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Flowering and individual survival of a population of the grass *Brachypodium sylvaticum* in Nåtö, Åland Islands, SW Finland

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A population of the grass *Brachypodium sylvaticum* (Hudson) Beauv., located in and outside a permanent quadrate (size 2 × 2 m) in a dense *Corylus* stand, was studied from 1964 to 1984. Each individual (tuft) was marked and the culms with spikelets counted every year. The vegetation of the quadrate, and the soil in its vicinity, were studied. During the study the population increased from four tufts with only one culm in one tuft in 1964 to more than 80 tufts with more than 3 000 culms in 1984. The succession of the vegetation revealed that the graminids increased continuously, especially after 1983, when all trees and shrubs were cut. The earliest observed tufts were still alive in 1984. The annual mortality of the tufts was absent, or very low during most of the time. It is suggested that *B. sylvaticum* is principally a stress-tolerant competitor.

Key words: *Brachypodium sylvaticum*, permanent quadrate, population dynamics, succession

INTRODUCTION

The flowering frequency of different plants may vary considerably from one year to another. This is characteristic of many fruit trees and other lignoses, of orchids, other herbs, and graminids too (e.g. Tamm 1948, 1956, 1972a, 1972b, Söyrinki 1985, 1987, Inghe & Tamm 1985, 1988, Hintikka 1988).

Studies on the performance of the individuals of a particular species are, however, rather few. The studies on reproduction, survival and flowering of perennial herbs made by Tamm (1948, 1956, 1971, 1972a, 1972b) and Inghe and Tamm (1985, 1988) are some of the very few long-term studies made on the individual level.

In Finland, the pioneer work on seedlings was carried out by Linkola (1930a, 1930b, 1935). Similar studies were also made by Perttula (1941). Studies on the demography of certain plant species have been done in recent years by e.g. Harper (1967, 1977), Sarukhán and Harper (1973), Sarukhán (1974), Jerling and Liljelund (1984), Eriksson (1986, 1987a, 1987b), Järvinen (1989), Järvinen and Järvinen (1991) and Eriksson and Bremer (1993).

In 1964, while researching wooded meadows in Nåtö, the author C.-A. H. established permanent quadrates, 2 × 2 m in size, in three different stand types (Hæggström 1983). One of these quadrates, Cq 50, located in a dense stand of *Corylus avellana*, contained four tufts of the grass *Brachypodium sylvaticum* (Hudson) Beauv. This species was not formerly known on the island of Nåtö, although for decades large stands have been known to grow on the small island of Idholm 1.5 km S of Cq 50 (Palmgren 1915).

Brachypodium sylvaticum is a caespitose species: it forms loose to compact tussocks without stolons (Raunkiær 1895–99, Ryberg 1967, Mühlberg 1970). Therefore, it was quite easy to recognise each individual tuft. Only six tufts were observed to divide into two or three separate tufts during the study period. Plants not forming tufts or stolons would, however, be more suitable for studies on the individual level (Tamm 1948).

Brachypodium. sylvaticum is mainly a European and west Asiatic woodland species, also occurring in northernmost Africa. It occurs discontinuously eastwards to the Himalayas, southern Asia, Sakhalin and Japan (Meusel *et al.* 1965, Hultén & Fries 1986). In Finland this grass is only known to grow in the Åland Islands, where it has been found in more than 20 localities. It usually grows as large, almost pure stands, in luxuriant deciduous woods, usually quite near the seashore (cf. Ryberg 1967). It often forms a belt a few metres in width and tens of metres in length along shores in *Alnus glutinosa* and *Fraxinus excelsior* stands.

Brachypodium sylvaticum seems to prefer calcium-rich soils in Sweden (Samuelsson 1922, Lindquist 1931). This grass is also bound to calcium-rich soils (*kalkstet*, Eklund 1946) in the Åland Islands.

