

## Dynamics of tundra and taiga populations of herbaceous plants in relation to the Tihomirov-Fretwell and Kalela-Tast hypotheses

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The Tihomirov hypothesis, according to which microtines have a strong impact upon the reproductive performance of northern plant populations, and the hypothesis of Kalela and Tast, stating that northern environments are characterized by strong, synchronous pulses of generative and vegetative reproduction, which create microtine cycles, were tested by studying fluctuations in the flowering intensity and population size of orohemiarctic populations of *Solidago virgaurea*, *Trollius europeus* and *Carex bigelowii* and in middle boreal populations of *S. virgaurea* during 1977-84 in relation to microtine herbivory.

The orohemiarctic populations failed to show any clear and widespread synchrony in reproduction between species or habitats, except for a synchronous low in 1983, associated with the highest vernal vole densities during the whole period and with high rates of injury in marked shoots of herbs. For boreal *S. virgaurea* populations, fluctuations in numbers of floral shoots were only pronounced in nutrient-poor habitats and were mainly attributable to fluctuations in survival rates. The results suggest that apparent flowering cycles in northern areas are mainly a consequence of fluctuations in microtine populations, as proposed by Tihomirov.

A review of available productivity data does not support the assumptions of the Kalela-Tast hypothesis. The field layer of subarctic habitats tends to be more productive than that of more southern forests. Thus, there is no obvious reason why subarctic herbs would need to accumulate resources over several years in order to reproduce, as proposed by Kalela and Tast.

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### Introduction

According to a traditional idea, microtine cycles in northern environments are somehow associated with synchronous changes in the fertility and numbers of key food plants (Tihomirov 1959, Kalela 1962, Pruitt 1966, 1968, Tast and Kalela 1971). This conventional wisdom has been recently confirmed in long-term surveys of boreal (Hansson 1979) and subarctic (Laine and Henttonen 1983) plant populations. Two diametrically opposite explanations for the phenomenon have been provided. Tihomirov suggests that the underlying cause is a predator-prey type interaction between herbivores and the plant cover of the tundra (see also Lack 1954). This idea can be connected to the hypothesis of exploitation

ecosystems (Fretwell 1977, Oksanen et al. 1981). According to the hypothesis, grazers of moderately unproductive ecosystems are strictly resource-limited and therefore exert strong influence upon the vegetation.

According to Tast and Kalela (1971), the cause lies in the opposite direction: favourable climatic conditions create a synchronous pulse of generative and vegetative reproduction in northern plant communities. After such a pulse, a period of low reproductive effort follows, because plants, according to this hypothesis, need time to replenish their energy reserves in the supposedly stressful conditions of the tundra and the northernmost forests. The reproductive pulses are interpreted as periods of abundant high-quality food for microtines, causing high survival and reproductive rates, whereas the

converse situation prevails during times of low reproductive effort in plants.

The Kalela-Tast hypothesis has been tested at Kilpisjärvi, Finnish Lapland, for almost two decades. However, the results obtained so far are rather contradictory. The initial results appeared to be strongly supportive: the fertility of *Solidago virgaurea* and *Eriophorum angustifolium* fluctuated in good correlation with the vole cycle and *E. angustifolium* behaved similarly on open sample plots and within supposedly rodent-proof exclosures (Tast and Kalela 1971). In the 1970s, however, corresponding patterns have been vague, and there has been a major discrepancy in the flowering of *E. angustifolium* between the two sample areas (1973 was a flowering peak in the material of Laine and Henttonen (1983) but a rock-bottom year in the material of Järvinen and Tast (1980)). No correlation between the flowering of *E. angustifolium* and the development of the microtine populations was found by Laine and Henttonen (1983). The data on interspecific flowering synchrony reported by Laine and Henttonen were equally vague. Positive signs prevailed in their correlation matrix, and 10 out of the 45 correlation coefficients were significantly positive. However, this hardly amounts to strong interspecific flowering synchrony, sufficient to be the underlying cause of small mammal cycles.

