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Genet age in marginal populations of two clonal *Carex* species in the Siberian Arctic

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During a Swedish-Russian expedition to northern Siberia 1994, we sampled two marginal populations of two *Carex* species at two high arctic sites (*C. stans* Drej. on Faddeyevsky Island and *C. ensifolia* V. Krecz ssp. *arctisibirica* Jurtz. at north-eastern Taymyr Peninsula), both north of previously documented localities in that areas for the two species. These populations were composed of a few distinct patches of ramet colonies, some of them shaped like fairy rings with dead centres. We measured the size of all colonies and collected samples for detailed morphometric analyses of rhizome growth. By using RAPD (random amplified polymorphic DNA) analysis we established that the largest colony at each site consisted of a single genet, based on 41 polymorphic bands amplified with three primers. Pooled samples from each of two additional colonies of *C. stans* on Faddeyevsky Island were analysed and showed that clones of the same species at the same site were relatively dissimilar (Dice's similarity index 0.26–0.43). We then assumed that each ramet colony represented a single genet. Based on the morphometric data, we developed a deterministic growth model that simulates the clonal growth of these species and enabled estimates of the time since establishment of the genets. The estimated age of the five *C. stans* clones varied from 17 to 154 yr and the age of the two *C. ensifolia* ssp. *arctisibirica* clones was well over 3000 yr.

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Various rhizomatous *Carex* species are an important component in tundra vegetation. To be able to understand tundra vegetation dynamics, studies are needed on population dynamics of these pronounced clonal plants, at both the ramet and the genet level. There are several studies at the ramet level in arctic *Carex* species while studies at the genet level are rare. One reason for this is that establishment of new genets in closed vegetation is apparently far too infrequent to be observed in conventional population studies (Jónsdóttir 1995, Jonsson et al. 1996). However, a study on genetic variation in populations of *Carex bigelowii* in Iceland revealed high levels of variation and genet diversity, comparable

to out breeding plant populations with frequent establishment of new genets (Jonsson et al. 1996). This may indicate that some genets survive for a very long time and during that time a considerable number of their offspring may get the chance to establish successively. It is therefore crucial to get estimates of genet age in genet level studies of clonal plants.

Published records indicate potential for extreme genet longevity among some clonal plant species with the highest record of 10000 yr in *Populus tremuloides* (Kemperman and Barnes 1976). However, most studies have used phenotypic characters to identify genets, as for example morphological markers and self-incom-

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patability systems in grasses (Harberd 1961, 1967), or it has been assumed that a well-defined colony of ramets constitutes a single genet (Oinonen 1967, 1969, Vasek 1980). Usually, individual *Carex* genets cannot be distinguished on morphological characters, but studies using molecular markers show that individual genets do not intermingle much (Jonsson 1995, Steinger et al. 1996). In their study of the compact species (i.e. phalanx-type, sensu Lovett Doust 1981), *Carex curvula*, from alpine grasslands in the Central Alps, Steinger et al. (1996) used a DNA-based approach to identify different genets. Estimated annual rate of horizontal growth was then used to calculate genet age. The estimated age of the largest clone in their plot was at least 2000 yr.

Population dynamics of common rhizomatous *Carex* species with loosely packed ramets, closer to the guerrilla-type (sensu Lovett Doust 1981), was studied in relation to climate and herbivory during a Swedish-Russian expedition along the whole Eurasian coast, Tundra Ecology – 94 (Jónsdóttir et al. unpubl.). Here we report on a study of genet age in two of these species, *C. stans* Drej. and *C. ensifolia* V. Krecz ssp. *arctisibirica* Jurtz., found at two high arctic sites visited during the expedition, north of earlier published records for the species in that areas (Hultén and Fries 1986, Tolmachev 1996) (Fig. 1). The dominance of *Carex* species in Eurasian tundra vegetation tends to decline towards the north (Chernov and Matveyeva 1997, Jónsdóttir et al. 1999) and at these two high arctic sites we encountered only widely separated circular patches of ramet colonies. Some of the colonies formed fairy rings with empty centres, a phenomenon more commonly observed among clonal plants closer to the phalanx-type of lateral spread (Watt 1947, Shirreffs and Bell 1984, Cain et al. 1991, Adachi et al. 1996a). If granted that each ramet colony represents a single genet, this kind of situation provides a unique opportunity to gain new insight in genet level population

dynamics of clonal tundra plants that would be impossible at sites with more tightly packed and overlapping genets.

We measured the size of each ramet colony and sampled them for genet identification by RAPD (random amplified polymorphic DNA) analyses. Morphometric characters that may influence the rate of horizontal spread were measured, but the short time spent at each site during the expedition (2 d) allowed us only to obtain detailed data from one large fairy ring per site. A deterministic growth model was developed and used to estimate the age of the genets based on the morphometric data and the size measurements of genets. The implication of the results for genet level population dynamics within remote populations of clonal tundra plants at the extremes of species distribution is discussed.

Materials and methods

The species and sites

The two species studied, *Carex stans* Drej. and *Carex ensifolia* V. Krecz ssp. *arctisibirica* Jurtz. (here just called *C. ensifolia*), both belong to the section *Acutae*. The first species is sometimes considered to be a subspecies of *C. aquatilis* and the latter species a member of the species complex *Carex bigelowii* s. lat. (Murray 1994). Both species form dense populations in the tundra vegetation zone with declining dominance towards north (Chernov and Matveyeva 1997, Jónsdóttir et al. 1999), but the distribution limits of *C. stans* extend further north than the limits of *C. ensifolia* (Fig. 1). They appear to have different but partly overlapping habitat preference: *C. stans* grows mainly at wet to moist sites whereas *C. ensifolia* grows at mesic to dry sites and is restricted to more acid bedrock. In the absence of *C. ensifolia*, *C. stans* may, however, also

Fig. 1. General distribution of *Carex stans* and *C. ensifolia* ssp. *arctisibirica* in Eurasia. The two study sites were Faddeyevsky Island (site number 13.1) and north-eastern Taymyr Peninsula (site number 10). Based on Hultén and Fries (1986) and Tolmachev (1996).

