plant community B in maximum and intermediate water levels at the 90% probability level, but there was no significant difference at the minimum water levels although the mean minimum level of plant community A is almost 23 cm lower than that of plant community B.

The average median water level of plant community B was about 45 cm in 1981 and 65 cm in 1982 below the soil surface. Only for a short period during early spring, was the water table near or above the soil surface. The duration lines of this group differed significantly at the t 0.01 and t 0.05 levels from the group of plant community D at maximum, intermediate and minimum water levels. The differences in duration lines between plant communities B and C+E were also considerable: the maximum and intermediate water levels differed at the t 0.01 level and the minimum water levels differed at the t 0.10 level.

Plant communities C+E and D had a long dura-

◀ Fig. 19. Duration lines for the sites with plant communities A–E for 1981 (I) and 1982 (II). A. Duration lines for the sites with plant community A, B. Duration lines for the sites with plant community B, C–E. Duration lines for the sites with plant communities C+E and D. Duration lines for the sites with plant community D. Numbers 0–14 indicate the measuring tubes (see also Fig. 18).

tion of inundation. The inundation lasted for about 8 weeks in 1981 and for about 6 weeks in 1982, on average, during the growing season in plant communities C+E. The inundation lasted for almost all the time in 1981 and for about 16 weeks in 1982, on average, during the growing season in plant community D. Considerable differences were found in the maximum water levels, at the t 0.05 level, between these two groups of duration lines. The intermediate and minimum water levels, however, differed only at the t 0.10 level.

3.3.3 Soil moisture content

The yearly variation of soil moisture content during the growing season of 1981 is shown in Table 5. In the early spring and late autumn the soil moisture reached high values, while during the active growing season, especially during June and July, it fell to rather low values. But there was nearly always water available to the plants in these wet meadows. The fluctuation range of topsoil moisture for the sites with plant community A was 53.4−19.2 (as percentage by volume), for the sites with plant community B 57.3−27.0, for those of plant community C 58.1−38.9, and 69.9−46.5 for those of plant community E. The sites with plant community D were inundated almost the year round in 1981 and the soil moisture content should be rather constant, which was around 56.9 as percentage by volume. The fluctuation range was large in the relatively dry sites and decreased towards the wet sites.

It is quite obvious that the soil moisture content in the study area is predominantly influenced by the ground water table. In addition, temperature, precipitation, evaporation, degree of development of the vegetation and the porosity of the soil should also be taken into account.

Table 5. The yearly variation (during the growing season of 1981) of soil moisture content. Means ($\bar{x}$) and standard deviations ($\pm$ s.d.) are given for every sampling site (n=4). The figures are expressed in terms of percentage by volume.

Plant community	Sampling site	Porosity (%)	Sampling date 26.4	22.5	23.6	25.7	27.8	26.9	24.10
A	50 m	65.9	53.4 ±3.3	39,7 ±4.1	25.1 ±1.9	30.9 ±3.6	43.7 ±1.7	38.9 ±4.5	51.1 ±6.1
A	480 m		42.3 ±13.0	22.2 ±3.8	19.2 ±1.1	29.3 ±5.5	36.9 ±9.6	36.1 ±10.4	46.7 ±8.9
B	100 m		57.3 ±7.1	45.9 ±2.5	29.7 ±1.6	41.3 ±1.6	41.6 ±2.8	39.8 ±2.3	57.1 ±1.2
B	150 m	67.1	53.4 ±8.0	40.1 ±1.3	27.0 ±1.0	33.2 ±2.8	43.5 ±2.1	43.5 ±2.7	50.9 ±4.5
B	200 m		55.7 ±3.8	39.7 ±2.5	31.8 ±3.3	35.9 ±1.0	44.3 ±2.7	45.4 ±2.4	51.9 ±2.4
B	250 m		49.3 ±6.5	35.6 ±1.0	35.8 ±1.4	33.3 ±1.1	43.9 ±1.4	44.7 ±3.6	56.3 ±4.5
C	280 m	73.3	58.1 ±5.6	43.9 ±3.4	41.2 ±3.5	38.9 ±4.2	42.7 ±2.0	50.7 ±6.2	52.5 ±3.0
E	460 m	71.5	68.3 ±8.1	49.2 ±1.9	49.1 ±2.8	46.5 ±3.8	50.9 ±5.1	64.2 ±9.9	69.9 ±4.4
D	400 m	68.6	-	-	-	-	56.9 +2.5	-	-

3.4 Conclusions

From the results of this investigation, the following four main ground water regimes in the study area could be recognized:

I. Plant community A with *Poa pratensis* and *Alopecurus pratensis* occurs on the borders of the reserve area at an altitude of 2.40−1.90 m (above sea level, system 1970), where drainage conditions are rather good. The characteristic duration lines are concave-shaped. The maximum level was 17.5 cm (1981) and 11.3 cm (1982), on average, below the soil surface. The intermediate level was 70.5 cm (1981) and 97.5 cm (1982) and the minimum water level 101.3 cm (1981) and 117.5 cm (1982), on average, below the soil surface. These sites thus were never flooded during the observation period. The fluctuations in topsoil moisture content were considerable.

II. Plant community B with *Arrhenatherum pubescens* and *Alopecurus pratensis* occurs mainly on the mesic sites at an altitude of 1.90−1.65 m a.s.l. The maximum water level was 2 cm (1981) and 12 cm (1982), on average, above the soil surface. The intermediate water level was 43.4 cm (1981) and 64.8 cm (1982), and the minimum water level was 68 cm (1981) and 93 cm (1982), on average, below the soil surface. The characteristic duration lines are concave-shaped. Some sites may occasionally be flooded during early spring or late autumn, but only for short periods (less than 10% of the growing season). Considerable fluctuations in topsoil moisture content were found.

III. Plant community D with *Carex acuta* occurs on the wettest and lowest sites at an altitude of 1.40−0.90 m a.s.l. The characteristic duration

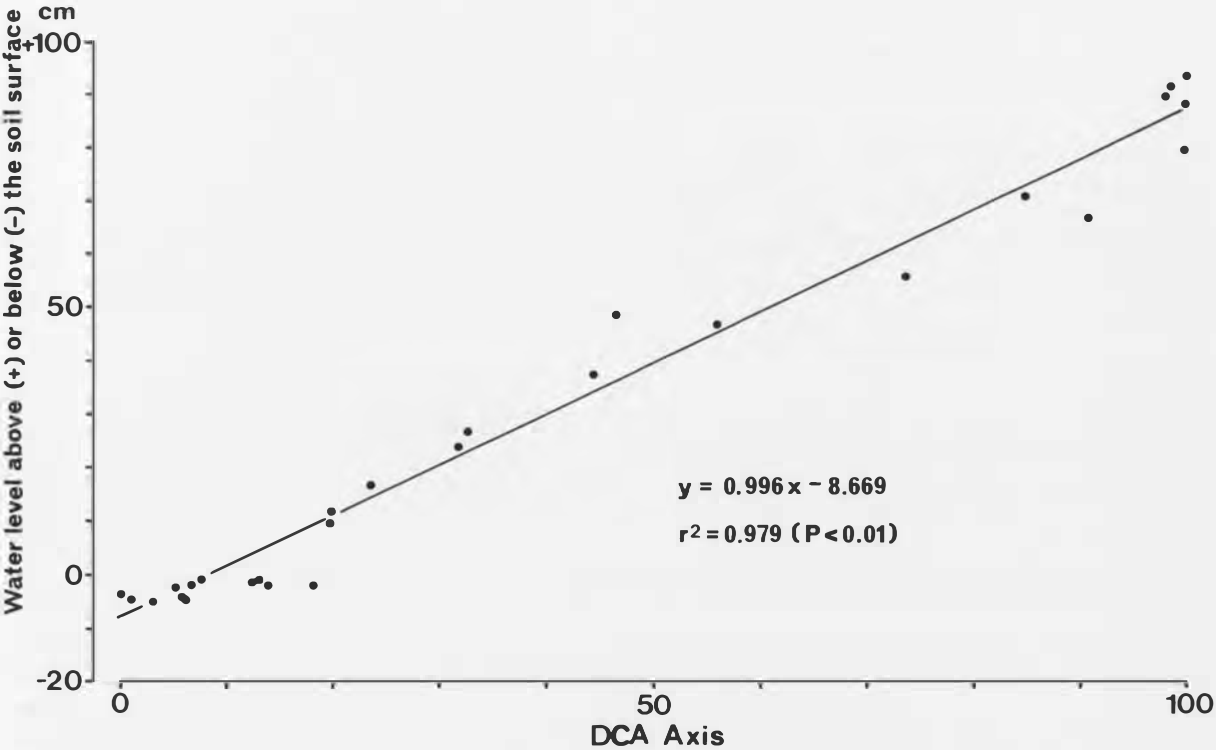


Fig. 21. Correlation between position on DCA ordination axis I and maximum water level during the growing season of 1982 for the 28 relevés along a transect within the Kungsängen Nature Reserve.

lines are convex-shaped, being characterized by prolonged high water levels above the soil surface and by peak high water flooding. The maximum water level was 31.7 cm (1981) and 78 cm (1982), and the intermediate water level was 18.3 cm (1981) and 1.7 cm (1982), on average, above the soil surface. The minimum water level was 1.7 cm (1981) above the soil surface and 33.3 cm (1982) below the soil surface. However, these figures were obtained from the interspaces between the tussocks. The average height of the tussocks is 20–50 cm. These sites were inundated in 1982 during more than half of the growing season and were almost permanently inundated in 1981. The soil moisture content was probably constant.

IV. The transition between the sites with plant communities B and D is at an altitude of 1.65–1.40 m a.s.l. These smaller but distinct parts are occupied by plant communities C and E, characterized by *Carex disticha* and *Carex caespitosa*, respectively. The maximum, intermediate and minimum water levels, as well as the duration of flooding, were similar for these two communities, apparently due to the same topographical positions. However, plant community E is a tussock vegetation with *Carex caespitosa* as the dominant species. The height of the tussocks is 15–30 cm and the ground water level was measured from the soil surface between the tussocks. The characteristic duration lines are convex-shaped. The maximum water level was 3.3 cm (1981) and 46.6 cm (1982), on average, above the soil surface. The intermediate water level was 7.7 cm (1981) and 25.3 cm (1982) below, and the minimum level was 26.7 cm (1981) and 58.3 cm (1982), on average, below the soil surface. These sites were periodically flooded and the period of inundation was about or less than 25% of the growing season. The topsoil moisture content was under the direct influence of the ground water table and moderate fluctuations in soil moisture content were found.

A significant correlation is found between the position on DCA ordination axis I and the maximum water level during the growing season of 1982 for 28 relevés along the transect where the water level was measured (Fig. 21; $r^2 = 0.98$, $P<0.01$). Apparently the variation in the vegetation composition is strongly related to the variation in the ground water regime in the study area (including inundation) and the soil-water conditions are one of the controlling factors in determining the variation in the vegetation.

4 Analyses of soil physical and chemical properties

Soils are the immediate physical and nutritional supports to plants and therefore are one of the direct controls on plant and community performance. Soil conditions in the Kungsängen area are well-known through the investigations of Westerberg (1910), Sjöström (1921), Giöbel (1933) and especially through the study of Torstensson & Eriksson (1941) in connection with agrogeological mapping at 1:8000 for the soil type, the soil reaction and the contents of phosphorus and potassium. However, a detailed investigation of soil conditions within the reserve area is lacking, particularly in relation to the different plant communities and the soil-water regimes. During the period of 1981–82 analyses of soil physical and chemical properties were carried out. The aim has been to provide necessary information on physical and chemical conditions of the substratum as an abiotic part of the ecosystem and to give a characterization of soil conditions in the different zones of vegetation, mainly as a function of different soil-water regimes.

4.1 Methods

4.1.1 Soil sampling

Soil is an extremely complex medium and its variability causes many problems. The apparently random spatial variability in soil physical and chemical parameters even in soils which are morphologically uniform and support the same vegetation has been shown by many soil scientists and ecologists (Ball & Williams 1968, Troedsson & Tamm 1969). Because of this, intensive sampling may be required. However, a compromise between effort and accuracy is essential (Ball & Williams 1971).

The soil samples were taken from the five plant communities along a transect. Four to five replicate samples were taken from each of the sampling sites at random: The *Poa pratensis—Alopecurus pratensis* community (A), the *Arrhenatherum pubescens—Alopecurus pratensis* community (B), the *Carex disticha* community (C), the *Carex acuta* community (D) and the *Carex caespitosa* community (E). For the tussocky vegetation of the *Carex acuta* community and the *Carex caespitosa* community the soil samples were taken from the interspaces between the tussocks since it was difficult to take the samples from the top of the tussocks. Each sample consisted of three subsamples, that is, subdivided into 0–10, 10–20, 20–30 cm horizons. Soil cores were taken with an auger of 48 mm diameter, which had a volume of 181 cm^3 for each horizon, and the soil core obtained was used as volume-determined for the measurement of physical and chemical properties. The soil samples were taken in September 1981. They were put in polythene bags and transported as soon as possible to the laboratory where they were treated immediately or were stored in a frozen state for later analyses.

4.1.2 Definitions and methods of analyses

Most of the definitions and the methods are according to Andersson (1970a) and Allen et al. (1976).

Dry bulk density, *Yt*, is the weight of the volume units of soil in undisturbed stratification dried at 105°C to constant weight.

Reduced bulk density, *Ytr*, is the weight of the fine earth per unit volume of soil, which means that the weight of roots and particles larger than 2 mm are excluded.

Porosity, *P*, is the volume of pore space as a percentage of a given volume of soil which is calculated according to the formula:

$$P = 100\,(1 - \frac{Yt}{S})$$

The soil samples were sieved through 2 mm mesh. Dead and living roots and mineral particles larger than 2 mm were removed and weighed. The following analyses were based on the remaining fine earth.

Specific gravity, *S*, was determined on the fine earth dried at 105°C to constant weight. A soil sample of known weight was placed in a volume-determined flask and the volume of the pores was determined by expelling the air with 95% alcohol.

pH was measured in water extract and in 0.2 M KCl extract. The extraction was prepared according to Sjörs (1961) and Hytteborn (1975). Samples were shaken on a rotating board for three hours. Because of their high clay content, the extracts were centrifuged for 30–60 minutes. Then pH was measured electrometrically with a combined glass and reference electrode (Beckman Expandomatic). The values were determined after the pH had stabilized. The pH values measured in KCl extract were roughly 0.5–1.0 units lower than the ones measured in water extract due to ion exchange—hydrogen ions being released (Peech 1965, Troedsson 1973).

Loss on ignition is an approximate expression of organic matter. Before the ignition, the water content was determined by oven-drying to constant weight at 105°C. Then the samples were put into a muffle furnace at a temperature of approximately 550°C for about one hour. According to Ekström (1927), correction should be made for water losses from samples with high clay content. The correction was applied for all the soil samples taken from this study area.

Total nitrogen, N-total, was determined by means of the macro-Kjeldahl method. Digestion was made with concentrated H_2SO_4 and catalyzed by K_2SO_4. H_2O_2 was added during the digestion. Distillation was done with 40% NaOH into a receiving flask with 0.1 M HCl containing indicators. Titration was made by an automatic titrator (Titrierautomat E 326 and Dosimat E 412) with 0.1 M NaOH.

The cation exchange capacity was determined as the sum of exchangeable metallic cations (Na^+, K^+, Ca^{2+}, Mg^{2+} and Mn^{2+}) and hydrogen ions (H^+). The replicate samples were mixed to a homogeneous composite sample, which considerably reduced the time and labour and rendered the same result as the means of separate determinations, but without information on the deviation. About 20 g of fresh fine earth (moisture content determined) were taken from each of the composite samples and the soil samples were rotated in a polythene flask together with 100 ml 1 M ammonium acetate (AmAc) of pH 7.00 for five hours and then filtrated.

The exchangeable hydrogen ions were determined by measuring the pH of the filtrated soil extracts. The concentration of hydrogen was read off from a pH standard curve obtained by titration of the neutral 1 M AmAc solution with 0.100 M HCl (Brown 1943).

Metallic cations were analysed directly in diluted AmAc extracts (50 ml extract was made up to 100 ml with deionized water) on a Varian Techtron Atomic Absorption Spectrophotometer, Model 1000, acetylene-air burner.

The degree of neutralization or percentage base saturation (Sjörs 1954) was obtained by dividing the sum of exchangeable Na^+, K^+, Ca^+, Mg^{2+} and Mn^{2+} equivalents by the cation exchange capacity determined as the same sum plus exchangeable H^+.

The composite samples were also used for the measurement of the phosphorus content in soil. There are several methods available for the determination of phosphorus (Ståhlberg 1980). In this investigation, analyses of easily soluble P (available to plant) were made according to the Swedish AL-method (Egnér et al. 1960). For total P (stored P), the HCl-method was used. Acetate-Lactate solution (110 g lactic acid d 1.20, 85%, 119 g acetic acid d 1.06, 96%, 80 g ammonium acetate per liter, when used, diluted to 10 times with distilled water) and 2 M HCl were used as the extractants respectively. After digestion and filtration of the air-dried soil samples, the colorimetric method was used for the determination of phosphorus based on the development of molybdenum blue with ammonium molybdate-sulphuric acid reagent and stannous chloride reagent. The concentration of PO_4-P was read off from a standard curve obtained by measuring the optical density at 872 nm using water as a reference on a spectrophotometer Turner Model 330.

The results for N-total, P-AL, P-HCl and exchangeable cations were multiplied by the reduced bulk density to convert them to concentration by volume, since comparison of properties for ecological purposes are more adequate on a volume basis.

4.2 Results

4.2.1 Description of the soil profiles

The soil types within the reserve area were, according to Torstensson & Eriksson (1941), in the sector ranging from light clay with fine sand to heavy clay. The different horizons in the clay profile resulted from the formation of the deposits (Hofman-Bang 1938). The clay content was high, especially in the low-situated sites with the *Carex acuta*, the *Carex disticha* and the *Carex caespitosa* plant communities. In these sites the content of heavy clay was high even in the humus layer. In the relatively high-situated sites with the *Poa pratensis—Alopecurus pratensis* and the *Arrhenatherum pubescens-Alopecurus pratensis* plant communities, the soils were more or less mixed with silt and fine sand which provided a fairly good physical structure at these sites. The differences between the contents of clay were caused by an uneven deposition of the clay fraction during the formation of the deposits (Torstensson & Eriksson op. cit.). No mineral particles larger than 2 mm were found in the samples taken from the study area.

All profiles showed distinct hydromorphic features and the macromorphological features were apparently dependent on the variation in ground water regimes in the study area. The humus layer was 11–12 cm thick in plant community A and 13–14 cm in plant community B. The humus type was a mull, dark brown in colour with a crumb structure, particularly in plant community B which had a typical coarse crumb structure due to large earthworms. The boundary between the humus layer and the underlying layer was not sharp. The soil-moisture regime there allowed adequate aeration in the upper part of the soil. Fissures were frequent in the underlying layer with rusty mottles. The humus layer was 6–8 cm thick in plant community C and 8–10 cm in plant community E with black colour in the upper part and dark grey colour in the lower part. The humus type resembled mull, being a black, structureless humus type well mixed with mineral material. Due to a frequent fluctuation of the ground water table close to the upper part of the soil, the reduced features dominated over the oxidized features there. The humus layer in plant community D was 4–6 cm thick. The humus type could be assigned to mull-like moder, a black, structureless humus with a substantial mineral admixture and smell of ink. The boundary between the humus layer and the underlying layer was rather sharp, and the latter was of a pale grey colour which indicated a predominantly reduced feature developed by a high water table throughout the year.

4.2.2 Humus content

The humus content of the fine earth expressed as the percentage of loss on ignition after the correction, shows a slightly horizontal variation and a more clearly vertical variation (Table 6). Expressed as percentage of dry weight, the average losses on ignition for the plant communities were: 11.1±0.74 (A), 9.8±1.6 (B), 11.9±0.74 (C), 9.7±1.17 (D) and 10.7±0.56 (E) respectively, in the upper 10 cm horizons. The vertical variation showed the highest values in the upper 10 cm and the values decreased considerably with depth.

Table 6. Survey of soil structural properties. Means ($\bar{x}$) and standard deviations (SD) of loss on ignition in weight % (ign. loss), dry bulk density (Yt; g/cm^3), reduced dry bulk density (Ytr; g/cm^3), specific gravity (S; g/cm^3) and porosity in volume % (P). SD at 95 % confidence limits. n = number of samples. m = the value of the composite samples.

Community type	Depth (cm)	n	ign. loss		Yt		Ytr		S	P
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	m	m
A	0-10	4	11.10	0.74	0.86	0.26	0.84	0.06	2.51	65.9
	10-20	4	3.63	0.80	1.19	0.07	1.18	0.07	2.53	53.1
	20-30	4	2.25	0.21	1.26	0.01	1.26	0.01	2.59	51.2
B	0-10	5	9.80	1.60	0.84	0.07	0.80	0.07	2.55	67.1
	10-20	5	4.50	1.04	1.11	0.07	1.10	0.07	2.59	57.3
	20-30	5	2.00	0.67	1.22	0.07	1.22	0.07	2.73	55.3
C	0-10	5	11.90	0.74	0.68	0.04	0.64	0.05	2.55	73.5
	10-20	5	1.93	0.40	1.30	0.04	1.29	0.04	2.71	52.2
	20-30	5	0.53	0.33	1.31	0.04	1.31	0.04	2.75	52.3
D	0-10	4	9.68	1.17	0.79	0.07	0.76	0.07	2.53	68.6
	10-20	4	1.05	0.45	1.35	0.04	1.34	0.03	2.76	51.0
	20-30	4	0.15	0.39	1.40	0.06	1.40	0.06	2.79	49.9
E	0-10	5	10.68	0.56	0.73	0.08	0.69	0.08	2.55	71.5
	10-20	5	3.45	0.82	1.03	0.08	1.02	0.08	2.59	60.4
	20-30	5	1.13	0.50	1.23	0.09	1.23	0.09	2.71	54.5

The losses on ignition in the humus layer were within the variation measured by Sjörs (1961) in samples classified as mull from grassland and other open sites.

4.2.3 Dry bulk density and reduced bulk density

The dry bulk density of the soil in plant communities A–E were 0.86, 0.84, 0.68, 0.79 and 0.73 g/cm^3, respectively, in the upper 10 cm. As to the vertical variation, maximum values of 1.22–1.40 g/m^3 were found in the lower 20–30 cm. The influence of organic matter on dry bulk density was obvious (Fig. 22). At high percentages of loss on ignition the dry bulk density would be largely determined by porosity; similar relationships have been reported by Sjörs (1961) and Andersson (1970 a).

A comparison of dry bulk density with the reduced bulk density showed a variation in the upper part of the soil, which corresponded to the rooting

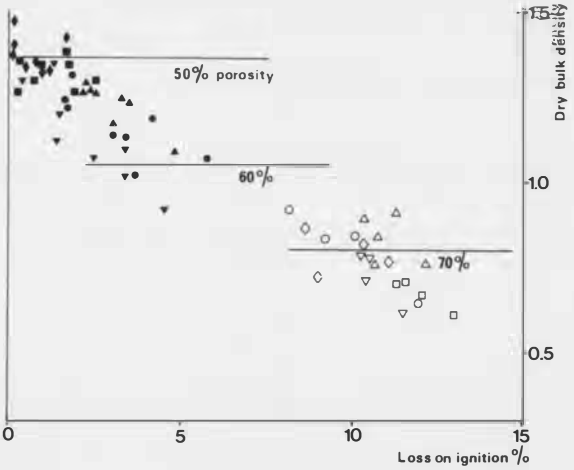


Fig. 22. Relationship between dry bulk density, loss on ignition and porosity of the soil samples taken from plant communities: A (△, 0–10 cm, ▲, 10–30 cm), B (○, ●), C (□, ■), D (◇, ◆) and E (▽, ▼) in the Kungsängen Nature Reserve.

depth. The variation was mainly caused by the differences in root distribution.

4.2.4 Specific gravity

The specific gravity showed no significant differences between the different sampling sites (Table 6). A slightly vertical variation parallel to the distribution of organic matter was confirmed, with the lower specific gravity (2.51–2.55) in the upper 10 cm and high values (2.59–2.79) in the 20–30 cm horizons. This meant decreasing specific gravity with increasing organic matter.

4.2.5 Porosity

Generally, the pore space made up more than 50% of the soil volume at all sampling sites (Table 6). The greatest variations were found in the upper 10 cm, with 65.9 % for plant community A, 67.1% for community B, 73.5% for community C, 68.6% for community D and 71.5% for community E. The porosity in the 20–30 cm level showed small differences, ranging from 49.9 to 55.3%. The porosity of soil was influenced by the nature of the soil texture, the degree of packing and the soil organic matter. The influence of soil organic matter on porosity can be seen in Fig. 22.

4.2.6 pH

The horizontal and vertical variations of pH_{water} and pH_{KCl} are presented in Table 7. A comparison of determinations of fresh sample in water and KCl solutions was made. The differences between pH values from these two extracts varied from 0.6–1.5 pH units with, as could be expected, large differences in the more acid samples (with more exchangeable hydrogen ions).

The pH_{water} values were below 7 in the soil sam-

Table 7. Comparison between pH_{water} and pH_{KCl}. Figures calculated as means ± standard deviation, n = number of samples.

Plant community		A	B	C	D	E
Type of extract	Depth cm	n = 4	n = 5	n = 5	n = 4	n = 5
H_2O	0-10	5.93 ± 0.22	6.64 ± 0.08	7.52 ± 0.07	7.54 ± 0.06	7.46 ± 0.14
	10-20	5.92 ± 0.06	7.79 ± 0.06	7.69 ± 0.05	7.72 ± 0.06	7.73 ± 0.05
	20-30	6.26 ± 0.06	7.88 ± 0.04	7.81 ± 0.03	7.81 ± 0.06	7.81 ± 0.03
KCl	0-10	4.89 ± 0.24	5.53 ± 0.14	7.03 ± 0.05	6.92 ± 0.06	6.76 ± 0.15
	10-20	4.57 ± 0.08	7.11 ± 0.06	7.08 ± 0.05	7.02 ± 0.04	6.97 ± 0.04
	20-30	4.83 ± 0.08	7.18 ± 0.04	7.17 ± 0.03	7.18 ± 0.03	7.04 ± 0.02

Table 8. Vertical distribution of exchangeable cation content for plant communities A – E along the transect.