According to Sjörs (1967) and Ryberg (1967), *Brachypodium sylvaticum* belongs to the ecological group of broad-leaved nemoral grasses. It is a characteristic species (*Charakterart*) of the vegetation class *Querco-Fagetea* and it belongs to the *Galeobdolon* group of plants growing in deciduous woodlands of central Europe (Ellenberg 1963).

During the successive years of studying the permanent quadrate Cq 50, growth was observed in the population of *Brachypodium. sylvaticum*. The aim of this study was therefore to evaluate the growth, flowering and individual survival of this grass.

The field work for the present study was done by C.-A. H. during the 1960s and by both authors during the rest of the study period.

MATERIAL AND METHODS

The *Corylus* stand (sampling area 7), in which Cq 50 is located, was described in detail by Hæggström (1983). The tree and shrub layer around Cq 50 comprised a few formerly pollarded *Fraxinus* trees and a dense stand of *Corylus avellana*. The area was a wooded meadow managed by mowing, pollarding and grazing during the 18th, 19th and early 20th centuries.

The vegetation in Cq 50 and its vicinity was almost undisturbed by man from 1964 until 1978 when a shed was built some 5 metres from the quadrate, and a few sheep occasionally grazed in the area. The stand of *Brachypodium sylvaticum* was rather heavily grazed, as were some other species, e.g. *Dryopteris filix-mas*, *Hepatica nobilis* and *Lathyrus vernus* (Hæggström 1990).

In 1981 two *Corylus* shrubs just W of Cq 50 were cut. A summer cottage in the vicinity was being used more frequently, causing increasing disturbance to Cq 50. In April 1983 the whole area was heavily disturbed as all trees and shrubs were cut. The changing light conditions resulted in a sharp increase in some species, including *Brachypodium sylvaticum*. Since 1985 the *B. sylvaticum* population has been partly cut by a lawn mower. Therefore the study of Cq 50 and the stand of *B. sylvaticum* was discontinued in 1985.

Between 1964, when the quadrate Cq 50 was established, and 1984, every tuft of *Brachypodium sylvaticum* was registered, marked and mapped, both inside and outside the quadrate. During some years, seedlings of this grass occurred abundantly, but they were not mapped. As the number of individuals increased remarkably in 1971, the marking was done from then onwards with white flexible plastic markers, about 10 cm long and 1.5 cm broad. The markers were pushed into the soil just south of each grass tuft, where they were easily found year after year.

The number of flowering culms per tuft was counted every year. Furthermore, during certain years, the length of a few, or all culms was measured and the number of spikelets per culm counted. The dates for these studies varied between 6th of August and 4th of October, usually falling between 26th of August and 4th of September.

Some vegetation was slightly trampled, especially at the border of Cq 50, when we counted the tufts and culms and analysed the vegetation (see Hæggström 1983). However, we tried to be careful, stepping on boulders and bare spots on the soil whenever possible.

Fig. 1. Summer aspect of Cq 50 on July 26, 1971. The grasses *Brachypodium sylvaticum* and *Melica nutans* grew mostly in the northern part (to the right) of the quadrate. Other field layer species visible are e.g. *Hepatica nobilis, Dentaria bulbifera, Lathyrus vernus, Laserpitium latifolium* and *Convallaria majalis*. View from the east. All photos by C.-A. Hæggström.

The vernal and summer aspects of Cq 50 and samples of the soil were analysed according to the methods described by Hæggström (1983). The vegetation samples of the different analyses were compared with each other using the similarity index (*SI*) of Sørensen (1948). Both the similarity index of the presence (SI_{sp}) and the cover values (SI_{co}) of the species (taxa) were calculated.

The soil was investigated in 1966 (pH only) and 1971 (pH and some exchangeable nutrients; for the methods see Hæggström (1983)).

