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advised on phytosociological problems, Dr O. WILDI (Swiss Federal Institute of Forestry Research SFIFR) helped with the mathematical analysis and Dr H. FUNK (Geological Institute ETH) with geological nomenclature. The advice of Ms C. BROWN, who made many valuable suggestions on style and use of the English language is greatly appreciated. I have had useful discussions on various points with PD Dr A. GIGON. Mr E. SCHäFFER assisted in the field, and Ms A. HONEGGER typed the manuscript; my sincere thanks are addressed to all these persons as well as to numerous colleagues from the Geobotanical Institute who occasionally helped throughout the course of the work.
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2. Description of the study areas

The four study areas are localized in northern Switzerland, within the Jurassic mountains belonging to the community of Merishausen 7.5 km NNW of Schaffhausen (National Grid Reference 688 500 / 291 000, Fig. 1). The substratum consists of Upper Jurassic limestone. The soils are of a mull-like rendzina type; the content of calcium carbonate within the uppermost 5 cm of soil ranging from 29 to 60 per cent, the corresponding pH values vary from 7.6 to 8.0. Climatic conditions are diagrammatically presented in Fig. 2.

The vegetation within all study areas corresponds to grassland of the *Mesobrometum* type. In the region of Schaffhausen this meadow type is usually cut once a year in mid June and very rarely or not at all fertilized. Prior to experimental management, two study areas had been used for hay-making (study areas 1 and 2), two others having been abandoned for ten and twenty years, respectively (study areas 3 and 4). One of the areas used until experimental management was started was drier and poorer in nutrients (study area 1) than the other (study area 2).

The phytosociological classification of the study areas offers some problems as far as nomenclature is concerned. According to ZOLLER (1954), who studied the dry grasslands in this region, our study area 1 should be considered as a *Medicago falcatae-Mesobrometum*, whereas study area 2 should correspond to a *Dauco-Salvio-Mesobrometum*; the study areas 3 and 4 abandoned for ten and 20 years respectively would represent the *Seselio libanotidis-Mesobrometum*.