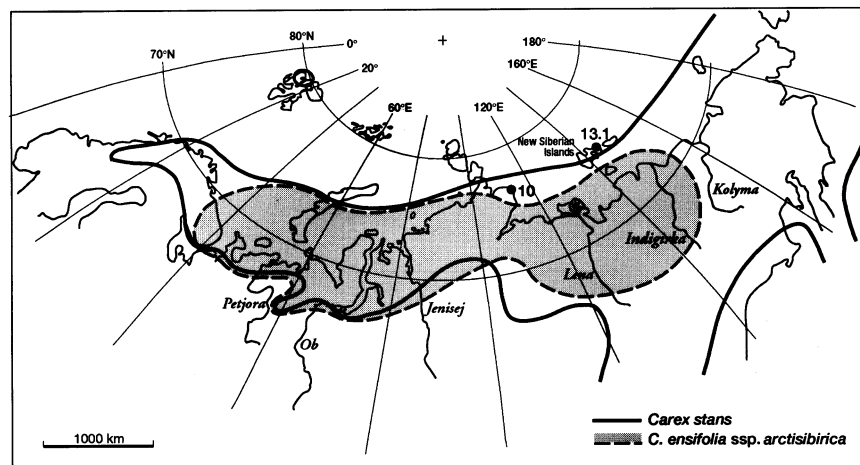


Table 1. Size and shape of all ramet colonies encountered Faddeyevsky Island (*C. stans*) and north-eastern Taymyr (*C. ensifolia* ssp. *arctisibirica*) and the distance between colonies within sites.

Colony	Radius (m) ¹	Fairy ring formed	Distance from S1 or E1 (km)
<i>C. stans</i>			
S1 ²	3.67	yes, intact	0
S2	0.40	no	0.7
S3	1.50	no	ca 2
S4	2.25	no	ca 2 (ca 30 m from S3)
S5	2.00	yes, intact	ca 2 (ca 30 m from S3)
<i>C. ensifolia</i>			
E1 ²	15.0	yes, fragmented	0
E2	20.0	yes, fragmented	0.2

¹ The radius of the fairy rings was calculated as the maximum diameter divided by 2. This is a conservative measure since the origin of the ring may have been off centre. ² Colonies on which morphometric analyses were done.

grow at mesic to dry sites. *Carex stans* has a distinct ramet differentiation into long and short rhizome ramets. Only the long rhizome ramets produce roots and daughter ramets. Although rhizome lengths vary considerably in *C. ensifolia*, there is no such clear-cut ramet differentiation in this species.

Both study sites are high arctic and according to Russian terminology they belong to a vegetation subzone of the Eurasian Arctic called arctic tundra (Chernov and Matveyeva 1997). Faddeyevsky Island (75°29'N, 143°09'E) is one of the New Siberian Islands. Mean annual temperature at the closest meteorological station (Sannikova Strait) is –14.9°C, mean July temperature 2.3°C (Goryachkin et al. 1994) and July mean 1993 and 1994 was 2.1 and 2.7°C, respectively (Kotelnny Island, Obninsk Meteorological Data Center). At this site we encountered ramet colonies of *C. stans*, ca 200 km north of the previously published northernmost record for the species on the Islands (Hultén and Fries 1986, Tolmachev 1996). The second site, at north-eastern Taymyr Peninsula (76°27'N, 111°13'E), is within the general distribution limits of *C. stans* (Fig. 1), although we did not find it there. We did, however, find colonies of *C. ensifolia*, ca 300 km north of the closest, previously published record for this species on Taymyr (Hultén and Fries 1986, Tolmachev 1996). The mean annual temperature at the closest meteorological station (Andrey Island) is –15.3°C, mean July temperature 3.0°C (Goryachkin et al. 1994) and the July mean 1993 and 1994 was 0.8 and 3.5°C, respectively (Andrey Island, Obninsk Meteorological Data Center).

Sampling

Carex stans at Faddeyevsky

On 10–11 July 1994 we visited Faddeyevsky Island. Five isolated and almost circular ramet colonies of *C. stans* (called S1–S5) were found at some distance from each other (Table 1) within an area of several square kilometres. Evidence of flowering was only found in the largest colony, S1, where 3% of the ramets had flowers

at an early stage of development (*Carex* ramets that will flower during the current season are easily identified long before anthesis). Two colonies (S1 and S5) formed regular fairy rings where the ring itself was about one metre wide encircling an empty centre. The size of the colonies and the intervening distance was measured. For later identification of genets by use of RAPDs, 23 green shoots were collected at random from S1 and kept cool until transferred to a –80°C freezer on board the expedition vessel. In addition, one pooled sample consisting of 10 randomly chosen shoots, was collected from each of two smaller colonies, S3 and S4.

More detailed samplings and measurements were taken from the S1 fairy ring (Fig. 2a). This ring was on dry, level ground on the rim of a shallow ravine, with 80% vegetation cover, dominated by scattered tussocks of *Luzula* spp. with lichens in between. Ten clonal fragments (= a branch of a larger clone, consisting of a number of interconnected ramet generations and more numerous ramets) were sampled at random and pressed dry for later analysis of variables that were assumed to be important for horizontal growth of a genet. Each excavated fragment consisted of a minimum of three, but more usually of five to seven, interconnected ramet generations. Before excavating the fragments we measured the branching angles. Ramet generation time (= the period from “birth” of a ramet to first production of own daughter ramets) was assessed by carefully studying these fragments and comparing them with earlier studies, based on detailed observations on clonal growth in *Carex* at time intervals (Jónsdóttir 1991). The following was recorded for each ramet of the sampled fragments (Fig. 3): 1) the apical meristem status (alive or dead). 2) Whether the ramet was established (i.e. whether a horizontal rhizome had turned upwards to differentiate into a vertical shoot, rooted or unrooted). 3) If established, rhizome length was measured and number of internodes on rhizome counted. 4) The number of daughter ramets produced per ramet. 5) The position of daughter ramets, i.e. dorsally, ventrally or at either the right or left side of the mother rhizome. 6) Category of daughter ramet [with long, intermediate or

short rhizome; only those with long and intermediate rhizomes (collectively termed “spreading ramets”) produced daughter ramets in their turn, the short rhizome ramets being “dead ends” in terms of horizontal growth]. 7) The number of dormant buds.

For ramets with dead apical meristems (“below ground ramets”), i.e. those ramets that give an estimate of final daughter ramet and bud production per ramet (e.g. Callaghan 1976, Jónsdóttir 1991), the following was calculated, based on measurements 1–7: 8) potential daughter ramet production (mean values of “4” + “7”). 9) Proportion of ramets with a long or an intermediate rhizome, i.e. spreading ramets. 10) The number of spreading ramets produced per mother ramet (the mean value of “4” × “9”). 11) The frequency of spreading ramets originating ventrally, dorsally, on the right side, and on the left side of the mother rhizome. 12) Probability of establishment among spreading ramets (number of established ramets divided by total number of ramets).

