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SEASONAL RHYTHM OF PLANT COMMUNITIES OF URAL ALPINE TUNDRA

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A phenorhythmic periodization of the growing season in the alpine tundra of the high-mountain boreal zone (as exemplified by the Urals) is proposed; its periods and stages are characterized; the course and ecological dependence of the phenophases, and the relative representation of the phenorhythmic groups of plants, are discussed.

The rhythm of seasonal development is one of the most characteristic features of plant communities (Sukachev, 1903; Shennikov, 1964; Rabotnov, 1978; Braun-Blanquet, 1951). Unfortunately, this feature has not been sufficiently well revealed for many types of vegetation. This applies particularly to the vegetation of high mountains. Gams (1927) in his time postulated that in subalpine and alpine belts the summer phases of plant development are omitted and the spring period is followed directly by autumn. Subsequent investigations (Narinyan, 1958; Nakhutsrishvili, 1964; Gadzhiev, 1967), however, showed that, although the growing season is shortened in high mountains, the vegetation passes through the usual series of seasonal stages. As yet there have been very few investigations of the seasonal rhythm of boreal high mountains. All we can cite are the papers of Malyshev (1960) and Krasnoborov (1971) on the high mountains of Siberia, and the work of Gorchakovskii (1975), in which the most general features of the seasonal rhythm of Ural alpine tundras were characterized, the main aspects were described, and the phenological spectra of some plant communities were examined. In the present paper we devote our main attention to a phenorhythmic periodization of the growing season, the course of the phenophases in alpine tundras, and the relative representation of different phenorhythmic groups of plants.

REGION, OBJECTS, AND METHODS OF INVESTIGATION

The investigations were conducted in the Northern Urals, on Mt. Konzhakovskii Kamen'. As objects we selected four alpine-tundra associations: the *Dryas* (stony), the whortleberry–crowberry (low shrub–moss), the dwarf birch–*Hylocomium* (shrub–moss), and the sedge–*Rhacomitrium*–*Hylocomium* patchy (grass–moss) associations. These associations belong to the same ecological-genetic series and reflect the main trends of succession in the alpine-tundra vegetation (Gorchakovskii, 1975). On 100-m^2 sampling areas situated in the alpine-tundra belt at a height of about 1100-1230 m above sea level we conducted phenological observations on 55 species of flowering plants, mainly by Beideman's method (1974), in each community during the growing seasons of 1971 and 1972. The characteristics of the phenological state of the plants were recorded every five days at the start and end of the season and once every three days at the height of flowering. In all cases we determined the percentage representation of the phenophases of the individual species. On a field meterological station observations of the temperature and air humidity at a height of 2 m above the ground were made, and the precipitation was measured. In 1972 the temperature at the soil surface was measured with minimum, maximum, and periodic thermometers, the soil temperature at different depths was measured (with Savinov thermometers), and the air humidity determined, in the investigated types of tundra. The phenological spectra obtained from these observations can be found in a previous paper (Gorchakovskii, 1975).

PHENORHYTHMIC PERIODIZATION OF GROWING SEASON

The growing season begins in alpine tundras, according to the results of observations over two years, in the first two-thirds of June and ends in early or mid September. Its total duration is 75-90 days.

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On the basis of a consideration of the turning points in meteorological conditions and the phenological rhythm of the plants we can subdivide the growing season into three periods: spring (with early- and late-spring stages), summer (with early-, middle-, and late-summer stages), and autumn.

Spring Period. The first thawed patches do not appear in the alpine tundras till late May to early June. The continuous snow cover frequently persists till the end of the first third of July. The subsequent thawing of the snow, however, is very rapid. By the beginning of the last third of June the bulk of the snow has dispersed, although in depressions and at the foot of north and northeast slopes, where a large amount of drifted snow accumulates, patches of snow can persist for a long time (until early or mid July). In alpine tundras in spring there are frequent long spells of heavy rain, lasting for 10-12 days, which assist the rapid dispersal of the snow cover. The temperature conditions at this time are unstable, ground frosts are common, and the mean diurnal air temperature is about +5°C. The soil heats up slowly, especially in moss tundras. For instance, the temperature at a depth of 30 cm on an area of grass–moss tundra was about 0°C or lower up to June 30 inclusive. In the stony tundra at this time the soil temperature at the same depth was +1 to +6°C.