We have tried to elucidate the situation by a study on populations of three herbaceous plants (*Solidago virgaurea*, *Carex bigelowii* and *Trollius europaeus*) on the tundra and, in the case of *S. virgaurea*, also in taiga habitats. The taiga study has been designed to answer the following two questions: (1) Does the amplitude of fluctuations in the numbers of floral shoots depend on the productivity of the habitat? (2) Does the number of floral shoots observed in late summer correlate with the number of floral shoots observed in early summer? An affirmative answer to question (1) is vital for the Tihomirov-Fretwell hypothesis, although such an answer does not rule out the Kalela-Tast hypothesis. Conversely, the Kalela-Tast hypothesis requires that question (2) is answered affirmatively, though such an answer can also be reconciled with the Tihomirov-Fretwell hypothesis (by emphasizing winter grazing). The tundra work focuses on the question (3) whether fluctuations in the numbers of floral shoots and in the total number of shoots are persistently synchronous between species and habitats, as predicted by the Kalela-Tast hypothesis, or whether the synchrony only manifests itself during those times when rodents have exerted strong grazing pressure upon the vegetation, as implied by the Tihomirov-Fretwell hypothesis.

## Material and methods

### Taiga studies

During 1977–1984, floral and vegetative shoots and seedlings of *Solidago virgaurea* were marked with plas-

tic pins and censused in early summer (early June) when the floral shoots started to elongate. The censusing of floral shoots was repeated after the actual flowering period (late August–early September). The censusing was performed on three sample plots, each 3 × 5 m in size, located in small herb-rich depressions of the *Geranium-Oxalis-Myrtillus* type (GOMT, Kalela 1961), within middle boreal heath forests (mainly *Vaccinium-Myrtillus* type, VMT, locally *Deschampsia-Myrtillus* type, DeMT) on the forested hill Pyttisberget in Västerbotten, northern Sweden. (For a detailed description of the study area, see Ericson 1977). The vole populations of the area have been surveyed by B. Hörnfeldt (unpubl.). During 1983 (a year of low vole densities) and 1984 (a year of strong vole population increase), late summer censuses of floral shoots of *S. virgaurea* were performed in 15 additional sample plots, representing a gradient from very barren heath forest of *Empetrum-Vaccinium* type (EVT) to luxuriant meadow forests of *Geranium-Oxalis-Maianthemum* type (GOMaT). The plots were ranked on the basis of the presence and abundance of plants which indicate good nutrient and moisture conditions. For each sample plot, the number of floral shoots in 1984 was divided by the number of floral shoots in 1983, to provide an index for the flowering pulse which, in accordance to the Kalela-Tast hypothesis, ought to have caused the strong population rise in the vole population in 1983.

### Tundra studies

Floral and vegetative shoots of *S. virgaurea*, *Carex bigelowii* and *Trollius europaeus* were annually censused during 1977–80 and 1982–84 on permanent plots located in the following four tundra habitats on Finnmarksvidda, Norwegian Lapland (species censused and sample plots used are in parentheses).

- 1) windbarren (*Solidago virgaurea*, sample plot 10 m<sup>2</sup>)
- 2) typical tundra heath (*Carex bigelowii*, 7 plots of 0.6 m<sup>2</sup> each)
- 3) snowbed (*Carex bigelowii* on 7 plots of 0.6 m<sup>2</sup> each, *Solidago virgaurea* on a sample plot of 40 m<sup>2</sup>)
- 4) mesic meadow tundra (*Solidago virgaurea* and *Trollius europaeus*, 7 plots of 0.6 m<sup>2</sup> each).