The nomenclature of the vascular plants is based on Hämet-Ahti *et al.* (1986) and of the bryophytes on Koponen *et al.* (1977). *Ranunculus auricomus* is treated as a collective species as only basal leaves of this buttercup were found. *Corydalis solida* is a polymorphic species in Nåtö, but as we have never found a pure *C. solida* subsp. *laxa* (cf. Lidén 1991), the taxon in Nåtö is treated as *C. solida* subsp. *solida*. *Heracleum sphondylium* is represented by subsp. *sibiricum*.

RESULTS

Vegetation of the permanent quadrate Cq 50

The cover percentages of the tree and shrub layer and the field layer are presented in Table 1. The summer aspect analyses are treated before the vernal aspect analyses, as *B. sylvaticum* is a typical summer aspect species (Ellenberg 1963).

The dominant species of the field layer were *Hepatica nobilis* and *Brachypodium sylvaticum* in the summer aspect (Fig. 1). The vernal aspect was fairly well developed with *Anemone nemorosa* as the dominant species (Fig. 2).

The ground layer comprised mosses and a liverwort. The cover of these was low, about 2–3%. *Plagiomnium undulatum, Cirriphyllum piliferum* and *Rhytidiadelphus triquetrus* grew on the humus, and *Brachythecium populeum, Homomallium incurvatum, Hypnum cupressiforme* and *Plagiochila porelloides* partly covered three boulders which protruded from the ground.

The vegetation in Cq 50 became more grass-dominated during the 21 years of study: the cover of the graminids (the grasses, *Luzula pilosa* and *Carex digitata*) was estimated at about 1.5% in 1964 compared to about 8% in 1971, 64.5% in 1975 and 60.5% in 1983 (Fig. 3). By 1984 *Brachypodium. sylvaticum* had increased considerably, covering approximately 98% of Cq 50.

The cover of *Hepatica nobilis* decreased considerably from 1975 to 1983. This may be due to competition from the grasses and perhaps also to grazing in 1978: sheep eagerly eat *Hepatica* which then becomes much smaller and weaker (Hæggström 1990). *Melampyrum nemorosum* increased in 1983, probably because of the change in light conditions after the cutting of the tree and shrub layer. As much of the soil surface lay bare, this annual species could flourish for some years before perennials take over.

According to the species presence, SI_{sp} (Table 2), both the summer and vernal aspects show a fairly high and rather uniform similarity. It is a well-known fact that similarity indices based on species presence alone are much higher than indices based on quantitative data (Hæggström 1983). This is also the case regarding Cq 50; the SI_{co} values are much

Table 1. The vegetation in Cq 50 in 1964–83. Cq 50 was analysed 16.VIII.1964 (summer aspect = s), 10.VI.1966 (vernal aspect = v), 28.V.1971 (v), 26.VII.1971 (s), 2.IX.1975 (s), 13.VI.1983 (v) and 26.VIII.1983 (s). The figures are cover estimates (percentages). A cover considerably less than 1/2% is marked +. A taxon not found or annotated is marked with –.