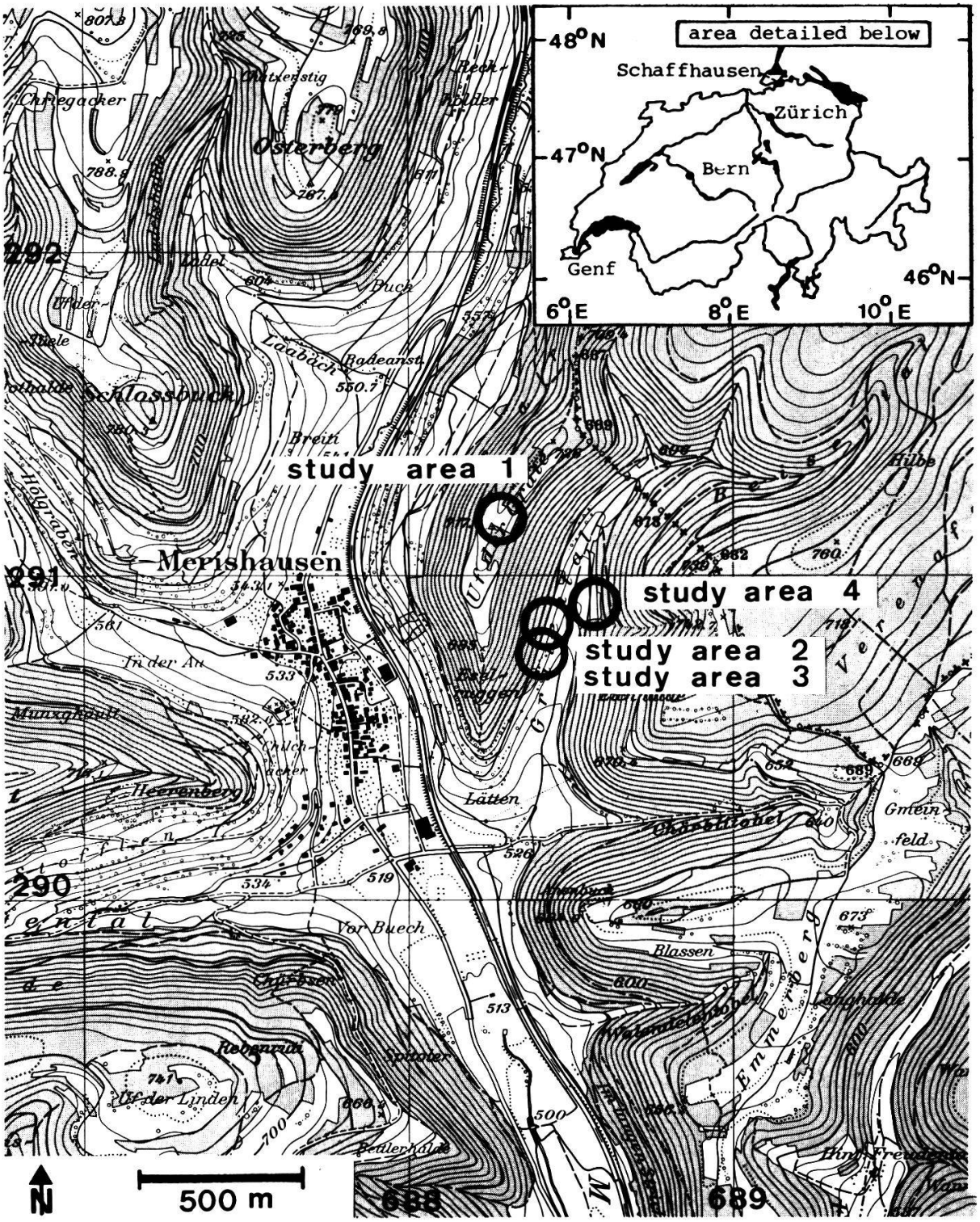

Fig. 1. Location of the four study areas investigated and (inset) their relationship to other places in Switzerland. Scale 1:25000. (Reproduced with permission of the Swiss Federal Office of Topography from May 6, 1981).

The nomenclature proposed by ZOLLER (1954) not being generally recognized, the classification of OBERDORFER (1957, 1978) was followed. According to this author, our study areas 1 and 2 correspond to a *Mesobrometum* Br.-Bl. 1925, the first area being a type with *Trisetum flavescens* and *Medicago falcata* whereas the second, having a soil richer and more humid, represents a type with *Trisetum flavescens* and *Centaurea jacea*. The study areas 3 and 4 correspond to successional stages towards a *Geranion sanguinei*, the former area representing a less advanced stage than the latter.

The floristic composition of the four study areas is shown in a frequency table based upon 18 relevés per area (Table 1); the resemblance of the 72 relevés considered is shown in Figs 3 and 4 representing scatter diagrams constructed by principal component analysis using a cross product matrix. Further characteristics of the four study areas are summarized in Table 2. The study areas will be referred to by their respective numbers in further parts of the present paper.

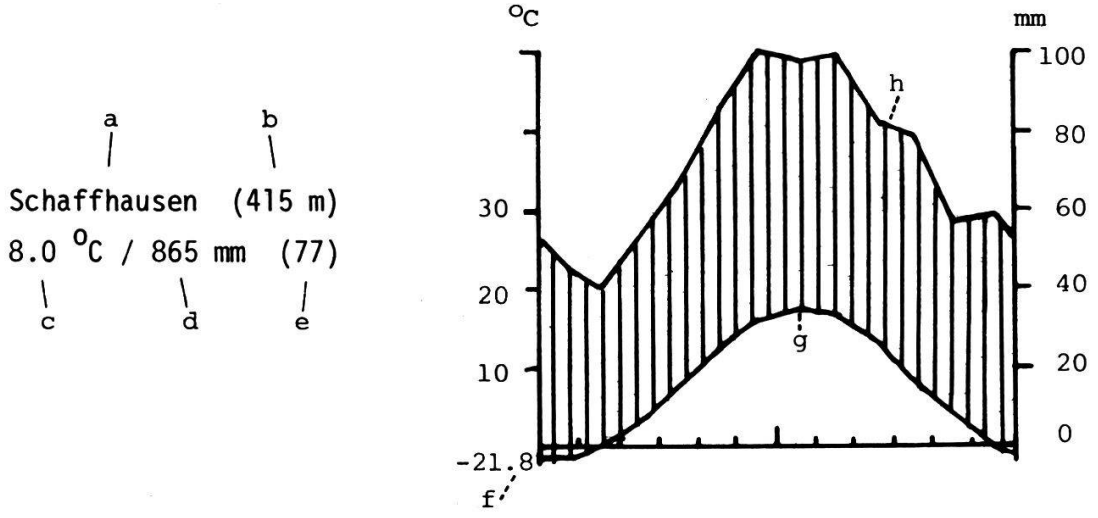

Fig. 2. Climatic diagram of Schaffhausen (from WALTER and LIETH 1960-1967).

a: station
b: hight above sea level
c: mean annual temperature (°C)
d: mean annual precipitation (mm)
e: duration of observations (years)
f: lowest temperature recorded (°C)
g: curve of mean monthly temperature
h: curve of mean monthly precipitation

Ordinate: one division = 10 °C or 20 mm rain
Abscissa: months (January-December)

Table 1. Frequency table representing the floristic composition of the four study areas based upon 18 relevés (50 m^2) per each area (*: value is less than 0.05, 'species value': see page 21).