		Exchangeable cation meq/dm^3							
Community type	Depth (cm)	H^+	K^+	Na^+	Mg^{2+}	Mn^{2+}	Ca^{2+}	Sum metallic cation	Degree of neutralization
A	0-10	39.9	9.26	0.80	34.4	0.125	115.5	160.0	80.1
	10-20	33.1	3.97	1.10	56.3	0.030	160.3	221.7	87.0
	20-30	28.1	2.13	1.99	71.5	0.011	167.2	242.8	89.6
B	0-20	20.5	2.85	1.19	21.8	0.010	194.9	220.8	91.3
	10-20	-	1.93	1.86	17.9	0.008	328.8	350.5	100.0
	20-30	-	1.76	2.42	19.8	0.008	346.9	371.0	100.0
C	0-10	-	2.29	5.10	21.1	0.028	284.9	277.4	100.0
	10-20	-	1.70	5.96	25.0	0.167	341.3	374.1	100.0
	20-30	-	1.30	5.95	30.6	0.069	325.7	363.7	100.0
D	0-10	-	2.41	2.69	16.7	0.026	298.4	320.3	100.0
	10-20	-	1.00	2.78	17.9	0.764	322.6	345.0	100.0
	20-30	-	0.94	3.33	24.5	0.031	333.2	362.0	100.0
E	0-10	-	2.29	6.13	13.4	0.009	215.5	237.3	100.0
	10-20	-	1.39	7.66	9.8	0.007	291.9	310.8	100.0
	20-30	-	1.06	7.23	9.8	0.007	288.3	306.4	100.0

ples from plant community A, which might partly be due to the gyttja content in the eastern part of the reserve area (Giöbel 1933).

4.2.7 Exchangeable cations and degree of neutralization

In Table 8 the exchangeable cations, degree of neutralization and cation exchange capacity are given. In general, the cation exchange capacity was rather high in the study area, ranging from 200 to 374 meq/dm^3. The samples with highest exchange capacity were in wet sites of the study area and relatively dry sites had lower values. There was no obvious correlation between the exchange capacity and the organic content, perhaps because of the high content of clay. A relationship between the pH and the percentage of exchangeable metallic cations existed in this study (cf. Gorham 1953, Sjörs 1961). There was an increasing percentage of neutralization from 80% to 100%, from plant community A towards community D. Samples with a higher percentage value had also a higher Ca^{2+} content, which was a dominant exchangeable metallic ion, ranging from 116 to 347 meq/m^3. As to the amount of exchangeable Ca^{2+} and the sum of exchangeable metallic cations, there was a marked differentiation, similar to that found for the degree of neutralization.

Exchangeable H^+ was mainly presented in plant community A. The K^+ and Mg^{2+} contents were higher in plant community A than in the others. The Na^+ was slightly higher in plant communities E and C than in the others. No trend was noticed for the rather irregular Mn^{2+} content in the samples except that the amount in plant community D (at 10–20 cm) was much higher than in the other samples, and the amounts in plant communities E and B were very low.

Sjörs (1961) gives a variation of 41–95 for the degree of neutralization for grassland mull, 144 to 274 meq/dm^3 for cation exchange capacity, 2.3 to 5.3 meq/dm^3 for K^+ content, 13 to 186 meq/dm^3 for Ca^{2+} content, 0.3 to 1.6 meq/dm^3 for Na^+ content. The corresponding values obtained from the humus layer at the study area were mostly within the ranges given by Sjörs and in some cases, slightly higher.

4.2.8 Nitrogen

The horizontal and vertical variations of N-total are presented in Table 9. The mean values for the plant communities were: 5.13 (A), 4.45 (B), 4.08 (C), 4.01 (D) and 4.0 g/dm^3 (E) respectively, in the upper 10 cm. A vertical variation existed in all sampling sites; the N-total content decreased with

Table 9. N-total and P-AL, P-HCl contents in different horizons for plant communities A – E. Figures for N-total content are expressed in g/dm^3, as means ± standard deviations n = number of samples. Figures for P-AL and P-HCl content are the mean value of the composite samples, in mg/dm^3.

Community type	Depth (cm)	N-total g/dm^3 n = 4	P-AL mg/dm^3	P-HCl mg/dm^3
A	0-10	5.13 ± 0.62	39.4	629
	10-20	1.88 ± 0.22	18.6	690
	20-30	0.84 ± 0.19	17.2	670
B	0-10	4.45 ± 0.58	15.5	469
	10-20	3.21 ± 0.52	25.6	673
	20-30	1.71 ± 0.06	26.7	717
C	0-10	4.08 ± 0.20	19.3	369
	10-20	2.00 ± 0.35	24.9	773
	20-30	1.30 ± 0.27	20.9	771
D	0-10	4.01 ± 0.46	31.3	487
	10-20	1.45 ± 0.08	32.2	882
	20-30	1.23 ± 0.20	29.7	928
E	0-10	4.00 ± 0.31	44.1	462
	10-20	2.09 ± 0.74	26.0	663
	20-30	1.15 ± 0.31	26.3	769

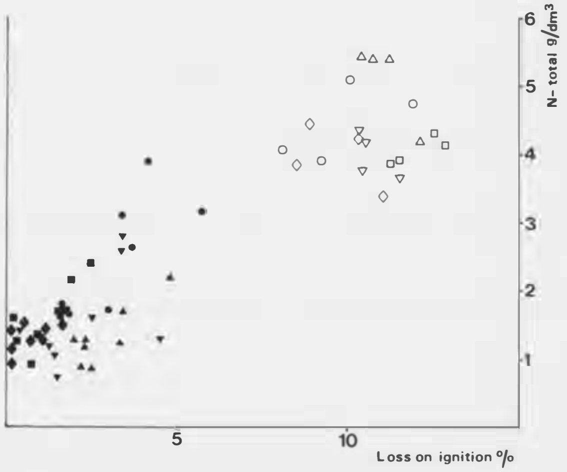


Fig. 23. Relationship between loss on ignition and N-total for the soil samples taken from plant communities: A (△, 0–10 cm, ▲, 10–30 cm), B (○, ●), C (□, ■), D (◇, ◆) and E (▽, ▼) in the Kungsängen Nature Reserve.

depth, but in plant community B not as sharply as in the others. This may be explained by the abundant presence of earthworms there.

There was a close correlation between the N-total content and the soil organic content (Fig. 23). The N-total contents in the humus layer at all the sampling sites were within the range of 2.0–6.7 g/dm^3 reported by Sjörs (1961) for mull from grassland and other open sites.

4.2.9 Phosphorus

The results of determination of P-AL and P-HCl are presented in Table 9. Ståhlberg (1976) has classified the available and stored phosphorus into five levels; a high value gives a higher class. Compared with these classes, the values for P-AL for plant communities A and E fall into 3, for plant communities C and D into 2 and for plant community B into 1 (upper 10 cm horizon). The values for P-HCl for communities A, D and E fall into class 4, and for communities B and C into 3. In general, there were, however, no particular differences between the P-HCl values, neither in the horizontal nor in the vertical distribution.

A range of 240–860 mg/dm^3 for P-total, and of 4–31 mg/dm^3 for P-AL is given by Sjörs for mull from grassland. The corresponding values obtained in the study area were within these ranges, and a few values were higher.

5 Primary production

The investigation of the plant community production at the Kungsängen Nature Reserve mainly aimed at providing information on the potential yield of hay-making, while establishing the differences in standing crop between the plant communities with reference to some soil physical and chemical properties as well as the soil-water regime.

5.1 Methods

The measurement of net primary production by determining the biomass at the beginning and the end of a study period has been widely used by agronomists and plant ecologists on managed grassland (Milner & Hughes 1968). In this study area, the above-ground living biomass at the beginning of the growing season is negligible. By the end of June the above-ground biomass reaches its maximum and thereafter there is a gradual decline (according to the manager). It was decided to estimate above-ground biomass only once when the maximum standing crop is reached.

The study was carried out in July 1981. During that year the whole vegetation transect was protected from mowing, which was done over the rest of the area during the period June 18–21. Samples were taken from the four plant communities A–D, except the *Carex caespitosa* community. This community type occurs only in a relatively small area and moreover, its tussocks and large interspaces made sampling difficult. By using the restrictive random method (Goldsmith et al. 1976), the sites along the transect under study were divided systematically into eight sub-divisions, each 50 m long, and each sub-division then was sampled at random. In this way each part of the transect had a good chance of being sampled and at the same time as the data obtained were suitable for statistical analysis. Sampling plots of 50×50 cm were used as recommended for grassland vegetation by Shimada (1959)) and Milner & Hughes (1968). The number of plots varied from one community to another between 6 and 27, the heterogeneity and the range of the plant community type being taken into account:

A. *Poa pratensis-Alopecurus pratensis* community	6
B. *Arrhenatherum pubescens-Alopecurus pratensis* community	27
C. *Carex disticha* community	12
D. *Carex acuta* community	9

Harvest data from the plots gave standard errors of the means for each plant community type ranging from 4.2 to 7.0%, with a mean of 5.6%. This is within the acceptable standard of an error of 10% of the mean (Milner & Hughes 1968).

All sampling plots were clipped with a pair of scissors (July 6–8, 1981) down to the litter and bryophyte layer at a level of about 2 cm above the soil surface. This way of harvesting proved to have no lethal effect on the vegetation. The freshly cut material was put into polythene bags and transported to the laboratory within a few hours, where it was stored frozen.

The harvested material from each sampling plot was sorted into four categories: (1) living graminids, (2) living herbids, (3) dead graminids and (4) dead herbids.

Living and dead graminids and herbids were weighed fresh and subsequently oven-dried to a constant weight at 80°C for 72 hours, and weighed again on a balance sensitive to 0.01 g. In presenting the results mean and a standard deviation, in g/m^2, were calculated on the basis of the restrictive random samples for each community type.

The estimation of the underground biomass was considered as well, but not realized. Two main difficulties were the separation of living from dead roots and the removal of soil particles adhering to root hairs (Milner & Hughes 1968). Besides, the root production measurement is very time-consuming. Nevertheless, some root analyses were made during September 1981, when four to five soil cores of 4.8 cm diameter were taken randomly from each plant community site for analyses of soil physical and chemical properties. The roots were separated from 0–10, 10–20 and 20–30 cm soil horizons, then washed, oven-dried and weighed.

5.2 Results

The mean and standard deviation of the peak standing crop, the proportion of graminids and herbids, and the ratio of dead and living standing crops are presented in Table 10. A statistical analysis (t-test) was carried out to compare the mean peak standing crops between these four plant communities and the results are presented in Table 11.

The differences in the peak standing crop were considerable. The highest value of the peak standing crop was found in plant community A with a mean value of 585 g/m^2, which was significantly higher than for any other plant community ($P<0.01$). The lowest value for the peak standing crop was found in plant community C with a figure of 340 g/m^2. The difference in the peak standing crop between plant communities C and D was significant ($P<0.01$) and that between plant communities C and B was considerable ($P<0.05$). The values for the mean standing crop of plant communities B and D were intermediate, with figures of 407 g/m^2 and 446 g/m^2 respectively, and there was no significant difference between these two plant communities ($P>0.10$).

Table 11. Comparison of the means of peak standing crop between plant communities A, B, C and D. t-test, t = calculated value, t' = expected value at significance level 0.05, t" = expected value at significance level 0.01. xx = significant at $t_{0.01}$, x = significant at $t_{0.05}$, N.S. = no significance.

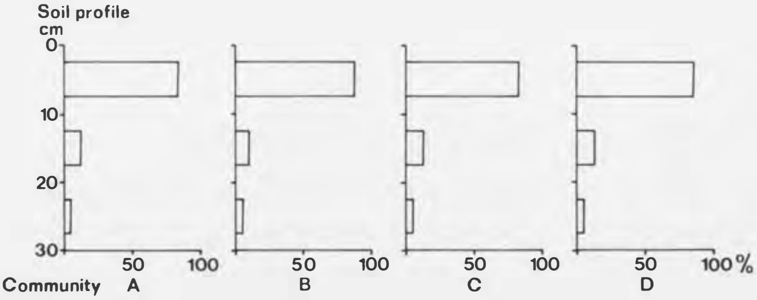
Compared communities	t	t'	t"	significance
Communities A - B	4.67	2.04	2.75	xx
Communities A - C	7.98	2.12	2.92	xx
Communities A - D	3.40	2.16	3.01	xx
Communities B - C	2.42	2.02	2.70	x
Communities B - D	1.17	2.04	2.75	N.S.
Communities C - D	3.41	2.09	2.86	xx

Considering the proportion of graminids and herbids, these plant communities were graminid-dominated ones: the herbids in all harvests from these four communities showed very low values both in the absolute weight and in the proportion of the total standing crop, generally not more than 7%. In plant community A the graminids contributed 98.9% of the total standing crop, of which the most abundant species were the tall-grasses *Poa pratensis, Alopecurus pratensis, Agropyron repens* and the tussocky species *Deschampsia caespitosa*. The herbids accounted only for 1.1% of the total standing crop. Plant community B was relatively herbid-rich, accounting for 6.7% of the total standing crop, the highest proportion among the plant communities under study. The graminids

Table 10. Means and standard deviations of total standing crop, proportions of graminids and herbids, and ratio of dead and living standing crops for plant communities A, B, C and D. n = number of sample plots. Dry weight in g/m^2, dried at 80°C, 3 days.

Community type	A n = 6	B n = 27	C n = 12	D n = 9
Total standing crop	585 ± 66.9	407 ± 87.4	340 ± 59.5	446 ± 83.9
Graminids	578 ± 68.5	380 ± 80.6	334 ± 59.5	433 ± 82.6
% in total	98.9	93.3	98.0	97.1
Herbids	6.7 ± 3.6	27.4 ± 15.7	6.6 ± 7.0	12.8 ± 5.5
% in total	1.1	6.7	2.0	2.9
Standing dead crop				
Graminids	64.2 ± 22.1	49.1 ± 16.9	54.4 ± 8.8	58.9 ± 19.8
Herbids	2.8 ± 1.8	3.5 ± 2.9	0.6 ± 0.6	2.0 ± 1.1
Ratio of dead and living standing crops	0.12	0.13	0.16	0.14

Fig. 24. Root distribution in the soil profiles (0–30 cm) in plant communities A–D.



constituted 93.3% of the total standing crop, of which the most abundant species were *Deschampsia caespitosa, Alopecurus pratensis, Arrhenatherum pubescens* and *Festuca rubra*. In plant community C, *Carex disticha* was the most dominant species, with sparsely distributed species such as *Alopecurus arundinaceus, Deschampsia caespitosa, Festuca rubra* and others. The herbids constituted only 2.0% of the total standing crop. In plant community D, *Carex acuta* accounted for more than 90% of the total standing crop and only a few other graminids and herbids could survive there, reaching very low cover. The herbids accounted for 2.9% of the total standing crop.

The ratio of the standing dead and living crops at harvesting time varied from 0.12 to 0.16 in these plant communities. The figures for sedge communities C and D were higher than those for plant communities A and B, which may suggest that the maximum standing crop was reached earlier in communities C and D.

The percentage distributions in relation to the depth of soil profiles in these four plant communities are shown in Fig. 24. Most of the shallow roots, which constituted more than 90% of the total root crop, were restricted to the upper 20 cm where the soil had good texture and structure, and the nutrient conditions were sufficient for grass development.

6 Vegetation dynamics

Vegetation dynamics can be defined as the changes in time in the composition of vegetation at a site. Austin (1981) stressed that it is important to partition dynamical variability into its components, such as the differential effects of climatic changes, environmental changes and biotic factors. Numerical classification and ordination can assist in such a clear partitioning of types of dynamical behaviour (Austin et al. 1981). This approach has been used successfully, especially in grassland, first in dune grassland to reveal successional relationships between plant communities (van der Maarel 1969), further in a lawn to show the changes of vegetation composition from year to year (Austin 1977), and in a long-term experiment in grassland to study the dynamical behaviour under different treatments (van Hecke et al. 1981).

An approach to the ecological interpretation of the vegetation, which can also be used in studies of vegetation dynamics, is the use of ecological indicator values of species, as developed by Ellenberg (1974) for Central Europe. On this basis, sites can be interpreted in terms of soil moisture, acidity, nitrogen status, etc., by assigning a value to each plant species for these important factors. The values are based on general experience, including measurements.

The interpretation can be further facilitated by combining the indicator value approach with an independently derived ordination based on the compositional variation of the sites involved (Persson 1980, 1981).

As has been mentioned in the previous sections, the vegetation at the Kungsängen Nature Reserve had been used for hay-making long before the establishment of the reserve and the soil-water conditions are mainly responsible for the differentiation of the vegetation at the study area. This study is focused on the vegetation dynamics in the reserve area over 41 years. By applying the dynamical approach based on repeated observations on permanent plots, the development of vegetation is described with multivariate techniques. Furthermore, as environmental data for 1940 were unknown, the system of ecological indicators is applied to interpret the dynamical changes in the vegetation. At the same time it is interesting to test whether Ellenberg's general system fits the real local situation outside Central Europe.

6.1 Methods

6.1.1 Observation sites

Permanent plots with yearly or at least regular recording are now generally considered as necessary for studies of vegetation dynamics (Austin 1981). An alternative to span a longer period without observations in the years between is the reestablishment, with acceptable accuracy, of plots once used and analyzed by other investigators (Persson 1980). The vegetation of the reserve area was described by Sandberg in 1940 (Sandberg 1948). He laid out a 495 m long transect which ran across the study area from east to west and covered most of the representative plant community types (see chapter 2, Fig. 5, plot numbers 1–28). Twenty-eight 2×2 m plots along this transect were sampled in the middle of June 1940 for vegetation analysis and the positions of these plots as well as the accompanying information were given by Sandberg (1948). The investigation was repeated by the present author in the middle of June 1981, using Sandberg's 1940 plot system. The 28 plots could be traced back almost to the nearest dm due to Sandberg's excellent description and his personal inspection of the transect in 1981.

The phanerogams were recorded for each plot and the quantitative occurrence of each species was estimated according to the Hult-Sernander-Du Rietz scale which was also used in Sandberg's investigation, thus simplifying the comparison with the older data.

6.1.2 Numerical methods

The multivariate data set consisted of cover estimates for 76 species in the same twenty-eight plots at two different times (1940 and 1981), thus reducing a three dimensional matrix of sites × species × times to a two dimensional one of site-times × species.

To obtain recognizable vegetation types and to follow their persistence over time, a numerical classification with the TABORD program was applied. The clusters were described in terms of the mean species cover value and the frequency of occurrence of species. The calculation of the mean cover value was according to Sjörs (1954), taking into account the exponential character of the Hult-Sernander-Du Rietz scale. Species dynamics were roughly divided into three groups:

I. decreasing cover or frequency
II. increasing cover or frequency
III. cover value or frequency more or less constant

By treating the data recorded for the 28 plots in 1940 and 1981 respectively as observations, the Principal Component Analysis (PCA) produced an ordination diagram in which the records for individual years of these plots appeared as points. The corresponding points on the ordination diagram were joined up to indicate the trajectory of each permanent plot through time in the floristic space defined by the axes of the PCA ordination. The patterns of behaviour among the permanent plots could then be analysed in relation to underlying environmental gradients.

6.1.3 Ecological indicator value

The so-called "ecological behaviour" of the species (Ellenberg 1974) has been expressed by the indicator values representing nine or twelve degrees, on an arbitrary scale, of "behaviour" with regard to the occurrence of species in relation to:

a) soil moisture or water level (moisture figure)
b) soil acidity (reaction figure)
c) the ammonia or nitrate supply (nitrogen figure)

The indicator value in relation to the general response of a species to the phosphorus status in a habitat has been presented by Kruijne et al. (1967), on the scale −100 −+100.

Characteristic indicator values (CIV_{jk}) for each plot were calculated according to Persson (1981):

$$CIV_{jk} = \frac{\Sigma\, C_{ij} Z_{ik}}{\Sigma\, C_{ij};\ Z_{ik} \neq 0}$$

where C_{ij} is the cover value (Hult-Sernander-Du Rietz scale) for the i-th species in each plot (j) and Z_{ik} is the indicator value for the i-th species and environmental factor (k), in this case including soil moisture, acidity, nitrogen and phosphorus status.

In cases where the indicator value was missing or marked unknown in the tables of Ellenberg and Kruijne et al., the respective species was deleted from that calculation. Only the species with the determined indicator values were taken into account for the calculation of *CIV*.

The proportion of unknown or indifferent indicator values in the present example was: soil moisture 21%; reaction 60%; nitrogen 27%; phosphorus 27%. If a large proportion of the indicator values was unknown or indifferent, the calculated *CIV* became unreliable; in this study the factor reaction was less satisfactorily indicated.

6.2 Results

6.2.1 Vegetation types

Six clusters were obtained in the final table of the TABORD classification with the 28 permanent plots and 76 taxa for two years (plot numbers 1−28 for 1940 and 29−56 for the corresponding plots in 1981). The resulting 6 clusters were based on an initial classification array of 10 clusters, with the options: a minimum cluster size of 3, threshold value of 0, frequency limit of 0.60 and fusion limit of 0.70. The frequencies and the mean cover values (HSD scale) of species in these 6 clusters are presented in Table 12.

Cluster 1 was composed of eighteen permanent plots from 1940 and five plots from 1981. *Agropy-*

Table 12. Species composition of the clusters. a = Frequency. b = Average cover value (HSD scale) of species when frequency is more than 50 % and when frequency is less than 50 % the symbol + is used. Species presented less than 50 % in all clusters are listed in the Addenda.

Cluster number	1		2		3		4		5		6	
Number of plots	23		14		4		4		4		7	
Average number of species per plot	21		25		14		14		8		7	
	a	b	a	b	a	b	a	b	a	b	a	b
Agropyron repens	96	3	21	+	75	2	-	-	-	-	-	-
Taraxacum sp.	100	2	43	+	25	+	-	-	-	-	-	-
Alopecurus pratensis	91	3	86	2	50	+	-	-	-	-	-	-
Festuca pratensis	87	1	86	1	-	-	-	-	-	-	-	-
Phleum pratense	78	1	100	1	-	-	-	-	-	-	-	-
Stellaria graminea	48	+	64	1	-	-	-	-	-	-	-	-
Trifolium pratense	4	+	64	1	-	-	-	-	-	-	-	-
Trifolium repens	39	+	86	1	-	-	-	-	-	-	-	-
Arrhenatherum pubescens	9	+	100	2	-	-	-	-	-	-	-	-
Galium verum	22	+	57	1	-	-	-	-	-	-	-	-
Cerastium caespitosa	52	1	50	+	-	-	-	-	-	-	-	-
Achillea millefolium	39	+	64	1	-	-	-	-	-	-	-	-
Festuca rubra	74	1	100	2	25	+	25	+	-	-	-	-
Poa pratensis	100	3	93	1	100	1	50	+	-	-	-	-
Fritillaria meleagris	65	1	100	1	75	1	-	-	-	-	-	-
Lathyrus pratensis	70	1	100	1	50	+	25	+	-	-	-	-
Ranunculus acris	91	1	100	1	25	+	-	-	-	-	-	-
Ranunculus auricomus	91	1	100	1	100	1	25	+	-	-	-	-
Vicia cracca	83	1	100	1	25	+	25	+	-	-	-	-
Rumex acetosa	52	1	79	1	25	+	-	-	-	-	-	-
Geum rivale	39	+	93	1	25	+	75	1	-	-	-	-
Galium uliginosum	52	1	64	1	75	1	25	+	-	-	-	-
Ranunculus repens	70	1	14	+	75	1	25	+	75	2	-	-
Deschampsia caespitosa	100	4	100	3	100	3	75	1	50	+	-	-
Poa trivialis	39	+	64	1	25	+	50	+	75	1	-	-
Potentilla anserina	35	+	21	+	100	1	50	+	100	4	-	-
Alopecurus pra. x arun.	26	+	36	+	100	4	75	1	-	-	-	-
Alopecurus arundinaceus	9	+	-	-	100	4	50	+	50	+	14	+
Carex disticha	-	-	14	+	25	+	100	4	-	-	29	+
Filipendula ulmaria	22	+	43	+	50	+	75	1	-	-	14	+
Carex caespitosa	4	+	29	+	-	-	75	1	-	-	-	-
Polygonum amphibium	-	-	50	+	-	-	75	1	-	-	100	1
Carex acuta	-	-	7	+	-	-	50	+	100	5	100	5
Equisetum fluviatile	-	-	-	-	-	-	-	-	-	-	71	1
Lemna minor	-	-	-	-	-	-	-	-	-	-	86	1
Lemna trisulca	-	-	-	-	-	-	-	-	-	-	86	1
Lysimachia thyrsiflora	-	-	-	-	25	+	25	+	50	+	86	1

Addenda of other species (frequency less than 50 %)

Urtica dioica, Veronica chamaedrys, Thalictrum flavum, Stellaria palustris, Ranunculus sceleratus, Ranunculus polyanthemus, Polygonum aviculare, Plantago major, Pedicularis palustris, Oenanthe aquatica, Myosotis palustris, Matricaria inodora, Matricaria matricarioides, Lysimachia nummularia, Lotus corniculatus, Leontodon autumnalis, Heracleum sphondylium, Glechoma hederacea, Galium boreale, Galeopsis sp., Cirsium vulgare, Carum carvi, Cardamine pratensis, Capsella bursa-pastoris, Caltha palustris, Anthriscus sylvestris, Alisma plantago-aquatica, Alchemilla sp., Scirpus palustris, Poa palustris, Poa annua, Phalaris arundinacea, Glyceria maxima, Dactylis glomerata, Carex sp., Briza media, Agrostis stolonifera, Agrostis canina.

Table 13. Cluster number to which vegetation type each permanent plot belonged in 1940 and 1981 showing the development of the vegetation in the 28 permanent plots. For distribution of the permanent plots see Fig. 5.

Plot number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Cluster number																												
1940	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	3	5	5	5	5	4	1	1	1	2
1981	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	4	4	4	6	6	6	6	6	6	6	2	2	1

ron repens, Alopecurus pratensis, Poa pratensis, Deschampsia caespitosa and *Taraxacum* sp. were the dominant species. The species *Ranunculus repens, Festuca pratensis, Festuca rubra, Phleum pratense, Lathyrus pratensis, Ranunculus acris, R. auricomus, Fritillaria meleagris* and *Vicia cracca* were frequent but had low cover values. The mean number of species per plot was 21.