	summer aspect (s)				vernal aspect (v)		
	1964	1971	1975	1983	1966	1971	1983
Tree and shrub layer							
Corylus avellana	80	60	60	+	20	4	–
Fraxinus excelsior	5	15	20	–	1	1	–
Field layer							
Brachypodium sylvaticum	1/2	3	40	50	+	1/2	20
Hepatica nobilis	15	25	30	10	15	35	10
Primula veris	3	1	1	1	3	1	1
Lathyrus vernus	2	10	6	3	3	3	5
Laserpitium latifolium	2	5	4	5	1	2	5
Fraxinus excelsior	2	+	1	1/2	+	+	1/2
Dentaria bulbifera	1	2	–	+	8	3	2
Ranunculus auricomus	1/2	1/2	–	–	+	1	1/2
Acer platanoides	1/2	+	1/2	–	+	+	+
Geranium sylvaticum	1/2	1	1	1	1	1/2	1/2
Heracleum sphondylium	1/2	1	–	–	-	1/2	–
Convallaria majalis	1/2	+	2	3	+	+	5
Carex digitata	1/2	1/2	1	+	+	1/2	–
Melica nutans	1/2	4	8	1/2	+	1	1/2
Dryopteris filix-mas	+	+	2	2	+	–	–
Viola mirabilis	+	–	–	–	–	–	–
V. riviniana	+	1/2	1	+	–	+	–
Veronica chamaedrys	+	2	1	+	+	1/2	–
Paris quadrifolia	+	–	–	–	–	+	–
Poa nemoralis	+	+	10	2	+	+	1
Anemone nemorosa	–	2	+	+	60	40	50
Listera ovata	–	1	–	–	1	+	1/2
Melampyrum nemorosum	–	1/2	1/2	12	–	1	1
M. sylvaticum	–	1/2	–	–	–	–	2
Dactylis glomerata	–	1/2	5	8	–	+	4
Moehringia trinervia	–	+	–	–	–	–	–
Geum rivale	–	+	–	–	–	–	–
Sorbus aucuparia	–	+	–	–	–	+	–
Luzula pilosa	–	+	1/2	–	–	+	–
Poaceae, young	–	+	–	–	–	–	–
Betula pubescens	–	–	–	+	–	–	–
Epilobium sp.	–	–	–	+	–	–	–
Anemone ranunculoides	–	–	–	–	5	5	2
Gagea lutea	–	–	–	–	1/2	1/2	1/2
Corydalis solida	–	–	–	–	+	+	–

Fig. 2. Vernal aspect of Cq 50 on May 29, 1971. The field layer is dominated by *Anemone nemorosa*. Other vernal aspect species visible are *A. ranunculoides, Hepatica nobilis* and *Lathyrus vernus*. The grasses are not prominent. View from the east.

Fig. 3. Summer aspect of Cq 50 on August 25, 1983. The field layer is totally dominated by *Brachypodium sylvaticum*. View from the east.

lower and vary considerably, showing a general decrease in similarity, especially in the summer aspect, as time elapsed. This is due to successional changes in the vegetation.

The soil

In addition to an inconspicuous surface litter layer, the soil profile comprised three layers, viz. the humus, a transitional layer and the underlying mineral soil (Hæggström 1983). The humus layer consisted of 10 to 14 cm of mull-like moder (Kubiëna 1953). The largest humus grains occurred in the upper part of the humus layer. The organic content of the humus as loss on ignition was 12.9% in 1971. The approximately 10 cm thick transitional layer consisted of unaggregated humus intermingled with stones, gravel, sand and fine sand. The underlying mineral soil was mainly fine sand.

The pH and exchangeable nutrients are presented in Table 3. Most of these values are higher than the corresponding mean values measured in *Corylus* stands on Nåtö; exceptions are the values of Ca in the humus and all values of P (Hæggström 1983).

Flowering and survival of the individual tufts

In 1964 there were only four tufts of *Brachypodium sylvaticum* (Fig. 4, Table 4). The population increased slowly until 1971, when records showed 41 seedlings beside 32 larger tufts. Most of these seedlings probably died, as the number of tufts did not increase until 1974. In the following ten years, between 1974 and 1984, the number of tufts almost doubled.

In 1964 only one tuft had one culm. The number of culms increased almost every year until 1975 when there were 505 culms, a number not surpassed until 1982. During some years, e.g. 1970 and 1972 and especially 1976 and 1978, the number of culms was lower than in the previous year. The reason for this may be a result of depletion of the reserve nutrients of the tufts. In 1978 the low number of culms was, at least partly, also a result of grazing by sheep.

When the two hazels were cut in 1980, and especially when all trees and shrubs were cut in 1983, the number of culms began to increase rapidly. In 1984 more than 3 000 culms were recorded. The ratio between the flowering tufts and all tufts fluctuated during the study period (Table 4).

The average length of the five tallest culms was 102.2 cm (max. 115 cm) in 1975, 93.3 cm (max. 97.5 cm) in 1976, 94.6 cm (max. 102 cm) in 1977, and 123.8 cm (max. 131 cm) in 1983. Weak culms with only 1–2 spikelets could be as short as 30 cm. The number of spikelets of the tall and well-developed culms was usually 5–8, occasionally only 4, with an average number of about 6.