	Study area 1	Study area 2	Study area 3	Study area 4
Total number of species (herbs/shrubs/cryptogames)	96 (79/3/14)	98 (88/3/7)	120 (103/9/8)	144 (111/21/12)
Mean number of species per 50 m^2 (range):	54.8 (48- 62)	54.1 (42- 62)	55.4 (42-68)	62.7 (52- 70)
- herbs	47.4 (43- 53)	51.3 (39- 59)	50.0 (36-62)	54.5 (43- 65)
- shrubs	0.8 (0- 2)	0.6 (0- 2)	2.0 (1- 4)	4.4 (1- 17)
- cryptogames	6.6 (5- 10)	2.2 (1- 5)	3.4 (2- 5)	3.8 (1- 6)
Mean cover-percentage (range)				
- herbs	98% (90-100)	84% (75- 95)	81% (50-95)	80% (60- 95)
- shrubs	<1% (0- <1)	<1% (0- <1)	2% (<1-10)	4% (<1- 20)
- cryptogames	42% (10- 90)	91% (70-100)	81% (50-95)	89% (70-100)

Species	frequency f. (%)	mean cover m.c. (%)	species value s.v.	frequency f. (%)	mean cover m.c. (%)	species value s.v.	frequency f. (%)	mean cover m.c. (%)	species value s.v.	frequency f. (%)	mean cover m.c. (%)	species value s.v.
Prunella grandiflora	95	1.5	1.4	-	-	-	-	-	-	-	-	-
Chrysohypnum chrysophyllum	72	6.2	4.5	6	0.2	*	6	0.1	*	6	0.1	*
Galium verum	72	1.0	0.7	-	-	-	-	-	-	-	-	-
Festuca pratensis	72	0.7	0.5	-	-	-	6	0.1	*	-	-	-
Centaurea scabiosa	44	0.4	0.2	-	-	-	6	0.1	*	-	-	-
Scleropodium purum	44	0.4	0.2	-	-	-	-	-	-	17	0.8	0.1
Anthoxanthum odoratum	39	0.4	0.2	-	-	-	-	-	-	-	-	-
Polygala comosa	33	0.3	0.1	-	-	-	-	-	-	-	-	-
Anacamptis pyramidalis	33	0.3	0.1	-	-	-	-	-	-	-	-	-
Cladonia cf. *rangiferina*	17	0.2	*	-	-	-	-	-	-	-	-	-

Trisetum flavescens	100	1.2	1.2	83	1.0	0.8	-	-	-	6	0.1	*
Trifolium campestre	67	0.7	0.4	100	1.5	1.5	-	-	-	-	-	-
Rhinanthus minor	100	1.3	1.3	39	0.4	0.2	-	-	-	-	-	-
Potentilla heptaphylla	95	1.1	1.1	22	0.2	0.1	6	0.1	*	-	-	-
Achillea millefolium	100	1.1	1.1	83	1.2	1.0	95	4.1	3.9	11	0.2	*
Carex verna	95	1.6	1.5	100	1.2	1.2	50	0.9	0.4	6	0.1	*
Centaurea jacea	39	0.4	0.2	100	7.7	7.7	67	0.7	0.5	6	0.1	*
Camptothecium lutescens	100	20.8	20.8	22	1.2	0.3	78	6.6	5.1	6	0.1	*
Euphorbia cyparissias	95	1.0	1.0	22	0.3	0.1	72	0.8	0.6	22	0.2	*
Inula conyza	-	-	-	6	0.1	*	44	0.4	0.2	-	-	-
Convulvulus arvensis	-	-	-	6	0.1	*	44	0.4	0.2	11	0.1	*
Koeleria cristata	-	-	-	-	-	-	39	0.4	0.2	-	-	-
Medicago sativa	-	-	-	6	0.1	*	27	0.3	0.1	6	6	*
Geranium sanguineum	-	-	-	-	-	-	22	0.4	0.1	-	-	-
Vicia sepium	-	-	-	89	1.0	0.9	95	1.0	1.0	17	0.2	*
Satureja vulgaris	-	-	-	67	0.7	0.4	100	9.7	9.7	17	0.3	0.1
Silene nutans	17	0.2	*	83	1.9	1.6	78	1.1	0.9	6	0.1	*
Sedum sexangulare	-	-	-	95	1.3	1.2	56	0.6	0.3	-	-	-
Pastinaca sativa	-	-	-	39	0.4	0.2	95	1.0	0.9	6	0.1	*
Silene vulgaris	11	0.1	*	33	0.4	0.1	67	0.8	0.5	6	0.1	*
Cerastium caespitosum	17	0.2	*	67	0.7	0.4	17	0.2	*	6	0.1	*
Thlaspi perfoliatum	-	-	-	17	0.2	*	56	0.6	0.3	-	-	-
Geranium pyrenaicum	-	-	-	39	0.4	0.2	33	0.3	0.1	-	-	-
Rumex acetosa	17	0.2	*	44	0.4	0.2	22	0.2	0.1	-	-	-
Trifolium repens	17	0.2	*	44	0.4	0.2	17	0.2	*	-	-	-
Heracleum sphondylium	-	-	-	33	0.3	0.1	17	0.2	*	6	0.1	*
Peltigera canina	6	0.1	*	50	0.5	0.3	-	-	-	-	-	-
Glechoma hederaceum	-	-	-	39	0.4	0.2	-	-	-	11	0.1	*
Mysotis arvensis	6	0.1	*	22	0.2	0.1	-	-	-	-	-	-
Thesium bavarum	-	-	-	17	0.2	*	11	0.1	*	83	1.2	1.0
Quercus petraea (seedlings)	-	-	-	28	0.3	0.1	-	-	-	50	0.5	0.3
Origanum vulgare	-	-	-	28	1.0	0.3	-	-	-	33	0.4	0.1