On the snow-free areas, which are grayish yellow due to the dead grass of the previous year, the plants begin to wake from their winter rest and turn green. The spring period lasts two to three weeks on the average. Depending on the meteorological conditions of the particular year, spring can begin early or be late, covering the period from the earliest days of June to June 15-18, or from June 10-12 to June 23-26, but it sometimes does not begin till the last third of June and lasts till the beginning of the following month. On the well-heated southern slopes spring is shorter and more intense than on north and northeast slopes, where this period is rather protracted.

In the colder early-spring stage the alpine tundras owe their characteristic appearance to the dead, grayish yellow sedge foliage of the previous year and the brown leaves of the undershrubs. At this time *Betula nana* and *Arctous alpina* begin to bloom, although the shoots are still not invested with fresh leaves; *Empetrum hermaphroditum* also flowers.

In the late-summer stage many species of plants grow vigorously, and green leaves appear on *Vaccinium uliginosum, Dryas octopetala, Betula nana, Eritrichium villosum, Pachypleurum alpinium,* and *Lagotis uralensis.* At this time buds appear on *Carex bigelowii, Lloydia serotina, Anemone biarmiensis, Pedicularis oederi,* and *Rhodiola rosea.* By the end of the period *Lloydia serotina* begins to flower, together with a few specimens of *Anemone biarmiensis, Carex bigelowii,* and the willows *Salix lanata* and *S. reticulata,* which along with *Rhodiola quadrifida* and *Ranunculus borealis* impart a slightly colorful, yellowish-white aspect.

Summer Period. Summer in the alpine tundras lasts 47-53 days, from the end of June to August 8-12. In this period the mean diurnal air temperatures are close to +10°C. Although night ground frosts occur (especially at the beginning and end of the period), they are fairly rare. The daytime temperatures during the first half of the period steadily rise, reaching a peak (mean diurnal temperature 15°C, maximum temperature +28°C) by mid July. At the start and end of the period the relative air humidity is high (about 90%) and the amount of precipitation is high, whereas in mid summer the humidity is lower, and the precipitation is much less. The adequate moistening of the soil and the establishment of steady mean diurnal temperatures above +10°C in mid July promote the vigorous and rapid growth of the plants and their extensive flowering. The gradual, but sometimes sharp, drop in temperature in late July (to 0°C on certain days) leads to a reduction of the number of flowering species.

The early-summer stage, depending on the conditions of the year, lasts 10-17 days – from June 24-28 to July 3-14. At this time ground frosts occur on certain days (down to -0.1°C in the stony tundra, and to −6.9°C in the grass–moss tundra). The soil is still not sufficiently warm. At a depth of 5 cm the temperature is +6.3 to +11.0°C (stony tundra) and +2.5 to +5.7°C (moss tundra), while at depth 30 cm it is +2.5 to +8.0 and −0.2 to +0.6°C, respectively. Nevertheless, the minimum temperatures on the soil surface are positive (+5.6°C in the stony tundra, and +3.8°C in the grass–moss tundra), and by day the sun heats the soil surface to +18°C. In this period the tundra very rapidly turns green, a process that is assisted by the high air humidity (80% on the average during the stage), the frequent heavy rain (thunderstorms are common), and mists.

At this stage many species bloom: *Pedicularis oederi, Androsace bungeana, Silene acaulis, Salix arctica,* and *Eritrichium villosum.* By the end of this stage up to 8-9 species are in flower.

The mid-summer stage lasts 14-20 days — from July 4-16 to July 23-29. At this time negative temperatures are not observed on the soil surface, and the soil is much warmer than in early summer. In the stony tundra the mean diurnal temperature at a depth of 5 to 30 cm varies from +14.8 to +12.5°C, and in the grass–moss tundra it varies from +7.2 to +3.1°C. The maximum temperature of the ground layer of air is +26°C and the minimum +7°C. The air is much drier: Its relative humidity does not exceed 76%, and the precipitation is half of that of the early-summer or late-summer stages. The meteorological conditions of this stage are most congenial for plants: At this time most of the species are flowering extensively. At the start of this stage *Dryas octopetala, Anemone biarmiensis, Androsace bungeana, Silene acaulis, Carex bigelowii, C. vaginata, Cerastium krylovii,* and *Salix reticulata* bloom abundantly, and *Lagotis uralensis, Vaccinium vitis-idaea, V. uliginosum, V. myrtillus, Valeriana capitata,* and *Saxifraga punctata* less abundantly; *Rumex acetosa* and *Cortusa matthioli* begin to flower. Some species (*Lloydia serotina, Rhodiola quadrifida,* and *Draba lactea*) set fruit. The willow catkins drop off.