Cluster 2 consisted of thirteen permanent plots from 1981 and one from 1940. This cluster shared many species with cluster 1, but the frequency and the mean cover value of *Agropyron repens, Taraxacum* sp., *Alopecurus pratensis* and *Poa pratensis* were lower. On the other hand, *Festuca rubra, Arrhenatherum pubescens* and *Geum rivale* had higher frequencies and cover values in cluster 2 than in cluster 1. The vegetation was rich in species and the mean number of species per plot was 25.

Cluster 3 included only four plots from 1940. This cluster was characterized by the abundance of *Alopecurus arundinaceus, A. pratensis* × *arundinaceus, Deschampsia caespitosa* and *Agropyron repens.* The species *Poa pratensis, Ranunculus repens, Fritillaria meleagris, Ranunculus auricomus, Potentilla anserina* and *Galium uliginosum* were frequent. The mean number of species per plot was 14.

Cluster 4 comprised three permanent plots from 1981 and one from 1940. *Carex disticha* was the most dominant species. *Deschampsia caespitosa, Geum rivale, Alopecurus pratensis* × *arundinaceus, Filipendula ulmaria, Carex caespitosa* and *Polygonum amphibium* were frequent but had low cover values. The mean number of species per plot was 14.

Cluster 5 contained only four permanent plots from 1940. This cluster was characterized by the dominance of *Carex acuta* and *Potentilla anserina. Ranunculus repens* and *Poa trivialis* also had a relatively high frequency and cover value. The vegetation was poor in species and the mean number of species per plot was about 8.

Cluster 6 included only seven permanent plots from 1981. This cluster resembles cluster 5 in several ways. Namely, the vegetation was poor in species and the mean number of species per plot was 7, and *Carex acuta* was the dominant species. However, the species *Ranunculus repens, Potentilla anserina* and *Poa trivialis* were not found in this cluster and instead *Polygonum amphibium, Equisetum fluviatile, Lemna minor* and *Lemna trisulca* occurred.

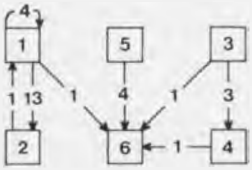


Fig. 25. Diagram of cluster transitions in the permanent plots of the Kungsängen Nature Reserve. Numbers in arrows indicate number of transitions and numbers in squares indicate cluster numbers.

The occurrence of the 6 clusters in space and time is shown in Table 13 which indicates the vegetation types to which each permanent plot belonged in the years 1940 and 1981 respectively, thus describing changes of vegetation in terms of clusters over 41 years. The following main developments could be noticed (Fig. 25).

(1) In the wettest sites, i.e., in permanent plots 19–25, a transition towards cluster 6 was quite clear, mainly from the plots which once belonged to cluster 5 but also from a few plots which once belonged to clusters 3, 4 and 1. The species like *Carex acuta, Equisetum fluviatile, Polygonum amphibium, Lysimachia thyrsiflora, Lemna minor* and *Lemna trisulca* which indicate frequent inundation conditions (Ellenberg 1974), increased their presence or appeared in the plots belonging to cluster 6, while the species indicating moist soil conditions such as *Potentilla anserina, Ranunculus repens, Deschampsia caespitosa* and *Poa trivialis,* which once occurred in the plots now belonging to cluster 6, disappeared.

(2) In the nowadays relatively wet sites, i.e., in permanent plots 16–18, a transition from cluster 3 towards cluster 4 was observed. The dominant species *Carex disticha,* according to Ellenberg's value, indicates wet, often not well aerated soil conditions and flooding. Many species once in cluster 3 had disappeared or decreased their frequencies and cover values since 1940. Among these species, which indicate moderately moist soil conditions, *Agropyron repens, Ranunculus repens, Potentilla anserina, Poa pratensis, Deschampsia caespitosa, Fritillaria meleagris, Ranunculus auricomus,*

Galium uliginosum and *Alopecurus pratensis* × *arundinaceus* can be mentioned.

(3) In the mesic sites, i.e., in permanent plots 5–15, 26 and 27, a transition from cluster 1 towards cluster 2 was recorded. In cluster 2 *Festuca rubra* and *Arrhenatherum pubescens,* which indicate a relatively poor nutrient status, especially a low P-status (Kruijne et al. 1967), had higher frequencies and cover values than in cluster 1, while species indicating a relatively high nutrient status (Ellenberg 1974, Kruijne et al. 1967) such as *Alopecurus pratensis, Agropyron repens, Ranunculus repens, Taraxacum* sp. and *Poa pratensis* had lower frequencies and cover values in cluster 2.

(4) In the relatively dry sites which were located on the borders of the reserve area, the vegetation in permanent plots 1–4 was quite stable over the 41 years and they remained in cluster 1. Permanent plot 28 was an exception to the main trends of vegetation development in the study area, as it changed from cluster 2 to cluster 1. The species which occurred in these plots indicate, according to Ellenberg and Kruijne et al., high nutrient status and mesic soil conditions. The ground water investigation and the soil analyses (see chapters 3 and 4) confirmed that the sites on the border area in the reserve, where permanent plots 1–4 and 28 were located, had a fairly good drainage and nutrient status.

6.2.2 Ordination

The first four axes of the PCA ordination accounted for 0.371, 0.107, 0.089 and 0.066 of the total variance. Only the first two axes could be interpreted. The 6 clusters indicated in the TABORD classification table could be drawn as discrete entities on the first and second axes diagram of the PCA stand ordination (Fig. 26). The 6 clusters established appeared reasonable and rather homogeneous. The dynamical relationships of the individual plots were indicated by the time

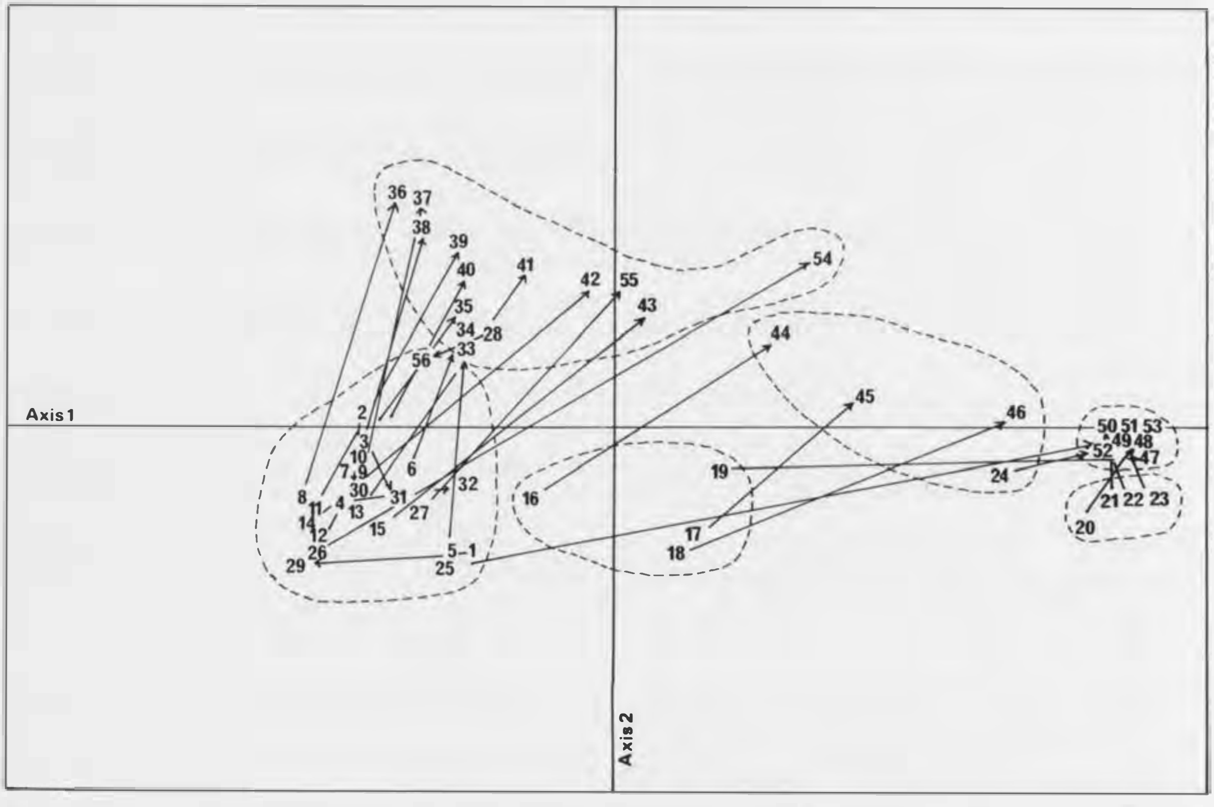


Fig. 26. PCA stand ordination of 28 permanent plots through time; 1–28 refer to the plots observed in 1940 and 29–56 the plots observed in 1981. Time trajectories are shown as lines linking individual plots observed in 1940 and 1981. The clusters derived from the TABORD classification are also shown on the first and second axes of the PCA ordination.

trajectories of the corresponding plots which were traced through the species-space of the ordination. The general patterns of dynamics could be discerned by a comparison of the trends among these time trajectories. The following trends were observed.

There were considerable changes over 41 years in a majority of the permanent plots. Two patterns of development could be recognized. The trend of development over 41 years in permanent plots 16–19 and 24–26 was more or less similar and the time trajectories were skewed along the first axis of the PCA ordination. The time trajectories of permanent plots 5–15 and 27 showed a more or less similar trend which, although slightly oblique to the first axis, was roughly parallel to the second axis of the PCA ordination.

There were relatively small changes in one group of plots. The trend of development in permanent plots 20–23 was rather clear and the corresponding plots were separated by two discrete clusters, but the amount of changes seemed to be slight over the 41 years. There was no clear trend of development in permanent plots 1–4. The amount of changes was also rather small and the corresponding plots of 1940 and 1981 remained in the same cluster, which may suggest that the vegetation in these plots was more or less stable. The amount of changes in plot 28 was small but its corresponding plots belonged to two different clusters obtained from the TABORD classification.

It is interesting to note that both the spatial pattern of the vegetation types and their changes in time can be recognized in this diagram of the PCA ordination. Most of the corresponding plots observed in 1940 occur on the lower part of the diagram, while those observed in 1981 occur mostly on the upper part of the diagram. The distribution of the different clusters at different times reveals the relationships between the spatial variation and the temporal development of the vegetation in the study area.

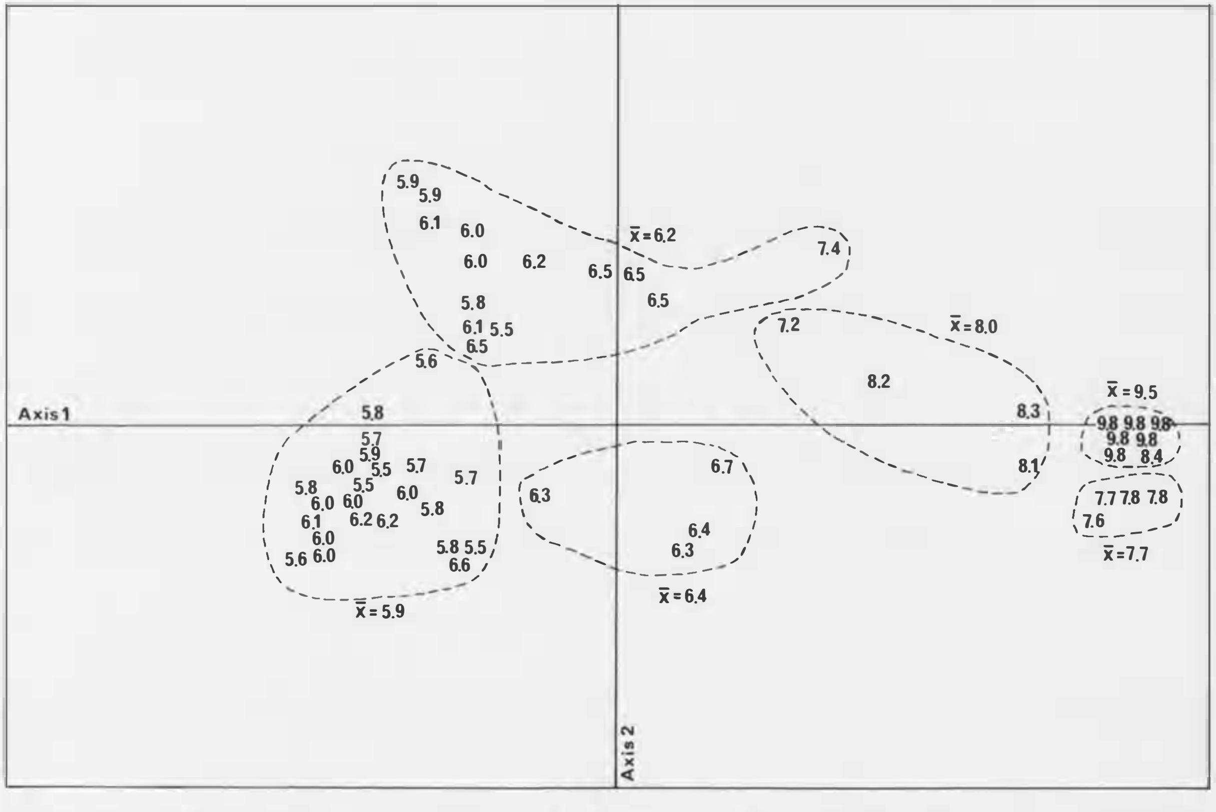


Fig. 27. Characteristic indicator values (*CIV*) for soil moisture in each plot on the first and second axes of the PCA stand ordination.

6.2.3 Characteristic indicator value

To test the hypothesis that the axes of the PCA ordination can be related to the underlying environmental gradients and to interpret the observed trends of vegetation development, the calculated characteristic indicator values (*CIV*) of each plot, including observations both in 1940 and 1981 for the different environmental factors, were plotted on the first and second axes diagram of the PCA stand ordination.

Plotting of the calculated *CIV* for soil moisture on the PCA ordination diagram gave a very clear pattern (Fig. 27). The first axis was strongly related to a gradient of increasing soil moisture, ranging from the relatively dry sites on the left of the diagram, mostly with values between 5.5–6.0 (which according to Ellenberg, indicate mesic soil conditions), to the wet sites on the right of the diagram, mostly with values between 8–10 which indicate wet, often not well aerated or frequently inundated soil conditions. A plot of the *CIV* for soil moisture

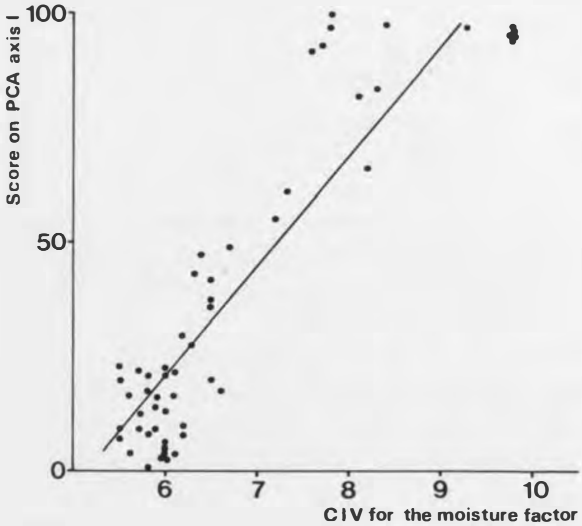


Fig. 28. The relationship between position on PCA ordination axis *I* and characteristic indicator value for moisture for the 28 permanent plots observed in 1940 and 1981. The linear regression between PCA axis *I* score (Y) and *CIV* for moisture (X) is $Y = -124.3 + 24.1X$; $r^2 = 0.83$, $P<0.01$.

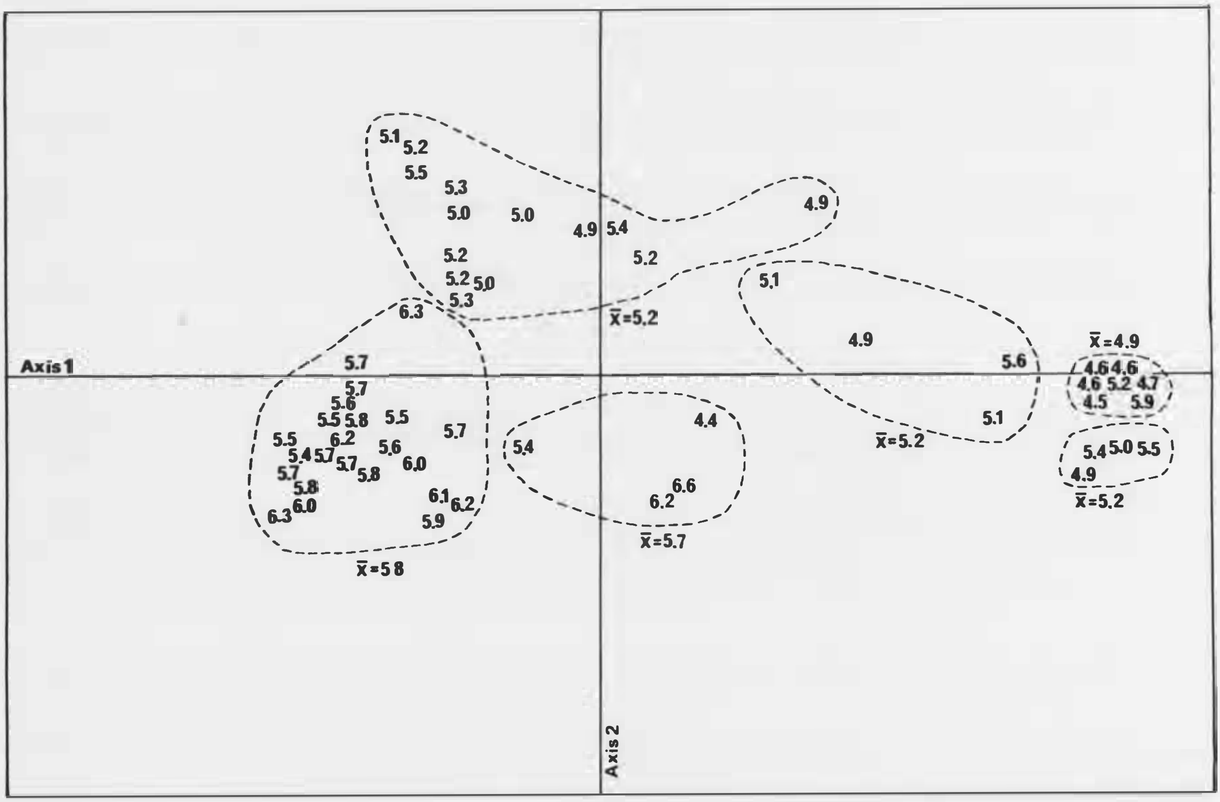


Fig. 29. Characteristic indicator values (*CIV*) for nitrogen supply in each plot on the first and second axes of the PCA stand ordination.

against the first axis of the PCA ordination revealed a fairly clear linear relationship (Fig. 28, $r^2 = 0.83$, $P < 0.01$).

Plotting of the calculated *CIV* for nitrogen status on the PCA ordination diagram gave a complex pattern (Fig. 29). Two gradients could be recognized. There was one gradient of decreasing nitrogen status from the relatively dry sites on the left of the PCA ordination diagram, mostly with values between 5.5–6.5 (soil rather rich in mineral nitrogen), to wet sites on the right of the diagram, mostly with values between 4.5–5.0 (relatively poor in mineral nitrogen). Another gradient of decreasing nitrogen status was from the lower part of the PCA ordination diagram in which most plots observed in 1940 occurred, to the upper part of the diagram in which most plots were observed in 1981. This may be explained in terms of a spatial-temporal pattern. The gradient of decreasing nitrogen status which was related to the first axis of the PCA ordination could be explained as a spatial variation of nitrification capacity. As van Duuren et al. (1981) pointed out, Ellenberg's nitrogen indicator value refers to the N-mineralization rates for separate species and Williams (1968) has demonstrated in his investigation of some wet meadows that there is a close negative correlation between soil moisture conditions and the nitrification capacity of the soils. The gradient of decreasing nitrogen status which was related to the second axis of the PCA ordination may indicate a temporal development, a diminishing availability of nutrients from the soil.

The pattern of displaying the calculated *CIV* for phosphorus status on the PCA ordination diagram (Fig. 30) was more or less similar to that of the *CIV* for nitrogen status. Two gradients of decreasing phosphorus status, especially the temporal variation, could be recognized and this spatial-temporal pattern could also be explained as that for nitrogen status.

The display of the *CIV* for reaction shows no obvious pattern (Fig. 31), since the variation in the *CIV* for reaction among these plots was small and a large proportion of the indicator values for reaction

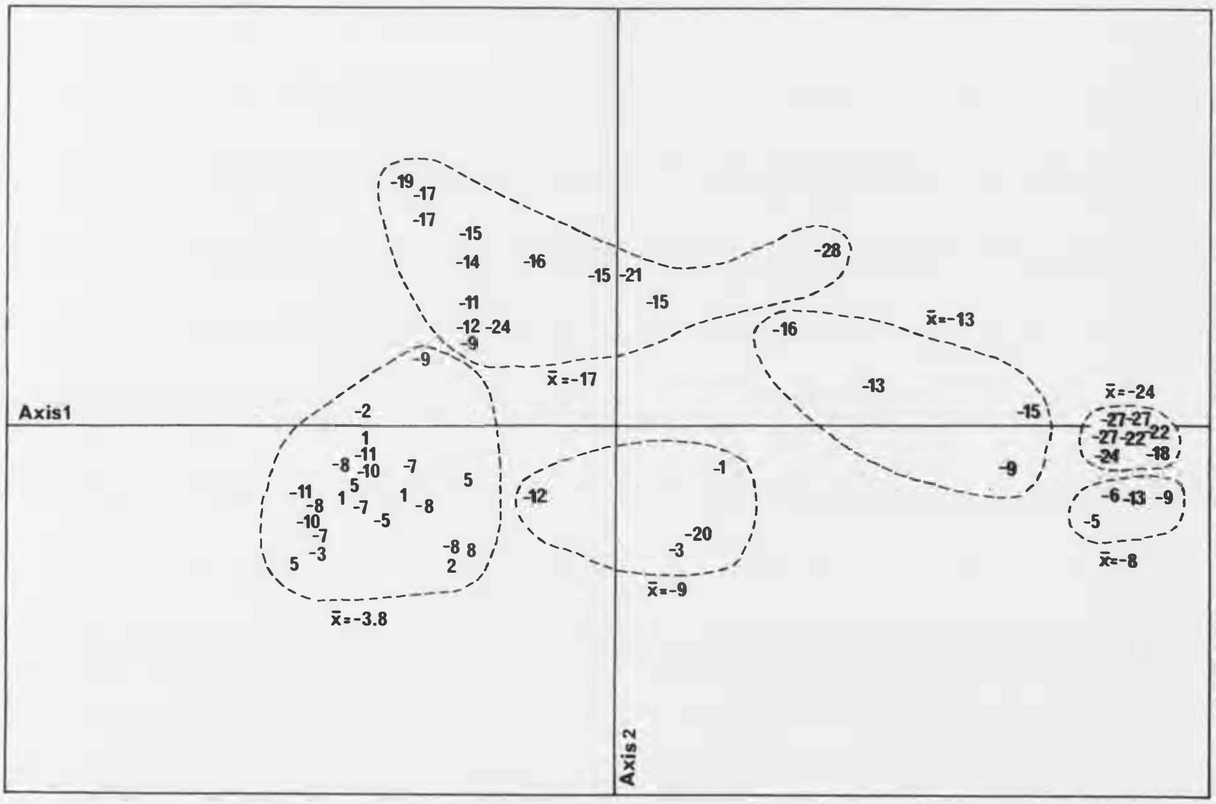


Fig. 30. Characteristic indicator values (*CIV*) for phosphorus status in each plot on the first and second axes of the PCA stand ordination.

were indifferent or unknown.

The mean *CIV*'s for soil moisture, nitrogen and phosphorus status for each cluster derived from the TABORD classification were calculated (Table 14). Considerable differences with regard to these environmental factors were found between the clusters, especially between the corresponding clusters 1–2, 3–4 and 5–6, which revealed the main trends of vegetation development from 1940 to 1981.

6.2.4 Comparison of the *CIV* with the measurements of environmental variables

The efficiency of using the system of ecological indicators depends on whether or not there is a high correlation between the *CIV* for plots and actual measurements of environmental variables for the same plots (Ellenberg 1974, Persson 1981). From the results of ground water investigations and soil analyses during the period 1981–82 (see chapters 3

Table 14. Mean Characteristic Indicator Value (CIV) for soil moisture, nitrogen status and phosphorus status for each cluster derived from the TABORD classification.