Table 1 (continued)

Species	Study area 1			Study area 2			Study area 3			Study area 4		
	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.
Scabiosa columbaria	95	1.1	1.0	83	1.0	0.8	11	0.1	*	100	1.3	1.3
Linum catharticum	100	1.6	1.6	39	0.4	0.2	6	0.1	*	61	0.7	0.4
Onobrychis arenaria	100	1.4	1.4	33	0.3	0.1	6	0.1	*	28	0.3	0.1
Fissidens taxifolius	95	3.2	3.0	-	-	-	-	-	-	17	0.2	*
Pinus silvestris (seedlings)	50	0.5	0.3	-	-	-	-	-	-	22	0.2	0.1
Carex flacca	95	2.8	2.6	-	-	-	28	0.4	0.1	100	2.1	2.1
Rhytidium rugosum	39	0.4	0.2	-	-	-	83	6.5	5.4	89	42.0	37.3
Aster amellus	95	1.0	0.9	-	-	-	11	0.1	*	95	4.7	4.5
Medicago falcata	100	1.6	1.6	-	-	-	22	0.4	0.1	17	0.2	*
Thuidium tamariscifolium	78	3.5	2.7	-	-	-	11	0.1	*	39	1.9	0.8
Gentiana ciliata	56	0.6	0.3	-	-	-	11	0.1	*	50	0.5	0.3
Leontodon hispidus	67	0.7	0.4	11	0.1	*	28	0.3	0.1	72	1.8	1.3
Trifolium medium	100	1.9	1.9	11	0.1	*	28	0.4	0.1	33	0.6	0.2
Ononis repens	95	10.3	9.8	28	0.3	0.1	33	0.5	0.2	83	1.7	1.4
Trifolium pratense	89	1.2	1.1	83	1.0	0.8	17	0.2	*	44	0.4	0.2
Chrysanthemum leucanthemum s.l.	100	1.8	1.8	100	1.7	1.7	39	0.4	0.2	39	0.4	0.2
Salvia pratensis	100	7.0	7.0	100	20.6	20.6	6.1	8.4	5.2	22	0.2	0.1
Plantago media	100	2.3	2.3	100	1.8	1.8	6.1	0.6	0.4	39	0.4	0.2
Primula veris s.l.	95	1.0	0.9	100	2.6	2.6	100	3.3	3.3	100	8.5	8.5
Buphthalmum salicifolium	56	0.6	0.3	100	1.4	1.4	100	5.0	5.0	100	11.4	11.4
Thymus froehlichianus	28	0.3	0.1	89	2.3	2.1	95	2.3	2.2	89	3.3	3.0
Thymus pulegioides	17	0.2	*	100	6.7	6.7	100	4.7	4.7	100	9.9	9.9
Lathyrus heterophyllus	17	0.2	*	67	0.8	0.5	100	4.1	4.1	100	1.2	1.2
Acer pseudoplatanus (seedlings)	17	0.2	*	56	0.6	0.3	61	0.6	0.4	61	0.6	0.4
Lathyrus pratensis	11	0.1	*	100	1.9	1.9	100	1.3	1.3	95	1.0	1.0
Daucus carota	6	0.1	*	100	2.0	2.0	95	1.5	1.4	39	0.4	0.2
Veronica chamaedrys	-	-	-	78	0.9	0.7	50	0.5	0.3	39	0.4	0.2
Fraxinus excelsior (seedlings)	-	-	-	67	0.7	0.4	33	0.3	0.1	22	0.2	0.2
Asperula cynanchica	-	-	-	56	0.6	0.3	78	1.0	0.8	72	1.1	0.8
Viola hirta	-	-	-	39	0.4	0.2	78	1.4	1.2	100	4.7	4.7