In the middle of this stage the number of simultaneously flowering plants reaches a maximum (from 8 to 22 in the different alpine-tundra associations). The flowering plants make a colorful picture — a combination of white (*Anemone biarmiensis, Cerastium krylovii, Dryas octopetala, Valeriana capitata*), pink (*Polygonum bistorta*), crimson (*Silene acaulis, Cortusa matthioli*), blue (*Myosotis asiatica, Eritrichium villosum*), yellow (*Ranunculus borealis, Pedicularis oederi*), and claret (*Sanguisorba officinalis*).

By the end of this stage (July 23-29) *Polygonum bistorta* and *Polygonum viviparum* flower abundantly, and the grasses *Festuca supina* and *Deschampsia flexuosa* shed their panicles. Everywhere *Anemone biarmiensis, Dryas octopetala, Carex bigelowii,* and *C. vaginata* shed their flowers and set fruit. By July 20 the leaves of the sedges and *Betula nana* begin to turn yellow, and the first autumn tints can be seen on the foliage of *Dryas octopetala, Polygonum bistorta,* and *P. viviparum.*

The late summer stage occupies the last third of July and the first half of August and lasts for 19-23 days. At this time the air temperature drops and there are even brief snowfalls, after which warm dry weather returns for a short time and the snow thaws. The minimum temperature on the soil surface drops to +5.4°C in the stony tundra and +2.8°C in grass–moss tundra, the diurnal maximum temperatures fluctuate around +15°C, although they can still reach +25°C on certain days. The soil temperature gradually decreases (to +10°C in stony tundra and to +2.9°C in grass–moss tundra). Protracted drizzle and mists are frequent, accompanied by a general reduction of air temperature. The relative air humidity is 80-90%. In the period of protracted rains the tundras, especially the moss tundras, become waterlogged; streams of water flowing down the slopes can be found among the boulders under the moss at a depth of 10-20 cm.

At the start of the late-summer stage 5-9 species are in flower at the same time, whereas at the end there are now more than 3-5 flowering species left. In late July the grasses *Festuca supina, Anthoxanthum alpinum, Deschampsia flexuosa* begin to flower, *Polygonum bistorta* and *Valeriana capitata* continue to flower, and several species, including *Crepis chrysantha,* flower again, adding, along with *Saxifraga hirculus*, yellow tones to the pink and white aspect. The blue heads of *Campanula rotundifolia* and the claret inflorescences of *Sanguisorba officinalis* are occasionally seen. The majority of plants, however, are in fruit. Many species disperse their fruits and seeds: the sedges at the start of this stage, and subsequently the representatives of other families of flowering plants. By the end of the second third of August only odd flowers of *Saxifraga hirculus, Polygonum bistorta, Sanguisorba officinalis,* and *Cerastium krylovii* are occasionally seen. The leaves of *Betula nana* begin to turn yellow, as do the sedges, grasses, and willows (*Salix reticulata, S. lanata*), while the leaves of *Vaccinium vitis-idaea, Rumex arifolius,* and *Rhodiola rosea* show reddish tints.

Autumn Period. In alpine tundras autumn occurs in the second half of August and the beginning (sometimes middle) of September. There are years when the snow falls very late — not until late September or even early October. The autumn period can accordingly be reduced to 17 days, or extend to 34 days, depending on the conditions of the year. In this period the air temperature drops, sometimes gradually, but usually sharply; ground frosts, thick mists, protracted drizzle, frequently with snow, occur. A dry clear autumn in the alpine tundras of the Northern Urals is a rare event.

