# Phytogeographical Studies of *Calamagrostis sachalinensis* (Gramineae)

# II. Origin and Dispersal

Tuguo Tateoka

*Department of Botany, National Science Museum,
Shinjuku, Tokyo 160*

The place of origin and the direction of migration of *Calamagrostis sachalinensis*, which has the boreal — montane distribution pattern and represents an apo-amphimictic complex by itself, have been discussed on the basis of the combination of the information on the internal structure of this species and the existing circumstantial evidence. It is without a doubt that *Calamagrostis* belongs to a primitive group within the tribe Aveneae, and its existence in Eurasia since the late Miocene period can not be questioned. Amphimictic tetraploids of *C. sachalinensis* seem to have originated in the mountains of Japan from some ancestors which invaded Japan in the Neogene period or earlier, considering the distributional and ecological attributes of the tetraploids and the related tetraploid species. The hexaploids and octoploids of *C. sachalinensis* with the apomictic manner of seed formation are apparently of a derived type and have most probably been brought forth from the tetraploid races in the mountains of Japan. The climatic oscillations during the Pleistocene period seem to have greatly facilitated the northward migration of the hexaploids and octoploids. The present range of *C. sachalinensis* extending from the mountains of Japan to Sakhalin and southern Kamtchatka may therefore have been established mainly by the migration from the southern montane areas to the northern lowlands. The usual interpretation for the derivation of the boreal — montane distribution which postulates the migration from the north to the south can hardly be applicable in the case of *C. sachalinensis*. It is pointed out that the role of autochthonous development in the formation of the montane flora of Japan has probably been more important than hitherto recognized.

As described in the first paper of this series (Tateoka, 1974b), *Calamagrostis sachalinensis* Fr. Schm. comprises four infraspecific races. Two of them are tetraploid with $2n=28$ chromosomes and are amphimictic in reproduction. One of the remaining two is hexaploid ($2n=42$) and the other is octoploid ($2n=56$), and both are usually apomictic in seed formation. Fig. 1 shows the distribution area of this species. So far as confirmed, the two tetraploid races are limited in range, while the assemblage of apomictic races extends from Shikoku to Sakhalin and Kamtchatka. Fig. 2, which was prepared mainly on the basis of my field observations, indicates the vertical distribution of *C. sachalinensis* in various areas of Japan. It is clear that temperate or boreal habitats are needed for the growth of this plant.

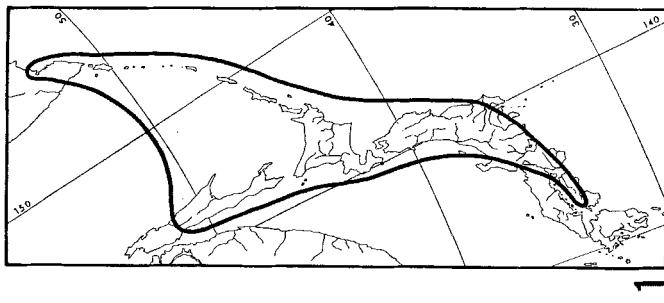The following can be enumerated as the taxa which are related to *C. sachalinensis*
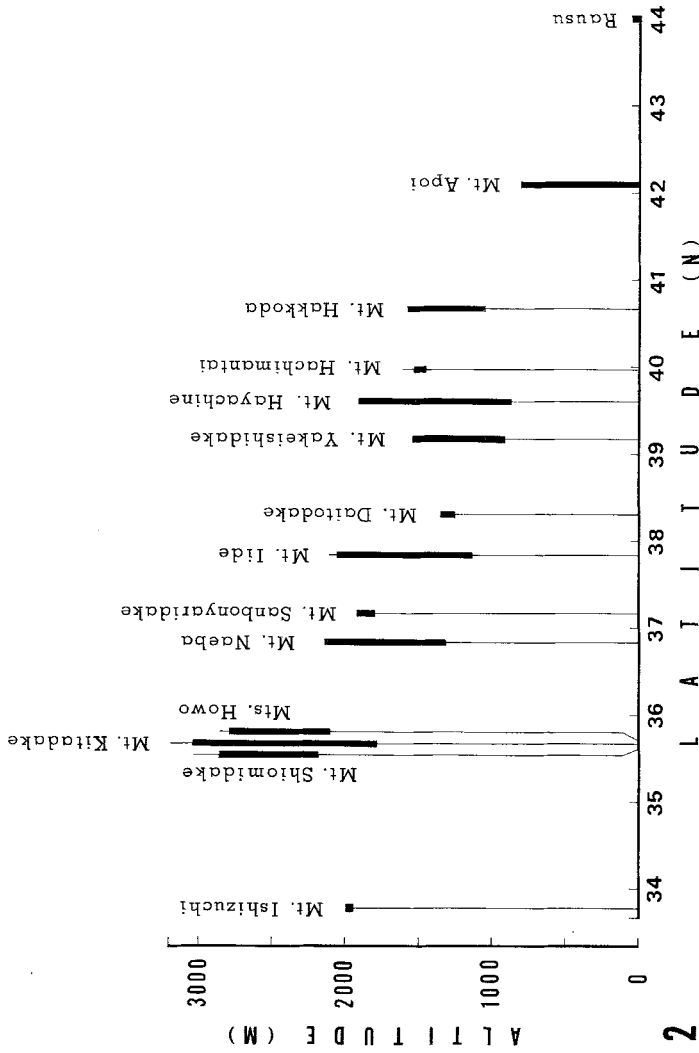
Fig. 2. Altitudinal distribution of *Calamagrostis sachalinensis* in various localities. Length of vertical line represents the height of each mountain, and the range of *C. sachalinensis* is shown by broad lines. Note that the lower critical altitude gradually goes down as the position of mountains shifts northward. Prepared on the basis of field observations by the present author except for the distribution on Mt. Iide, which was cited from Nishiyama (1972).