The censusing was usually done in the last days of July or in the first week of August (the exact time was determined on phenological grounds, see Oksanen and Oksanen 1981), although on the snowbed, sampling was delayed to September during years of late snowmelt. The area was not visited in 1981. The counts of floral shoots for that year were made on the basis of their remains in 1982 which appeared to be a reliable procedure in habitats 1–3. (Remains of old shoots were readily visible and could be distinguished from still older ones by their colour.) On the meadow where the rate of decay is more rapid, this estimation procedure was not applied. A summary of the habitat characteristics and

Tab. 1. The study habitats in the tundra area and the outlines of their vegetation (abundances of major plant groups; Hult-Sernander Scale, names of the dominating constituents) and the ranges of variation in the number of all shoots (n) and floral shoots (f) of the focal plant species

	1 windbarren	2 heath	3 snowbed	4 meadow
altitude (m)	430	430	600	430
characteristics of the site	sandy ridge	level moraine	stony slope	depression in heath
vegetation:				
shrubs (h > 30 cm)		1, <i>Betula nana</i>	-	4, <i>Salix</i> spp.
dwarf shrubs	1, <i>Empetrum hermaphroditum</i>	2, <i>Vaccinium myrtillus</i>	3, <i>Salix herbacea</i>	1, <i>Empetrum hermaphroditum</i>
herbs	1, <i>Solidago virgaurea</i>	+, <i>Pedicularis lapponica</i>	2, <i>Sibbaldia procumbens</i>	4, <i>Solidago virgaurea</i>
graminids	1, <i>Juncus trifidus</i>	1, <i>Deschampsia flexuosa</i>	2, <i>Deschampsia flexuosa</i>	3, <i>Carex vaginata</i>
cryptogams	5, <i>Stereocaulon paschale</i>	5, <i>Dicranum fuscescens</i>	5, <i>Dicranum fuscescens</i>	3, <i>Hylocomium splendens</i>
populations (min, max):				
<i>Solidago virgaurea</i>	n: 867,1044 f: 24, 113		n: 24,255 f: 3, 62	n: 437,545 f: 48,121
<i>Carex bigelowii</i>		n: 177,289 f: 15, 59	n: 306,607 f: 30,102	
<i>Trollius europaeus</i>				n: 92,112 f: 4, 38
<i>Solidago</i> -seedlings (min, max)	n: < 10		n: < 5	n: 105,701

plant population data is provided in Tab. 1 (for detailed descriptions, see Oksanen and Oksanen 1981).

The vole populations of the area were surveyed by means of the small quadrat method of Myllymäki et al. (1971). Habitats 1 and 2 were trapped each spring except 1981 with at least 5 quadrats (each quadrat amounts to 24 trap nights), and in 1978, 1979, 1983 and 1984 also in the autumn. Habitat 4 was trapped even in spring 1981, although by a different person. Two quadrats were allocated to habitat 3, trapped as in habitats 1 and 2.

In 1983 (the year with exceptionally high spring densities of rodents), 70 emerging *Solidago* shoots were marked when they had barely started to be visible (about 15 June) by plastic pins in habitats 1 and 4. In habitat 2 where herbs were extremely rare, we marked 30 shoots of *Pedicularis lapponica*.

The marked shoots were checked in early August and allocated to three categories: intact or almost intact (the greatest part of every leaf was present), lightly grazed (at least one leaf was severed, but the number of intact leaves exceeded the number of grazed leaf bases) and severely grazed (most leaves were bitten off or the entire shoot was clipped at its base). Cases where the growth of a shoot cluster had made the identity of the marked shoot ambiguous were removed from the sample (a few pins were also lost during the summer). To get a more complete picture on the between-habitat variation of grazing pressure, 70 shoots of *Geranium*