Carex ensifolia at north-eastern Taymyr Peninsula

On 10–12 August we visited north-eastern Taymyr Peninsula and searched seemingly suitable habitats for

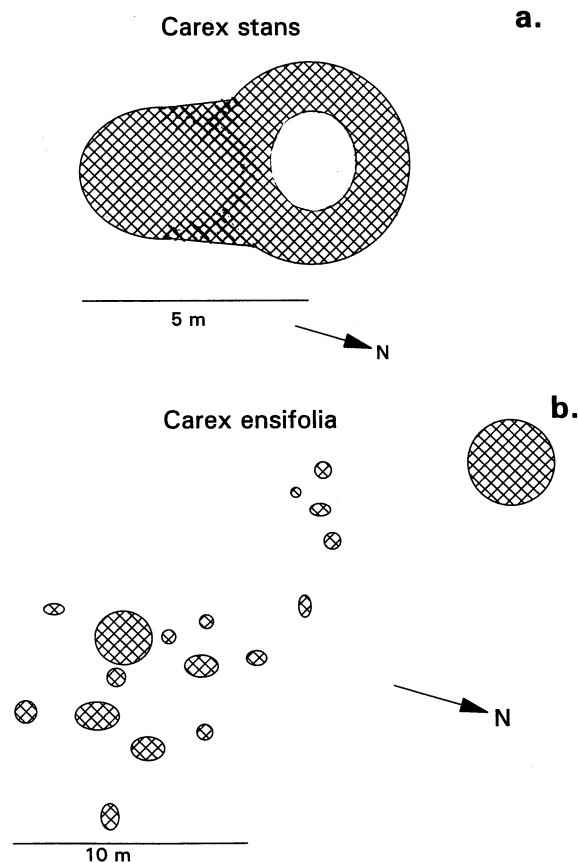


Fig. 2. a. Sketch of an intact *Carex stans* fairy ring (S1) at Faddeyevsky Island. b. Sketch of a fragmented *C. ensifolia* ssp. *arctisibirica* fairy ring (E1) at NE Taymyr.

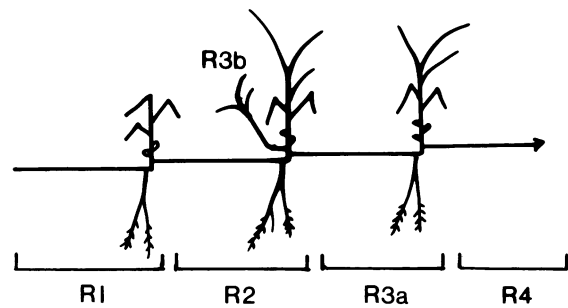


Fig. 3. Schematic clonal fragment of *Carex* that consists of four ramet generations. Ramet generation 1, R1, is represented by an established ramet with dead apical meristem (only dead leaves attached, cannot produce any more leaves, daughter ramets or buds), one spreading daughter ramet and two dormant buds. R2 is established, with living apex, two daughter ramets (one spreading and one with short rhizome) and two dormant buds. R3a is established, with living apex, one daughter ramet and three buds. R3b is an established short rhizome ramet, with living apex. R4 is not established (still growing as a horizontal rhizome), with living apex. For further explanations, see text.

Carex over several square kilometres. We only found two large, but fragmented ramet colonies of *C. ensifolia* (called E1 and E2) ca 200 m apart. Each colony formed an irregular fairy ring. No evidence of flower development was found in either colony. Due to lack of time we only managed to do detailed measurements on, and collect samples from E1 before we were forced to return to the expedition vessel. This colony was on level ground on top of a small hill and was composed of 18 discrete patches (Fig. 2b). The total vegetation cover was 50–60%, dominated by *Luzula* spp., *Oxyria digyna*, *Salix* spp., *Alopecurus* spp., bryophytes and lichens. For DNA analysis, we collected one green shoot from each of the 18 patches, plus another two shoots from the two largest patches. These samples were treated in the same way as at the previous site. For later detailed morphometric analysis, clonal fragments were collected from 10 randomly chosen patches. Measurements of branching angles before fragment excavation are missing, but they are assumed to be similar to what has been found in a close relative from Iceland, *C. bigelowii* s. str., or 60° on average (Jónsdóttir unpubl.). The fragments were analysed in the same way as described for *C. stans* above, except that the daughter ramets were not divided into different rhizome length categories.

RAPD analysis of *Carex*

Samples and DNA isolation

A total of 25 samples from three colonies in Faddeyevsky (23 single-shoot samples from the largest colony, S1, and one pooled sample from each of two smaller colonies, S3 and S4) and 20 samples from one colony (E1) at NE Taymyr were analysed at the DNA-

laboratory at Balsgård, Sweden. Genomic DNA was isolated using the method of Nybom and Schaal (1990), except that the RNase treatment of the DNA preparation was omitted.

RAPD analysis

Two samples from the two different sites were screened with 14 decamer primers (Operon Technologies, Alameda, CA, USA). Six primers (OPB-05, OPB-07, OPB-11, OPB-12, OPB-17 and OPB-18) were then selected for further analysis since they yielded polymorphic and reproducible bands. The size of amplified DNA fragments ranged from 230 to 1750 base pairs. All 45 samples were analysed with three of the primers in order to identify putative clones. To get more bands for calculations of similarity values, representatives of each genotype were then analysed with the rest of the six primers.

In a final volume of 25 µl, each PCR reaction contained 20 ng of DNA, 1 × reaction buffer IV (Advanced Biotechnologies, Epsom, Surrey, U.K.), 1.5 mM MgCl₂ (Advanced Biotechnologies), 0.6 µM primer, 0.2 mM PCR Nucleotide Mix (Boehringer Mannheim Scandinavia, Bromma, Sweden) and 1.0 unit Taq DNA Polymerase (Advanced Biotechnologies). The thermal cyclor (MJ Research) was programmed for 1 cycle of 5 min at 94°C followed by 40 cycles of 1 min at 94°C, 1 min at 36°C and 2 min at 72°C and finally by 1 cycle of 7 min at 72°C. DNA fragments were separated by electrophoresis in 1.8% agarose gels with a TPE buffer system. Gels were stained with ethidium bromide, visualized by UV light and the fragment patterns were photographed for further analyses. Molecular Weight Marker VI (Boehringer Mannheim) was used to determine the size of the DNA fragments.