Cluster number	1	2	3	4	5	6
Soil moisture (F)	5.9±0.3	6.2±0.4	6.4±0.2	8.0±0.5	7.7±0.1	9.5±0.5
Nitrogen status (N)	5.8±0.3	5.2±0.2	5.7±1.0	5.2±0.3	5.2±0.3	4.9±0.4
Phosphorus status (P)	-3.8±3.4	-16.7±5.2	-9.2±9.0	-13.4±3.0	-7.8±3.6	-23.9±3.4

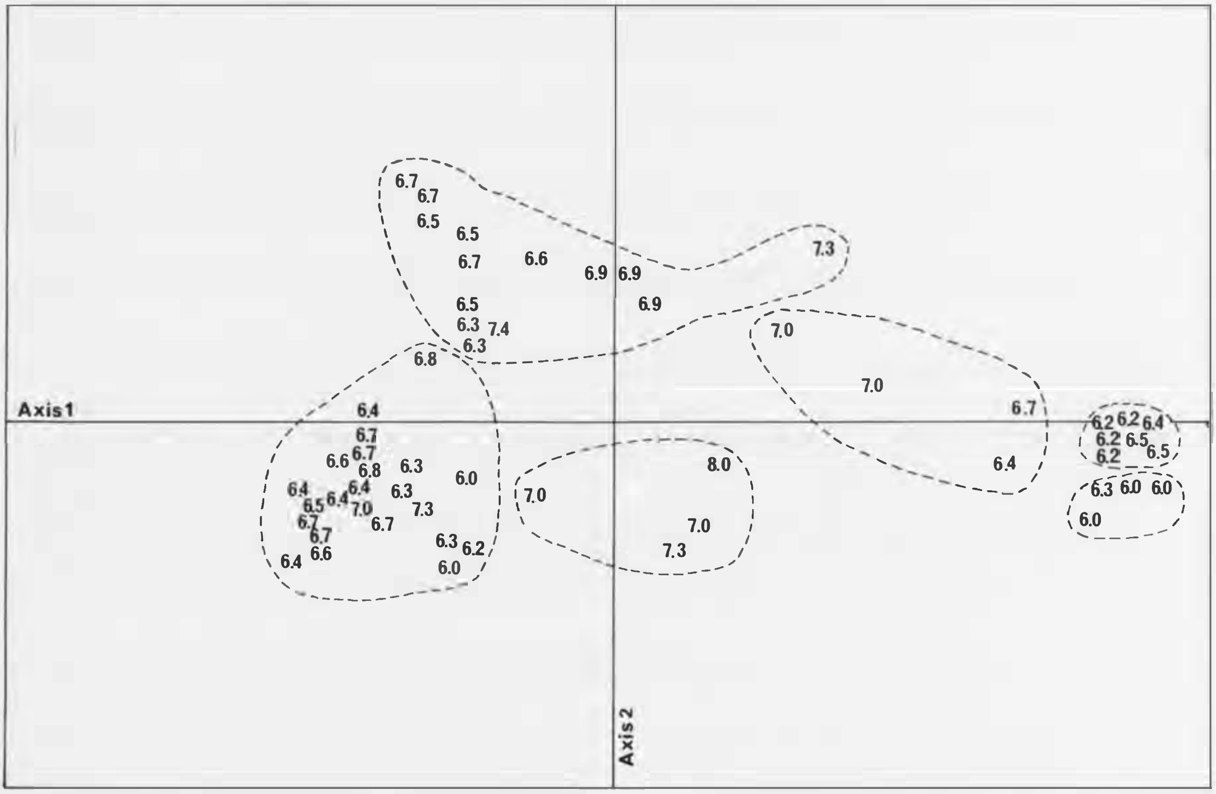


Fig. 31. Characteristic indicator values (*CIV*) for reaction in each plot on the first and second axes of the PCA stand ordination.

and 4), a test between the *CIV* for the 28 plots observed in 1981 and the actual measurements can be made.

A highly significant correlation both between the maximum water level during the 1982 growing season and the *CIV* for soil moisture ($r^2 = 0.96$, $p < 0.01$), and between the maximum water level and the position on the PCA ordination axis *I* ($r^2 = 0.94$, $P < 0.01$) for the 28 plots observed in 1981 has been found (Fig. 32). It is noteworthy that the correlation is less for a number of plots which are situated on the highest and lowest sites at the two ends of the regression line. This may suggest that the influence of a particular ground water regime, in relation to the height of the site above the water table, is different (van der Laan 1979); the water level beyond a certain range has less influence on the vegetation.

The comparisons of the *CIV* for nitrogen, phosphorus status and reaction with the actual measurements for the 28 plots, which have been grouped into five plant community types according to the results of vegetation classification (see chapter 2), are presented in Table 15. In general, the correlations between the *CIV* and the actual measurements for these environmental variables are fairly good at the mesic sites (plots 1–15, 27 and 28), while those at the wet sites (plots 16–26) are less

Table 15. Comparison of the CIV's for nitrogen, phosphorus status and reaction with the actual measurements for the 28 plots in the Kungsängen Nature Reserve.

Community type	A	B	C	D	E
Plot number	1-4, 28	5-15, 27	16-18	19-25	26
N-total (0-10 cm) g/dm^3	5.13 ± 0.62	4.45 ± 0.58	4.08 ± 0.20	4.01 ± 0.46	4.00 ± 0.31
N-CIV	6.02 ± 0.34	5.19 ± 0.19	5.20 ± 0.36	4.87 ± 0.43	4.90
P-AL (0-10 cm) mg/dm^3	39.4	15.5	19.3	31.3	44.1
P-HCl (0-10 cm) mg/dm^3	629	469	369	487	462
P-CIV	2.8 ± 2.8	-15.1 ± 3.5	-14.7 ± 1.4	-23.9 ± 3.4	-28.4
pH_{water} (0-10 cm)	5.93 ± 0.22	6.64 ± 0.08	7.52 ± 0.07	7.54 ± 0.06	7.46 ± 0.14
pH-CIV	6.38 ± 0.29	6.63 ± 0.21	6.90 ± 0.17	6.31 ± 0.15	7.25

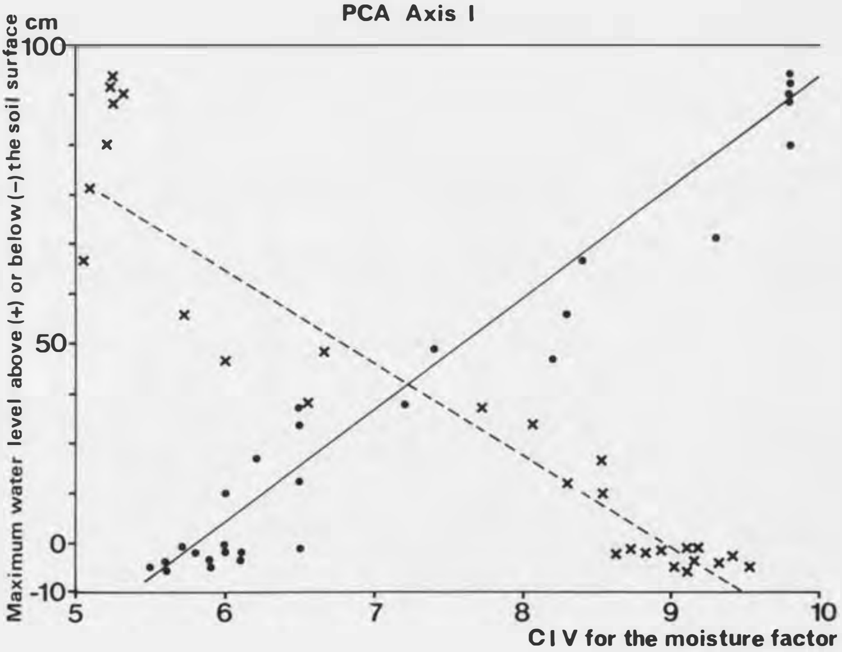


Fig. 32. Correlation between maximum water level during 1982 and position on PCA ordination axis *I* (x, $r^2 = 0.94$, $P<0.01$), and between maximum water level during 1982 and characteristic indicator value for moisture (●, $r^2 = 0.96$, $P<0.01$) for the 28 permanent plots observed in 1981.

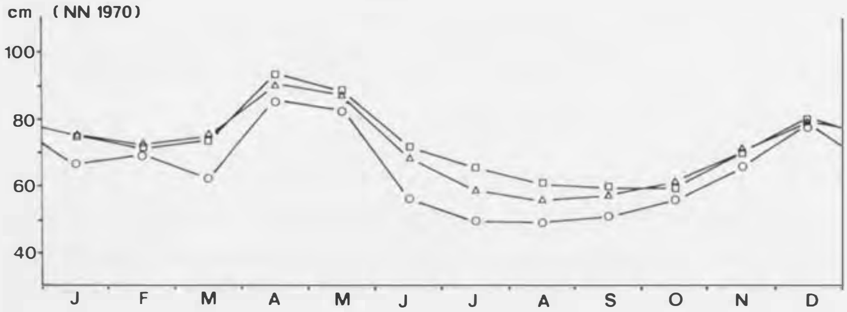


Fig. 33. The monthly mean water levels in the River Fyris at Ultuna during the period of 1938–42 (o), 1943–67 (△) and 1968–80 (□). The water level is expressed in cm above sea level in system 1970. The data for the period of 1938–67 obtained from Hallgren & Sandsborg (1968) and for the period of 1968–80 from Anders Bjerketorp (unpublished). Redrawn by the author.

Table 16. The characteristic water level (m) of Lake Mälaren before and after regulation. The figures for the period 1900-1982 were obtained from SMHI.

Period	1900-1942	1943-1967	1968-1982
Highest maximum level	5.45 (June 1924)	4.85 (Dec. 1944)	4.62 (May 1970)
Mean maximum level	4.65	4.48	4.46
Mean water level	4.12	4.11	4.15
Mean minimum level	3.75	3.85	3.98
Lowest minimum level	3.44 (Nov. 1939)	3.54 (Dec. 1959)	3.72 (Oct. 1976)

satisfactory. This can be explained by the fact that both the number of species per plot and the species with known indicator values at the wet sites are very low, thus being more likely subject to chance effects. Furthermore, as the vegetation at the wet sites is tussocky, the habitat conditions of the tussocks and interspaces could be quite different (Regnell 1980) and the soil samples for measurements were taken from the interspaces.

Although measurements of ground water level in the study area in 1940 were not available, the ground water investigation during the period of 1981–82 has indicated a close correlation between the ground water levels in the study area and the water level in the River Fyris which is, in turn, closely related to the water level in Lake Mälaren. Lake Mälaren was regulated twice, in 1942 and 1968, as a land improvement in order to avoid salt water, to reduce high water levels and to raise the low water level for boats (Ehlert 1970). The characteristic water level for Lake Mälaren before and after the regulation is shown in Table 16. It has been shown that the low water level has been raised considerably, while the high water level has been reduced. According to investigation of water level variations in the River Fyris at Ultuna, which is 2–3 km south of the study area, for the period 1938–67 (Hallgren & Sandsborg 1968) and 1968–80 (Anders Bjerketorp, unpublished data), it has been shown that the low water level in the River Fyris has been raised as a result of the regulation of Lake Mälaren. In spite of considerable variations in water levels between years, depending on weather conditions, this rise of the water level in the River Fyris is still obvious if a comparison of the monthly mean water level in the River Fyris for the period of 1938–42, 1943–67 and 1968–80 is made (Fig. 33). It seems reasonable, thus, to assume that the ground water level, especially during the growing season, within the Kungsängen Nature Reserve area has been raised since 1940, which has induced the changes in vegetation observed in the wet meadows. This also justifies the efficiency of using the ecological indicators for aiding in the deduction of environmental changes from the changes in the vegetation.

7 Introductory description of *Fritillaria meleagris* L.

7.1 Geographical distribution

Fritillaria meleagris L., a member of the family *Liliaceae*, is a characteristic bulbous perennial. Its geographical distribution is rather wide, extending from Scandinavia right across Europe, as far as the Balkan peninsula and from Britain eastwards to Central Russia (Hollman 1972). According to Hollman (op. cit.) this species is fairly common in the phytosociological class of the *Molinio-Arrhenatheretea* with an optimum in the transition between the orders *Molinietalia* and *Arrhenatheretalia.* In NW. Europe it is a differential species of the subassociation *Arrhenatheretum elatioris alopecuretosum.* More phytosociological and phytogeographical aspects will be treated in a separate paper.

Nowadays *Fritillaria meleagris* is considered as a rare species (e.g. Harper 1981). It has been greatly affected by changes in agricultural practice such as drainage, grazing and fertilization. Formerly fairly common in wet meadows and pastures in Europe, it is becoming rare (Proctor 1981).

The Kungsängen Nature Reserve near Uppsala contains probably the largest Swedish population of *Fritillaria meleagris.* The Swedish name of this plant is "Kungsängslilja" and this colourful plant is the symbol of the province of Uppland. However, it is not a native species here. It may have escaped from the garden in Uppsala established by Rudbeck. According to Sernander (1948) this species was found in the catalogues from 1658, 1666 and 1685 listing the plants in that garden. According to Almquist (1965) it was cultivated in several gardens in Uppsala during the 17th century and may thus have escaped from other gardens than that of Rudbeck. At that time the gardeners in Holland were leading this field, so it could have been introduced from that country. It was first discovered on the Kungsängen wet meadows by Sten Carl Bjelke, a friend of Carl von Linné, during 1742 or 1743 and published in 1745 in Linnés Flora Suecica (Sernander 1948). How *Fritillaria meleagris* spread from gardens in Uppsala to the wet meadows is still uncertain. However, its buoyant seeds or bulblets may have been spread by wind or water to suitable habitants where the species eventually has become naturalized.

One of the conservation objectives for the establishment of the Kungsängen Nature Reserve was to preserve the fritillary population in those wet meadows. The species occurs with highest density in the *Arrhenatherum pubescens—Alopecurus pratensis* plant community of

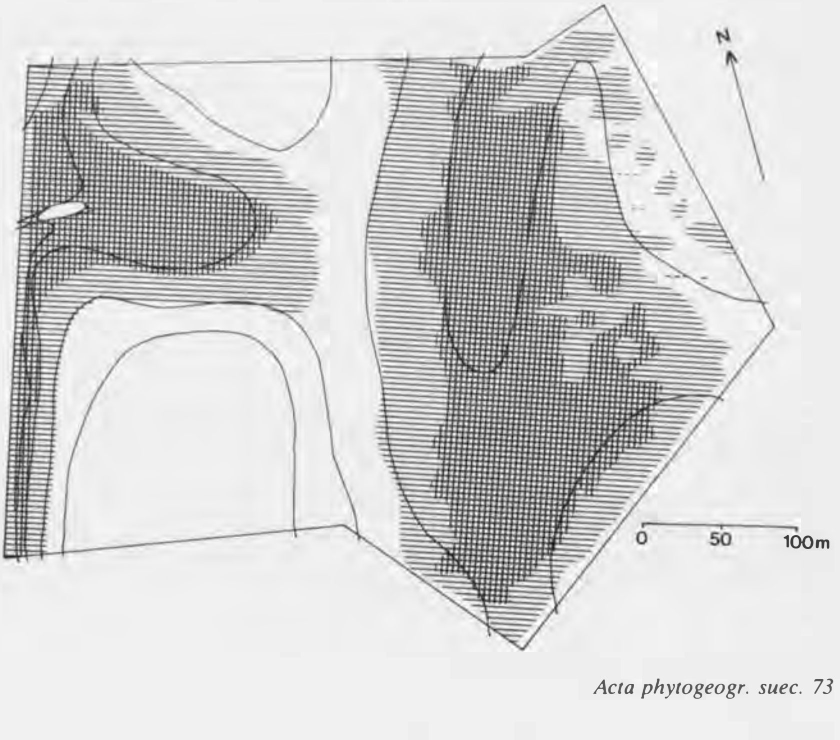


Fig. 34. The distribution of *Fritillaria meleagris* L. in the Kungsängen Nature Reserve, mid-May 1982. ▤ <500 flowering individuals per 100 m^2, ▦ >500 flowering individuals per 100 m^2.

the reserve area. According to the observation of Sernander in 1938 and my own observations in 1981–83, a maximal density of about two thousand flowering individuals could be found in some 10×10 m plots. During the flowering season (mid May) most of the reserve area except the driest and wettest parts is covered by a rich-purple blanket of colour from thousands of these flowers. The distribution of flowering individuals in the whole reserve area was estimated during the middle of May, 1982 (see Fig. 34).

7.2 The "age-states" within the population

Fritillaria meleagris is a bulbous perennial and its bulb is renewed annually. For the population of this species the precise age of an individual plant cannot be determined unless by following marked individuals from seeds. Furthermore, age is a poor predictor of size or reproductive activity among plants in general (Harper 1977). Many investigators have used the concept of "age-state" (Barkham 1980a, Gatsuk et al. 1980) or "size-class" (Rabotnov 1969. Kawano et al. 1982) and found it particularly useful for perennials. In the present study I have adopted the concept of "age-state" and classified the population of the fritillary on the basis of their ontogenetic (or developmental) states, their size of bulbs, number of foliage leaves and their reproductive activity. Six categories of age-state are distinguished in field populations according to the criteria mentioned above. They have been described as follows (see Fig. 35):

1. Viable seeds in the soil: 3–6 mm in size and 0.5–2.0 mg in dry weight, mainly on the soil surface.

2. Seedlings: developed directly from the germination of seeds. Consist of a green cylindrical cotyledon and radicle. At the end of the growing season a small bulb, 1–3 mm in size, is formed, mainly in the soil at a depth of 0–1 cm.

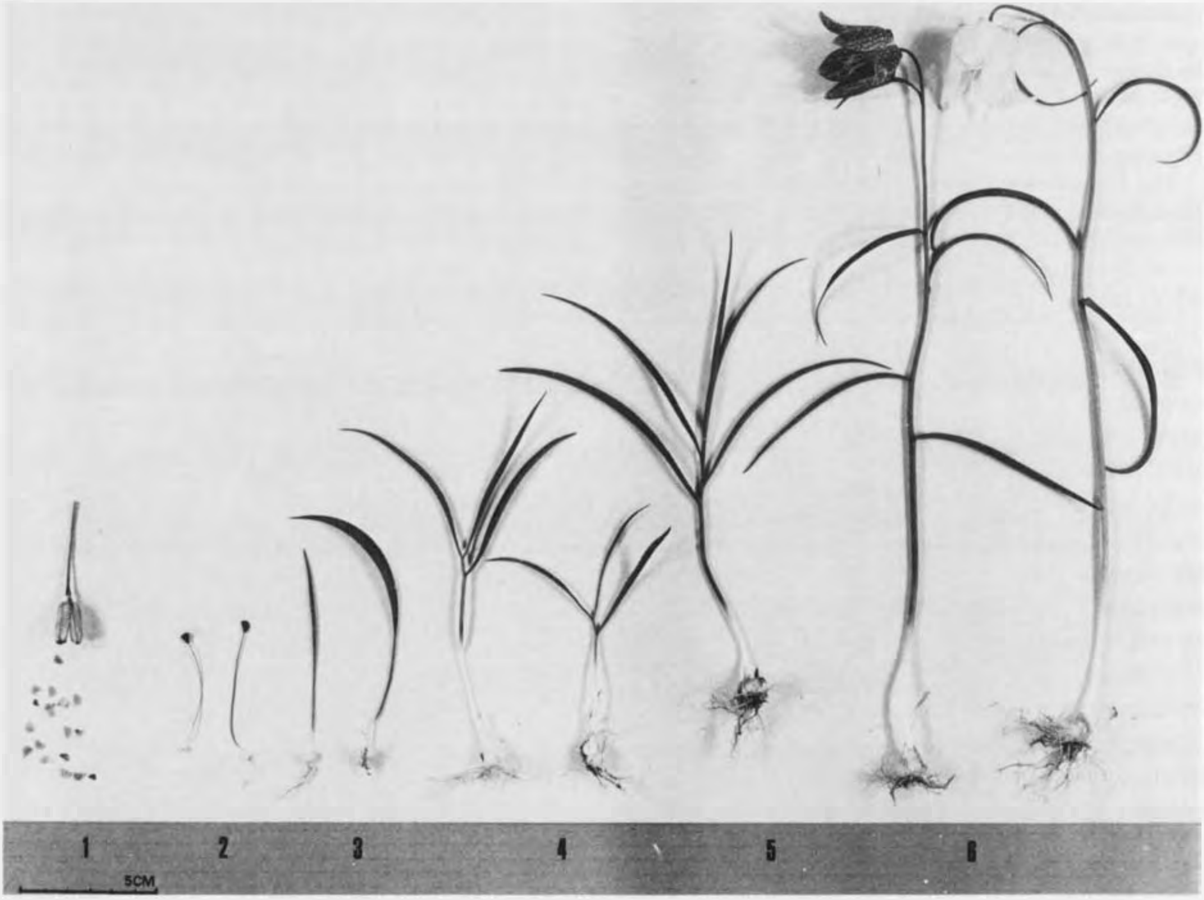


Fig. 35. Individuals of *Fritillaria meleagris* belonging to the different age-states. 1) viable seed, 2) seedling, 3) juvenile, 4) subadult, 5) vegetative adult and 6) reproductive adult. For detailed explanation, see text.–Photo. Author. May 1982.

3. Juveniles: individuals with one true foliage leaf, bulb size 2–7 mm. They can be derived from seedlings or vegetative offsprings (bulblet produced by adult bulb). The bulbs are mainly located in the soil at a depth of 1–3 cm.

4. Subadults: individuals with two or three foliage leaves, bulb size 6–11 mm. The bulbs are mainly located in the soil at a depth of 2–5 cm.

5. Vegetative adults: individuals with four to eight foliage leaves, bulb size 10–17 mm. The bulbs are mainly located in the soil at a depth of 5–8 cm.

6. Reproductive adults: flowering individuals with four to eight foliage leaves, bulb size 12–20 mm. The bulbs are mainly located in the soil at a depth of 5–8 cm.

Normally the age-states follow a development sequence from seeds to adults. However reverse changes can also occur, e.g. from adults to subadults or juveniles. These changes seem to depend upon diminishing size of the bulbs at the annual renewal. This phenomenon will be discussed further in chapters 8 and 9.

7.3 Morphology

Fritillary meleagris is, cytologically, diploid with 2n=24 chromosomes (Beck 1953).

The seed of the fritillary is flat and weakly winged. It consists of a brownish seed coat enclosing a small amount of endosperm. The embryo is a simple axis; a radicle and single cotyledon. The radicle usually points towards the micropyle in the seed coat.

The seedling consists of a green cotyledon and some adventitious roots developed from the bottom of the radicle. A small bulb is gradually formed on the bottom of the radicle during its development.

Although the juvenile, subadult and vegetative adult differ in size of the plant and number of foliage leaves, their structure is more or less the same. The terminology for describing their structure follows Raunkiaer (1895–99). The bulbs in these age-states are composed of two thick bulb leaves, somewhat hemispherical outside and concave inside. The bulb leaves are food storage organs. Between them emerges a stalk (Fig. 36). Loew & Kirchner (1913–14) found that two stalks sometimes developed on a bulb, but this phenomenon has not been found in the population of the fritillary at the Kungsängen Nature Reserve. At the base of the stalk, it carries 5 or 6 scale-like low leaves which are below the soil surface. The stalk is slender and has one to eight foliage leaves (depending on their age-state) alternately placed on it. The foliage leaf is linear, somewhat glaucous. Adventitious roots develop from the bulb base.

The structure of the reproductive adult is similar to those described above except for the reproductive organ (flower bud, flower and fruit). The reproductive organ is carried on the top of the stalk, usually one flower or very seldom two flowers. The perianth is very broadly campanulate, usually in red-purple colour with dark spots, but white and the intermediate pink colours are also frequent. The nectary is linear, green and the stigma is trifid (Fig. 36). The fruit is a capsule consisting of three parts which are green when young, turn yellow when matured, open into three columns and release numerous seeds. The flowers of the fritillary are protogynous and cross-fertilized. The pollination is brought about mainly by bumble-bees and honey-bees (Ingemar Hedström pers. comm.).

Individuals of the fritillary renew their vegetative body annually. The previous year's bulb is replaced by a new daughter bulb each year, which is formed by the two inner low leaves. A shoot bud is formed on the inner side of one of the bulb leaves (see also section 9.2.1). The origin of bulbs is: from seeds (seedlings)—new genets, and from vegetative propagation by bulblets—ramets which develop at the bulb base of the parent plant and grow independently in the following year when the old bulb leaves are sloughed off. It is not possible in the field to distinguish between these different origins of adult plants.

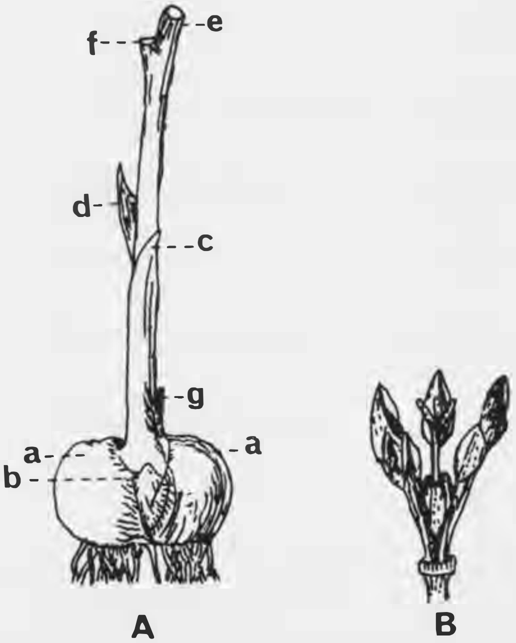


Fig. 36. A. Bulb (a) and lower part of stalk (e) of the fritillary. Low leaves (b, c, d), rest of previous year's stalk (g) and foliage leaves (f). (After Raunkiaer 1895–99.) B. Flower with perianth removed showing pistil and stamen with anthers (after Beck 1953).

8 Demographic study

Many plant ecologists have observed that the study of demographic characteristics of herbaceous perennial species involves several problems, such as the overlapping of generations (Harper 1977), the little or no possibility of estimating chronological age in the field populations (Kawano et al. 1982), the long period of pre-reproduction and the longevity of individuals (Tamm 1972a, b), the existence of both vegetative and sexual reproduction (Barkham 1980a), the irregular reproductive behaviour (Tamm op. cit.) and the non-appearance in some years of above-ground parts (Wells 1967, Tamm op. cit.). Therefore, the long-term observation of a marked population is necessary before a complete demographic account is possible (Harper 1977). The long-term study over a 30-year period carried out by Tamm (1972 a, b) on some perennial herbs in Swedish meadows and forests has provided an excellent example of what can be done along such lines.

The demography of the field population of *Fritillaria meleagris* at the Kungsängen Nature Reserve was studied during 1981–1983. The population distribution and flux on the permanent plots were recorded over a period of three years. However, due to problems involved in the study of a perennial species such as the fritillary, several components of demographic characteristics were difficult to establish in such a short time. The preliminary results presented here are mostly, thus, tentative and may hopefully encourage the continuation of this work by others in further observations.