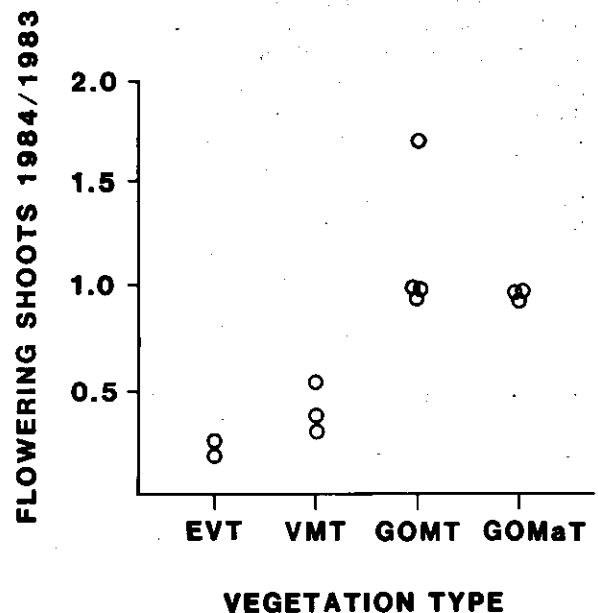


Fig. 1. The ratio between flowering shoots present in 1984 and 1983 for different localities along a productivity gradient. Data from the middle boreal zone (Västerbotten, Sweden). The order between the localities within each vegetation type based on the composition of the field layer. Abbreviations: EVT, *Empetrum-Vaccinium* type; VMT, *Vaccinium-Myrtillus* type; GOMT, *Geranium-Oxalis-Myrtillus* type; GOMaT, *Geranium-Oxalis-Maianthemum* type.

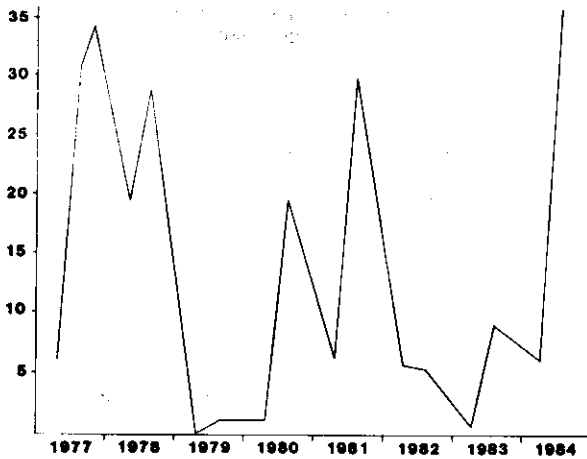


Fig. 2. Fluctuations in the density of microtines in Västerbotten, Sweden during 1977–84. Unpubl. data provided by B. Hörnfeldt.

*silvaticum* were similarly marked and evaluated in a luxuriant meadow (an almost pure stand of *G. silvaticum*). The vole densities of this habitat have exceeded the values for other habitats almost through the whole study period (see Oksanen and Oksanen 1981).

### Results

In the more productive middle boreal forest types (GOMT, GOMaT) flowering intensity was about equal in 1983 and 1984. The only notable exception was a patch of luxuriant (GOMT) forest within a paludified drainage system (Fig. 1). (This patch was covered by solid ice during the winter 1983/1984.) In the less productive habitats (EVT, VMT), flowering intensities were invariably lower in 1983 (a year of low vole densities) than in 1984 (a year of strong population rise, see Fig. 2). There was significant positive correlation between the ratio flowers in 1984/flowers in 1983 (RF) and the productivity rank (PR) of the habitat ( $r = 0.77$ ,  $p < 0.01$ ,  $n = 12$ ). This correlation did not depend on the inclusion of the somewhat special GOMT patch in the drainage system: removal of this patch from the material actually lead to better correlation between PR and RF ( $r = +0.89$ ,  $p < 0.001$ ,  $n = 11$ ).

The *Solidago* population on Pyttisberget showed rather marked density variations. The most clear changes occurred in 1980–82 (Fig. 3) when the numbers first

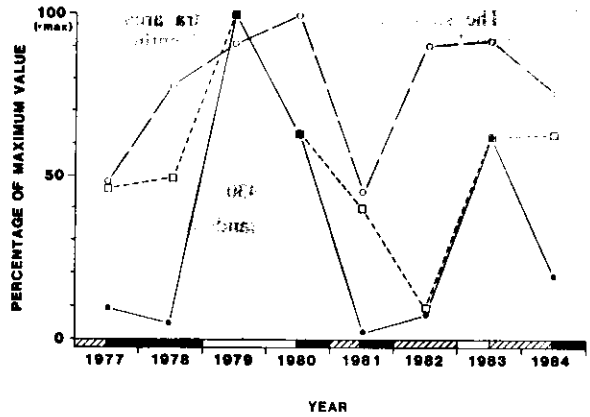


Fig. 3. Fluctuations in the number of developing floral shoots in early June (dots; max 42, min 3), the number of floral shoots present in late August - early September (squares; max 42, min 1), and the number of vegetative rosettes (circles; max 192, min 85) for *Solidago virgaurea* in small GOMT depressions on Pyttisberget, Västerbotten. Vole index values given on the x-axis: black > 10%, shaded 3–10% open < 3% (cf. Fig. 2).