Fig. 1. Outline of the distribution area of *Calamagrostis sachalinensis*.

in distribution: *Trautvetteria japonica* (Ranunculaceae), *Trollius riederianus* (do.), *Polygonum weyrichii* (Polygonaceae), *Macropodium pterospermum* (Cruciferae), *Vaccinium smallii*, *V. praestans* (Ericaceae), *Bryanthus gmelini* (do.), *Arcterica nana* (do.), *Cassiope lycopodioides* (do.), *Fragaria iinumae* (Rosaceae), *Prunus nipponica* (do.), *Sorbus sambucifolia* (do.), *Epilobium fauriei*, *E. dielsii*, *E. foucaudianum* (Oenotheraceae), *Euonymus tricarpus* (Celastraceae), *Hypericum kamtschaticum* (Guttiferae), *Conioselinum filicinum* (Umbelliferae), *Tilingia ajanensis* (do.), *Pedicularis yezoensis* (Scrophulariaceae), *Lonicera chamissoi* (Caprifoliaceae), *Poa radula* (Gramineae), *Carex scita*, *C. hakkodensis*, *C. middendorffii*, *C. stenantha*, *C. flavocuspis*, *C. jacens* (Cyperaceae), *Ephippianthus schmidtii* (Orchidaceae), *Platanthera tipuloides* (do.). Most of these plants have their southern limit of distribution in central Honshu, and a few extend to Shikoku or Kyushu. They occur in boreal areas adjacent to Japan, but none reaches the Arctic. These plants therefore belong to the boreal — montane element.

The most prevalent explanation for the derivation of the distribution pattern as found in these plants is as follows: the plants primarily existed in the boreal region, extended their range southward during the Pleistocene glacial periods, and went up to high mountains and remained there in warm postglacial (interglacial) periods (cf. Hara, 1959, pp. 92–93). This view is sometimes regarded to be almost axiomatic and is introduced in textbooks and popular literature. *Dryas octopetala* may be one of the best examples demonstrating the migration from the north to the south during the Pleistocene. According to Tolmachev (1960) whose discussions stand on ample paleobotanical evidence, *Dryas octopetala* was absent in the alpine flora of Europe throughout the early Pleistocene, thrived in lowlands of Central Europe together with other northern or alpine plants which composed the "dryassic flora" in later cold stages, and is localized in the present time to the arctic and alpine areas.

It may be reasonable to suppose that this kind of southward migration, which is not an assumption but a fact, is the main factor which has caused the interrupted boreal — montane distribution. Nevertheless, a pitfall apparently rises if this concept is exaggerated, since the boreal — montane distribution pattern can equally be brought forth by the northward, instead of southward, migration. There is no reason to believe that the northward migration from the southern montane areas to the northern lowlands has not occurred at all in plants with the boreal — montane type of distribution. It is becoming increasingly clear that tropical to warm-temperate montane areas include primitive and original forms of a number of taxa at present flourishing in temperate and boreal areas (cf. Maekawa, 1965; Takhtajan, 1969). Hotta (1967) pointed out that basic components of the modern Japanese flora consist of the China — Himalayan (=Sino — Japanese) element and its derivatives, and suggested that some of the derivatives might have obtained the distribution area extending from Japan to Sakhalin and Amur.