The highest number of culms per tuft, namely 182, was recorded in 1984. Four more tufts with more than 100 culms were recorded in that year. The highest number of culms in the previous years was 72 in 1983. Tuft No. 1 had the highest number of culms between 1964 and 1973 and in 1975. Tuft No. 28a had the highest number of culms in 1978 and 1980–82.

Tufts can survive for several years, the longest run observed being 21 years for Nos. 1–3 and 4a and 20 years for Nos. 5 and 6.

Only one tuft (No. 1) flowered each year and several of the others were first observed as culmless tufts for two to four years, whereupon they flowered for the rest of the study period, and could be assigned to "the old guard" (Inghe & Tamm 1985).

Table 2. Similarity indices (%) of the field layer vegetation of Cq 50 in different years. SI_{sp} = similarity indices calculated on the basis of species (taxa) presence, SI_{co} = similarity indices calculated on the basis of cover values.

Aspect and interval	SI_{sp}	SI_{co}
Summer aspect		
1964–1971	75	61
1964–1975	77	34
1964–1983	75	36
1971–1975	81	54
1971–1983	75	32
1975–1983	87	68
Vernal aspect		
1966–1971	85	72
1966–1983	83	68
1971–1983	81	62

Table 3. pH and exchangeable nutrients (mg l^{-1} in 1971) of Cq 50.

Soil layer	pH 1966; 1971	Ca^{++}	K^{+}	N	P
Humus layer	6.55; 6.90	733	119	41	5
Transitional layer	7.00; 6.70	1435	30	35	4
Mineral soil	7.40; 6.95	1065	21	41	5