At the start of the period 1-3 flowering species can still be found (*Senecio resedifolius,*

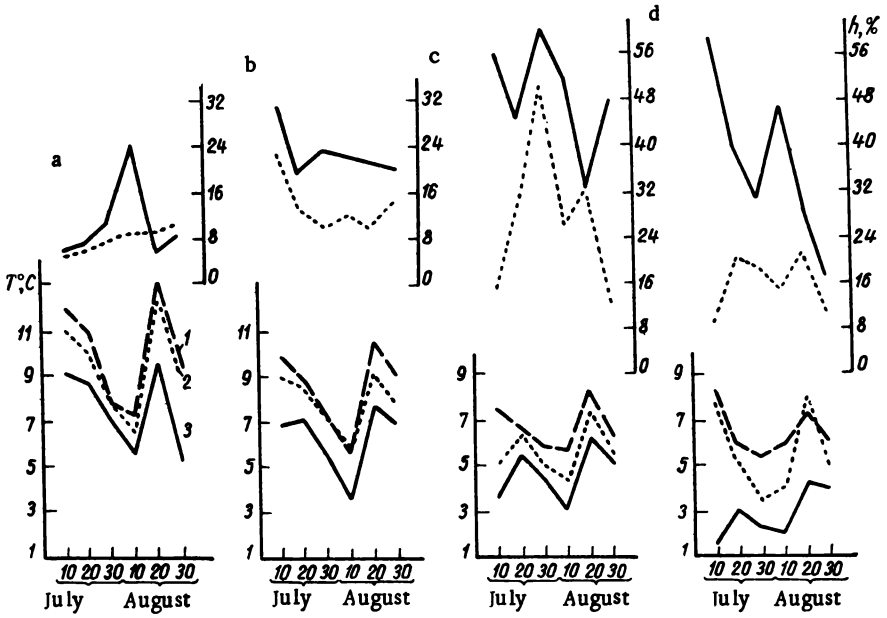

Fig. 1. Seasonal dynamics of mean diurnal temperatures (T, °C), and moisture content (h, %) of soil in alpine tundras: a) *Dryas*; b) wortleberry—crowberry; c) dwarf birch—*Hylocomium*; d) sedge—*Rhacomitrium—Hylocomium;* 1) 5 cm; 10 cm; 3) 30 cm.

Saussurea alpina, Saxifraga hirculus). Many plants bear fruit and disperse their fruits and seeds. By the end of this period the leaves of most species (apart from evergreens) die and the period of winter dormancy begins. An autumn aspect is imparted to the tundra by the brown leaves of the undershrubs *Vaccinium uliginosum* and *Dryas octopetala*, the yellow foliage of sedges and grasses, willows, and *Betula nana*, and the purple patches of foliage of *Rhodiola quadrifida* and *Arctous alpina*.

COURSE OF PHENOPHASES AND THEIR ECOLOGICAL CONDITIONALITY

The main parameters of the environmental conditions in the different periods and stages of the growing season in their most general form are compared with the number of flowering species in Fig. 2. As Fig. 2 shows, the mid-summer stage as a whole is characterized by the most stable and prolonged regime of relatively high temperatures and low relative air humidity. Cold spells during the growing season are accompanied by an increase in air humidity and lead to a reduction in the number of flowering species. In all the investigated alpine tundra associations, the number of flowering species increases steadily from early spring and reaches a maximum in the mid-summer stage. After this the number of flowering species gradually declines. Short warm spells in the autumn period are accompanied by only a slight rise in the flowering curves for some tundra associations.

The seasonal course of temperature and soil moisture content during the period from July 10 to August 30 is illustrated in Fig. 1. The graphs reveal that the curves of the soil temperature at different depths are similar only in general features to the air temperature curve (compare Fig. 2), and do not coincide with it. The course of the soil temperature curves depends to a much greater extent on the seasonal changes in soil moisture: In periods of high moisture content the soil temperature drops to its minimum values, and in periods of low moisture content it reaches its maximum.

The thermal regime of the soil is different in the different associations. The *Dryas* (stony) tundra is characterized by the lowest moisture content, and the greatest warmth. The moisture content is highest in soils of the dwarf-birch—*Hylocomium* (shrub—moss) and sedge—*Rhacomitrium—Hylocomium* (grass—moss) tundras; here the soil has a thick peat layer and heats up poorly.