In order to advance our understanding on the formation of the Japanese montane flora, it may be of significance to clarify whether *Calamagrostis sachalinensis* penetrated

from boreal regions to the mountains of Japan or should be regarded as having originated in the mountains.  For this reason, I have tried to examine the probable place of origin and migration routes of *C. sachalinensis* by combining the results of the analysis of the internal structure of this species (Tateoka, 1974b) with existing circumstantial evidence.  The present paper deals with this subject.

## Antiquity of *Calamagrostis*

Since *Calamagrostis* (incl. *Deyeuxia*) requires temperate or boreal habitats, it occurs in high altitudes or grows in cold seasons in tropical and subtropical areas.  This habitat preference is common to members of the tribe Aveneae (s. lat.) to which *Calamagrostis* belongs and also to most of the other tribes of the subfamily Festucoideae.  Discussions on the probable time of origin of several genera of this subfamily have been made by some authors on the basis of the information from the present distribution and ecology of the taxa in question and other plants with which the taxa are associated and also from the paleobotany and geology of the areas concerned (cf. Tateoka, 1968a).

Aveneae comprises about 50 genera.  Some of them are not markedly specialized in morphology and have wide distribution: *Helictotrichon*, *Amphibromus*, *Trisetum*, *Koeleria*, *Deschampsia*, *Calamagrostis*, *Agrostis*, etc.  These genera are interconnected one another.  *Calamagrostis* is close to *Trisetum* and *Deschampsia* on the one hand and to *Agrostis* on the other.  *Trisetum* is connected with *Koeleria* and *Helictotrichon*, which is in turn very close to *Amphibromus*.  Aveneae also includes many small genera with specialized morphology and a restricted range, as well as a few relicts with primitive features such as *Metcalfia* in central and southern Mexico and *Pseudodanthonia* in western Himalaya.

Lengthy discussions which are needed to elucidate the interrelationships of genera of Aveneae are here put aside, but the point closely related to the present work must be stated.  It is that many small genera with specialized morphology and habits are found particularly in the Mediterranean region and their ancestral forms can often be sought in the widespread genera.  For example, the Mediterranean annuals *Triplachne* and *Gastridium* have quite specific spikelets (cf. Maire, 1953) and are probably derived from the *Calamagrostis*-like ancestors.  Holub (1958, 1961, 1962) indicated that the ancestral forms of *Avena*, *Arrhenatherum*, *Pseudoarrhenatherum* and *Avenochloa*, of which centers of distribution are all in the Mediterranean region, can be looked for in *Helictotrichon*.  The Mediterranean *Lophochloa* and *Avellinia* may be derivatives of *Koeleria* (Larsen, 1960).  The group consisting of *Calamagrostis* and the other widespread genera can be regarded to represent the parent body from which various derivatives have been produced.  The origin of some of the derivative genera may be as recent as in the Pleistocene (cf. Stebbins, 1956), but the origin of some other genera, particularly those including perennial species, may date back up to the Miocene epoch as advocated for *Dactylis* by Stebbins and Zohary (1959) and for *Secale* by Khush (1962).  The old age of *Calamagrostis* is thus suggested from the interrelationships of the genera of Aveneae.

*Calamagrostis* is a large genus with over 150 species. Although it thrives in cool and temperate regions of the Northern Hemisphere, the number of species is more numerous in the mountains of low latitudes. There are two regions which are particularly rich in species of *Calamagrostis*. One of them is the highlands of tropical and subtropical South America (Venezuela, Colombia, Ecuador, Peru and Bolivia). About 40 species are found there and most of them are endemic. Another region lies from Szechwan — Yunnan to Pamir — Alai of the Soviet Union via the Himalayas. Here again, about 40 species are found. It is noteworthy that 26 species occur in southeastern Australia and all of them are endemic (after Vickery, 1940). Malaysia is poor in habitats suitable for *Calamagrostis*, but about 10 species with limited range can be recognized in this region. In Central America about 10 species are also recognized, and no species is common to Central America and North America. *Calamagrostis* is scanty in Africa, though a closely related genus *Leptagrostis* is found in Ethiopia. There are not many species found in southern South America and New Zealand either.