Solidago virga-aurea	-	-	-	22	0.2	0.1	33	0.3	0.1	95	1.0	1.0
Seseli libanotis	-	-	-	17	0.2	*	44	0.6	0.3	100	7.1	7.1
Campanula rapunculoides	-	-	-	17	0.2	*	83	1.0	0.8	28	0.3	0.1
Prunus spinosa	-	-	-	17	0.2	*	22	0.9	0.2	28	0.3	0.1
Galium pumilum	6	0.1	*	6	0.1	*	61	0.8	0.5	22	0.2	0.1
Fragaria vesca	-	-	-	-	-	-	78	4.2	3.2	100	2.1	2.1
Cornus sanguinea	-	-	-	-	-	-	39	1.1	0.4	56	2.8	1.5
Tragopogon minor	-	-	-	-	-	-	39	0.4	0.2	50	0.5	0.3
Aegopodium podagraria	-	-	-	-	-	-	33	4.4	1.5	17	0.2	*
Acer campestre	-	-	-	-	-	-	33	0.6	0.2	50	0.5	0.3
Prunus avium	-	-	-	-	-	-	33	0.3	0.1	39	0.4	0.2
Clematis vitalba	-	-	-	-	-	-	22	2.4	0.5	17	0.2	*
Carex ornithopoda	-	-	-	-	-	-	17	0.4	0.1	89	1.6	1.4
Anthericum ramosum	-	-	-	-	-	-	17	0.2	*	83	2.4	2.0
Euphorbia verrucosa	-	-	-	6	0.1	*	17	0.2	*	39	0.4	0.2
Carex montana	-	-	-	-	-	-	-	-	-	95	8.1	7.7
Aquilegia atrata	-	-	-	-	-	-	-	-	-	89	1.6	1.5
Polygala amarella	-	-	-	-	-	-	-	-	-	89	1.0	0.9
Carlina simplex	-	-	-	-	-	-	-	-	-	83	2.3	1.9
Gentiana germanica	-	-	-	-	-	-	-	-	-	83	1.3	1.1
Cephalanthera longifolia	-	-	-	-	-	-	-	-	-	78	0.8	0.6
Orobanche alsatica	-	-	-	-	-	-	6	0.1	*	61	0.6	0.4
Hylocomium splendens	-	-	-	-	-	-	-	-	-	50	10.8	5.4
Phyteuma orbiculare	-	-	-	-	-	-	-	-	-	50	0.6	0.3
Gymnadenia conopea	-	-	-	-	-	-	-	-	-	50	0.5	0.3
Melittis melissophyllum	-	-	-	-	-	-	6	0.1	*	44	0.4	0.2
Teucrium chamaedrys	-	-	-	11	0.1	*	6	0.1	*	39	0.8	0.3
Viburnum lantana	-	-	-	-	-	-	-	-	-	39	0.4	0.2
Rhytidiadelphus triquetrus	-	-	-	-	-	-	-	-	-	33	2.0	0.7
Agrimonia eupatoria	-	-	-	-	-	-	-	-	-	33	0.4	0.1
Carlina vulgaris	-	-	-	-	-	-	-	-	-	33	0.4	0.1
Chrysanthemum corymbosum	-	-	-	-	-	-	-	-	-	22	0.3	0.1
Sorbus aria	-	-	-	-	-	-	-	-	-	22	0.2	0.1
Thalictrum saxatile	-	-	-	-	-	-	-	-	-	17	0.3	0.1
Hepatica triloba	-	-	-	-	-	-	6	0.1	*	17	0.2	*
Hieracium murorum	-	-	-	-	-	-	-	-	-	17	0.2	*
Orchis pallens	-	-	-	-	-	-	-	-	-	17	0.2	*

Table 1 (continued)