declined dramatically and then increased again. The decline occurred during a vole peak and the recovery took place when the vole populations were declining. Proximately, these changes were caused by variation in survival or production of new shoots from established rhizomes, as seedling numbers were generally low and seedling survival was virtually nil (Tab. 2). The year 1982 when the population size was more than doubled from its 1981 level thus seems to represent an especially pronounced pulse in the vegetative reproduction of *Solidago*.

The late-summer censuses on Pyttisberget showed a strong variation in the numbers of *S. virgaurea* inflorescences (Fig. 3). The apparent flowering peaks occurred during the years of low vole densities (1979, 1983). Out of the years with low flowering intensity, one (1982) can be attributed to copious vegetative propagation (see above) which must have reduced the amounts of resources available to the production of inflorescences. All other low years (1977, 1978, 1981, 1984) can be attributed to low survival rates of floral shoots during the summer. The spring samples indicated a rather constant reproductive effort from year, and the coefficient of variation for spring censuses (0.48) was less than half of that for late summer counts (1.09). Only one year (1979) can be characterized as a strong flowering pulse. This was the deepest crash year in the entire small

Tab. 2. The numbers of 1st-year seedlings (c) of *Solidago virgaurea* and their survival to the following year (c+1) in GOMT depressions on Pyttisberget. Data from the same sample plots as in Fig. 3.

No. of Seedlings	c	Germination year							
		1977	1978	1979	1980	1981	1982	1983	1984
	c	21	148	55	112	3	73	32	35
	c+1	0	2	1	0	0	1	0	not counted

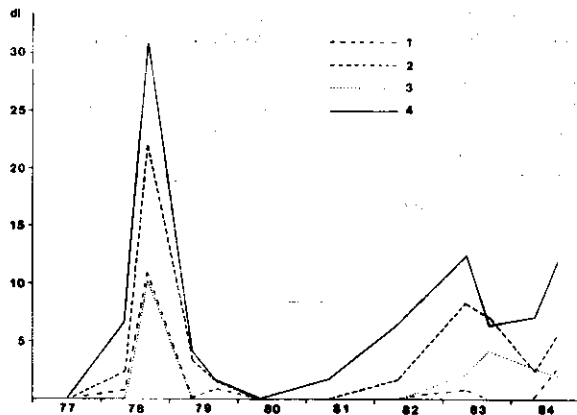


Fig. 4. Fluctuations in microtine densities (di, no. captures per 100 trap nights) on Finnmarksvidda during 1977-84. 1: windbarren, 2: blueberry-lichen-moss heath, 3: snowbed, 4: golden-rod-globe flower meadow with willows.

mammal material (Fig. 2). Excluding 1982 (the year with copious vegetative reproduction), the best single factor explaining variation in late summer counts of floral shoots is herbivory. The correlation between numbers in late summer and survival rate from the spring is almost perfect ( $r = 0.94$ ,  $p < 0.01$ ,  $n = 7$ ).

Microtine populations on Finnmarksvidda fluctuated pronouncedly although less regularly than those of Västerbotten, with a sharp peak in 1978 and an extended period of relatively high densities in 1982-84. The phases of high densities were clear on the herb-grass meadow and also on the relatively barren blueberry-lichen heath, while the occurrence of voles on dry heaths and snowbeds was more sporadic (Fig. 4).