The outline of distribution of *Calamagrostis* noted above shows that this genus must have a long span of existence. Distance dispersal may be more or less responsible for the wide range of this genus, but it can hardly be imagined that long-distance dispersal in the recent geological time has played a decisive role for the present distribution of *Calamagrostis*, which includes numerous species endemic to a small area. Plants of this genus seem not to be particularly suitable for such dispersal, and examples suggestive of long-distance dispersal, e.g. occurrence of species with disjunctive range between North America and South America (cf. Raven, 1963), are scarcely encountered. The fact that the highlands of southeastern Asia include many *Calamagrostis* species is particularly interesting. Takhtajan (1969) pointed out that this region includes an abundant number of primitive forms of many orders or families of the Angiosperms. Diploid plants of *Calamagrostis* with 2n=14 chromosomes have not been detected so far, and it would seem possible to find diploid plants in southeastern Asia. *Calamagrostis* has most probably existed in this region for a long time.

Mention should be made of fossil records of grasses. Although macrofossils of grasses are scanty as in other herbaceous plants, Elias (1942) reported fossil fruits of the tribe Stipeae from the Miocene and Pliocene deposits of the North American Great Plains, and later (1946) noted that even the earliest fruits from the lower Miocene rocks have the essential characteristics of Stipeae. Stebbins (1947) confirmed that the fruits from the mid-Pliocene beds of this fossil flora are undoubtedly those of the modern genus *Piptochaetium*. This genus by no means belongs to a primitive group, since its one-flowered spikelet has various advanced features. *Calamagrostis* and other Aveneae are not known paleobotanically, but the existence of modernized grass genera in the Neogene period is clearly substantiated by the paleobotanical evidence.

The origin of *Calamagrostis* perhaps dates back to the Paleogene or the Cretaceous period, and its place of origin may probably be in the uplands of the paleo-tropical or paleo-subtropical zones. Setting aside details of these matters, we can safely conclude that plants of this genus must have existed in Eurasia since at least the late Miocene

period, in which conspicuous modernization of the woody flora of Japan and vicinity has been confirmed (Tanai, 1963; Huzioka and Uemura, 1973).

## Invasion of *Calamagrostis* to Japan

Fortunately enough, the historical vicissitudes of the topography of Japan can be visualized from the palaeogeographical maps and descriptions given by Minato *et al.* (1965). Furthermore, Kobayashi and Shikama (1961), Tanai (1967), Chaney (1967) and others have presented a review on the Tertiary floral changes of Japan.

According to these writers, Japan was part of the Asiatic continent and largely under subtropical climate in the Eocene period. In the Oligocene period, the climate gradually became cooler, and the continental stage of Japan ended by the latest Oligocene period. The Arcto-Tertiary geoflora gradually increased in eastern Asia during this period. The island arc stage of Japan opened at the dawn of the Neogene period. Passing through a transitional vegetation type in the earliest Miocene, the Aniai-type flora which represents temperate or rather cool temperate vegetation predominated in the early Miocene period. In the middle Miocene, a warmer climate again prevailed and the Daishima-type flora involving many evergreen hardwoods flourished. In the latest Miocene period, Japan was united with the continent, and the climate again became cooler. In the early Pliocene period, Japan became separated from the continent, and no drastic climatic changes occurred during this period. The woody floral composition of Japan much modernized since the late Miocene period.

The above sketch of the geohistorical vicissitudes of Japan shows that the habitats suitable for the growth of temperate plants as *Calamagrostis* were fairly wide spread in Japan since the ancient Tertiary period. Recently, Huzioka and Takahasi (1973) reported on the middle Miocene flora of Shimonoseki in southwestern Honshu. Though this epoch was the warmest during the Neogene period (vide supra), the floral composition of the Shimonoseki flora was estimated to correspond roughly to the modern assemblages now growing on mountain slopes at 300–1000 m altitudes in Kyushu. It is noteworthy that two species of *Calamagrostis*, *C. adpressi-ramea* and *C. brachytricha*, are now growing abundantly on mountain slopes at 300–1000 m altitudes in northeastern Kyushu. The climatic conditions of Japan, even in the southwest, were therefore not so warm throughout the Neogene period that the growth of *Calamagrostis* was suppressed to any degree.