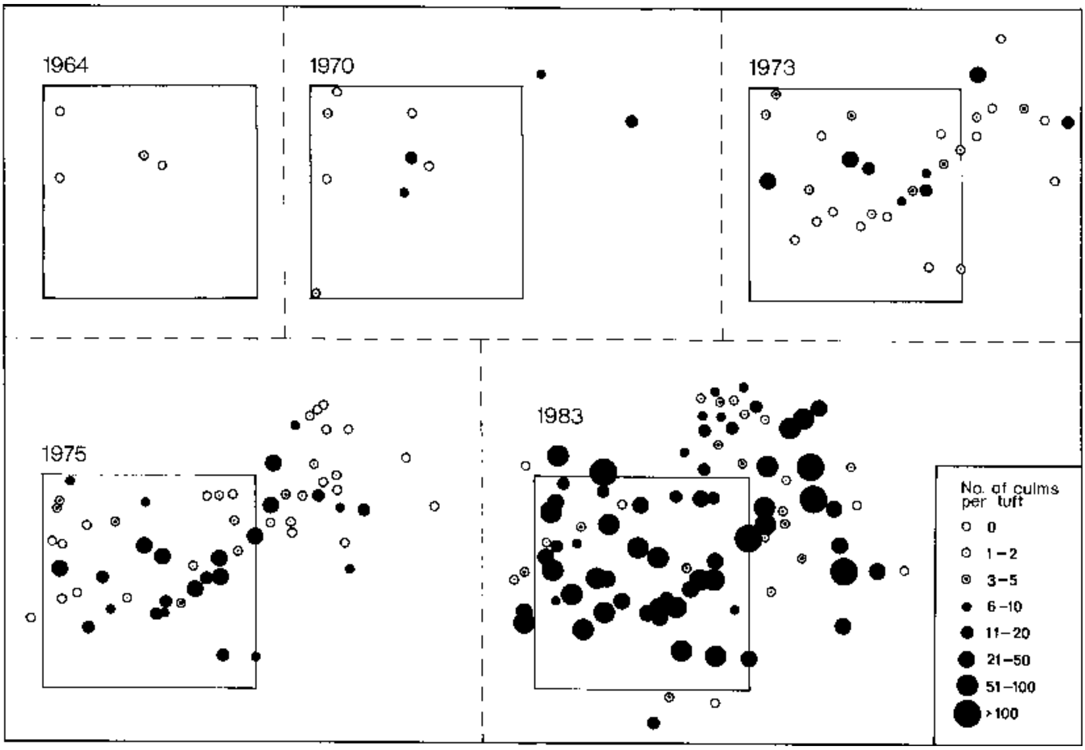

Fig. 4. The development of the population of *Brachypodium sylvaticum* in and around Cq 50 (the square) in 1964, 1970, 1973, 1975 and 1983.

Many others were culmless from one to eight years before flowering for the first time. A few short-lived tufts were also observed.

The survival rate (Treshow & Harper 1974) for the total number of tufts and the tufts with culms, the mortality of the population between each successive year and 1984, and the annual mortality of the population are presented in Table 5. The survival rate, calculated as the ratio between the number of tufts in 1984 and each previous year of study, is a way of expressing mortality. All the values were greater than 1.0, which is typical of an increasing population. The mortality between each year of study and 1984 varied between 0.0% and 25.4%, being highest during the mid 1970s. The annual mortality was usually very low, rising to 20.0% only once (between 1970 and 1971).

DISCUSSION

The population of *Brachypodium sylvaticum* expressed as the number of tufts increased during the 21 years of observation. The succession in the permanent quadrate Cq 50 revealed that even without any prominent human disturbance, changes in vegetation occur in a rather closed *Corylus* stand. The most prominent change was the increase in graminids, especially *B. sylvaticum*. This indicates that *B. sylvaticum* is a strong competitor in shady deciduous forests.

Although *Brachypodium. sylvaticum* is a shade tolerant woodland species, it also may persist in quite open areas (Hubbard 1968, Pedersen 1974). According to the three primary strategies of Grime (1974, 1977), *B. sylvaticum* seems principally to be a stress-tolerant competitor.

As soon as the trees and shrubs were cut, the population of *Brachypodium sylvaticum* began to flourish. This was due both to the changed light conditions and the assart effect (Romell 1957), i.e. fertilising of the soil by nitrogen and other nutrients which were released from decaying roots, mycorrhizas, etc. Some commonplace grass species, e.g. *Deschampsia flexuosa* and *Calamagrostis* *arundinacea*, and a few of the broad-leaved nemoral grasses, e.g. *Milium effusum* (Palmgren 1915, Ryberg 1967), react in the same way. It is obvious that *B. sylvaticum* also belongs to those grasses which benefit from the removal of trees and shrubs. *B. sylvaticum* itself is, however, sensitive to both cutting (Ryberg 1967) and grazing as its vitality suffers from these types of disturbances.

The flowering of certain species is affected by a pervious summer's drought conditions, as was shown by Inghe and Tamm (1985, 1988) regarding *Dactylorhiza sambucina, Listera ovata* and *Sanicula europaea* and by Hintikka (1988) regarding *Calamagrostis arundinacea*. To test if this is also the case in *Brachypodium sylvaticum,* we used regression analysis to compare the formation of culms to the summer (June to August) and growing season (May to October; see Hæggström 1983) precipitation of both the previous and the same year. The number of culms does not, however, seem to be strongly dependent on the summer precipitation. As a late summer aspect species of shady habitats, *B. sylvaticum* seems to get enough moisture, especially since in the Åland Islands precipitation in August is quite often higher than the combined precipitation in June and July. A multiple regression analysis (of the

Table 4. The development of the *Brachypodium sylvaticum* population in and around Cq 50.