Variation in the intensity of flowering on Finnmarksvidda does not show any persistent synchrony between species or habitats. The visual impression of the data is

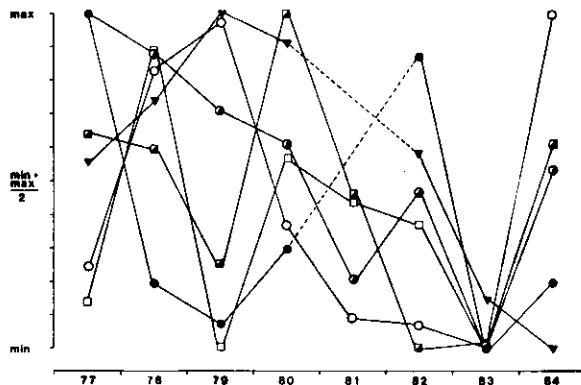


Fig. 5. Fluctuations in the number of floral shoots of *Solidago virgaurea* (circles), *Carex bigelowii* (squares) and *Trollius europaeus* (triangles) on windbarren-heath (white), snowbed (black and white) and meadow (black) habitats of Finnmarksvidda during 1977-84. Stubs of severed floral shoots are not included.

diffuse (Fig. 5). All correlations between the flowering intensities of different populations - whether different species in the same habitat or the same species in different habitats - are non-significant (Tab. 3a). However, positive correlations prevail in the correlation matrix, and if the individual  $r$ -values are treated as variables, their mean value ( $\bar{r} = +0.21 \pm 0.08$ ) is significantly greater than zero ( $t = 2.67$ ,  $P < 0.01$ ,  $n = 15$ ). This weak synchrony is critically dependent on the inclusion of 1983 with simultaneously low flowering intensity in all species (Fig. 5). If this year is removed from the material, individual correlation coefficients (Tab. 3b) and the material as a whole fail to show the slightest semblance of flowering synchrony ( $\bar{r} = 0.04 \pm 0.10$ ).

In summer 1983, the marked samples of herbs were strongly affected by voles in all habitats except for the luxuriant *Geranium* meadow (Tab. 4). *Trollius* was subjected to intense shoot clipping both in 1983 and in 1984: the counts for intact floral shoots totalled 13 for these two years, whereas 39 bases of clipped floral shoots were then recorded on the sample plots. The grazing culminated on the relatively unproductive heath (habitat 2) where a moderate density of microtines (Fig. 4) was combined with a scanty resource basis (Oksanen and Oksanen 1981, see also Kalliola 1939). The barren habitat 1 with very few microtines and the meadow habitats with much more forage had lower intensities of grazing.

The total numbers of shoots showed neither substantial nor synchronous fluctuations, except for a continuous downward trend in the numbers of *Solidago* seedlings on the meadow and a deep dip in the number of *Solidago* shoots on the snowbed in 1983 (Fig. 6, Tab. 5). The dip was clearly caused by grazing: the only relatively intact shoots were observed on a boulder. (Remains of shoots lacking any intact leaves were consistently excluded from censuses).

Tab. 3. Pairwise correlations between the numbers of fertile shoots of *Solidago virgaurea*, *Carex bigelowii* and *Trollius europaeus* on habitats 1. through 4.  $r$ -values multiplied by 100. a. year 1983 included; b. year 1983 excluded.

a.	<i>S. vir</i> 1.	<i>C big</i> 2.	<i>S. vir</i> 3.	<i>C big</i> 3.	<i>S vir</i> 4.
<i>C big</i> 2.	+47				
<i>S vir</i> 3.	+52	+22			
<i>C big</i> 3.	+33	+53	+51		
<i>S vir</i> 4.	-47	-12	+42	+00	
<i>T eur</i> 4.	+14	-22	+52	+26	+08

b.	<i>S vir</i> 1.	<i>C big</i> 2.	<i>S vir</i> 3.	<i>C big</i> 3.	<i>S vir</i> 4.
<i>C big</i> 2.	+35				
<i>S vir</i> 3.	+35	-13			
<i>C big</i> 3.	+14	+39	+26		
<i>S vir</i> 4.	-86	-38	+16	-27	
<i>T eur</i> 4.	-15	-57	+24	+00	-16

Tab. 4. Percentages of injured and severely injured shoots and fractions of severed inflorescences in the samples of *Solidago virgaurea* (windbarren, transition, mesic meadow), *Pedicularis lapponica* (heath) and *Geranium silvaticum* (luxuriant meadow) shoots.