Species	Study area 1			Study area 2			Study area 3			Study area 4		
	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.
Bromus erectus	100	55.5	55.5	100	35.6	35.6	100	15.4	15.4	100	15.1	15.1
Sanguisorba minor	100	1.0	1.0	100	2.3	2.3	100	3.0	3.0	95	1.7	1.6
Knautia arvensis	100	1.2	1.2	100	2.3	2.3	95	2.8	2.7	100	1.7	1.7
Medicago lupulina	100	1.2	1.2	100	1.0	1.0	83	0.8	0.7	100	1.1	1.1
Festuca ovina	100	1.1	1.1	100	21.5	21.5	83	4.9	4.1	95	3.2	3.0
Pimpinella saxifraga	72	0.7	0.7	100	2.0	2.0	100	1.0	1.0	100	1.1	1.1
Plantago lanceolata	100	1.6	1.6	95	1.5	1.4	89	0.9	0.8	83	0.9	0.7
Campanula rotundifolia	89	1.0	0.9	100	1.0	1.0	95	1.4	1.3	83	0.8	0.7
Lotus corniculatus	78	0.8	0.6	100	1.6	1.6	95	1.0	1.0	89	1.3	1.2
Thuidium abietinum	83	4.0	3.3	100	93.3	93.3	100	56.2	56.2	78	16.0	12.4
Galium album	61	0.7	0.4	100	5.6	5.6	100	7.4	7.4	89	1.3	1.2
Arrhenatherum elatius	95	1.0	0.9	100	8.5	8.5	100	12.6	12.6	50	0.7	0.3
Picris hieracioides	95	1.7	1.6	100	2.9	2.9	89	0.9	0.8	61	1.0	0.6
Briza media	100	1.2	1.2	83	0.9	0.7	67	0.7	0.4	95	1.0	1.0
Brachypodium pinnatum	100	4.1	4.1	67	0.7	0.4	89	1.8	1.6	100	9.4	9.4
Hippocrepis comosa	100	1.1	1.1	95	1.2	1.2	33	0.4	0.1	100	3.9	3.9
Anthyllis vulgaris s.l.	100	1.6	1.6	72	0.8	0.6	67	1.7	1.2	95	2.6	2.5
Dactylis glomerata	95	1.0	0.9	100	1.1	1.1	78	0.8	0.6	56	0.6	0.3
Poa angustifolia	50	0.5	0.3	100	1.9	1.9	100	2.5	2.5	72	1.1	0.8
Ranunculus bulbosus	95	1.0	0.9	100	1.0	1.0	39	0.4	0.2	89	0.9	0.8
Hieracium pilosella	50	0.5	0.3	78	0.8	0.7	89	1.1	1.0	89	0.9	0.8
Arabis hirsuta	83	0.8	0.7	100	1.0	1.0	83	0.8	0.7	33	0.3	0.1
Helictotrichon pubescens	56	0.6	0.3	95	1.3	1.2	89	1.7	1.5	33	0.3	0.1
Hypericum perforatum	50	0.5	0.3	72	0.7	0.5	78	0.9	0.7	56	0.6	0.3
Taraxacum officinale s.l.	61	0.6	0.4	83	0.8	0.7	11	0.1	*	50	0.5	0.3
Vicia cracca	33	0.3	0.1	78	1.0	0.8	50	0.7	0.4	39	0.4	0.2
Weisia viridula	50	0.5	0.3	39	0.4	0.2	6	0.1	*	33	0.3	0.1
Entodon orthocarpus	33	1.2	0.4	17	0.7	0.1	56	3.4	1.9	17	0.2	*
Fagus silvatica	11	0.1	*	6	0.1	*	6	0.1	*	22	0.2	0.1
Festuca rubra	17	0.2	*	17	0.2	*	-	-	-	6	0.1	*
Allium sp.	-	-	-	11	0.1	*	22	0.2	0.1	6	0.1	*

Brachyhecium rutabulum	6	0.1	*	11	0.1	*	6	0.1	*	11	0.1	*
Potentilla reptans	-	-	-	-	-	-	11	0.1	*	22	0.2	0.1
Mnium rostratum	17	0.2	*	11	0.1	*	-	-	-	-	-	-
Rosa canina	-	-	-	-	-	-	17	0.2	*	6	0.1	*
Geum urbanum	-	-	-	-	-	-	17	0.2	*	6	0.1	*
Pirus malus	-	-	-	-	-	-	6	0.1	*	17	0.2	*
Tragopogon orientalis	17	0.2	*	-	-	-	-	-	-	6	0.1	*
Ligustrum vulgare	-	-	-	-	-	-	11	0.3	*	6	0.1	*
Ophrys insectifera	6	0.1	*	-	-	-	-	-	-	11	0.1	*

Species only found in one or two relevés

Study area 1: *Ctenidium molluscum (2x), Dianthus carthusianorum (2x), Agrostis stolonifera (1x), Bellis perennis (1x), Brachythecium laetum (1x), Campanula patula (1x), Euphrasia rostkoviana (1x), Nostoc communis (1x), Peucedanum cervaria (1x).*

Study area 2: *Campanula patula (1x), Festuca arundinacea (1x), Malva moschata (1x), Orobanche vulgaris (1x), Valerianella locusta (1x).*

Study area 3: *Sedum maximum (2x), Stachys recta (2x), Epipactis latifolia (1x), Erigeron acer (1x), Linaria vulgaris (1x), Melandrium diurnum (1x), Melilotus officinalis (1x), Senecio erucifolius (1x), Veronica hedericifolia (1x), Tortella tortuosa (1x).*

Study area 4: *Corylus avellana (2x), Crataegus oxyacantha (2x), Rhamnus cathartica (2x), Carex digitata (1x), Campanula persicifolia (1x), Cephalanthera damasonium (1x), Cephalanthera rubra (1x), Coronilla coronata (1x), Evonymus latifolius (1x), Festuca duriuscula (1x), Hedera helix (1x), Juniperus communis (1x), Lactuca perennis (1x), Lonicera alpigena (1x), Melampyrum pratense (1x), Platanthera bifolia (1x), Picea abies (1x).*