As a whole the differences in length of the growing season in the different alpine-tundra communities are slight (from 3 to 8 days in different years). In communities with relatively dry, more easily warmed, soils (*Dryas* tundra) the growing season is longer than in

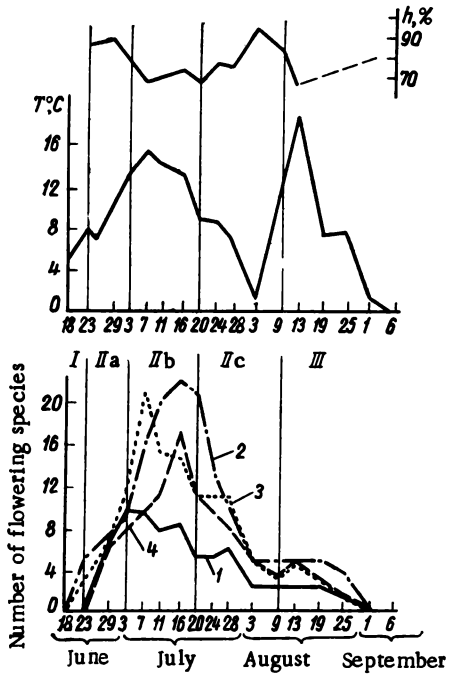

Fig. 2. Relation between seasonal dynamics of mean diurnal temperatures (T, °C) and relative humidity (h, %) of air and number of flowering species in alpine tundras: 1) *Dryas;* 2)whortleberry – crowberry; 3) dwarf-birch – *Hylocomium;* 4) sedge – *Rhacomitrium* – *Hylocomium.* I) Spring period; II) summer period a) early-summer; b) mid-summer; c) late-summer stage; III) autumn period.

communities with moister and colder soils (dwarf-birch – *Hylocomium*, sedge – *Rhacomitrium* – *Hylocomium* tundras).

The general nature of the course of the phenophases in the investigated associations is approximately the same (Fig. 3). The prefloral period is very short: Two or three days later, when the plants start to grow, budding and flowering occur. The budding and flowering curves are mainly unimodal, with steep ascending branches (which indicates vigorous development of the vegetation in the spring – early-summer period) and gentle descending branches. Individual small peaks on the descending branches are due to seasonal changes in the heat and moisture regime and the onset of budding and flowering of late-summer species. Mass flowering occurs for 15-25 days. The fruiting phase is characterized by curves with relatively symmetric ascending and descending branches; the period of mass fruiting extends to 40 days. The nature of the dissemination curves indicates that by the end of the growing season the fruits and seeds of many species are not all disseminated; this process is completed during the winter season.

PHENORHYTHMIC PLANT GROUPS

Alpine-tundra plants, depending on the association of their flowering with particular periods and stages of the season, can be subdivided into six groups: early-spring, late-spring, early-summer, mid-summer, late-summer, and autumn.

1. Early spring (5.4% of species): *Arctous alpina, Betula nana, Empetrum hermaphroditum.*
2. Late spring (14.6% of species): *Carex bigelowii, Lloydia serotina, Ranunculus borealis, Rhodiola quadrifida, Rh. rosea, Salix glauca, S. reticulata, S. lanata.*
3. Early summer (14.6% of species): *Androsace bungeana, Anemone biarmiensis, Draba lactea, Eritrichium villosum, Salix arctica, Silene acaulis, Pachypleurum alpinum, Pedicularis oederi.*
4. Mid summer (56.4% of species): *Anthoxantum alpinum, Carex capillaris, C. halleri, C. sabynensis, C. vaginata, Cortusa matthioli, Dryas octopetala, Festuca supina, Lagotis uralensis, Melandrium apetalum, Myosotis asiatica, Polygonum bistorta, P. viviparum, Potentilla crantzii, Pyrola grandiflora, Sanguisorba officinalis, Saxifraga punctata, S. hieracifolia, S. hirculus, Scorzonera ruprechtiana, Senecio campester, S. resedifolius, Trientalis europaea, Thalictrum alpinum, Vaccinium uliginosum, V. vitis-idaea, V. myrtillus Valeriana capitata, Viola biflora.*
5. Late summer (5.4% of species): *Campanula rotundifolia, Deschampsia flexuosa.*
6. Autumn (last third of August to first or second third of September; 3.6% of species): *Saussurea alpina, Solidago virgaurea.*