8.1 Methods

The soil-water conditions in the study area are important for the differentiation of vegetation (chapter 3). This seems also to apply to the distribution of the fritillary, which occurs mainly in

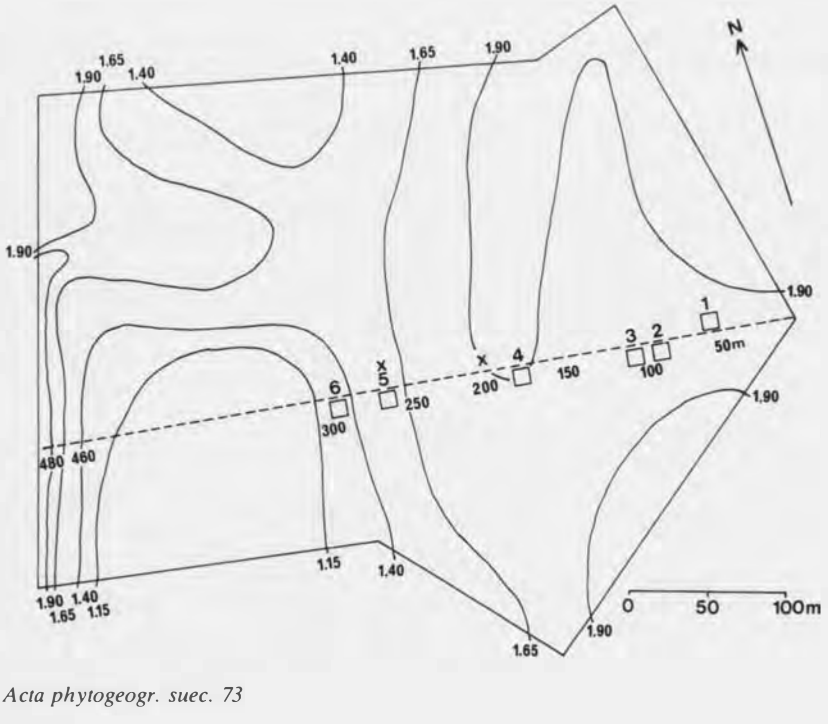


Fig. 37. Map of the Kungsängen Nature Reserve showing the position of the transect and six 10×10 m plots used for recording of total number of flowering individuals of the fritillary in 1938 and 1981–83, as well as the location of the permanent plots for demographic study.

the *Arrhenatherum pubescens—Alopecurus pratensis* plant community. A series of permanent plots, each 1×1 m in size, was chosen subjectively along a vegetation transect to include a range of population densities and a variety of soil-water conditions in which the fritillary was commonly found. Twenty-nine permanent plots were established (Fig. 37) and were distributed as follows (number of plots in parenthesis): 50 m (1), 100 m (2), 150 m (8), 200 m (8), 250 m (2), 460 m (2) and 480 m (6).

The permanent plots were marked at the four corners with plastic rods. The position of each above-ground shoot within the plots was determined by using a square 1 m^2 aluminium frame with a grid of 100 10×10 cm sections (Fig. 38) and was mapped on co-ordinate paper. The fritillary specimens are well-defined individuals and can be easily mapped. Using this method, it was possible to return to the same plant in successive years. The study started in 1981 and continued until 1983. Recordings were carried out once each year, in the middle of May. For each plant, the number of leaves and the reproductive activity was recorded. For the flowering individuals the counts of capsules with or without seeds or damaged by animals were made in the middle of June each year. The plants recorded were classified into the different age-states according to the criteria mentioned earlier (chapter 7). However, the seedlings were not given particular attention in this study, since it was difficult to carry out the very time-consuming and perhaps destructive or otherwise disturbing search for seedlings, which had only a tiny cotyledon in the natural sward. The re-inspecting of juveniles, subadults, vegetative and reproductive adults was performed as carefully as possible. The results of population distribution and flux were drawn up from these data.

8.2 Results

8.2.1 Number of individuals along the transect

Table 17 shows the number of individuals per m^2 in the different sites along the transect for three consecutive years. There was a significant variation in the distribution of the fritillary within the study area. The density of plants was high in the mesic sites at 150 m and 200 m and low at the relatively dry sites on the borders of the reserve area (100 m, 480 m and especially low at 50 m). At these relatively high-situated and mesic sites the year-to-year changes in density were small and the popula-

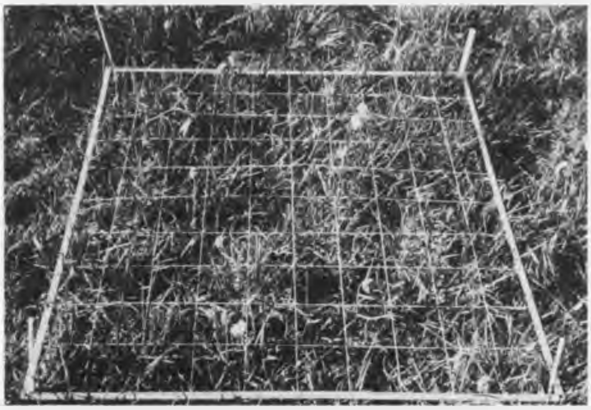


Fig. 38. The 1 m^2 aluminium frame delimited each permanent plot and helped in the census of *Fritillaria meleagris* individuals. Note that the plants of the fritillary are well scattered and well defined individuals.—Photo Author. May 1981.

Table 17. Density and age-state structure of the fritillary at different sites along a transect within the Kungsängen Nature Reserve. Mean number of individuals per m^2 with percentage values in parentheses are given for the period 1981-83.

Site	Altitude	Year	Juvenile	Subadult	Veg. adult	Repro. adult	Total
50 m	1.89 m	1981	0	0	2 (66.7)	1 (33.3)	3
		1982	2 (40.0)	0	2 (40.0)	1 (20.0)	5
		1983	2 (40.0)	0	1 (20.0)	2 (40.0)	5
100 m	1.87 m	1981	9 (18.8)	9 (18.8)	20 (41.7)	10 (20.8)	48
		1982	9 (18.8)	6 (12.5)	15 (31.3)	18 (37.5)	48
		1983	9 (17.0)	6 (11.3)	19 (35.8)	19 (35.8)	53
150 m	1.90 m	1981	23 (30.7)	11 (14.7)	19 (25.3)	22 (29.3)	75
		1982	29 (36.7)	7 (8.9)	33 (41.8)	10 (12.7)	79
		1983	30 (36.1)	10 (12.0)	27 (32.5)	16 (19.3)	83
200 m	1.90 m	1981	22 (31.4)	12 (17.1)	20 (28.6)	16 (22.9)	70
		1982	24 (32.4)	10 (13.5)	32 (43.2)	8 (10.8)	74
		1983	26 (31.7)	11 (13.4)	28 (34.1)	17 (20.7)	82
250 m	1.60 m	1981	11 (39.3)	4 (14.3)	9 (32.1)	4 (14.3)	28
		1982	30 (47.6)	16 (25.4)	16 (25.4)	1 (1.6)	63
		1983	50 (52.1)	19 (19.8)	21 (21.9)	6 (6.3)	96
460 m	1.65 m	1981	39 (54.1)	10 (13.9)	19 (26.4)	4 (5.6)	72
		1982	15 (45.4)	9 (27.3)	7 (21.2)	2 (6.1)	33
		1983	50 (60.2)	6 (7.2)	23 (27.7)	4 (4.8)	83
480 m	1.96 m	1981	18 (37.5)	6 (12.5)	14 (29.2)	10 (20.8)	48
		1982	17 (37.8)	5 (11.1)	16 (35.6)	7 (15.6)	45
		1983	27 (45.0)	5 (8.3)	18 (30.0)	10 (16.7)	60

tion size remained fairly stable over the three years, perhaps as a result of fewer effects from waterlogging.

At the wettest sites between 280–440 m along the transect (altitude below 1.40 m) there was no fritillary at all. Large changes in density were found between years at the relatively low-situated and wet sites (250 m and 460 m). The number of plants in 1981 or 1982 was very low, while the number of plants in 1983 was high and exceeded that of the two other years.

8.2.2 Age-state structure

The proportions of juvenile, subadult, vegetative adult and reproductive adult at each site are also presented in Table 17. The proportion of adults (including both vegetative and reproductive adults) in the mesic sites (100 m, 150 m, 200 m and 480 m) was rather high and relatively stable over the three years, ranging from 47 to 72% of the total number of plants. The proportion of adults in the relatively wet sites (250 m and 460 m) was low and varied from 27 to 46%. The proportion of juveniles was fairly high at the wet sites, ranging from 39 to 60%.

The number of reproductive adults varied considerably from site to site and from year to year on most sites. The number and the proportion of reproductive adults were high in the mesic sites and were very low in the wet sites, which may suggest that soil-water conditions were important in influencing the flowering frequency. At most sites the proportion of flowering individuals showed alternate marked rises and falls in consecutive years except at the site at 100 m. The number of flowering individuals was high in 1981 and 1983 and low in 1982.

8.2.3 Disappearance and origin of the plants

By comparing the different maps made each year during the period of 1981–83 the fate of the individual plants could be followed. However, it is extremely difficult to construct a life table for a perennial species such as the fritillary, because the plants renew the vegetative body completely (bulb, root, stalk and leaves) each year and there is probably no gradual senescence of the plant in the normal sense of the term (Harper 1977). The individual plants are able to change from one age-state to another (see section 8.2.4). A further complication was that the exact causes of death and origin of plants were not identified in this study.

Plants recorded as absent in one year cannot be simply considered dead as they may appear again in later years. It might be possible to determine the fate of absent individuals by digging up the location of absent plants and examining their underground bulbs, but this has not been done since the long-term observations would not allow such destructive disturbances.

Two processes can be involved in the origin of newly recorded plants. Newly recorded plants of juvenile age-state could originate from seedlings or vegetative bulblets, both of which have a small bulb (1–2 mm in size) and develop into juveniles with one foliage leaf in the following year. The second process of origin of newly recorded plants can be involved in all the age-states. The plants had been, for some reason, missed in the previous year's recording and had remained as underground bulbs. This process should account for the origin of the newly recorded subadult, vegetative and reproductive adults since the seedlings and the vegetative set-off bulblets were very small (bulb size 1–2 mm) and could only produce one tiny foliage leaf in the next year, thus being unable to attain the age-states of subadult and adult so soon. The second process could also be involved in the origin of the newly recorded juveniles.

Numerous droppings and the absence of plants on the grazed grass sward suggested that voles and hares might be responsible for the absence of some plants. From the field observations it was clear that such attacks mainly occurred in winter and early spring when the stalk and foliage leaves of the fritillary had approached the soil surface but not emerged above ground. Very few plants became totally grazed after their emergence above ground. Soil-water conditions may also be responsible for the absence of plants in some years. The large changes in density at the wet sites (250 m and 460 m) were caused by the large proportion of plants which were absent in some years or were newly recorded.

An experiment was designed to examine the non-appearance of some individuals in some years.

Twenty individuals of different age-states were dug up from the field in the early spring of 1983 when their above-ground part had not emerged above the soil surface. The bulb size and fresh weight of each individual were determined. Then the upper parts of the stalk with foliage leaves were cut off in an attempt to resemble the possible damage caused by animals in the field. The bulbs were planted in a pot with natural soil at a depth of 1–5 cm under the soil surface. The pot was kept in a growth chamber at a temperature of 15°C and 12 hours light/dark regime for about two months. The pot was kept in a good moisture condition. During the active growth phase no above-ground parts (stalk and foliage leaves) occurred and at the end of the experiment the bulbs were excavated and examined. The results (Table 18) showed that although no stalk and foliage leaves appeared, a new bulb with a new bud for next year's growth inside could be formed by the transition of nutrients and food reserve from the old bulb which was completely empty and sloughed off by the end of the active growth period. The bulb size and fresh weight of the new bulbs were reduced to some extent due to respiration. The "mobility efficiency" (fresh weight of new bulb/fresh weight of old bulb) ranged from 0.40 to 0.70. This gives an explanation of the origin of newly recorded plants which were absent in some years in the field but were obviously still alive underground.

Table 18. The mobility of bulb reserves in a range of the fritillary individuals of different size. The plants were taken from the field in early April 1983, the upper part of the stalk with foliage leaves was cut off and the bulbs were planted in a pot with natural soil, kept in a growth chamber at 15°C with 12 hours light/dark regime for about two months.

No.	Before planting (2/4-83)		After planting (20/5-83)		Mobility
	Bulb diameter	Fresh weight	Bulb diameter	Fresh weight	efficiency
1	1.75 cm	2.724 g	1.50 cm	1.634 g	0.600
2	1.75	2.311	1.45	1.619	0.700
3	1.70	2.080	1.40	1.454	0.699
4	1.60	1.753	1.35	0.966	0.551
5	1.55	1.516	1.35	0.932	0.615
6	1.55	1.474	1.30	0.874	0.593
7	1.40	1.177	1.15	0.639	0.543
8	1.25	1.053	1.10	0.566	0.537
9	1.25	0.929	1.10	0.565	0.609
10	1.25	0.919	1.05	0.485	0.528
11	1.25	0.978	1.10	0.559	0.572
12	1.15	0.844	1.05	0.506	0.600
13	1.15	0.868	1.00	0.425	0.490
14	0.75	0.335	0.70	0.216	0.645
15	0.65	0.293	0.55	0.196	0.669
16	0.55	0.217	0.50	0.136	0.627
17	0.45	0.190	0.35	0.105	0.553
18	0.35	0.091	0.30	0.050	0.549
19	0.25	0.025	0.20	0.013	0.520
20	0.25	0.025	0.20	0.010	0.400

Table 19. Subsequent behaviour in 1982 for the plants of different age-states which were recorded in 1981 in twenty-nine 1 m^2 permanent plots within the Kungsängen Nature Reserve.

1981	1982					
	numbers	juvenile	subadult	veg.adult	repro.adult	absent
Juvenile	580	52.2 %	10.5 %	2.4 %	0.2 %	34.7 %
Subadult	258	7.8 %	32.6 %	41.9 %	1.6 %	16.3 %
Veg.adult	494	1.8 %	3.8 %	52.0 %	24.3 %	18.0 %
Repro.adult	405	0.5 %	4.9 %	60.0 %	22.5 %	12.1 %

8.2.4 Population flux

A summary of the flow diagram of the population changes from 1981 to 1983 for all the twenty-nine plots is presented in Fig. 39. The complexity of the population changes is apparent. The plants changed their age-state very frequently each year and the proportions of plants which were newly recorded or absent were considerable.

The total number of plants within the twenty-nine 1 m^2 plots was 1,737 in 1981 and remained about the same in 1982 (1,775). The number rose to 2,160 in 1983 and the increase was due to an additional large number of newly recorded plants in the wet sites. The proportion of different age-states remained rather stable over the three years. The juveniles accounted for 33.4–38.6%, subadults for 12.3–14.9% and adults (both vegetative and reproductive adults) for 49.1–51.7%, respectively.

Considerable changes in individuals constituting the population occurred each year. It is necessary to examine each age-state as it changes over time. The subsequent behaviours of the 1,737 individuals recorded in 1981 within all the twenty-nine plots are presented in Table 19.

The subsequent behaviours of the 580 juveniles which were recorded in 1981 showed that 52.2% of them remained in the same age-state in 1982, which may indicate that the juvenile state is rather long in this species, perhaps due to the relatively short active growth period (mainly from late April to late June). 10.5% of the juveniles entered into the subadult state in 1982 and very small proportions entered into vegetative and reproductive adult states in 1982, 2.4% and 0.2% respectively. It is noteworthy that a considerable proportion of juveniles (34.7%) were recorded as absent in 1982.

Altogether 258 subadult individuals were recorded in 1981, of which 32.6% remained in the same age-state in 1982 and 41.9% entered into the vegetative adult state. The proportion of subadults which entered into the juvenile state and reproductive adult state was small, only 7.8% and 1.6%

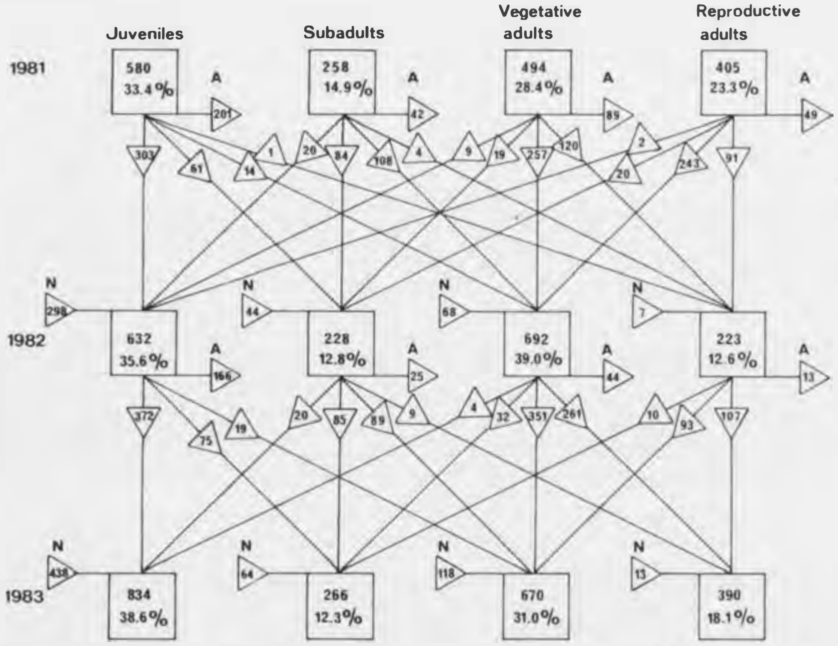


Fig. 39. Population flux of the four age-states in *Fritillaria meleagris* within the 29 1 m^2 permanent plots over the period 1981–83 in the Kungsängen Nature Reserve. The proportions of the different age-states in each year are also presented in squares (%). N = Newly recorded plants, A = Absent. For the explanation, see text.

respectively, the proportion of absence for subadults being 16.3%.

For 494 vegetative adults recorded in 1981, 52.0% of them remained in the same age-state in 1982 and 24.3% entered into the reproductive adult state. A small proportion of vegetative adults, 1.8% and 3.8%, entered into the juvenile and subadult states respectively, and 18.0% of vegetative adults were recorded as absent in 1982.

Altogether 405 reproductive adults were recorded in 1981. Most of them, 60.0%, entered into the vegetative adult state in 1982 and 22.5% remained in the same age-state. The proportion suggests a tendency that a plant flowering in 1981 was more likely to become a vegetative adult in the next year. The proportion of reproductive adults that became juveniles or subadults was very small, being 0.5% and 4.9% respectively. The proportion of absence for reproductive adults was relatively low, being 12.1% in 1982.

The subsequent behaviour in 1983 of the individuals in each age-state which were recorded in 1982 within the 29 plots was about the same as in 1981–82, except that the proportion of reproductive adults remaining in the same age-state was slightly higher in 1982–83.

A total of 381 individuals of the population recorded in 1981 were absent in 1982. The subsequent behaviour of these individuals in 1983 is presented in Table 20. Of the 201 juveniles recorded as absent in 1982, 37.8% appeared as juveniles in 1983, 3.5% as subadults and 58.7% were again absent. Although the plants recorded as absent for two consecutive years may indicate a death, this cannot be stated with certainty as a number of adult individuals, although very few, were newly recorded in 1983 and did not appear in the census of 1981 and 1982. Of the 42 subadults recorded as absent in 1982, 19.0% appeared as juveniles in 1983, 14.3% as subadults, 19.0% as vegetative adults, 2.4% as reproductive adults and 45.2% as again absent in 1983. Of the 89 vegetative adults which were missing in the 1982 census, 5.6% appeared as juveniles, 10.1% as subadults, 41.6% as vegetative adults, 6.7% as reproductive adults

Table 20. Subsequent behaviour in 1983 for the plants of different age-states which were recorded in 1981 and were absent in 1982 in twenty-nine 1 m^2 permanent plots within the Kungsängen Nature Reserve.

1981	1983					
	Numbers	Juvenile	Subadult	Veg. adult	Repro. adult	Absent
Juvenile	201	37.8 %	3.5 %	-	-	58.7 %
Subadult	42	19.0 %	14.3 %	19.0 %	2.4 %	45.2 %
Veg. adult	89	5.6 %	10.1 %	41.6 %	6.7 %	36.0 %
Repro. adult	49	4.1 %	10.2 %	44.9 %	8.2 %	32.7 %

and 36.0% as again absent in 1983. Of the 49 reproductive adults recorded as absent in 1982, 4.1% appeared as juveniles, 10.2% as subadults, 44.9% as vegetative adults, 8.2% as reproductive adults and 32.7% as again absent in 1983.

Consequently, of the juveniles, subadults, vegetative adults and reproductive adults recorded in 1981, 20.3%,7.4%, 6.5% and 4.0%, respectively, were absent in two consecutive years. The data suggest that the mortality was not uniformly distributed over all age-states; the risk of dying among juveniles appeared to be higher and decreased with increasing plant size (as measured by bulb size and number of foliage leaves).

9 Phenology, life cycle and dry matter allocation

The way in which an organism allocates or partitions time and energy has been expressed in terms of "principle of allocation" by Cody (1966), "strategy and tactics" by Harper (1967) and "reproductive effort" including reproduction in particular by Ogden (1968). It is considered that the organism's quantitative program of energy allocation is an essential feature of its strategy. According to Harper & Ogden (1970), the way of dry matter or energy allocation by the organism in relation to the complex time and space pattern can be expressed in terms of "life cycle strategy" and the dry matter or energy allocation particularly associated with reproduction can be expressed in terms of "reproductive strategy".

Such considerations are of great interest in a bulbous perennial species like *Fritillaria meleagris*, which has active growth and dormant phases during its annual cycle and has both sexual and vegetative reproductive means. The study of seasonal growth and dry matter allocation pattern is needed to understand and interpret the life cycle strategy adopted by a species (Waite & Hutchings 1982).

The purpose of this study is to describe, in detail, the seasonal growth cycle (phenology) of the different age-states within the fritillary population at the Kungsängen Nature Reserve in relation to seasonal fluctuation of environmental regimes and to determine the pattern of dry matter allocation throughout the life cycle of the plant. The purpose is also to illustrate the reproductive and survival aspects of this species in terms of relative quantities of dry matter expenditure.

9.1 Material and methods

The field observations and samplings of the fritillary were carried out in the reserve area where the fritillary has its highest density (the zone between 150–200 m along the transect, see section 8.3). Sequential harvests of individuals of the juvenile, subadult, vegetative and reproductive adults were carried out in the field throughout the year. The sampling of the reproductive adults (flowering individuals) included a series of 13 harvests between April and November 1981. The juveniles, subadults and vegetative adults were sampled by a series of 6 harvests between April and November 1982. On the first sampling occasion on April 15, 1981, the fritillary had not emerged aboveground so the sampling was made by digging and collecting 20 individuals with a visible flower bud. After the emergence of plants the sampling was located to 1×1 m plots in which up to 20 individuals with a flower or fruit were collected. In June the flowering individuals were mapped in several plots for later sampling since the aboveground parts of the plant disappeared after June; this enabled subsequent location and collection of individuals of this age-state. The samplings of juveniles, subadults and vegetative adults in 1982 were done in the same way as for reproductive adults. At each harvest 20 individuals of each age-state were excavated using a hand trowel. They were brought into the laboratory within a few hours. The underground part of the plant was carefully cleaned with tap water and the total fresh weight of each individual was determined. The bulb size, number of foliage leaves and stalk length as well as their phenological characters such as dormancy, development of roots and leaves, and reproductive activity were recorded. The plants were then divided into their component organs: root, bulb, low leaves, stalk and foliage leaves and for the reproductive adults the reproductive organs, e.g. flower bud, flower and capsule or vegetative bulblet, if present, were also separated. They were dried at 80°C for 72 hours and then weighed again. Mean values of bulb size and length of the stalk were also measured. The mean dry weight distribution was calculated, both in terms of absolute weight and proportion.

9.2 Results

9.2.1 Life cycle and phenology

In the field, seed germination occurred in late March and April (see section 10.2). During the first year the only aboveground structure of seedlings was a cotyledon, which was thus the only photosynthetic organ during the first year's growth. Some thread-like adventitious roots and a small bulb were gradually developed after the establishment of seedlings. In late June the aboveground part of the seedling turned yellow roughly at the same time as those of the adults.

The general growth pattern was the same for the juveniles, subadults, vegetative and reproductive adults, although they differed in bulb size, number of foliage leaves and reproductive activity. The results presented below are based on the field observations during 1981–82 at the study area.

Before April, all individuals of the fritillary were hidden underground. As air and soil temperature rose, the unexpanded foliage leaves and stalk began to emerge above the soil surface from the middle of April. The foliage leaves and stalk expanded rapidly and at the same time, new adventitious roots developed from the base of the bulb. The previous year's bulb was consumed simultaneously and by early June it was completely emptied and sloughed off. Through the active photosynthesis of foliage leaves during May and June the two inner scale-like low leaves began to swell and form a new daughter bulb for preserving the assimilate products. A small new bud of next year's growth was already found inside the newly formed bulb in the plants sampled in late May. By late June, the foliage leaves and stalk had turned yellow and withered. The bulb underground was then a completely new one. The active growth (productive) phase for the fritillary was, thus, about two months, i.e. mainly in May and June.

Although the new daughter bulb was hidden underground until the coming spring, it did not mean that there was no growth activity at all. From the sequential harvests, it was found that a dormant stage in the fritillary occurred in summer, from late June through July and August. There were no apparent growth activities such as root development and elongation of the new bud. However, by the end of August, some contractile roots started to appear on the sides of the bulb and these contractile roots may bring about a movement of the bulbs to the proper depth in the soil; at the study area most bulbs of adult individuals being situated in a layer 5–8 cm below the soil surface. The new shoot bud began to develop and elongate simultaneously, although at a very slow rate. By the beginning of November it approached the soil surface and the low leaves, unexpanded foliage leaves and stalk, or the flower bud for flowering individuals, were well differentiated. They remained underground and after a second period of dormancy during winter, the foliage leaves and stalk started sprouting quickly in the following spring.

The reproductive adults had a recognizable flower bud before they emerged from the soil surface in spring. The flower bud developed rapidly after the sprouting of foliage leaves. The full flowering mainly occurred from the middle of May. The period of full flowering during 1981–82 was in agreement with the earlier observations made by Arnell (1914) and Sernander (1948) in the reserve area. By the end of May, most of the flowers had withered, and capsules formed and matured in late June. The seeds of the fritillary were shed in late June and July.

Fig. 40 summarizes the seasonal changes in soil temperature at 5 cm depth (data from the meteorological station at Ultuna) and in soil moisture content together with the phenological observation of flowering individuals of the fritillary in the study area during 1981. It is conspicuous from this diagram that the growth and dormancy phases corresponded well to the seasonal cyclical rhythms of the environmental variables. The most active phase in the growth and reproduction occurred from late April to late June when soil temperature and moisture conditions were moderate. The summer dormant stage occurred when soil moisture decreased and soil temperature increased. In autumn, when soil moisture and temperature became moderate, some growth activities took place. A further decrease of temperature induced the winter dormant stage.