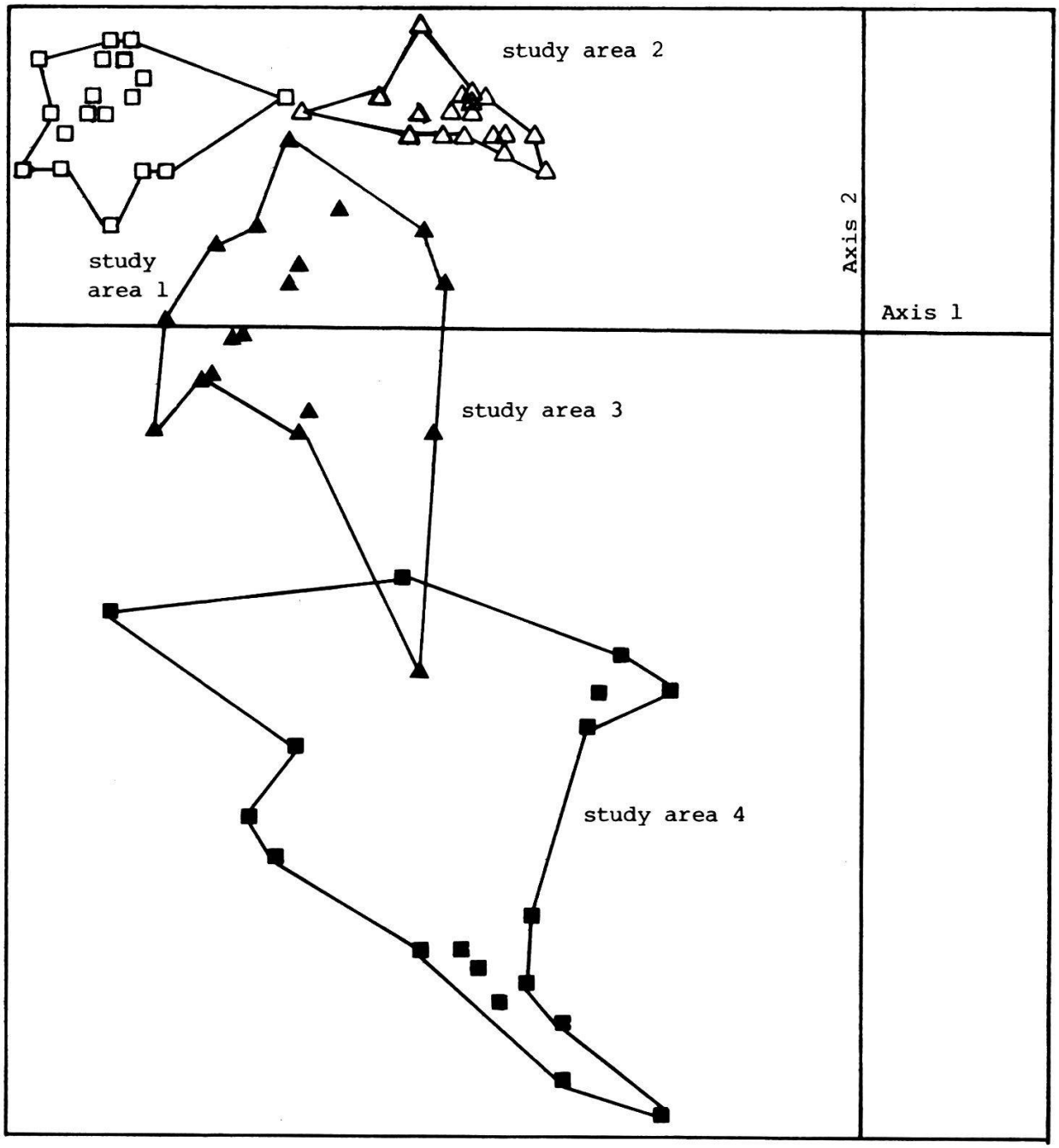

Fig. 3. Ordination by principal component analysis of 72 relevés (50 m^2) within the four study areas (18 relevés per each area).
Axis 1 and 2 are presented.
Axis 1: percentage of variation accounted for: 45.81%
range of co-ordinates: - 15.48 to 3.14
Axis 2: percentage of variation accounted for: 12.99%
range of co-ordinates: - 13.64 to 4.98