Year	Total number of tufts	Number of tufts with culms	Proportion of tufts with culms	Total number of culms	
1964	4	1	25.0	1	
1965	7	1	14.3	5	
1966	7	2	28.6	5	
1967	8	3	37.5	21	
1968	8	4	50.0	41	
1969	8	7	87.5	58	
1970	10	6	60.0	42	
1971	32	7	21.9	99	
1972	32	9	28.1	77	
1973	32	19	59.4	167	
1974	46	27	58.7	319	
1975	59	41	69.5	505	
1976	61	33	54.1	188	
1977	67	46	68.7	442	
1978	61	27	44.3	113	(1)
1979	62	31	50.0	144	
1980	63	34	54.0	164	(2)
1981	61	50	82.0	457	
1982	67	53	79.1	707	
1983	80	60	75.0	1481	(3)
1984	88	83	94.3	3083	

Disturbance: (1) – Shed built, light sheep grazing, (2) – Two hazels cut just W of Cq 50, (3) – All trees and shrubs cut in April

Table 5. The survival rate (S) for the total number of tufts of *Brachypodium sylvaticum* (S_{tot}) and the tufts with culms (S_{cu}) the mortality M (%) of the population between each year of study and 1984, and the annual mortality m (%) of the population.

Period	Survival rate S S_{tot}	S_{cu}	Period	Mortality M%	Period	Annual mortality m%
1984–1964	22.0	83.0	1964–1984	0.0	1964–1965	0.0
1984–1965	12.5	83.0	1965–1984	14.3	1965–1966	0.0
1984–1966	12.5	41.5	1966–1984	14.3	1966–1967	0.0
1984–1967	11.0	27.7	1967–1984	12.5	1967–1968	0.0
1984–1968	11.0	20.8	1968–1984	12.5	1968–1969	0.0
1984–1969	11.0	11.9	1969–1984	12.5	1969–1970	0.0
1984–1970	8.8	13.8	1970–1984	20.0	1970–1971	20.0
1984–1971	2.8	11.9	1971–1984	12.5	1971–1972	0.0
1984–1972	2.8	9.2	1972–1984	12.5	1972–1973	0.0
1984–1973	2.8	4.4	1973–1984	12.5	1973–1974	0.0
1984–1974	1.9	3.1	1974–1984	23.9	1974–1975	0.0
1984–1975	1.5	2.0	1975–1984	25.4	1975–1976	0.0
1984–1976	1.4	2.5	1976–1984	24.6	1976–1977	4.9
1984–1977	1.3	1.8	1977–1984	23.9	1977–1978	9.0
1984–1978	1.4	3.1	1978–1984	16.4	1978–1979	3.2
1984–1979	1.4	2.7	1979–1984	12.9	1979–1980	1.6
1984–1980	1.4	2.4	1980–1984	11.1	1980–1981	9.5
1984–1981	1.4	1.7	1981–1984	1.6	1981–1982	0.0
1984–1982	1.3	1.6	1982–1984	6.0	1982–1983	1.5
1984–1983	1.1	1.4	1983–1984	3.8	1983–1984	3.4

BDMP Programme Package) of the influence of the monthly precipitation and temperature and the difference between these and the monthly mean values of the period 1961–1990 did reveal that the number of culms is affected principally by the mean temperature in May (F = 44.64***) and the divergent precipitation in January, September and October (F = 39.94***, F = 18.46***, and F = 16.67**; significance levels: *** = P < 0.001, ** = P < 0.01). These climate factors seem, however, to be of minor ecological importance.

The formation of culms does not seem to be dependent on the snow cover. During the study period, there were only four snow-rich winters and several with very little, or even no snow at all.

On the basis of the data of Tamm (1956), Harper (1967) calculated the decay rate and the half-life of populations of *Centaurea jacea, Filipendula vulgaris* and *Sanicula europaea*. This was not, however, possible in the ever increasing population of *B. sylvaticum*. A much longer study period would have been required.

As the population of *Brachypodium sylvaticum* in Cq 50 was quite small in 1964 and increased subsequently, it had probably been established a few years earlier. The exact time cannot be given, but as none of the tufts were culmless for more than eight years before flowering for the first time, an extrapolation backwards in time sets the date in the late 1950s or early 1960s.

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