	wind- barren (habitat 1)	tran- sition (habitat 1-2)	heath (habitat 2)	mesic meadow (habitat 4)	luxuriant meadow
% injured.....	11	45	93	21	0
% severely injured.....	2	33	79	10	0
fraction severed.....	1/8	6/11	13/14	1/7	0
sample size.....	66	67	28	67	70

### Discussion

The differences in the flowering pattern of the Västerbotten populations of *Solidago virgaurea* were opposite to those predicted by the Kalela-Tast hypothesis: the population rise of microtines was accompanied by a reduction in the number of floral shoots, especially in the less productive habitats, as predicted by the Tihomirov-Fretwell hypothesis.

The data from Pyttisberget show that late summer counts of floral shoots can be misleading as indicators of fluctuations in the reproductive effort of plants. In this case, differences in survival during the summer months were responsible for most of the variation in the numbers of floral shoots in late summer. As the voles nevertheless showed pronounced population cycles, pulses in the reproductive effort of plants do not seem to have a critical role in the vole cycle.

The data from Finnmarksvidda suggest that 'flowering synchrony' in tundra plants can be restricted to synchronous lows, caused by grazing, as proposed by Tihomirov (1959). The pattern in grazing intensity conforms to the predictions of Fretwell's (1977, 1987) hypothesis: the most extreme rates of shoot mortality and injury were recorded in moderately unproductive habitats.

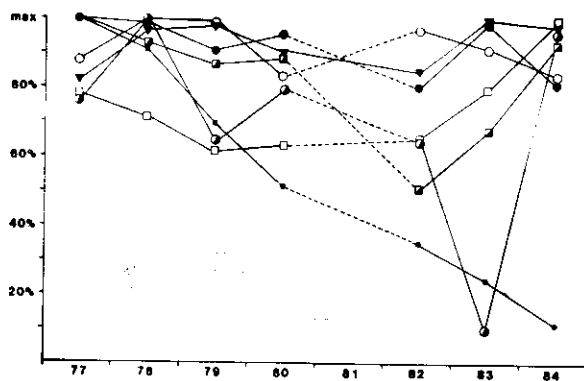


Fig. 6. Fluctuations in the total number of shoots of *Solidago virgaurea* (circles), *Carex bigelowii* (squares) and *Trollius europaeus* (triangles) on windbarren-heath (white), snowbed (black and white) and meadow (black) and in the numbers of *S. virgaurea* seedlings in the meadow (small dots) on Finnmarksvidda during 1977-84.

Our results thus suggest that the viewpoints of Tihomirov and Fretwell are more relevant for explaining pronounced between-year variations in the intensity of generative and vegetative reproduction of boreal and subarctic field layer plants than those of Tast and Kalela (1971). Some of the premises of Tast and Kalela were indeed confirmed. Individual clones of *S. virgaurea* seem to produce large numbers of inflorescences in certain years and then shift to a mainly vegetative existence at least for the next year. It is quite possible that occasional flowering pulses occur if some external factors synchronize these variations. It seems, however, that Tast and Kalela overestimated the strength of synchronizing factors and, especially, the role of temperature and underestimated the role of other factors (e.g., moisture, grazing by voles).

The emphasis on temperature in the Kalela-Tast hypothesis seems to be based on Kalela's (1962) assumption that subarctic field layer plants need to accumulate resources for reproduction over several years because of the generally unfavourable conditions prevailing in subarctic areas. The currently available data do not support this assumption. The total productivity of the vegetation is indeed higher in humid boreal and temperate areas than in subarctic and arctic ones, but the productivity of the field layer in mature plant communities seems to culminate in the timberline region (Fig. 7). The field layer of genuine forest ecosystems is much less productive, probably because of shading. Thus, subarctic and low-arctic areas seem to represent optimal conditions for field layer plants. The relative luxuriance of the field layer of subarctic plant communities is well depicted in Norin's (1961) classic work comparing the structure of