The timing of these processes can be influenced by climatic and environmental conditions. For example, the emergence of plants in spring was about two weeks later in 1981 than in 1982. This could be due to the fact that the mean temperature during

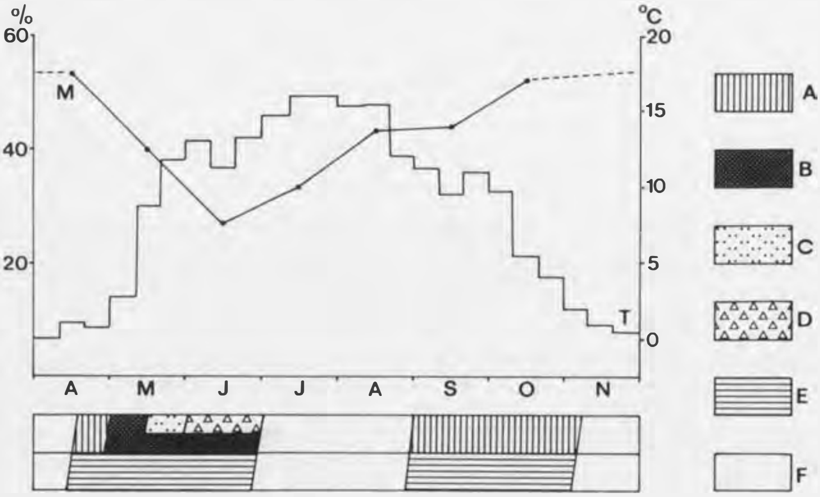


Fig. 40. Seasonal changes in ten-day means of soil temperature at 5 cm depth (T) (data from the meteorological station at Ultuna) and soil moisture (M, % by volume) and phenology of flowering individuals of *Fritillaria meleagris* during the observation period of 1981 in the Kungsängen Nature Reserve. A = unexpanded foliage leaves, B = expanded foliage leaves, C = flowering, D = fruiting, E = root development and F = dormancy.

April was 0.3°C lower in 1981 than in 1982. According to Sernander (1948) the flowering time could be either advanced or delayed for a few weeks in some extreme years.

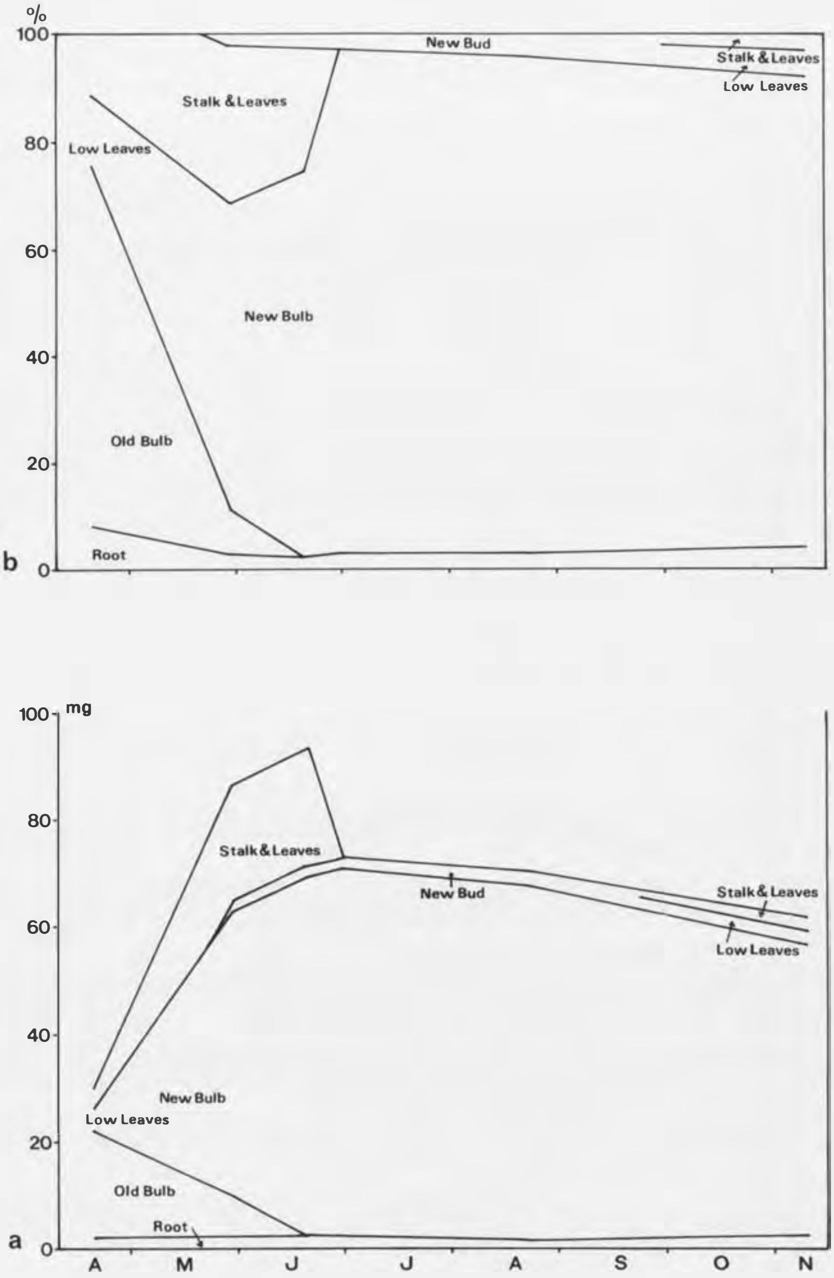
9.2.2 Dry matter allocation

The absolute amount and the proportional allocation of dry matter into root, bulb, low leaves, foliage leaf and stalk throughout the annual cycle in juvenile individuals are shown in Fig. 41a och b. From the middle of April the aerial foliage leaf and stalk grew rapidly and the dry matter of the foliage leaf and stalk increased from 3.4 ± 2.0 mg in absolute amount or 11.6% in proportional amount (April 19) to 22.0 ± 14.4 mg or 23% (June 20) respectively. The food reserves stored in the bulb from the previous year decreased from 19.9 ± 15.3 mg or 67.7% (April 19) and became completely consumed (June 20). The production of assimilate by the foliage leaf was rather high; the total biomass per individual increased from 29.4 ± 18.9 mg in the beginning of the active growth phase (April 19) to the maximal value of 93.3 ± 61.5 mg by the end of the active growth phase (June 20). A considerable amount of the assimilate products was translocated into the new bulb, which reached 68.7 ± 55.0 mg by the end of June. The absolute amount and the proportion of dry matter in roots were relatively low as compared with other component organs, being 2.2 ± 1.2 mg or 7.5% in April 19, remaining rather constant during the active growth phase, decreasing to 1.9 ± 0.7 mg or 2.7% during the summer dormancy as some of the roots were decaying, and increasing to 2.6 ± 1.4 mg or 4.2% in the autumn as new contractile roots developed. The increases of bulb size and total biomass in dry weight, on average, were from 4.6 ± 1.5 mm and 29.4±18.9 mg (April) to 6.1 ±2.0 mm and 61.4 ±37.8 mg (November); an annual increase of about 30 mg dry matter per individual was estimated for the juveniles.

The dry matter allocation pattern of the subadults and vegetative adults was the same as for the juveniles, although the bulb size and biomass differed greatly. The maximal biomass per individual of the subadults was 328± 105 mg (June 20) (Fig. 42a and b). The increases of bulb size and total biomass in dry weight were from 9.0 ± 1.3 mm and 103 ± 46 mg (April) to 11.2 ± 2.9 mm and 214 ±86 mg (November); an annual increase of about 110 mg dry matter per individual was estimated for the subadults.

The maximal biomass per individual of the vegetative adults was 751 ± 178 mg by June 20 (Fig. 43a and b). The increases of bulb size and total biomass in dry weight were from 13.7 ± 1.8 mm and 265 ± 90 mg (April) to 16.3 ± 1.5 mm and 499 ±81 mg (November); an annual increase of about 235 mg dry matter per individual was esti-

Fig. 41. Dry matter allocation into the different component organs in the juvenile age-state of *Fritillaria meleagris* from April to November 1982 in the Kungsängen Nature Reserve. a) in mg dry weight, b) in %. Twenty individuals were measured at each sampling and the mean values per individual are given.



mated for the vegetative adults.

No vegetative reproduction by bulblets was observed among the juveniles, subadults and vegetative adults sampled during April–November 1982. However, it still remains to be investigated if vegetative reproduction could occur among these age-states, since the observations were made on the individuals from 6 harvests during one single year. Nevertheless, it can be stated that vegetative reproduction is, at least, very rare among these vegetative age-states, thus being negligible.

It is worth noting that the proportional allocation of dry matter into the component organs during the annual cycle was quite similar among the juveniles, subadults and vegetative adults (Fig. 41b, 42b and

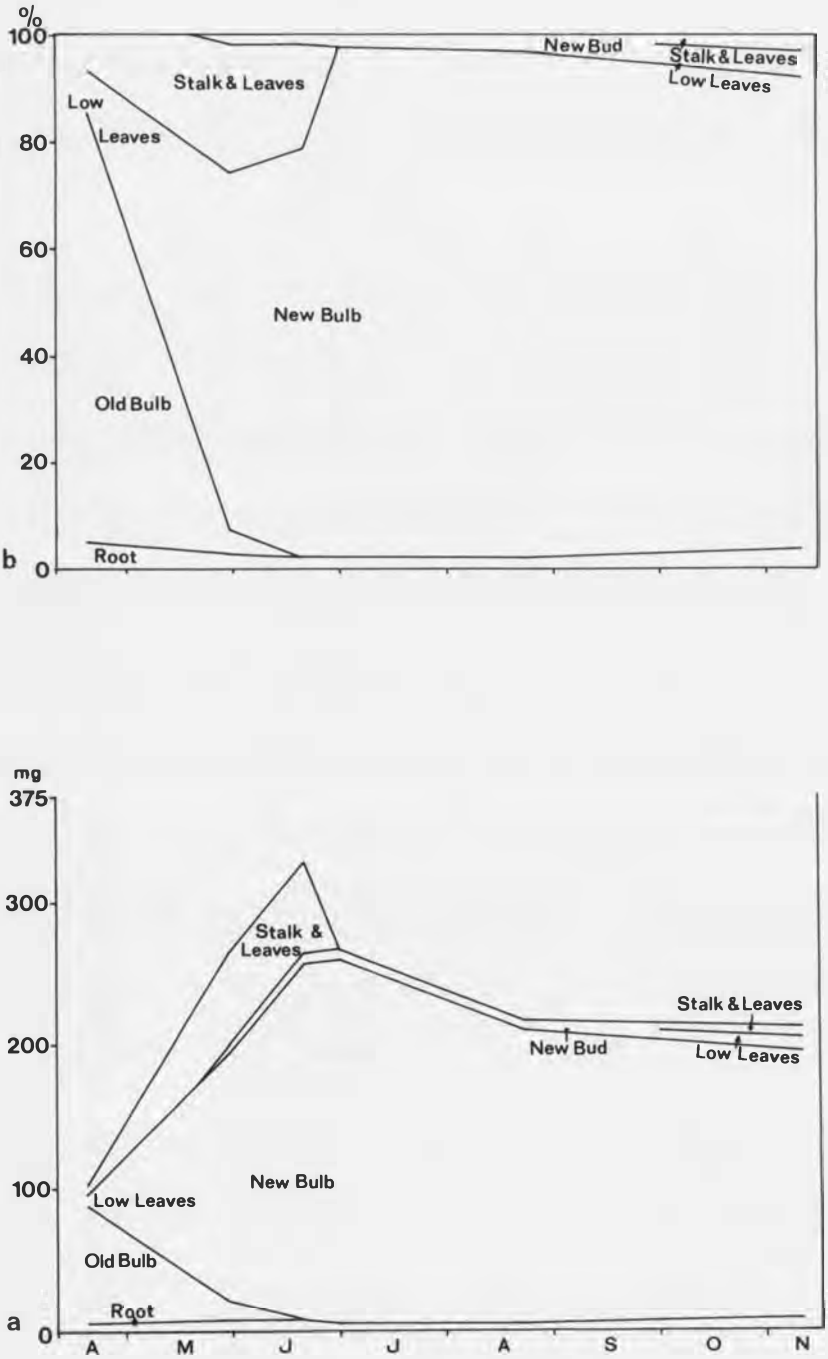


Fig. 42. Dry matter allocation into the different component organs in the subadult age-state of *Fritillaria meleagris* from April to November 1982 in the Kungsängen Nature Reserve. a) in mg dry weight, b) in %. Twenty individuals were measured at each sampling and the mean values per individual are given.

43b). This may suggest that the program of dry matter allocation is rather fixed for the fritillary.

The dry matter allocation of the reproductive adults throughout the year is presented in Fig. 44a and b, both by dry weight and proportion. The general annual cycle pattern of the reproductive adults was more or less similar to the vegetative age-states. However, during the active growth phase a considerable amount of the assimilate produced by the foliage leaves was allocated into the reproductive structures, i.e. flower, capsule and seeds. The absolute amount and the proportional allocation of dry matter into reproductive organs attained about 0.5 mg or 0.1 % of the total biomass at flower bud stage (April 15), gradually increased to 71 ± 18 mg or 12.6% at full flowering stage (May

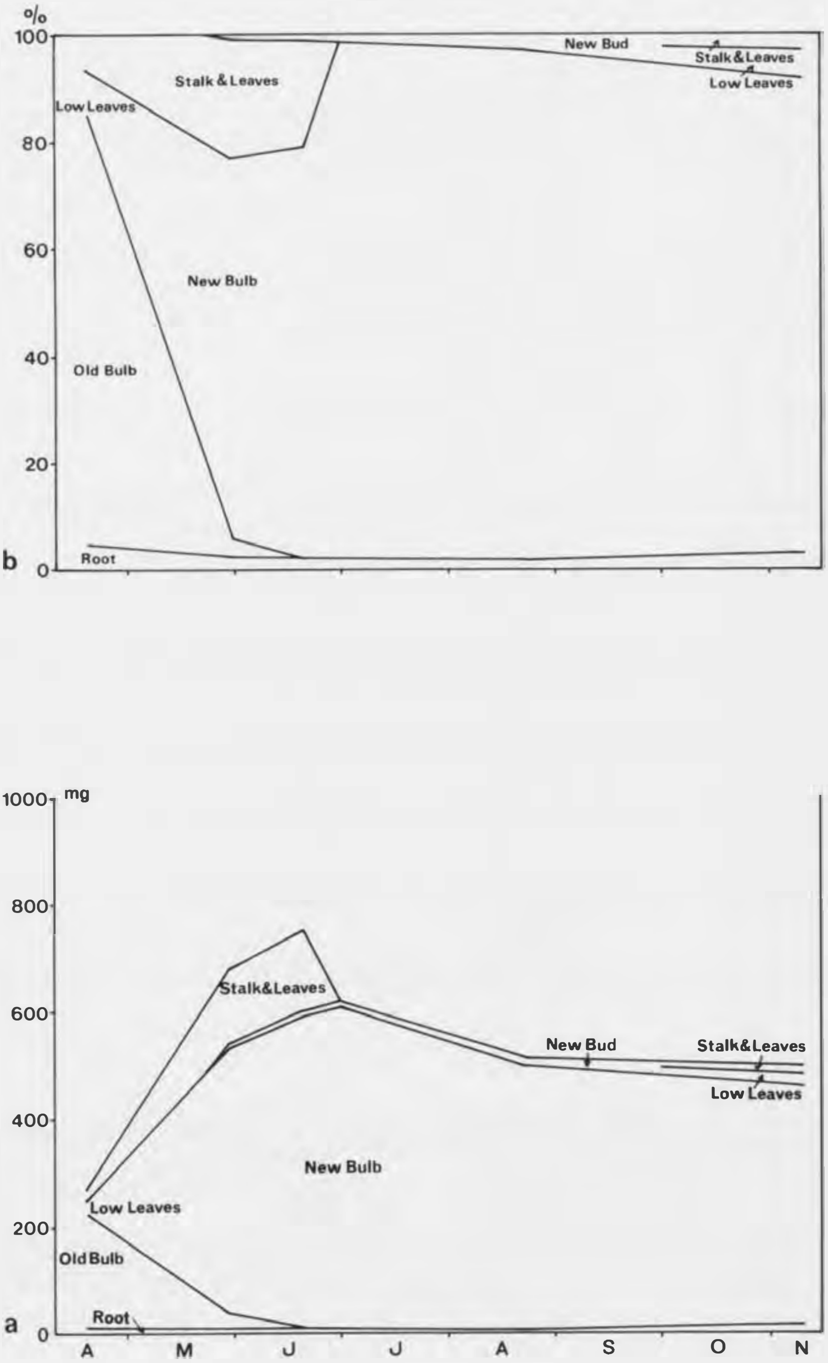


Fig. 43. Dry matter allocation into the different component organs in the vegetative adult age-state of *Fritillaria meleagris* from April to November 1982 in the Kungsängen Nature Reserve. a) in mg dry weight, b) in %. Twenty individuals were measured at each sampling and the mean values per individual are given.

24), then decreased to 32 ± 11 mg or 4.1% (June 9) and increased again to 155 ± 24 mg or 17.5% (June 24) at mature fruiting stage (capsule with seeds). The maximal biomass per individual of the reproductive adults was 885 ± 174 mg by June 24. During the active growth phase, vegetative reproduction by set-off bulblet formation also occurred on the newly-formed bulb. It was found that among the 120 flowering individuals sampled during May–July 1981, 16 individuals had one and 1 individual had two set-off bulblets, which sprouted from the new bulbs, apparently formed by vegetative propagation. These small bulblets were 1–2 mm in size, 1.2–10 mg in dry weight and accounted for 0.4–1.5% of the total dry matter allocation. However, if taking the occurrence frequency into

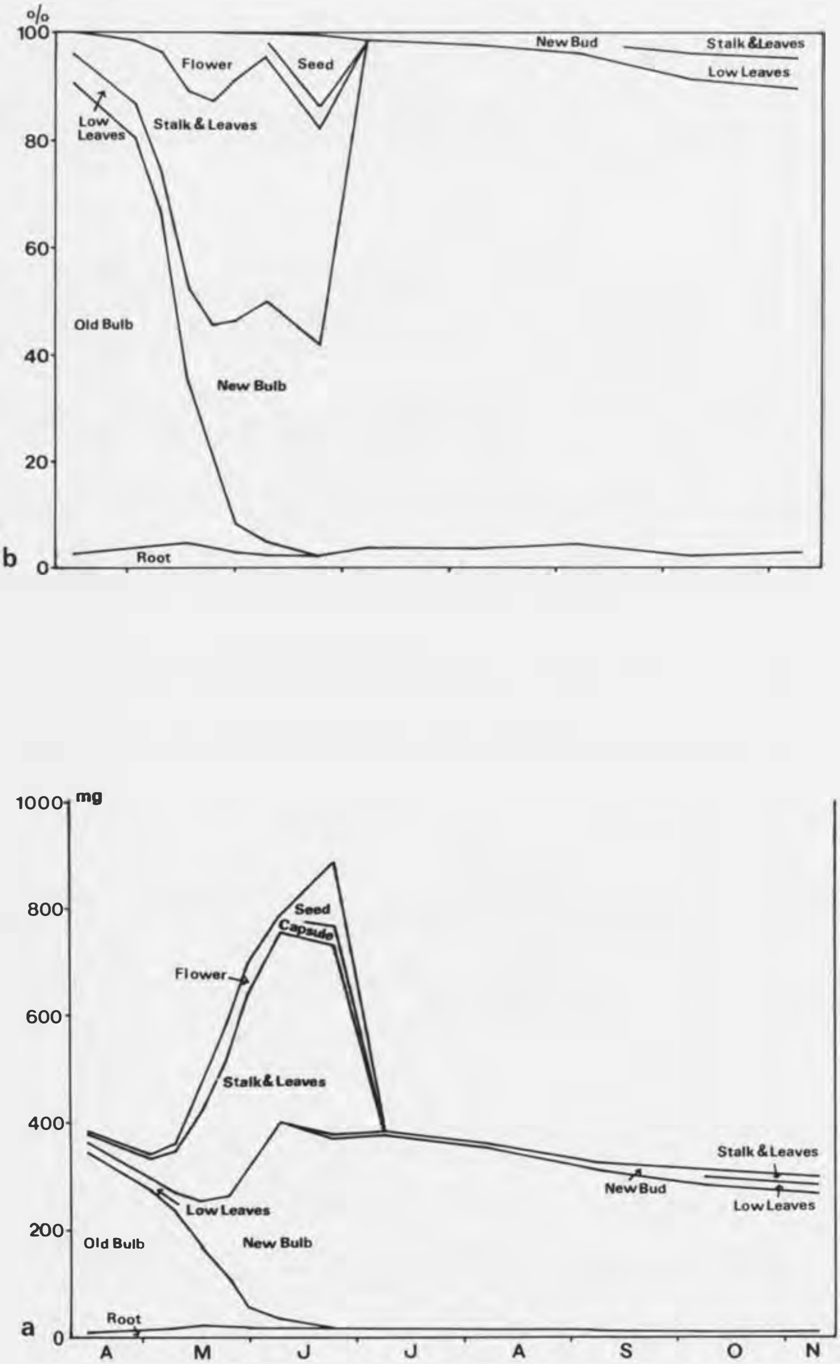


Fig. 44. Dry matter allocation into the different component organs in the reproductive adult age-state of *Fritillaria meleagris* from April to November 1982 in the Kungsängen Nature Reserve. a) in mg dry weight, b) in %. Twenty individuals were measured at each sampling and the mean values per individual are given.

account, it attained less than 0.2% of the dry matter allocation per flowering individual.

The reproductive effort was estimated by the ratio of seed production/total biomass at final harvest in dry weight, which is a crude approximation of the net reproductive effort defined by Harper & Ogden (1970). The proportion of dry matter in seeds per reproductive adult was 13.2% of the total biomass.

In contrast to the other vegetative age-states, the bulb size and total biomass in dry weight of reproductive adults decreased from 15.6±1.4 mm and 378±86 mg (April) to 14.5±1.6 mm and 299±106 mg (November); an annual decrease of about 80 mg dry matter per individual was estimated for the reproductive adults.

10 Seed production, seed bank in the soil and germination experiments

A plant population living in an area is often composed of two parts: viable dormant seeds and established individuals. Any attempt to discuss the population dynamics of individual species must include the quantified studies of these two parts (Harper 1977, Pavone & Reader 1982). Recently the dynamics of natural seed populations, the germination characteristics and the establishment of seedlings under natural conditions have attracted the attention of many plant ecologists (Harper et al. 1965, Sarukhan 1974, Harper 1977, Thompson & Grime 1979, Grime et al. 1981, Roberts 1981).

The study of the seed biology of the fritillary has attempted to acquire basic information on the seed production and the dynamics of the seed bank under field conditions, and to describe the germination characteristics both in the laboratory and in the field in relation to the mechanisms which control the time and place at which seed germination and seedling establishment occur under natural conditions. By combining this information with demographic data of established individuals, it should be possible to reach some knowledge of the interaction between the characteristics of the habitable sites and the species itself.

10.1 Material and methods

The investigation was performed within the Kungsängen Nature Reserve area where the fritillary is abundant.

10.1.1 Seed production

Counting of flowering individuals with seeded capsules and number of seeds per capsule could give an estimate of seed production in the population as a whole and also give some information on the variation in seed production from year to year.

The number of flowering individuals, the proportion of seeded, unfertilized and damaged (the reproductive organs, e.g. flowers and fruits were damaged by animals) flowering individuals were counted during the flowering and fruiting stages (May–June) in 1981 and 1982, in the same set of twenty-nine 1 m^2 permanent plots used for the demographic study. The capsules with seeds were collected randomly from the field population just after the annual mowing (during June 18–24). The capsules sampled were brought into the laboratory and air-dried. The ripe and unripe (apparently empty) seeds per capsule were sorted and counted. The ripe seeds were weighed and the mean weight per ripe seed for each capsule was calculated.

10.1.2 Seasonal changes of seed population in the soil

The study area is mown annually during the midsummer period when most capsules of flowering individuals are ripe but not dry enough to release seeds. The amount of seeds entering the seed bank in the soil not only depends upon the seed production of reproductive plants, but also upon the management practice, i.e. the date of cutting and collecting of hay. The seasonal changes of seed population in the soil as well as the influence of management practice on the size of the seed bank were assessed by collecting a series of soil samples in the enclosed area and the nearby mown area where the observations on reproductive activities of the flowering individuals were made. The soil cores, each 7.2 cm in diameter and 5 cm in depth, were collected: (1) on August 14, 1981 when seed set had been completed, (2) April 20, 1982 when spring germination started, (3) June 10, 1982 after seed germination in the field and before the supply of a new seed set and (4) July 19, 1982 when a new seed set had been added. On each occasion, 10–20 soil cores were collected from the mown area and the enclosed area, respectively, at random points along line transects. The soil samples were brought to the laboratory and sliced depthwise into two or three parts. The seeds of the fritillary are large (3–6 mm) enough to be separated from the soil by hand-sorting. The results are expressed as mean number of seeds/m^2.

10.1.3 Germination tests in the laboratory

Source of seeds

The seeds of the fritillary used in all experiments described here were collected from the field population in the study area in late June and early July 1981 and 1982. Immediately following collection, the ripe seeds were air-dried at laboratory temperature (about 20°C). They were then placed: (1) in dry storage in paper envelopes at temperatures of 4°C and 20°C respectively, (2) in moist storage in 9-cm diameter Petri dishes on filter paper saturated with distilled water and kept saturated throughout the storage both at temperatures of 4°C and 20°C and (3) in field storage where batches of seeds were placed in porous containers and put into the reserve area in July 1981 just beneath the soil surface. They remained there until June 1983 to test the germinability of the seeds under field conditions.

Initial tests

Before placing the seeds into different storage treatments, the capacity of the freshly-collected seeds for immediate germination was tested. One hundred seeds were placed in each 9-cm glass Petri dish on filter paper moistened with distilled water. The effect of gibberellic acid on the germination of freshly-collected seeds was tested at the same time, where the filter paper was soaked in a millimolar solution of gibberellic acid. These dishes were transferred into germination chambers with a 12 hours light/dark regime at constant temperatures of 12°C and 20°C, and into a temperature of 4°C in darkness apart from the exposure to diffuse laboratory light for a few minutes during the inspection of the germination.

Response to the different storage treatments

In each storage treatment, subsamples, each of one hundred seeds, were taken at intervals. They were tested for germinability at various temperatures. In the field storage treatment, subsamples on each collecting date were brought into the laboratory from the field containers and tested at a constant temperature of 12°C with a 12 hours light/dark regime. The viability of the seeds at the end of this experiment (June 1983) was tested by the reaction with 2,3,5-triphenyl tetrazolium chloride (Colbry et al. 1961).