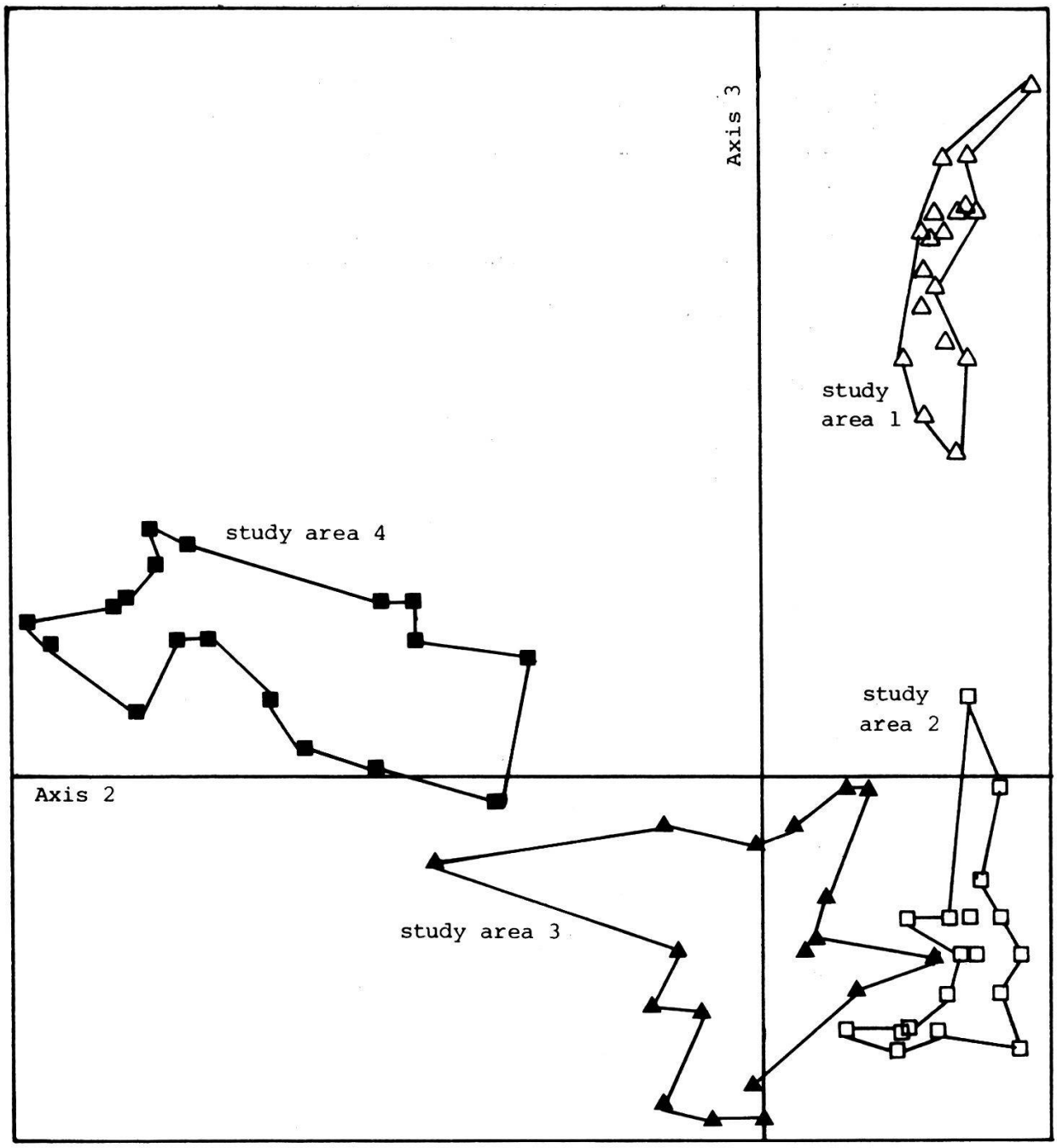

Fig. 4. Ordination by principal component analysis of 72 relevés (50 m^2) within the four study areas (18 relevés per area).
Axis 2 and 3 are presented.
Axis 2: percentage of variation accounted for: 12.99%
range of co-ordinates: - 13.64 to 4.98
Axis 3: percentage of variation accounted for: 11.10%
range of co-ordinates: - 6.07 to 12.55

Table 2. Characteristics of the four studied areas

Study area	Grassland type according to ZOLLER (1954)	Grassland form	Treatment prior to experimental management	Experimentally managed since	Geology	Aspect (°)	Slope (%)	Altitude a.s.l.
1	*Medicago falcatae-Mesobrometum*	dry	annually cut in mid June	1978*	Gamma-Marl	124 (SE)	27	710 m
2	*Dauco-Salvio-Mesobrometum*	dry-fresh	annually cut in mid June	1977**	talus of Beta-lime-stone	111 (SE)	45	565 m
3	*Seselio libanotidis-Mesobrometum*	dry	abandoned for 10 years	1977**		114 (SE)	47	570 m
4	*Seselio libanotidis-Mesobrometum*	dry	abandoned for 20 years	1977**		265 (NW)	43	588 m

* burnt for the first time in 1979
** burnt for the first time in 1978