Statistical evaluation

Bands were scored manually for absence and presence. Similarity between genotypes was evaluated by Dice's similarity index (Dice 1945), also known as Nei and Li's index as well as Lynch's index: $S = 2n_{ab}/(n_a + n_b)$, where n_a and n_b are the number of bands in genotypes a and b respectively, and n_{ab} is the number of bands shared by genotypes a and b.

Growth model

The aim of this model is to provide an estimate of the age of a genet of known size. In order to simplify the calculations we used average branching angles of ramets rather than the frequency distribution of observed branching angles, i.e. we employ a deterministic rather than stochastic method (e.g. Cain 1990, Cain et al. 1991, Adachi et al. 1996b). As is further shown below the estimated error introduced by this simplification is very small indeed.

To calculate the approximate age of the clones, we use the following model:

Clone radius =

$$\frac{\text{Average ramet length} \cdot \text{Divergence factor} \cdot \text{Age}}{\text{Average generation time}} \quad (1)$$

The radius of the clone is measured in meters, and denoted by R. We have the average rhizome length of a ramet, L, from the morphometric data (Table 2). The divergence, D, of the radial growth from the actual growth depends on the average branching angle of daughter ramets; while some daughter ramets grew at an angle of the mother ramet, others grew in the same direction as the mother. This divergence factor can be calculated using a trigonometric function:

$$D = L \cdot \cos\left(\frac{\bar{V}}{2}\right) \quad (2)$$

where \bar{V} is the average branching angle (Fig. 4).

By Taylor expansion the error introduced by using average branching angle can be estimated from:

$$E\left(\cos\frac{\bar{V}}{2}\right) \approx \cos\frac{\bar{V}}{2} - \frac{1}{2}\cos\frac{\bar{V}}{2} \cdot \text{Var}\left(\frac{\bar{V}}{2}\right) \quad (3)$$

which, for the typical variances in branching angles found in our data, means that the deterministic method introduces a deviation of < 5% from the estimated value.

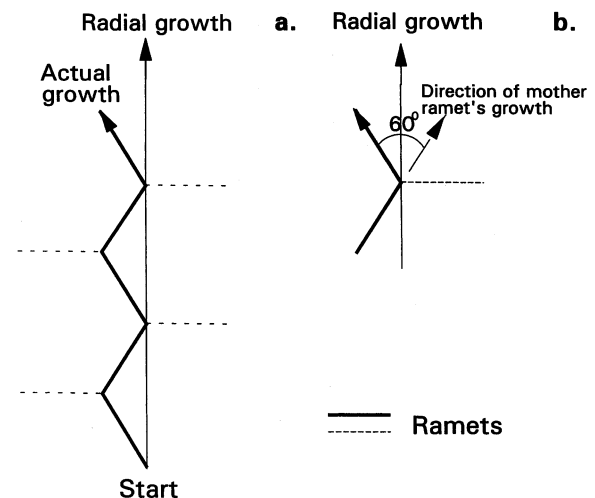


Fig. 4. An example of rhizomatous, clonal growth with branching ramets. a. Actual growth of consecutive, branching ramets vs radial growth of the clone. b. With daughter ramets branching at 60° angle from direction of growth of the respective mother ramet's, the average deviation between actual growth and radial growth is half the branching angle (in this case 60°/2 = 30°).

Similarly, by Taylor expansion a standard error of $V/2$ can be estimated from the formula:

$$\text{Var}\left(\cos \frac{V}{2}\right) \approx \text{Var}\left(\frac{V}{2}\right) \sin^2\left(\frac{\bar{V}}{2}\right) \quad (4)$$

giving a standard error (for the *Carex stans* clone of Table 2) of ca 2% of the mean.

The average generation time, T , depends on the minimum time it takes for a ramet to grow from its activation to the production of daughter ramets, t ; on the probability of the establishment of a daughter ramet, p ; and on the number of potential daughter ramets per mother ramet, N . We assume that a mother ramet activates one daughter ramet at a time, and that mortality among daughters occurs randomly. If the daughter ramet survives and becomes established, then all is well and the cycle is repeated all over again. If the daughter fails to become established, the mother ramet activates another daughter ramet the following year, which in turn may fail or succeed, and so on. If the mother ramet has an infinite number of potential daughter ramets, then even the most unlucky mother eventually will have a successful daughter. (As long as

the probability of establishment, p , is larger than zero, then with an infinite number of daughters there is no possibility that they all will fail.) The expected average generation time is calculated as a series. However, when the number of potential daughters is infinite, mortality occurs at random, and the mother activates one daughter per year, this series equals the function:

$$\langle T \rangle = \frac{t}{p} \quad (5a)$$

However, in our case, since it takes a mother ramet two years from establishment to the activation of the first daughter ramet, we have to modify eq. (5a)

$$\langle T \rangle = 1 + \frac{t}{p} \quad (5b)$$

to obtain the appropriate expected value of T . In our cases, with rather high probabilities of establishment of daughter ramets and around 4 potential daughters per mother ramet (Table 2), we found that the discrepancies between the values of T given by eq. (5b) and those

Table 2. Morphometric data from clonal fragments sampled from colonies S1 (*C. stans*, Faddeyevsky Island) and E1 (*C. ensifolia* ssp. *arctisibirica*, north-eastern Taymyr Peninsula). Letters in brackets denote the parameters used in the growth model.

Parameter estimates		<i>Carex stans</i>	<i>Carex ensifolia</i>
a.	Number of fragments analysed	10	10
b.	Number of ramets analysed	113	102
c.	Number of ramet generations per fragment (mean \pm SD)	5.7 ± 1.3	4.8 ± 2.7
d.	Length of rhizome (mean \pm SD) [L]	83 ± 55 mm (n = 113) ¹	14 ± 13 mm (n = 86) ²
e.	Branching angle (mean \pm SD) [V] ³	$57.8^\circ \pm 22.05$ (n = 61)	?
f.	Position of daughter ramets – proportions (“spreading ramets” ¹ within brackets):	n = 203 (n = 104)	n = 84
	• Angling to the right	0.246 (0.22)	0.190
	• Angling to the left	0.167 (0.15)	0.155
	• Same angle – ventral	0.365 (0.61)	0.500
	• Same angle – dorsal	0.222 (0.02)	0.155
g.	Generation time [t]	2 yr	2 yr
h.	Number ramets with dead apex	48	58
i.	Number of daughter ramets per mother (mean \pm SD)	2.41 ± 0.93 (n = 46) ^{4,5}	1.65 ± 1.05 (n = 51) ⁴
j.	Proportion of “spreading ramets” ²	0.417 (n = 103)	
k.	Number of “spreading ramets” per mother	1.005	
l.	Number of dormant buds per mother (mean \pm SD)	2.45 ± 1.06 (n = 38) ^{4,5}	2.13 ± 1.41 (n = 47) ⁴
m.	Number of potential daughter ramets per mother (mean \pm SD) [N]	4.92 ± 1.51 (n = 38) ^{4,5}	3.85 ± 1.89 (n = 47) ⁴
n.	Number of established ramets with dead apex	45	52
o.	Probability of establishment (n/h) [p]	0.9375 ⁴	0.8965 ⁴