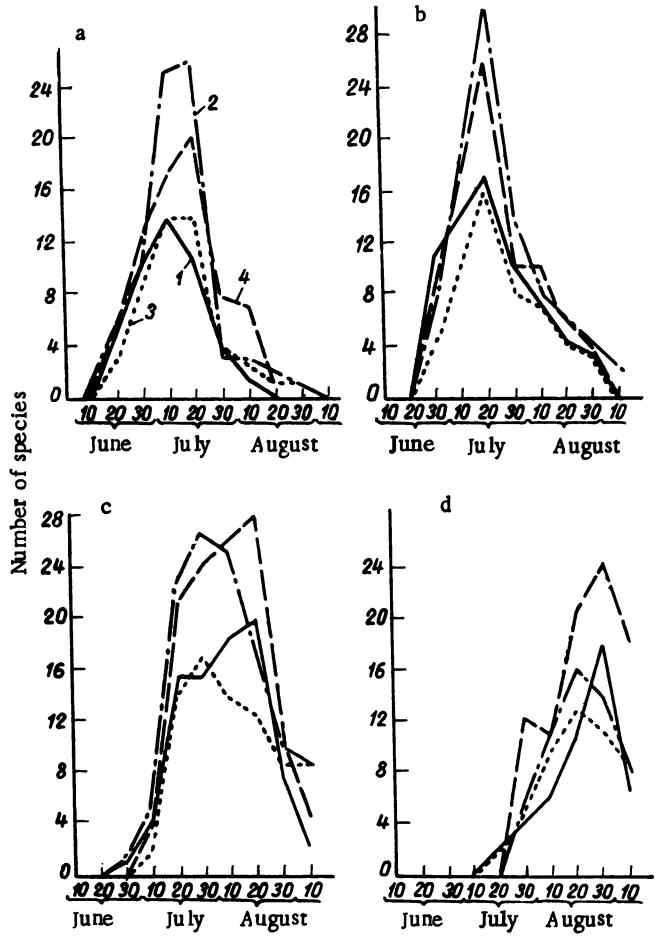

Fig. 3. Seasonal dynamics of phenological phases of plants in alpine tundras: a) budding; b) flowering; c) fruiting; d) dissemination; 1-4) same as in Fig. 2.

This division is arbitrary to some extent, since the flowering time of some species is protracted, and although their mass flowering occurs in only one stage, they can be found in flower in other stages too.

As the above list shows, many of the plant species occurring in alpine tundras belong in their flowering phases to the late-spring, early-summer, and mid-summer categories; the group of mid-summer plants, which includes more than half the species, is particularly large.

SUMMARY

1. In alpine tundras of the Northern Urals the growing season lasts 75-90 days, depending on the meteorological situation in the particular year, and also on the moisture content and degree of heating of the soils in the different plant associations. On the basis of the set of meteorological and phenological features the season can be subdivided into three periods: spring (with early-and late-spring stages), summer (with early-, mid-, and late-summer stages, and autumn. The shortness of the growing season is responsible for the rapid succession of periods and stages. The initial stages (early- and late- spring, early-summer) are particularly short; the late-summer and autumn stages are more protracted.

2. In alpine-tundra plant communities the prefloral period is very short (2-3 days), the onset of budding and flowering is very rapid, the period of mass flowering is 15-25 days, the period of mass fruiting extends to 40 days, and the dissemination of many plants is not completed by the end of the growing season.

3. The peak of flowering of alpine-tundra plants coincides with the warmer and drier mid-summer stage, when the mean diurnal air temperatures reach 10-15°C, and the relative air humidity usually does not exceed 70-80%. The peak of fruiting occurs in the late-summer stage, when the soil in alpine tundras is warmest.

4. Depending on the association of their time of flowering with the periods and stages of the growing season, six groups of alpine-tundra plants can be distinguished: 1) early-spring; 2) late-spring; 3) early-summer; 4) mid-summer; 5) late-summer and 6) autumn. The fourth group contains most species (57% of all the species considered) followed by the second and third groups (14.6% each), first and fifth (5.4% each) and, finally, the sixth (3.6%).

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