Tab. 5. Pairwise correlations between the numbers of shoots of *Solidago virgaurea*, *Carex bigelowii* and *Trollius europaeus* on windbarren (1), heath (2), snowbed (3) and meadow (4) sample plots. r-values multiplied by 100.  $F = +0.03 \pm 0.08$

	<i>S vir 1.</i>	<i>C big 2.</i>	<i>S vir 3.</i>	<i>C big 3.</i>	<i>C vir 4.</i>
<i>C big 2.</i>	-52				
<i>S vir 3.</i>	-08	+14			
<i>C big 3.</i>	-35	+30	+55		
<i>S vir 4.</i>	+00	-20	-02	+45	
<i>T eur 4.</i>	+18	+23	-22	+06	+17

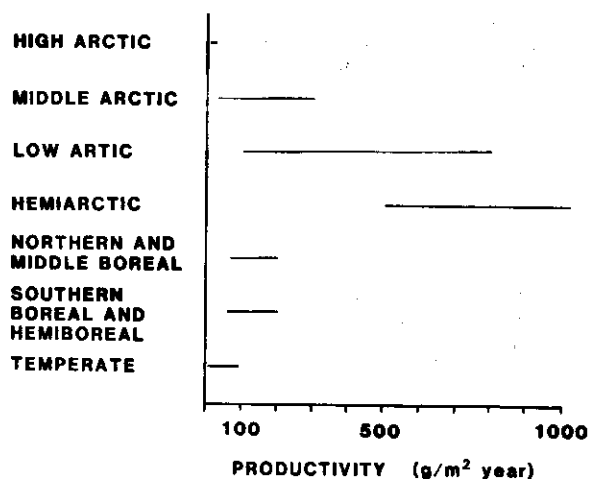


Fig. 7. Ranges of variation in reported values of field layer production in climax and late seral communities of the tundra, taiga and deciduous forest biomes. Sources: Bliss 1977 (high arctic = 'polar desert' in American terminology); Bliss 1977, Miller et al. 1980 (middle arctic); Kjelvik and Kärenlampi 1975, Wielgolaski 1975ab (low arctic); Holmen 1965, Kjelvik and Kärenlampi 1975 (hemiarctic); Havas and Kubin 1983, Astrologova 1977 (north and middle boreal); Mälkönen 1974, Persson 1980, Aulak 1970, 1975, Plewczynska 1970, Puszkar et al. 1972, Traczyk 1971 (south boreal and hemiboreal, including transitional areas with disputed zonal position, see Ahti et al. 1968); Traczyk 1967, Satoo 1970, Eber 1971 (temperate).

the field layer along a gradient from the southern taiga to the forest tundra. References to the high productivity of subarctic and subalpine meadows are also available in older Nordic literature (Kalela 1939, Nordhagen 1927, 1943; see also Hämet-Ahti 1963).

Tihomirov's notes on pronounced flowering fluctuation in tundra plants referred to much less productive middle arctic tundras (Fig. 7). If the perspective of Fretwell (1977, 1987) is realistic, the impact of microtines upon the vegetation should indeed be most pronounced and widespread in the middle arctic zone. In low arctic and subarctic areas, strong impact of herbivores upon the vegetation should be restricted to relatively barren habitats, (as it seems to be, see above), and fertility cycles due to grazing should be relatively vague (which also seems to be the case, see Fig. 5). On this point affirmative results have also been obtained by Andersson and Jonasson (1986) from northernmost Swedish Lapland: floral shoots became strongly grazed during 1974 when vernal rodent densities were high, but not so in 1978 when peak densities were restricted to the autumn in their study area. Also the data of Laine and Henttonen (1983) from Kilpisjärvi suggest better flowering synchrony in the mid 70s than later on. Moreover, Järvinen's (1987) study on *Ranunculus glacialis* suggests that flowering cycles caused by microtine grazing are more pronounced in the middle oroarctic (medioalpine) zone which is comparable to the middle arctic tundras studied by Tihomirov (1959) than in the boreal, orohemiarctic and lower oroarctic areas studied by us and by Andersson and Jonasson (1986).

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