¹ *Carex stans* had a marked ramet differentiation: ramets with short, intermediate, and long rhizome. Rhizome length was measured only on established “spreading ramets”, i.e. intermediate and long rhizome ramets that could continue horizontal growth through production of daughter ramets. ² Average rhizome length of all established ramets. There was no marked ramet differentiation in *C. ensifolia*. ³ Average branching angle is calculated as $V/2$, where $V = (\text{Proportions of left and right angling daughter ramets}) \times (\text{branching angle})$. For the daughter ramets having the same growth direction as the mother, there is no deviation. For the division by 2, see Fig. 4. We have no certain measurement for the branching angles of *C. ensifolia*; in the growth model we use an estimate of 60° , the results of the model are rather insensitive to angles lower than 60° . ⁴ Based on ramets with dead apex (below ground ramets) only (see h.), i.e. ramets that had terminated their apical growth due to death of the apical meristem, to get an estimate of the final number of daughters or buds produced. ⁵ Including potential “dead ends”, i.e. short rhizome ramets.

we obtained from the calculations of the series only occurred on the fourth decimal, and for our purposes eq. (5b) is sufficient.

We can now rewrite eq. (1) and solve it for Y, the number of years since the first establishment of the clone,

$$Y = \frac{R \left(1 + \frac{t}{p} \right)}{L \cdot \cos \left(\frac{\bar{V}}{2} \right)} \quad (6)$$

This equation, then, assumes a linear relationship between clone radius (R) and clone age (Y). Using our data the resulting relations become $Y_S = 42 \cdot R$ and $Y_E = 259 \cdot R$ for *C. stans* and *C. ensifolia*, respectively.

Results

The radius of the five *C. stans* colonies found on Faddeyevsky ranged from 0.4 to 3.7 m and the distance between them varied from 30 to 2000 m (Table 1). The two *C. ensifolia* colonies at NE Taymyr were much larger, with an estimated radius of 15 and 20 m (Table 1).

Morphometric analysis

The two rhizomatous tundra sedges show many similarities in their pattern of clonal growth (Table 2). When only the spreading ramets in *C. stans* are considered, the frequency of branches (i.e. daughter ramets) angling either to the left or right of the axis of the mother ramet was similar to that in *C. ensifolia*, or ca 35%. The other 65% of the daughter ramets had the same direction as the mother. Inspection of the different developmental stages of the ramets and at which stage daughter ramets are produced revealed the following pattern for the spreading ramets in *C. stans* and for all ramets in *C. ensifolia*: after initiation, a ramet grows as a horizontal rhizome during the first growing season (see R1 in Fig. 3). In the second season, the rhizome turns upwards and differentiates into a shoot (at this stage the ramet has a few green leaves and no old leaves attached). The ramet initiates its first daughter ramets during the third season (at this stage it has several green leaves and the last year's dead leaves attached, see R3a in Fig. 3). This gives a generation time of about two years. The probability of ramet establishment was also similar for the two species or close to 90%. Because each analysed fragment consisted of 5–6 different ramet generations, the morphometric data merges variation in ramet growth and establishment over 10–12 yr, given a generation time of two years.

There are three main differences between the species. First, the ramet differentiation found in *C. stans* into long (spreading) and short rhizome ramets is absent in *C. ensifolia*, where all established ramets appear to be potentially able to continue horizontal growth through production of daughter ramets (Table 2). Second, *Carex stans* is more robust with rhizomes that are on average almost six times as long as those of *C. ensifolia* if only the spreading ramets are considered (Table 2). Finally, the horizontal spread of *C. stans* is more of a guerrilla type than *C. ensifolia* (a rhizome length: shoot height ratio ca 0.7 in *C. stans* compared to 0.2 in *C. ensifolia*, if only spreading ramets are included; shoot height data not shown here).

RAPD analyses

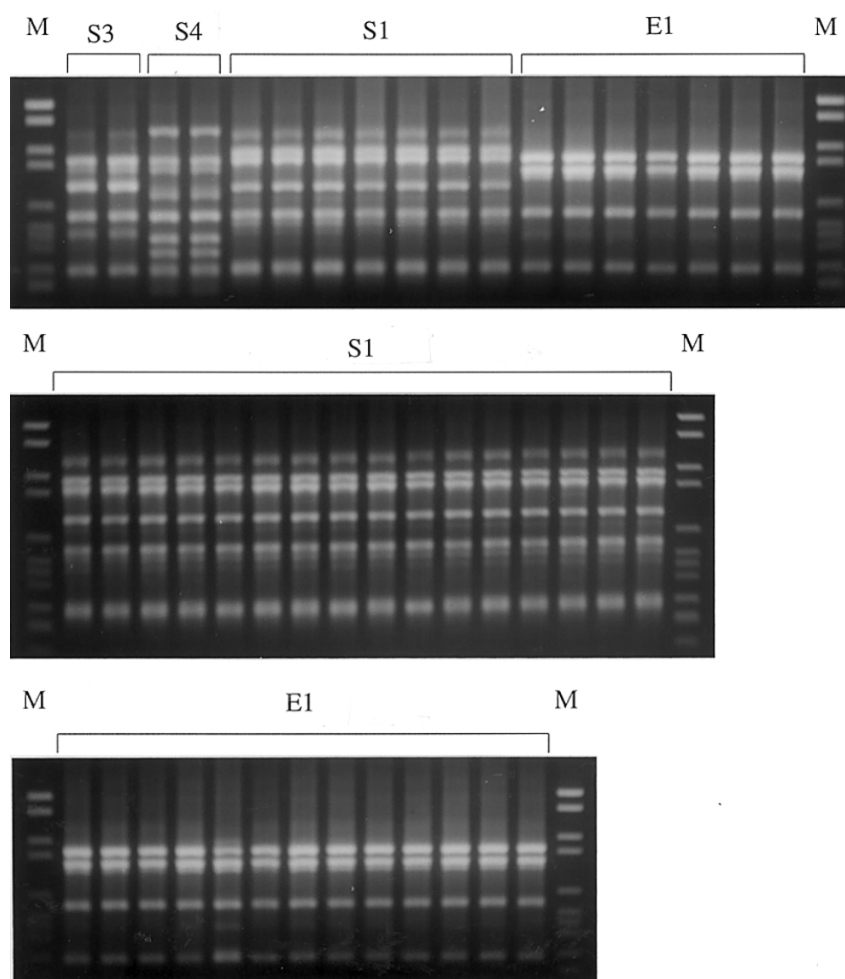
The profiles of the amplified fragments from each sample were compared to each other and a total of four different genotypes (putative clones) were found, based on 41 polymorphic bands amplified with three primers. All 23 samples analysed from the large regular fairy ring on Faddeyevsky, S1, showed identical band patterns (Fig. 5). The two analysed samples from colonies S3 and S4 showed unique band patterns which, however, may represent several genotypes since 10 shoots had been pooled from each of these colonies. Samples from S3 and S4 were amplified twice to ensure reproducibility. To conclude, the three Faddeyevsky colonies were represented by different genotypes, and the large colony appears to consist of a single genotype. Similarly, all of the samples from the large, fragmented fairy ring at NE Taymyr, E1, showed identical band patterns and therefore belong to the same genet (Fig. 5). The number of unique bands identifying different genotypes ranged from three to twelve (Table 3).