Response to temperature

The influence of temperature upon germination percentage and germination rate was studied at a wide range of both constant and fluctuating temperature conditions in germination chambers.

Each Petri dish was inspected at intervals of 1–7 days, depending on the germination rate of seeds. Germination is defined as the emergence of approximately 1 mm of radicle through the seed coat. Germinated seeds were recorded and removed. The minimum duration of a test was 30 days and continued until no germination occurred for 7 successive days. The results of all tests are presented as a final germination percentage and as the time required for 50% of the final germination percentage to be attained (half-time).

10.1.4 Germination in the field

The course of germination in the field was followed in an enclosed experimental site. A thin-walled wooden box, 50×50 cm without top and bottom, was pressed into the soil. The box was subdivided into twenty-five 10×10 cm plots. Three treatments were adopted: (1) the seeds were sown on the surface of sterilized soil, (2) just beneath the soil surface at a depth of 0.2–0.5 cm in sterilized soil and (3) on the soil surface with natural vegetation which resembled the seed dispersal under natural conditions. Four to one hundred ripe seeds were sown on or in each plot in the autumn of 1981. The box was covered with a plastic netting (1×1 cm mesh) to prevent predation by animals. The seedlings that emerged were recorded in the spring of 1982.

10.2 Results

10.2.1 Seed production

The total number of flowering individuals and the seed production within the twenty-nine 1×1 m permanent plots for the study period of 1981–82 are presented in Table 21.

The first remarkable point in these figures is the much higher total number of flowering individuals in 1981 than in 1982. The total number of flowering individuals with a seeded capsule was also higher in 1981. The differences between years in the percentage of flowering individuals producing a seeded capsule seems to depend on the availability of insect pollination and on damage caused by animals.

The differences in the mean number of ripe and unripe seeds per capsule as well as the mean weight of ripe seed were considerable between years (Table 22). This may be explained by the weather conditions during flowering and fruiting stages and by the management practice in the actual years. The mean monthly temperatures during May and June of 1982 were 2.0°C and 0.6°C lower than those of 1981. The mowing date was 4 days earlier in 1982 (June 18) than in 1981 (June 22). Both the mean number of ripe seeds per capsule and the mean weight of ripe seeds were higher in 1981 than in 1982, while the number of unripe seeds per capsule was higher in 1982. However, from the observation in the enclosed sites, the mean number of ripe seeds per capsule and the mean weight of ripe seeds were 96±27, 1.5±0.4 mg in 1981 ($n=25$), and 84±43, 1.3±0.3 mg in 1982 ($n=30$), respectively. In both years sampling took place in late June. There were no significant differences between years concerning the mean number of ripe seeds per capsule and the mean weight of ripe seed ($P>0.10$).

Consequently, these results provided an estimate of yearly seed production in the permanent plots. The estimate of seed production per unit area was 1,027±281/m^2 in 1981 and 226±99/m^2 in 1982. The seed production was strongly dependent on the number of flowering individuals producing a seeded capsule.

Table 21. Variation between years in the number of flowering individuals, the proportion of flowering individuals with a seeded capsule, with an unseeded capsule and with a damaged flower or capsule in the twenty-nine 1 x 1 m permanent plots in the Kungsängen Nature Reserve. The percentage value is shown in parenthesis.

Year	1981	1982
Total no. of flowering individuals	405 (100)	223 (100)
Total no. of flowering individuals with a seeded capsule	331 (81.7)	95 (42.6)
Total no. of flowering individuals with an unseeded capsule	47 (11.6)	44 (19.7)
Total no. of flowering individuals with a damaged flower or capsule	27 (6.7)	84 (37.7)

Table 22. Variation between years in the mean number of ripe and unripe seeds per capsule and the mean weight of ripe seed, and the mean seed production per unit area. Samples were collected from the field population in the Kungsängen Nature Reserve just after annual mowing. Number of capsules is indicated in parenthesis.

Sampling date	1981-06-22	1982-06-18
Mean no. of ripe seeds ± S.D per capsule	90 ± 25 (80)	68 ± 30 (30)
Mean no. of unripe seeds ± S.D per capsule	40 ± 17 (80)	59 ± 31 (30)
Total no. of seeds ± S.D per capsule	130 ± 24 (80)	127 ± 21 (30)
Mean no. of flowering individuals with a seeded capsule/m^2	11.4	3.3
Mean no. of ripe seed ± S.D per m^2	1,027 ± 281	226 ± 99

Table 23. Estimate of mean density ± S.D of seeds/m^2 of the fritillary on the soil in the mown and the enclosed sites in the Kungsängen Nature Reserve. Value in parenthesis is the number of samples collected.

Collection date	Mown site	Enclosed site
14 August 1981	369 ± 914 (10)	811 ± 1074 (10)
20 April 1982	152 ± 329 (14)	440 ± 656 (14)
10 June 1982	49 ± 128 (20)	123 ± 258 (20)
19 July 1982	74 ± 278 (20)	283 ± 629 (20)

10.2.2 Size and dynamics of seed population in the soil

Most seeds remained within the capsules before the annual mowing. Some seeds could be released during the period between cutting and collecting of hay, and thus become part of the seed bank. In the enclosed site, the seeds were released completely from the capsules in July. The size and dynamics of the seed bank in soil were estimated at both mown and enclosed sites. The seeds of the fritillary were found to be presented on the soil surface only, no seeds were found under 0.5 cm of the soil surface. The distribution of seeds on the soil surface was very clumped ($S^2/\bar{x} \gg 1$), in relation to the plot area (40.7 cm^2 each). The seed dispersal of the fritillary in the study area was apparently influenced by the hay-making management, as most seeds were released when hay was cut down and the capsules were close to the soil surface.

The results of the investigation (Table 23) show that a large proportion of seeds could not enter the seed bank due to the hay-making. This has been shown in the differences between the mown and the enclosed sites. The t-test on the differences of mean values was not significant ($P > 0.05$), depending on the very clumped distribution of seeds. On the other hand, Fisher's exact test gave significantly higher frequencies ($P < 0.01$) when comparing the differences between the mown and enclosed sites as well as between years. Regarding the mean values an estimate of 55% in 1981 and 74% in 1982 of the seeds were lost as a consequence of the annual hay-making. The differences in the size of seed banks in the soil between years depended, to a large extent, on the variation of yearly seed production and the date of annual mowing (see section 10.2.1).

The seasonal changes of the seed bank were similar at both sites (Table 23). The largest density of seeds in the soil was recorded just after seed set (July–August). The amount of seeds subsequently decreased as a result of predation, fungal attack and decay. Out of the seed population which had reached the soil in July-August 1981, 46–59% was lost at the beginning of field germination (April 1982); predation by small mammals such as voles and field mice may be important in reducing the seed population in soil as they were observed frequently in the field. Further decrease of seed population in the soil occurred as a result of flushes of seed germination in the field in spring (April–May). By the middle of June, before there was any replenishment with fresh seeds from the current year, the seed bank in the soil was almost exhausted. Most seeds left (amounting to 13–15% of the previous year's seed bank) were infected or empty. According to a laboratory germination test, about 10% of them were viable, but the chance of surviving to the next year was very little considering the effect of predation and fungal attack. The soil seed bank was replenished with fresh seeds from the current year again in July 1982.

10.2.3 Initial germination tests

The freshly-collected seeds of the fritillary were completely dormant at the initial germination test under a range of temperatures, 4°C–20°C. The treatment with a millimolar gibberellic acid could not replace the dormancy breaking requirement of the freshly-collected seeds.

10.2.4 Response to different storage treatments

The effects of different storage treatments on germinability of the fritillary seeds are shown in Table 24. The results revealed that the freshly-released seeds of the fritillary must experience a period of about three months of chilling (at low temperature and in moist conditions) before germination was possible. It has been observed in the laboratory that once the chilling requirement had been fulfilled, the seeds could germinate at a low temperature (4°C) and in darkness. The presence or absence of light seems to be of no importance for completing germination successfully.

It has been shown that the dry storage at 4°C and 20°C and the moist storage at 20°C for more than five months did not decrease the innate dormancy of freshly-collected seeds. It has also been found that seeds kept under dry storage at a temperature of 4°C for more than one year did not increase or decrease their germinability after pre-chilling treatment in laboratory.

Table 24. Germination percentage of the fritillary seeds after different storage treatments at the laboratory.

Germination temperature			4°C (dark)	12°C (light)	20°C (light)
Dry storage:	4°C	90 days	0	0	0
		160 days	0	0	0
	20°C	90 days	0	0	0
		160 days	0	0	0
Moist storage:	4°C	50 days	0	0	0
		90 days	45	52	16
	20°C	90 days	0	0	0
		160 days	0	0	0

10.2.5 Response to temperature

Seeds of the fritillary were set to germination tests at various constant temperatures and fluctuating temperature conditions in germination chambers after three months pre-chilling treatment (moist storage at a temperature of 4°C). The results (Table 25) show that at constant temperatures, the most rapid germination took place at 20°C (half-time 4 days) and the optimum temperature for maximum germination was at 12°C (germination percentage 52%). At the low temperature of 4°C, the germination percentage reached 47% but the germination rate was slow (half-time 23 days). The germination tests at fluctuating temperatures showed that the most rapid germination took place at 20–30°C (half-time 3 days) and the maximum germination was attained at 10–20°C (germination percentage 69%). The fluctuating temperatures increased the total germination percentage over that obtained at the constant temperatures.

It is noteworthy that with increasing temperature, the germination percentage decreased (16% at constant temperature of 20°C and 26% at fluctuating temperature of 20–30°C), possibly being a result of induction of dormancy due to high

Table 25. Germination percentage and rate (half-time in days, in parenthesis) of the fritillary seeds after three months' chilling treatment at various constant as well as fluctuating temperatures in germination chambers.

Germination temperature	4°C	12°C	20°C	20-10°C	20-15°C	30-20°C
Germination percentage and half time	47 (23)	52 (8)	16 (4)	69 (8)	49 (5)	26 (3)

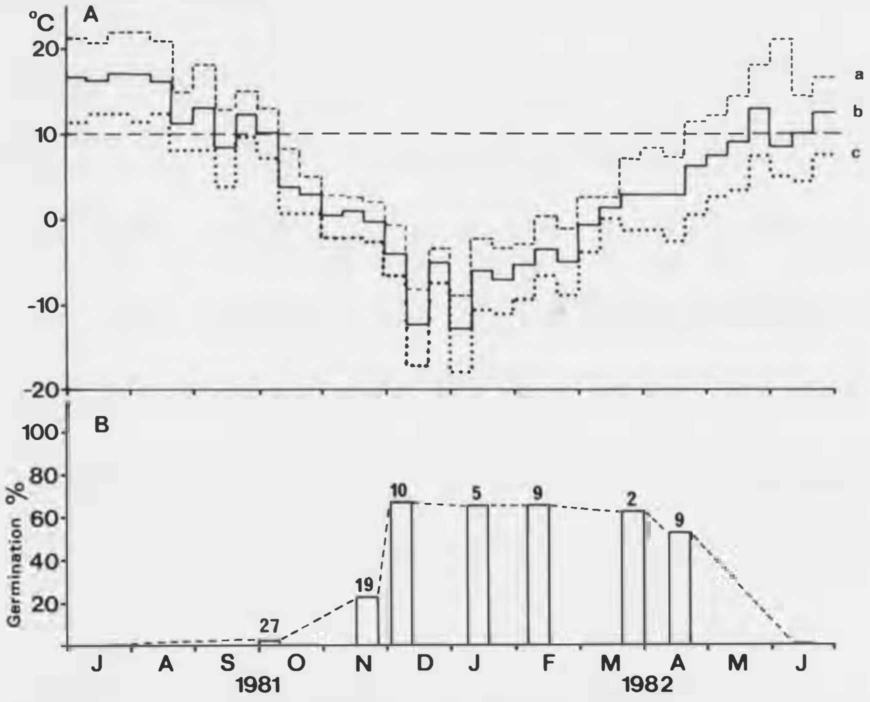


Fig. 45. Temperature and germinability of the fritillary seeds in porous containers in the field from July 1981 to June 1982.

A. Ten-day averages of daily maximum (a), mean (b) and minimum (c) temperatures based upon measurements at the meteorological station at Ultuna.

B. Germinability of the fritillary seeds after stored in the field for various lengths of time. Germination test at a constant temperature of 12°C with a 12 hour light/dark regime in a germination chamber. Germination rate (half-time in days) is also indicated. Only ungerminated seeds were used for the tests and the seeds that germinated in the field containers were removed.

temperature. After being subjected to re-chilling treatment (moist storage at a temperature of 4°C) for 30–60 days, the germination began again even at a low temperature of 4°C in darkness or in light. The final germination percentage for these seeds attained 66–70%.

10.2.6 Germination behaviour of the seeds stored in the field

The germination behaviour of the fritillary seeds stored in the field was studied by testing samples of seeds collected at various time over two years. The germination percentage and rate (half-time in days) are presented in Fig. 45B. The ten-day averages of daily maximum, mean and minimum temperatures during the experiment are presented in Fig. 45A (the data were based upon the measurements made at the meteorological station at Ultuna).

When stored in July 1981, the fresh seeds remained dormant until November. It is quite obvious that the breakdown of innate dormancy could be performed by low temperature and improved soil moisture conditions in the field from September to November, which was in agreement with the chilling requirement in the laboratory. When the chilling requirement had been fulfilled, the proportion of germinable seeds increased from 2% in October, through 23% in November to 67% in December 1981 and remained quite constant through January (66%), February (66%) and March (63%) 1982. The germination rate increased, as demonstrated by the decrease of half-time from 19 days in November 1981 to 2 days in March 1982. However, no seeds were found to have germinated in the containers in the field, apparently due to very low temperature near or below zero from November to March.

In late March when the temperature began to rise, the seeds in the containers started germinating. The seeds that germinated in the containers were removed and only the ungerminated seeds were kept in the containers for further tests, which gave a relatively lower germination percentage (53%) and slower germination rate (half-time 9 days) in April 1982 than in late March. During April and May 1982, a rapid flush of germination occurred in the containers. No germination occurred in the containers after May 1982. The germination test in the laboratory with the seeds left ungerminated in the containers in June 1982 showed no germination at 12°C. However, after being transferred to the re-chilling treatment at the laboratory for about 60 days, 10% of these seeds could germinate in the laboratory, which may indicate that a small proportion of seeds left ungerminated in the field were in an induced dormant state. Whether this small proportion of seeds could survive more than one year under natural conditions and be able to germinate successfully in the next spring was tested by keeping them in the field and testing the germinability in March 1983. The result revealed that about 15% of the seeds sampled in March 1983 from the field containers could germinate in the laboratory at 12°C. As a considerable amount of apparently dead seeds rotted off during the storage in the field, the germination percentage was slightly higher compared with that tested in June 1982. This means that a small proportion of seeds could survive more than one year in the field, but according to the results of soil seed bank investigation, this proportion was less than 1.5%, thus being negligible. None of the seeds which had remained in the containers for two years was still alive as tested by the reaction with 2,3,5-triphenyl tetrazolium chloride in June 1983.

10.2.7 Germination in the experiment plots

None of the seeds sown on the plots with three treatments was observed to germinate from July 1981 to March 1982. A rapid flush of seed germination occurred on all plots during late March and April, and no germination occurred after May. These results were compatible with the results of seeds stored in the containers in the field. In all the plots, the seedlings which emerged were allowed to establish themselves. The final emergence of seedlings was recorded in late May 1982. Since there was no significant difference between the plots with same treatment, the results of the number of sown seeds, the number of final emergence of seedlings and the etablishment percentage were, thus, combined for comparison of the effect of different treatments on the final emergence of seedlings. The results are shown in Table 26.

The results show that considerable differences in

Table 26. Final emergence of seedlings under three sowing treatments. The figures are the total number for each treatment. Number of plots, 10 x 10 cm in size, for each treatment is presented in parenthesis.

Sowing treatment	No. of sown seeds	No. of seedlings	Emergence %
On sterile soil surface	217 (10)	31	14.3
Beneath sterile soil surface	164 (5)	60	36.6
On soil surface with natural vegetation	288 (10)	14	4.9

seedling establishment between these three groups of plots were found and the emergence of seedlings was much greater from the sterilized soil which was kept free of vegetation. The inhibitory effects of vegetation on germination of the fritillary seeds was quite clear: in the plots with natural vegetation, the emergence of seedlings was only 4.9% of the number of sown seeds and the seedlings were often observed in the gaps in perennial vegetation. Seedling establishment was much higher in the sterilized soil at the depth of 0.2–0.5 cm (36.6%) than on the sterilized soil surface (14.3%).

It is well-known that continuous hydration is a prerequisite of seed germination (Harper & Benton 1966, Pemadasa & Amarasinghe 1982). A part of the effect of sowing seeds beneath the soil surface would be due to the protection of seeds against water loss. In support of this, a laboratory experiment was designed in which the seeds, after chilling treatment, were sown both on the sterilized soil surface and in the sterilized soil at a depth of 0.5 cm in a tray. They were kept in good moisture conditions in a germination chamber at a temperature of 12°C with a 12 hours light/dark regime. There was no difference in the final emergence of seedlings between these two treatments, although the germination rate was slower for the seeds sown beneath the soil surface. The final emergence of seedlings and germination rate (half-time) was 41%, 12 days for the seeds sown on the soil surface and 43%, 23 days for the seeds sown beneath the soil surface.

11 Changes in distribution of the fritillary population and the proportion of flower colours

After the regulation of Lake Mälaren in 1942 and 1968, the water level in the River Fyris had been raised, especially during the growing season, which influenced the ground water regime in the reserve area and caused considerable changes in the vegetation there (see section 6.3). The effects of habitable sites on the distribution of a species have been demonstrated by many plant ecologists (Jones & Etherington 1971, Harper 1981). This may suggest that the alteration of the ground water regime within the Kungsängen Nature Reserve may also cause a change in the distribution of the fritillary population there.

This study was undertaken to answer a question: what changes have taken place in the distribution of the fritillary population and in the proportion of flower colour over 40 years within the study area.

11.1 Methods

As the flowering individuals of the fritillary have, in most cases, one flower, or very seldom two, per individual and the flowering time is almost simultaneous, counting of the number of flowers within a unit of area at the flowering season can give a reasonable estimate of the density of flowering individuals and the variations between years. Furthermore, it can also give an estimate of the proportion of flower colours.

Sernander (1948) counted the total number of flowers and the proportion of red-purple, pink and white flowers in six sampling plots, each 10× 10 m, along a transect within the reserve area (Fig. 37) on May 24–25, 1938. These plots were revisited on May 25 during 1981–83. Each plot was delimited along the transect according to the description of Sernander (1948). The observations were not made on marked permanent plots and the errors of reestablishment of these plots could be ±2 m. Nevertheless, the field observation showed that there were no obvious differences in the density of flowering individuals around each plot. The countings may thus give a general survey of changes in the distribution of the fritillary population within the study area as well as the variation in the number of flowers between years.

On each visit the total number of flowers and the numbers of red-purple, pink and white flowers within each plot were counted, with no attempt made to follow specific individuals. The proportion of flower colours was calculated for each plot with the exception of the plots which had less than 50 flowers, since low numbers could lead to unreliable proportion figures.

11.2 Results

11.2.1 Changes in the density of flowers

The changes in the total number of flowers within each plot in 1938 and 1981–83 are presented in Table 27. In plot 1 which was close to the border of the reserve area, the density of flowering individuals was low and did not change very much over the years. There were 11 flowers in 1938, 16 in 1981, 39 in 1982 and 61 in 1983. The number of flowers in plots 2 and 3 increased from 19 and 149 in 1938 to 66 and 98 in 1981, 243 and 274 in 1982, 291 and 239 in 1983, respectively. There was a considerable increase in plot 4, that is, from 452 in 1938 to 2,145 in 1981, 1,132 in 1982 and 1,862 in 1983. In plots 5 and 6 the density of flowering individuals decreased drastically over 40 years. In plot 5 there were 1,932 flowers in 1938, only 48 in 1981, 7 in 1982 and 152 in 1983. In plot 6 there were 255 flowers in 1938 and they had disappeared completely in 1981–1983.

Table 27. Changes in the number of flowering individuals of Fritillaria meleagris in six sampling plots, 10 x 10 m each, along a transect within the Kungsängen Nature Reserve. Observations were made in 1938 and 1981-83.

Plot number	1	2	3	4	5	6	Total
Position along the transect (m)	45-55	80-90	97-107	170-180	255-265	286-296	
Altitude (m above sea level, system 1900)	1.43	1.44	1.44	1.46	1.17	0.91	
1938-05-25	11	19	149	452	1,932	255	2,818
1981-05-25	16	66	98	2,145	48	0	2,373
1982-05-25	39	243	274	1,132	7	0	1,695
1983-05-25	61	291	239	1,862	152	0	2,605

Table 28. The proportion of red-purple (R), pink (P) and white (W) flowers recorded in six 10 x 10 m plots in 1938 and 1981-1983 within the Kungsängen Nature Reserve.

Plot number	1			2			3			4			5			6		
Proportion %	R	P	W	R	P	W	R	P	W	R	P	W	R	P	W	R	P	W
1938-05-25	-	-	-	-	-	-	96	0	4	96	0	4	95	2	3	93	3	4
1981-05-25	-	-	-	91	3	6	94	2	4	96	1	3	-	-	-	-	-	-
1982-05-25	-	-	-	94	3	3	95	2	3	94	3	4	-	-	-	-	-	-
1983-05-25	95	2	3	96	1	3	95	1	4	94	2	4	94	3	3	-	-	-

Table 29. Comparison between the white and red-purple flower plants of Fritillaria meleagris in the Kungsängen Nature Reserve for some measurements of growth performance and reproductive effort. Means and standard deviations are given and the sample size is presented in parenthesis. Significance, t-test, N.S. = not significant (P >0.10).

Measurement	white flower plant	red-purple flower plant	Significance
Height of above ground part (1982-05-25)	35.3 ± 3.6 cm (30)	35.8 ± 4.0 cm (30)	N.S.
No. of leaves per ind.	4.7 ± 0.7 (30)	4.6 ± 0.6 (30)	N.S.
No. of ripe seeds per capsule	75 ± 32 (10)	68 ± 30 (30)	N.S.
Mean weight per seed	0.90 ± 0.2 mg (10)	0.89 ± 0.2 mg (30)	N.S.
Germination percentage 10-20°C	71.4 %	69.0 %	

There were considerable year-to-year variations in the number of flowers in 1981–1983. The total number of flowers in all six plots showed alternate marked rises and falls in consecutive years; being 2,373 in 1981, falling to 1,695 in 1982 and then rising again to 2,605 in 1983. However, there was no consistent pattern for the yearly fluctuation between the plots. There were always years in which the number of flowers in some plots was rising and in others falling. Plots 1, 2 and 5 had higher numbers in 1983 than in 1981 and 1982, plot 3 had a higher number in 1982 than in other years, while in plot 4 the number was higher in 1981 than in 1982 and 1983.

In spite of the large changes in the number of flowers between the years, a significant change in the density of flowering individuals within the reserve area over 40 years has been observed. The number of flowering individuals decreased considerably or disappeared completely in the relatively low-situated plots 5 and 6 (altitude 0.91–1.17 m, system 1900), while in the relatively high-situated plots 2, 3 and 4 (altitude 1.44−1.46 m) the density of flowering individuals increased.

11.2.2 Proportion of flower colours

The proportions of red-purple, pink and white flower recorded within each plot in 1938 and 1981−83 are presented in Table 28. It is very conspicuous that the proportion of flower colours has remained quite constant despite the different position of these observation plots and the great changes in the density of flowering individuals as well as the fluctuations in the number of flowers between years. The red-purple flower accounted for 91−96%, the pink flower 0−3% and the white flower 3−6% of the total number of flowers within each of these plots in all the observation years.

It was found from the field observations that there were no local perceptible patterns of distribution for the individuals with different flower colours. The white flower plants, although in a small proportion, were well scattered among the red-purple ones. It was also found that there were no perceptible differences in vigour between the individuals with red-purple and white flowers (Table 29). Both kinds of individuals carried 4−7 foliage leaves and there were no significant differences in the height of the above-ground part as measured in the field at random on May 25, 1982 ($P>0.10$). Significant differences were found neither in the mean number of the ripe seeds per capsule nor in the seed weights between capsules ($P>0.10$). The laboratory germination test showed that the germination percentage was 71.4 for the seeds collected from white flower plants and 69.0 for those from red-purple ones, after the seeds had received a three-month chilling treatment and then transferred to a germination chamber at a temperature regime of 10−20°C.

12 General discussion and conclusions

The wet meadows within the Kungsängen Nature Reserve are of great value from a nature conservation viewpoint. They are the principle site of *Fritillaria meleagris* in Sweden and one of the most important known in Europe. Nowadays such wet meadows have become rare due to human activities. A detailed knowledge of the species' life cycle and population biology together with knowledge of its environmental and biotic conditions helps to understand the ecology of the species and how to manage it (Harper 1982). The present study was undertaken to obtain detailed information on the ecology of *Fritillaria meleagris* both at the plant community level of the vegetation in which the species occurs and the population level of the species itself. Such knowledge may also provide a basis for optimal management of the nature reserve.

12.1 Vegetation study

The vegetation within the Kungsängen Nature Reserve was described by a combination of classification and ordination methods. Numerical classification, such as the TABORD program, provides an objective technique in summarizing the vegetation data and presenting a useful scheme of clusters on the basis of the species composition. The ordination technique enables an effective visual inspection of the spatial sequences and the variations in vegetation. The evident mutual benefits of classification and ordination for phytosociological studies have been illustrated with the application of both approaches in the present study of vegetation and that these two approaches generally agree in their arrangement of the main plant community types.

The vegetation study suggested that the major environmental variable is formed by the topographical moisture conditions, operating as a moisture gradient.

Five main plant community types were distinguished. *Fritillaria meleagris* occurs optimally in the *Arrhenatherum pubescens—Alopecurus pratensis* community.

12.2 Ground water and soil moisture

The results of ground water and soil moisture measurements show that the differentiation of vegetation in the study area is related to the differences in maximum, intermediate and minimum water levels, the duration of inundation and the topsoil moisture content. These strongly correlated differences can again be related to the topography in the study area.

Niemann (1973) has suggested that in order to reveal the relations between vegetation and hydrology, a number of conditions should be fulfilled (see also Grootjans & ten Klooster 1980):

The stands studied must be clearly characterized, so a large data set of relevés and accompanying ground water observations must be available. Classification at the level of subassociation is recommended.