Representatives of each genotype were then analysed with the rest of the six primers. Altogether, the six primers yielded 67 bands of which 59 were polymorphic (88%). Within *C. stans*, a total of 51 bands were found and 40 of these (78%) were polymorphic. The similarity between pairs of genotypes ranged from 0.04 to 0.43 (Table 4). The lowest similarity coefficients were found between the *C. ensifolia* genotype on the one hand and the three *C. stans* genotypes on the other hand (0.04–0.18). Pairwise comparisons among the three *C. stans* genotypes showed similarity indices of 0.26–0.43. The highest similarity coefficient (0.43) was not found between the closest *C. stans* genets (S3 and S4), but between S1 and S3 which are separated by ca 2 km.

Growth model

To calculate the approximate age of the two fairy rings, we inserted the values given in Table 2 into eq. (6). We

Fig. 5. RAPD patterns in the four different *Carex* colonies generated by primer OPB-18. M stands for molecular size marker. S1, S3 and S4: *C. stans* on Faddeyevsky Island. E1: *C. ensifolia* ssp. *arctisibirica* at north-eastern Taymyr Peninsula.



found that the *C. stans* fairy ring was ca 150 yr old, while the one of *C. ensifolia* was > 3800 yr old. Because of the high probabilities of ramet establishment and because the average branching angles were not too extreme, the factors that affected the results the most were the length of rhizomes and the radius of the fairy rings. The age of the other three *C. stans* clones at Faddeyevsky and the second *C. ensifolia* clone found at NE Taymyr were calculated by assuming that the model parameters had the same value for all clones

within species as for S1 and E1, respectively. The age of the other *C. stans* clones varied from 17 to 94 yr and the E2 clone was over 5000 yr (Table 5). These results should be seen as conservative measures. We assumed that the establishment had occurred at halfway along the widest extent of the clone. Any deviation from this assumption would result in even a higher age.

Discussion

In rhizomatous *Carex* species it is usually impossible to see the limits between the different genets because the individual genets are tightly packed and they lack distinct morphological markers. This was also true for the majority of the populations of three *Carex* species (including *C. stans* and *C. ensifolia* ssp. *arctisibirica*) that we studied at 14 different sites during the expedition to the Siberian Arctic (Jónsdóttir et al. unpubl.). However, the two marginal populations of *Carex* reported on here, where the genets formed well separated,

Table 3. Total number of RAPD bands and number of unique bands for the analysed *Carex* colonies from Faddeyevsky Island (S1, S3, S4) and north-eastern Taymyr Peninsula (E1), using three primers.

Genotype	Total number of bands	Number of unique bands
S3	16	3
S4	23	12
S1	21	7
E1	16	9

Table 4. Similarities between the different RAPD band patterns of *Carex stans* on Faddeyevsky Island (S1, S3, S4) and *C. ensifolia* ssp. *arctisibirica* at north-eastern Taymyr peninsula (E1).

	S3	S4	S1
S4	0.26		
S1	0.43	0.38	
E1	0.18	0.04	0.14

fairly circular colonies of ramets, made it possible to identify genets, to take measurements of their size and some critical growth variables, that were then used in a simple growth model for genet age estimation. Empty centres were found within the larger (and older) colonies and it apparently can take some time before they develop, or between 80 and 90 yr in the guerrillatype *C. stans*. In moderate to high genet density populations of a close relative to *C. ensifolia*, *C. bigelowii* (Jonsson et al. 1996), clones tend to fragment into units of 7–30 interconnected ramet generations (and more numerous ramets due to branching) (Kershaw 1962, Jónsdóttir and Callaghan 1988, Jónsdóttir unpubl.). The old genets of *C. ensifolia* formed fragmented rings, which may be due to independent mortality of such clonal fragments.

An intriguing question is whether the genet growth patterns observed in these marginal populations are general for arctic rhizomatous *Carex* species, even under higher genet density, only obscured by the more tightly packing of genets. To answer this question a detailed mapping of genets under variety of conditions using molecular markers would be needed. It is not fully understood yet under which conditions fairy rings are formed in clonal plants (Cain et al. 1991, Adachi et al. 1996b), and it is possible that genets never have as regular growth patterns under high genet density condition as in low density marginal populations. But if they do, such circular forms, or rings, may never become visible because, as ramets eventually die, non-occupied space is likely to be quickly colonized by ramets of other genets.

Table 5. Calculated approximate age of the identified *Carex* genets (S1 and E1) and other encountered colonies assumed to represent only one genet (eq. 6).

Colony	Age (years)
<i>Carex stans</i>	
S1	154
S2	17
S3	63
S4	94
S5	84
<i>Carex ensifolia</i> ssp. <i>arctisibirica</i>	
E1	3885
E2	5180

Genet identification

In our study, the different colonies were successfully identified using three primers. One should be aware that additional primers might have revealed more genotypes per colony. However, our primers produced rather many polymorphic bands, i.e. a total of 41 bands (the number of polymorphic bands amplified by the three primers was 15, 13 and 13), which were very clear and easy to score, and each of the primers could by itself discriminate between all four identified genotypes. The reason for these very clear band patterns may be that we used a method for DNA isolation that in previous studies has proven to yield DNA of high quality (Ny-bom and Schaal 1990). In our opinion, the number of polymorphic bands (i.e. 41) was quite sufficient to identify the different genotypes. For comparison, Gabrielson and Brochmann (1998) identified 13 clones among 93 ramets of the species *Saxifraga cernua*, using 38 RAPD markers. Escaravage et al. (1998) used 17 polymorphic AFLP bands to identify 32 genotypes in *Rhododendron ferrugineum*. These genotypes were subsequently verified by applying additional primers.

The RAPD based similarity values ranged from 0.04 to 0.43. Comparisons among the three genotypes of *C. stans* ranged between 0.26 and 0.43. This suggests that genotype differentiation is unusually pronounced in this species, since the similarity values are much lower than generally reported in the literature. Steinger et al. (1996) report of values ranging from 0.64 to 0.86 within the species *C. curvula*. However, they collected samples within a sampling plot of 2.0×0.4 m, whereas our colonies grew at larger distances from each other and, consequently, may be less closely related. In a study of both wild and domesticated species of *Echinochloa*, Hilu (1994) reports of large differences in similarity values between species, with values ranging from 0.17 to 0.85 (Dice's index). Within species, the similarity values were 0.64–0.69. The numbers of polymorphic loci reported by Steinger et al. (1996), 77% (*C. curvula*), and obtained in our study 78% (*C. stans*), are similar and quite high. In addition, high levels of allozyme variation have been found in other outbreeding rhizomatous *Carex* taxa (Jonsson et al. 1996).

Genet age

The morphological variables we used as parameter estimates for the growth models probably show some annual variation in response to weather. However, the clonal fragments we measured consisted of several ramet generations, on average 5–6, and our values can therefore be considered as integrated values for the last ten to twelve years given the ramet generation time of approximately two years. Although this is not a long time in the context of genet longevity these rather

detailed measurements together with the growth model give a much better approximation of genet age than simple measurements of annual rhizome growth and genet size.

Individual *Carex* genets can apparently reach very old age and at least in the case of *C. ensifolia*, of some thousands of years. Whether such extreme age is an exception or a rule is difficult to conclude from the low number of genets found at the two sites. However, a comparable genet age has been estimated using a similar approach in yet another *Carex* species, i.e. *C. curvula* from the Central Alps (Steinger et al. 1996). This implies that genet longevity of thousands of years cannot be regarded only as a rare exception. More studies are needed to reveal general patterns of genet age structures in different *Carex* populations.

Implication for genet dynamics

Knowledge on population dynamics at both the ramet and genet level in clonal plants is required to understand the dynamics of vegetation types where they are the major component, as for example in most vegetation types of the tundra (Jónsdóttir et al. 1996). This is particularly important when resilience to environmental change is considered. The individual genets that we encounter today might be the very same as those that were introduced and established thousands of years ago and hence, they may have experienced and survived different types of environmental change (Steinger et al. 1996). The Holocene history of climate and vegetation in northern Siberia is poorly known, but available data suggest an overall gradual cooling since ca 4500 yr ago until today, intervened by periods of warming (for example the Middle Ages) and more extreme cooling (the Little Ice Age) (Borisov 1970, Khotinsky 1977, Peterson 1993). Between three and five thousand years ago, when the old genets of *Carex ensifolia* ssp. *arctisibirica* were established at NE Taymyr Peninsula, the climate was thus most likely somewhat warmer than today and the probability of seed set greater.

The sparse occurrence of *Carex* genets at the two high arctic study sites probably reflects the fact that the populations are at the extreme of the species northern distribution limits. The absence of flowering in the *C. ensifolia* population and low flowering frequency and late flower development in the *C. stans* population imply a low seed production. In such marginal populations the importance of immigration may become more important for genet recruitment than in populations with considerable seed production. However, flowering in tundra plants often shows large annual fluctuation (Sørensen 1941, Laine and Henttonen 1983, Carlsson and Callaghan 1994, Jónsdóttir et al. unpubl.) which can be related to summer temperatures in the preceding years (long flower bud maturation time). On

Faddeyevsky Island, summer temperatures 1993 and 1994 were close to the long term average, while the July mean for 1993 at north-eastern Taymyr Peninsula was about two degrees below the average. Accordingly, it cannot be excluded that the populations may produce mature seeds during unusually favourable growing seasons.

The limited data that we present here do not allow us to draw any conclusions about genet level population dynamics, but rather generates some alternative hypothesis. It is possible that these populations, at the very fringe of the species' distribution, may simply be relicts of a previously frequently breeding population. Alternatively, in terms of metapopulation dynamics in a broader view (Husband and Barrett 1996, Hanski and Gilpin 1997), they may function as sink populations maintained by migration (of seeds) from breeding source populations (Pulliman 1988, Hanski and Simberloff 1997). Only infrequent migration would be sufficient to maintain these populations because once established, the genets can expand horizontally by clonal growth and some of them apparently survive to an old age.

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References

- Adachi, N., Terashima, I. and Takahashi, M. 1996a. Central die-back of monoclinal stands of *Reynoutria japonica* in early stage of primary succession on Mount Fuji. – *Ann. Bot.* 77: 477–486.
- Adachi, N., Terashima, I. and Takahashi, M. 1996b. Mechanisms of central die-back of *Reynoutria japonica* in the volcanic desert on Mt. Fuji. A stochastic model analysis of rhizome growth. – *Ann. Bot.* 78: 169–179.
- Borisov, P. M. 1970. Opyt rekonstruktsii ledjanogo pokrova poljarnogo basseina v posdne- i poslednikovoe vremja ("The experience of reconstructing the ice cover of the Polar Basin in the late- and post-glacial time", in Russian). – In: Severnyi Ledovityi Okean i ego poberezhje v Kainozoe. Gidrometeoizdat, pp. 61–70.
- Cain, M. L. 1990. Models of clonal growth in *Solidago altissima*. – *J. Ecol.* 78: 27–40.
- Cain, M. L., Pacala, S. W. and Silander, J. A. Jr 1991. Stochastic simulation of clonal growth in the tall goldenrod, *Solidago altissima*. – *Oecologia* 88: 477–485.
- Callaghan, T. V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment. Strategies of growth and population dynamics of tundra plants 3. – *Oikos* 27: 402–413.
- Carlsson, B. Å. and Callaghan, T. V. 1994. Impact of climate change factors on the clonal sedge *Carex bigelowii*: implications for population growth and vegetative spread. – *Ecography* 17: 321–330.
- Chernov, Y. I. and Matveyeva, N. V. 1997. Arctic ecosystems in Russia. – In: Wielgolaski, F. E. (ed.), *Ecosystems of the world 3. Polar and alpine tundra*. Elsevier, pp. 361–507.