All observations of the ground water table must be included in the analysis of the ground water regime. In vegetation with major ground water influences, the yearly course of the ground water level is considered as an appropriate parameter. However, extreme values (such as inundation and water depth) should also be taken into account.

The area under study must be situated in a climatologically and pedologically homogeneous region.

These conditions have been fulfilled in the present study. A large number of relevés have been used in the classification and the plant communities are characterized in detail (see chapter 2). A number of ground water observation sites are available for each of the plant communities. Some extreme values such as the peak flooding height and the water level above the soil surface have been included. The results of the soil analysis show that the substratum in the reserve area is fairly homogeneous, all stands being found on alluvial clay soils.

The analysis in this study leads to a rather detailed characterization of ground water regimes. It is concluded that in the Kungsängen Nature Reserve fairly good relations have been found between the plant communities and the ground water regime, including seasonal flooding. However, flooding of course varied greatly between years, probably more than the ground water regime. The positional effects of ground water are thus expressed in the vegetational zonation. The duration of flooding is less important, except for plant community D with *Carex acuta* where possibly other species are excluded from dominance by the high or long-lasting inundation in some years.

Apart from positional effects in the gradient of the ground water regime, other factors could also be important in the differentiation of the vegetation composition. From the observations during three years, it has been found that the local abundance of *Carex caespitosa* in some sites could be due to less cutting, since the tussocks of this species made mowing difficult. On the other hand, *Carex disticha*, which is a low-growing and not a tussock-forming sedge, was cut each year. Here conditional relationships may be involved. Some mowing experiments have demonstrated that mowing leads to a change in the structure of the vegetation (Bakker 1976).

12.3 Soil properties

The qualities of the humus layer within all sampling sites reveal the mull-like properties described by Sjörs for grassland and other open sites (1961). Compared with soil conditions reported for the park meadows in southern Dalecarlia by Sjörs (1954), for the wet meadows in Scania by Andersson (1970a) and for the deciduous woodland in Andersby by Hytteborn (1975), the soils in the Kungsängen Nature Reserve are rather fertile in most respects, including nutrient contents and minerals.

Both the degree of neutralization and the quantities of metallic cations, especially of calcium, are high. The nitrogen and potassium values in the humus layer in the study area are of roughly the same order as those registered by Andersson in three wet meadow communities and those presented by Hytteborn in a deciduous woodland. The amount of phosphorus is fairly high in the study area.

The results show that soils in the Kungsängen Nature Reserve are rather homogeneous with regard to humus content and specific gravity. The bulk density and porosity of the soil are largely determined by the humus content. There is no correlation between the humus content and the soil-water regime.

The most obvious feature in the humus layer is the slight increase in the acid-base status towards more basic conditions from the relatively dry sites to the wet sites, which is shown both by pH, exchangeable metallic cations (especially Ca^{2+}), and the degree of neutralization. The increase in pH values towards wetness is presumably due to the high calcium content of the ground water. However, the humus layers of all plant communities give a range of pH_{water} 5.9–7.6 and therefore they all represent circum-neutral conditions, the pH not being likely to control their floristic composition very strongly.

The analyses of N-total, P-AL and P-HCl show no clear pattern in relation to the soil-water regime in the study area. However, the N-total is only a parameter in terms of capacity. Nitrate and ammonium available to plants result from mineralization, i.e. nitrification and ammonification. It has been demonstrated by Williams (1968) that the amount and the rate of nitrification are controlled by the soil-water conditions. There is a decrease in the nitrification capacity with increase of wetness. The amount of available phosphorus is also controlled by soil-water conditions. The quantities in wet meadows decrease from relatively dry sites towards wet sites, but the amount of available phosphorus present in soil also varied considerably during the year (Williams 1968). However, this trend has not become clear in this investigation, although there are no significant differences in P-total between the sampling sites. Other factors such as the rate by which P is used by plants and the management practice may also influence the amount of available phosphorus in soil.

An accumulation of nutrients occurs in the upper layer of the soil due to high content of organic colloids. The soil structure in plant community B is apparently influenced by earthworms, which are probably responsible for most of the mixing of the soil material. This can be seen from the vertical distribution of the humus content and nutrients in that community.

There is no obvious correlation between the results of ordination and the nutrient conditions for these plant communities. Nevertheless, some differences between the plant communities can be noted. The nutrient conditions in the study area may be, to some extent, a factor determining the floristic composition and the production. The samples from plant community A show higher qualities than the others, especially the N-total, exchangeable K^+, P-AL and P-HCl in the humus layer. Since this community is on the borders of the reserve and close to cultivated fields, it may be influenced by the agricultural activities.

In the wet sites with plant communities D and E, the values of P-AL and P-HCl are fairly high. The management practice may be an important factor for the explanation of this, as these two plant communities are less frequently, or probably never, cut.

12.4 Production

The differences in the peak standing crop between the plant communities under study can partly be related to their different soil-water regimes and their nutrient status in the study area. The sites of plant community A had a high nutrient status with respect to N-total, P-AL and K^+, as revealed by the soil analyses (see chapter 4). The tall-growing graminid species such as *Poa pratensis*, *Alopecurus pratensis* and *Agropyron repens* also indicated a high nutrient status of the soil (Ellenberg 1974). The sites of plant community B had a relatively lower nutrient status than those of plant community A. The nutrient status in the sites of plant community C was the lowest among these plant communities and the ground water table was frequently close to the soil surface. In general, the variation in the peak standing crop could be related to the variation in the different soil-water regimes; the peak standing crop decreased from the relatively dry sites with high nutrient status towards the wetter sites with lower nutrient status, that is, from plant community A to plant community C. The relatively high peak standing crop in plant community D was probably due to its relatively high nutrient status, although it was situated in the wettest sites. The wettest sites, according to observations in the field, were almost never cut. Mowing can affect nutrient levels of the substrate (Grootjans 1980). The results of soil analyses revealed that the sites of plant community D had a rather good nutrient status, especially as regards phosphorus.

Compared with results from other investigations of above-ground production of meadows in other parts of Sweden, the Kungsängen wet meadows have a relatively high production because of their rather favourable water and nutrient conditions in general. Nilsson gives a value range of 150–400 g/m^2 in his investigation of the meadow production in Småland (Andersson 1966). Sjörs (1954) reports that production values from wet meadows in Dalarna vary between 115–490 g/m^2, while Andersson (1970b) gives values between 331–970 g/m^2 from an investigation of low growing—tall growing herbid and sedge wet meadows in the south of Sweden. Although there must be some methodological differences between these investigations, these results are still useful for comparison.

12.5 The development of vegetation over 40 years

The development of the vegetation within the Kungsängen Nature Reserve was investigated on the basis of the semi-permanent plots, which were established by Sandberg in 1940 and could be traced very accurately. The numerical classification of the site-times × species data set at the study area has revealed changes of vegetation types over the 41 years as well as species responsible for such changes. The ordination method, in which the positions of the permanent plots observed at different times are connected on the floristic space, has detected the spatial pattern of vegetation types and their changes in time. A clear partitioning of the trends of vegetation development in the 28 permanent plots has been recognized. This demonstrates the usefulness of multivariate methods in studies regarding temporal changes in vegetation (Austin 1977, van der Maarel 1980).

The application of Ellenberg's characteristic indicator value (*CIV*), which is based on the entire vegetation data set and weighted by species cover, confirms that the main trends of the vegetation development recognized in the classification and ordination have been effectively interpreted in terms of variations in soil moisture conditions and nutrient status.

On the basis of the analysis of the relationship between the vegetation variation extracted by the numerical methods and the environmental variations reflected by the *CIV*, it is reasonable to assume that changes of vegetation over 41 years in the study area can be related to changes in the ground water regime as well as the management practice of hay-making without fertilization.

There is a strong relationship between the spatial variation and the temporal development of vegetation; the differences in the trends of temporal development of vegetation appear to be related to the relative height of the sites in the study area. The effects of the alteration of ground water regime on the vegetation apparently differ at the different sites.

In the low-situated sites, especially on the edges of the depression (plots 16–19 and 24–26), a drastic change towards wetter vegetation types has been observed. The vegetation there is more sensitive to the alteration of the ground water regime and the hydrological condition has a profound influence upon its development.

In the relatively high-situated sites the effect of the alteration of the ground water regime is less pronounced. A development towards a vegetation type with diminishing nutrient availability has been indicated by the decreasing of the *CIV*'s for nitrogen and phosphorus status. The management practice may play an important role in these sites. Due to hay-making without fertilization, a diminishing availability of nutrients from the soil can be expected (van Duuren et al. 1981).

In the sites on the border of the reserve area (plots 1–4 and 28) where the drainage and nutrient conditions are relatively good, the vegetation has remained rather stable over the 41 years. This is also reflected by the fairly constant *CIV*'s for soil moisture, nitrogen and phosphorus status over time.

Consequently, the results described and reviewed here suggest that primarily soil moisture conditions (predominantly governed by the ground water regime in the study area) and availability of nutrients from the soil are the most important factors controlling the differentiation and development of the vegetation at the study area.

The system of ecological indicators is derived from the distribution of species in Central Europe. It has, however, proved useful in the south of Sweden (Persson 1980, 1981). It proved equally useful in this study as an aid when environmental data for 1940 were unknown. In conclusion, Ellenberg's indicator values can be used outside Central Europe in certain circumstances provided the ecological behaviours of most species are already known.

The study also confirms the viewpoint (Grootjans & ten Klooster 1980) that although many nature reserves are under stable and proper management, the vegetation in the reserves may be influenced by so-called land improvements in surrounding areas, in this case by changes in the water regime.

12.6 Demography

The variation in density of the fritillary within the study area appears to depend on differences in habitat conditions; soil-water conditions are probably the most important ones. This is reflected in the distribution pattern and age-state structure of the population along the hydrotopographical gradient. The distribution of the fritillary within the reserve area is limited both by too dry and too wet habitat conditions. In the relatively low sites with frequently high ground water tables, a considerable oscillation in the number of individuals and a large proportion of juveniles may be a result of limitations imposed by waterlogging and accompanying anaerobic conditions in the soil. A possible mechanism is that long spells of waterlogging will cause many individuals not to develop aboveground parts in some years and reduce their growth rate, thereby reducing their size (bulb size and number of leaves) and keeping them in the juvenile state.

The continual flux between the various age-states of the fritillary population seems to depend on the annual renewal of bulbs and the accompanying changes in amount of food reserve (bulb size) of a plant. A similar phenomenon has been reported by Barkham (1980a) for the bulbous perennial *Narcissus pseudonarcissus*. The present study indicates that the performance of individual plants is quite diverse; an individual may change between juvenile, subadult, vegetative adult and reproductive adult age-states over time as a consequence of the succession of the bulbs. The plant behaviour for the population as a whole shows that the growth rate is slow and, in general, it takes rather a long time for a seed or vegetative offspring to develop into a reproductive adult.

Irregularity of flowering has been reported for many polycarpic perennials (Tamm 1972a, b, Hawthorn & Cavers 1976, Harper 1977, Barkham 1980b). This character has also been observed in the fritillary. Many possible factors have been supposed to account for the irregularity of flowering but little is known. Observations in this study suggest that the variation of flowering individuals from year to year does not seem to be regulated by one single factor and there is evidence that the reproduction behaviour in one year seems to be influenced by the behaviour in the previous year; many of the reproductive adults become vegetative in the next year (65.4% in 1982 and 46.2% in 1983). Flowering frequency in the wet sites is low and the soil-water condition has, at least, an indirect effect as it reduces the growth rate of a plant. In bulbs of many geophytes, the size (amount of food reserve) seems to be the most important factor in the control of flower formation (Barkham 1980b).

One striking feature of the fritillary population biology that emerges from this study is the mobility of food reserves from a previous year's bulb to the next year's one, the plant thus being able to remain underground without appearing for some years.

A complete life table of the population cannot be achieved until more information about the birth rate, death rate and longevity of plants is obtained, which are the critical elements for a balance of the life cycle of a species (Sarukhan & Harper 1973). Some general conclusions can be drawn from this study. Observations over the 3-year period show no big changes in net population size when compared to the number of plants which were recorded and subsequently lost. Recruitment from seedlings or vegetative offspring does occur but is apparently a slow process. The survival of plants is primarily a function of plant size; the larger the plant (as measured by bulb size and number of leaves), the greater its survival probability. Similar results were obtained by Barkham (1980a) with *Narcissus* and Solbrig et al. (1980) with *Viola sororia*. This is reflected by the relatively high rate of absence and the relatively low proportion of juvenile and subadult states within the population. Kawano et al. (1982) attributed the high mortality in the juvenile stage of a bulbous perennial *Erythronium japonicum* to its shallow root system, thus being exposed to drastic heat and water stress or animal attack on the soil surface. The larger the plant grows, the deeper its root system and bulb become, thus providing more protection. This seems to apply to the fritillary too. The relatively high proportion of adult state within the population and the low rate of absence (both among vegetative and reproductive adults), suggest that the adults of the fritillary may attain a considerable age.

The relatively long life span, long juvenile period and low adult mortality rate of the fritillary are common traits among many perennial herbs. As Tamm (1972b) and Barkham (1980b) supposed, sudden changes in the population of a perennial herb like the fritillary are not likely, since there is a lag in the population response of a long-lived perennial plant to a significant environmental event and population changes are most likely caused by external factors (including competition from neighbouring species).

12.7 Life cycle and dry matter allocation

This study has examined various aspects of the life cycle strategy and reproductive strategy in the sense of Harper & Ogden (1970) for the field population of the fritillary. The most striking feature of this species is the clear division in time of growth and reproduction. This is shown in the life cycle pattern (phenology) in relation to seasonal environmental regimes, in the program of dry matter allocation and in the reproductive behaviour. These features can be regarded as a characteristic perennation strategy (Harper & Ogden op. cit.), which is achieved by the food reserve in the bulbs. The bulb of the fritillary contains the energy required for survival of the dormant phase and provides the food reserve for an early and rapid growth in spring.

The bulbs and roots of the fritillary are restricted to the upper soil horizon (usually 0–10 cm). Soil conditions are particularly important in this plant because the plant is entirely underground for the greater part of the year. The roots of the fritillary are adventitious and the proportion of the dry matter allocated to the roots is very low.

The fritillary requires quite a long period of vegetative growth before reaching its reproductive stage. The vegetative stage is well represented by the age-states of seedling, juvenile, subadult and vegetative adult within the population. During its vegetative stage the plant allocates a considerable amount of dry matter into the food reserve organ (bulb) and the plant gradually increases its size and biomass, but no reproduction occurs. According to the annual increase rate, it probably needs at least five years for a seed to develop into a reproductive adult under field conditions.

The change from vegetative to reproductive stages in the fritillary appears to be largely determined by the size of the plant. Harper (1977) has pointed out that among many perennials the period of vegetative growth seems to be related to the time needed to achieve some critical size necessary for reproduction. It has been confirmed by the results of this study that the reproductive adults of the fritillary have a bulb ranging from 12 to 20 mm in diameter and have at least four foliage leaves. The demographic observations (see chapter 8) show that the fritillary is polycarpic and many of the reproductive adults did not flower in the season following the one in which their reproductive activity took place. The economy of dry matter allocation shows that a considerable amount of the assimilates is allocated into sexual reproduction in the reproductive adults and subsequently their bulb size and biomass decrease at the end of the growth period. Thus, it can be assumed that the reproductive behaviour depends largely upon the accumulation of the food reserves in the bulb.

However, the investigation also shows that the vegetative adults of the fritillary have a bulb ranging from 10–17 mm in diameter and have the same number of foliage leaves as the reproductive adults. The switch mechanism from the vegetative to the reproductive forms and vice versa as well as the reproduction potential still need to be investigated. A long-term study of the exact growth process and chronology of the vegetative and reproductive plants may provide valuable information.

Although vegetative propagation by set-off bulblet formation occurs in the reproductive adults, the sexual reproduction seems to be much more important to the success of this species. Vegetative propagation is rather limited not only in terms of frequency but also in terms of the amount of dry matter allocation. The small set-off bulblets (1–2 mm in size) are close to the parent plants and located to rather deep layers (5–8 cm) under the soil surface. The respiratory burden for their aerial productive organ (foliage leaf) to reach up to the soil surface might be high and the competition with the parent plants for nutrients and water is probably severe. The lack of close clusters of individuals, as observed in the field (see also Fig. 38), seems to support this assumption.

The overall pattern of the life cycle strategy and the reproduction strategy of the fritillary is similar to those of many geophytes reported by Ogden (1974), Kawano & Nagai (1975), Ernst (1979) and Kawano et al. (1982). This perennation strategy is perhaps characteristic of organisms growing in an environment of a high predictability and stability in its abiotic as well as biotic factors (Zeide 1978).

12.8 Seed biology

The fritillary is a polycarpic perennial and the variation in seed production between years as observed in the field is strongly correlated with the changes in the number of flowering individuals. The variation in seed production is also, to some extent, related to the activities of animals. The fritillary is entomophilous and the proportion of capsules with seeds depends on the pollinating insect activity, which in turn depends on weather conditions during the flowering season. Damage caused by animals is also considerable in the field. Trist (1981) observed that damage to the fritillary flowers at all stages of growth by birds and small mammals such as pigeons, pheasants, rabbits and hares could be a problem in some years.

The variation in the mean number of seeds per capsule and the mean weight of ripe seeds between years are related to the management practice. An earlier hay-making date could prevent capsules from fully maturing and both the mean number of ripe seeds per capsule and the mean weight of ripe seeds would decrease while the mean number of unripe seeds per capsule would increase. From the field observations, the mean number of seeds per capsule and the mean weight of ripe seeds would remain relatively constant if the hay-making could be postponed to July, which would also allow more seeds to enter into the soil seed bank.

Numerous agents profoundly affect the number of seeds that can reach the soil. Primarily the variation in seed production between years and the hay-making management control the size of the seed bank in the soil after seed set. Once seeds have entered the seed bank, rodents and pathogens may become important in reducing the seed population as the relatively large seeds of the fritillary on the soil surface may be subject to a high rate of predation by small rodents. However, further studies are needed to confirm this assumption. After predation, fungal attack and spring germination in the field, the seed population in the soil is almost depleted by the time newly produced seeds are added to the seed bank, and there is almost no accumulation of viable seeds produced in different years in the soil.

Harper (1957) has distinguished three kinds of dormancy: innate, induced and enforced ones. Innate dormancy is caused by endogenous factors such as immaturity of embryo or the presence of inhibitors which can be broken by a period of after-ripening or by some seasonal stimulus such as a thermo-period. Induced dormancy develops when an adverse factor such as drought or high temperature acts upon seeds and produces a condition of inability to germinate that remains even after the causal factor has ceased to act. Enforced dormancy is imposed by an exogenous factor such as cold and lasts only as long as the factor acts upon the seeds.

These three kinds of dormancy mechanism are involved in the timing of natural germination of the fritillary. The results of laboratory experiments show that the fritillary seeds have a dormancy breaking requirement of a period of three months at low temperature and in moist conditions (chilling or stratification). The optimal temperature for germination (tested in laboratory) is about 12°C at a constant temperature. Fluctuating temperatures have a stimulatory effect on seed germination of the fritillary, which has also been reported for seeds of several other species (Popay & Roberts 1970, Thompson 1977). However, at high temperatures (>20°C) a large proportion of the fritillary seeds can produce an induced dormancy, which can only be removed after re-chilling treatment.

Grime et al. (1981) pointed out that the most satisfactory analysis is that in which the laboratory results are complemented by studies of the production and fate of seeds under field conditions. In the field, the germinability of the fritillary seeds changes with time and appears to be related to seasonal environmental changes, especially in temperature and soil moisture. The results of the experiments in which seeds were stored under field conditions, show that after the seeds entered the seed bank they spent several months at low temperature (below 10°C) and in moist conditions and by December the innate dormancy was removed. Then the seeds in the field entered into an enforced dormancy due to very low temperature (below 0°C) during the winter. As soon as the maximum soil surface temperature reached above 5°C in late March, many of the seeds began to germinate. The disappearance of germinability for a small proportion of seeds left in the soil might have been due to the induction of dormancy by high temperature or desiccation, but the amount and the chance for them to survive to next spring was very low under field conditions. The combination of these dormancy mechanisms is of great importance in causing the spring flush of germination in the field, thus preventing premature germination in autumn or winter.

Thompson & Grime (1979) have discussed the distinction between a transient seed bank and a persistent seed bank; a transient seed bank is defined as one without any accumulation of seeds produced in different years (the seed bank is replaced annually), while a persistent seed bank is defined as one with an accumulation of seeds produced in different years (some component seeds can keep their viable state for more than one year).

A classification has been proposed by Thompson & Grime (1979) on the basis of a study of seed banks of many herbaceous species in a wide range of habitats. The characteristics of seed bank and seed germination behaviour of the fritillary are mostly in agreement with those described for seed bank type II: species with transient seed banks present during the winter; the seeds are relatively large and usually remain on the soil surface, they have a pattern of innate and enforced dormancy followed by a flush germination in early spring and the seeds are able to germinate in darkness and at low temperatures. Although a small proportion of the fritillary seeds may keep their viable state, due to induced dormancy, for more than one year under field conditions, it is negligible with regard to the annual production of seeds and the size of the seed bank. Thus, it seems reasonable to suggest that the fritillary belongs to the group of species with seed bank type II. Such a pattern of seed germination behaviour appears to be of great advantage for this species as the growth conditions in autumn and winter are severe and the most favourable period for seedling establishment and growth occurs in spring. However, the risk of delaying germination until next spring can only be afforded in a predictable and stable environment (Thompson & Grime 1979).

Seed germination and seedling establishment in the field frequently have little relationship to the germination capacity of the seed samples in the laboratory tests (Harper et al. 1965). From the results of the field germination experiments, it is quite obvious that the number of seeds germinated and seedlings established is determined not only by the availability of seeds in the soil, but also by the availability of a "safe site" (Harper et al. 1961). Gaps in perennial vegetation and soil moisture conditions are most important for the seed germination and seedling establishment of the fritillary in the field. Only a tiny proportion of seeds present in the soil could germinate to give seedlings. High mortality occurs between the fresh seed production which entered into the soil seed bank and the seedling establishment under the field conditions. Thus, it seems correct to state that the recruitment, which is one of the crucial factors contributing to the regulation of the fritillary population in the field, is not only dependent on the seed production but is also regulated by the frequency of "safe sites".

12.9 Changes in the population distribution over 40 years

The changes in the distribution of the fritillary population were detected by comparing the results of the observations made by Sernander in 1938 and those made during this study period (1981–83). Although the observations in the six 10×10 m plots along a transect were made on the flowering individuals of the fritillary only and the vegetative individuals were not taken into account, the results of this study have clearly shown that the alteration of ground water regime due to the regulation of Lake Mälaren has caused a significant change in the distribution of the fritillary population within the reserve area over 40 years. The raising of the ground water table has forced the fritillary population to retreat from the low part in the study area and has pushed them up to the relatively high part. It seems quite obvious that the soil-water conditions are important in determining the distribution of the fritillary population in the Kungsängen Nature Reserve. A transplantation experiment has been designed to test the hypothesis relating to the effects of soil-water conditions on the performance of the fritillary individuals, which will be treated in a separate paper.

The fluctuation in the number of flowers between years was considerable in all the plots. There was no obvious correlation with this phenomenon and some weather variables as reported by Barkham (1980b) for *Narcissus*, in which the total number of flowers was significantly correlated with weather conditions in the previous year. The results of this study are consistent with those of Wells (1967), who found that neither a single nor several weather variables together, such as temperature, rainfall and hours of sunshine, controlled the reproductive behaviour of *Spiranthes spiralis*. As he suggested, if it was so, some uniformity in the behaviour of plants in any one year would be expected as climatic conditions had been the same for all members of the population. There was no such uniformity in the fluctuations of flower number between the observation plots, as in any one year the number of flowers rose in some plots and fell in others. The results of the demography and dry matter allocation investigation (chapters 8 and 9) in which the fate and the economy of dry matter allocation of individuals were followed, have revealed that the reproductive behaviour of the fritillary is strongly influenced by the behaviour of the plant in the previous year.

However, the differences in climatic conditions cannot be entirely dismissed as having no influence upon flowering, as weather conditions could have an indirect effect on the assimilation rate and the flower formation of the fritillary is, to a large extent, dependent on the size of the plant (bulb size, weight and number of foliage leaves).

The proportions of red-purple, pink and white flowers have remained remarkably stable for the fritillary population in the Kungsängen Nature Reserve over 40 years. Having the natural markers of flower colour, the population of the fritillary in the study area could be a useful subject when studying the effects of the selection and genetic drift (Ford 1975), which may explain the colour proportion observed in the field.

However, there are too many possible mechanisms which are still unknown, The exact mode of inheritance of flower colour in the fritillary is, so far, not known because of the long period of prereproduction for this species. As the flower of the fritillary is protogynous and self-incompatible and the plants are entomophilous, the activity of insect pollinators doubtless also plays an important role in the mating system of this species.

Although it has been shown from this study that there were no obvious differences in the growth performance and the reproductive effort or in the distribution pattern between the plants with red-purple and white flowers, the analysis has been on a much more limited scale. Clearly, this aspect deserves more detailed investigations. The selective importance of survival during the establishment of seedling and the juvenile phase has been stressed as a critical process to explain the number and distribution of a species (Harper & White 1974, Grubb 1977). The life span of already established individuals, the reproduction behaviour of adult individuals and the size of an effective population are also of importance in determining the frequency of plants (Ford 1975, Harper 1977). These kinds of information for a perennial plant such as the fritillary are difficult to obtain in a short time. A long-term census, following specific individuals, is needed to achieve conclusive evidence of selection or genetic drift.

Concluding remarks

Harper (1981) points out that "the rarity or abundance of a species depends on an interaction between characteristics of the habitable sites and characteristics of the species themselves". The results discussed here indicate that the restricted and local distribution of *Fritillaria meleagris* in low-lying hay meadows seems to result in part from its specific demand of habitable sites, i.e. its niche (Hutchinson 1965). The Kungsängen Nature Reserve, which is under a long-term stable hay-making management, provides such a habitable site for the local abundance of the fritillary. Mowing is one of the factors responsible for its existence. In this case a cut in late June or early July is preferable since it allows *Fritillaria meleagris* to set seed and prevents it from dying out in a crop that is too dense. Although from an agricultural viewpoint mowing should occur earlier in order to get a higher yield, the nature conservation viewpoint leading to later mowing should prevail for the benefit of this rare and popular species.

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