- Dice, L. R. 1945. Measurements of the amount of ecological association between species. – *Ecology* 26: 295–302.
- Escaravage, N. et al. 1998. Clonal diversity in a *Rhododendron ferrugineum* L. (Ericaceae) population inferred from AFLP markers. – *Mol. Ecol.* 7: 975–982.
- Gabrielson, T. M. and Brochmann, C. 1998. Sex after all: high levels of diversity detected in the arctic clonal plant *Saxifraga cernua* using RAPD markers. – *Mol. Ecol.* 7: 1701–1708.
- Goryachkin, S. V., Zlotin, R. I. and Tertitsky, G. M. 1994. Diversity of natural ecosystems in the Russian Arctic: a guidebook. – Reprocentralen, Lund Univ.
- Hanski, I. A. and Gilpin, M. E. (eds) 1997. Metapopulation biology. Ecology, genetics and evolution. – Academic Press.
- Hanski, I. A. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. – In: Hanski, I. A. and Gilpin, M. E. (eds), Metapopulation biology. Ecology, genetics, and evolution. Academic Press, pp. 5–26.
- Harberd, D. J. 1961. Observations on population structure and longevity of *Festuca rubra* L. – *New Phytol.* 60: 184–206.
- Harberd, D. J. 1967. Observations on natural clones in *Holcus mollis*. – *New Phytol.* 66: 401–408.
- Hilu, K. W. 1994. Evidence from RAPD markers in the evolution of *Echinochloa* millets (Poaceae). – *Plant Syst. Evol.* 189: 247–257.
- Hultén, E. and Fries, M. 1986. Atlas of North European vascular plants north of the tropic of Cancer. I. – Koeltz, Königstein.
- Husband, B. C. and Barrett, S. C. H. 1996. A metapopulation perspective in plant population biology. – *J. Ecol.* 84: 461–469.
- Jónsdóttir, I. S. 1991. Effects of grazing on tiller size and population dynamics in a clonal sedge (*Carex bigelowii*). – *Oikos* 62: 177–188.
- Jónsdóttir, I. S. 1995. The importance of sexual reproduction in arctic clonal plants and their evolutionary potential. – In: Callaghan, T. V. et al. (eds), Global change and arctic terrestrial ecosystems. Proc. of the Int. Conf., 21–26 August 1993, Oppdal, Norway. Comm. of the European Communities Ecosystems Res. Rep., Brussels.
- Jónsdóttir, I. S. and Callaghan, T. V. 1988. Interrelationships between different tiller generations of *Carex bigelowii*. – *Oikos* 52: 120–128.
- Jónsdóttir, I. S., Callaghan, T. V. and Headley, A. D. 1996. Resource dynamics within arctic clonal plants. – *Ecol. Bull.* 45: 53–64.
- Jónsdóttir, I. S., Virtanen, R. and Kärnefelt, I. 1999. Large-scale differentiation and dynamics in tundra plant populations and vegetation. – *Ambio* 28: 230–238.
- Jonsson, B. O. 1995. Old populations of the rhizomatous sedge *Carex bigelowii* show little intermingling of clones (genets). – *Abst. Bot.* 19: 105–113.
- Jonsson, B. O., Jónsdóttir, I. S. and Cronberg, N. 1996. Clonal diversity and allozyme variation in populations of the arctic sedge *Carex bigelowii* (Cyperaceae). – *J. Ecol.* 84: 449–459.
- Kemperman, J. A. and Barnes, B. V. 1976. Clone size in American aspens. – *Can. J. Bot.* 54: 2603–2607.
- Kershaw, K. A. 1962. Quantitative ecological studies from Landmannahellir, Iceland. III. Variation of performance in *Carex bigelowii*. – *J. Ecol.* 50: 392–399.
- Khotinsky, N. A. 1977. Golotsen severnoi Evazii (“Holocene of the Northern Eurasia”, in Russian). – Nauka, Moscow.
- Laine, K. and Henttonen, H. 1983. The role of plant production in microtine cycles in northern Fennoscandia. – *Oikos* 40: 407–418.
- Lovett Doust, L. 1981. Population dynamics and local specialisation in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. – *J. Ecol.* 69: 743–755.
- Murray, D. F. 1994. Floristics, systematics and the study of arctic vegetation – a commentary. – *J. Veg. Sci.* 5: 777–780.
- Nybom, H. and Schaal, B. A. 1990. DNA “fingerprints” reveal genotypic distributions in natural populations of blackberries and raspberries (*Rubus*, Rosaceae). – *Am. J. Bot.* 77: 883–888.
- Oinonen, E. 1967. The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn.) clones and certain periods of site history. – *Acta For. Fenn.* 83: 1–51.
- Oinonen, E. 1969. The time table of vegetative spreading in the lily-of-the-valley (*Convallaria majalis* L.) and the wood small-reed (*Calamagrostis epigeios* (L.) Roth.) in southern Finland. – *Acta For. Fenn.* 97: 1–35.
- Peterson, G. M. 1993. Vegetational and climatic history of the western Former Soviet Union. – In: Wright, H. E., Jr et al. (eds), Global climates since the last glacial maximum. Univ. of Minnesota Press, pp. 169–193.
- Pulliman, H. R. 1988. Sources, sinks and population regulation. – *Am. Nat.* 132: 652–661.
- Shirreffs, D. A. and Bell, A. D. 1984. Rhizome growth and clone development in *Anemone nemorosa* L. – *Ann. Bot.* 54: 315–324.
- Sørensen, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. – *Medd. Grønland* 125: 1–305.
- Steinger, T., Körner, C. and Schmid, B. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. – *Oecologia* 105: 94–99.
- Tolmachev, A. I. (ed.) 1996. Flora of the Russian Arctic. Volume II. Cyperaceae-Orchidaceae (J. G. Packer ed. English edition). – The Univ. of Alberta Press, Edmonton.
- Vasek, F. C. 1980. Creosote bush: long-lived clones in the Mohave Desert. – *Am. J. Bot.* 67: 246–255.
- Watt, A. S. 1947. Pattern and process in the plant community. – *J. Ecol.* 35: 1–22.