During the early to late Miocene periods, Japan was separated into a considerable number of islands by large-scale transgression. But, at the latest Miocene period, present-day Honshu, Shikoku and Kyushu formed a land mass which was connected to the continent. Fig. 3 shows the distribution of land and sea in Japan and vicinity of this period (prepared on the basis of the palaeogeographical map by Ichikawa *et al.*, 1970, by permission). The climate in this period was cooler than in the middle Miocene, and furthermore mountain ranges in southwestern Japan were situated mainly in the east-west direction (cf. Minato *et al.*, 1965). Migration of temperate and boreal plants between the continent, Kyushu, Shikoku and Honshu must have been possible

along hills or mountains or through chains of high peaks effective as stepping stones. Plants of *Calamagrostis*, which must have existed in Eurasia in the latter part of the Neogene period, may have found their way to Japan at that time or earlier under these topographical and climatic conditions. The above view is in conformity with Miki's (1956) opinion that the migration of *Pinus koraiensis* and some other subalpine plants to Japan might have commenced from the late Miocene period or earlier judging from the remains discovered.
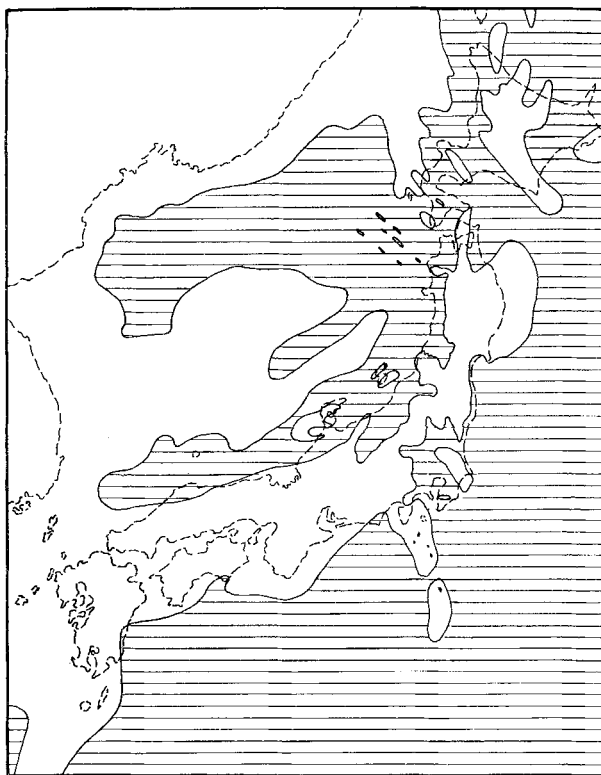
Fig. 3. Paleogeographical map of Japan and vicinity in the latest Miocene period, showing the distribution of land (white) and sea (hatched). The present shorelines are indicated by broken lines. Prepared on the basis of the paleogeographical map by Ichikawa *et al.* (1970) by permission.

## Birthplace of Tetraploid Races of *Calamagrotis sachalinensis*

As reported in a previous paper (Tateoka, 1974b), *Calamagrostis sachalinensis* represents an apo-amphimictic complex by itself and includes two amphimictic races. One of them is found in the subalpine belt of the mountains of central Honshu, and the other is restrictedly distributed in the exposed alpine belt of Mt. Apoi in Hokkaido. With the background of the inference that *Calamagrostis* may have existed in Japan at least since the latest Miocene period, the origin of these races must be considered.

The two tetraploid races are largely disjunctive in range. It is very unlikely that this disjunction (ca. 700 airline kilometers) has been caused by long-distance dispersal for the following reasons: (1) the two races as found at the present time are not identical but considerably deviated morphologically and ecologically, (2) the central Honshu race can be regarded to be a forest dweller which may have a very low possibility of long-distance dispersal (Raven, 1963), (3) the peculiar edaphic condition of Mt. Apoi (Watanabe, 1971) coupled with its climatic condition must be a strong obstacle for occassional immigration, and (4) seeds of the plants concerned seem to have no vehicle which causes long-distance dispersal over hundreds of kilometers, though as a general rule in the case of *Calamagrostis* strong winds may in part be responsible for making an interrupted range like stepping stones from mountains to mountains. The alpine flora of Mt. Apoi is known to include many relicts or rare species of disjunctive distribution (Hara, 1959), and the rich montane flora of central Honshu likewise includes relicts, such as *Anemonopsis macrophylla* and *Hakonechloa macra*. It is most likely that the two tetraploid races of *Calamagrostis sachalinensis* at present located in remote areas are derivatives or remnants of a tetraploid taxon which was formerly extensively spreading from Honshu to Hokkaido.

Of the two tetraploid races, the central Honshu race seems to be closer to the ancestral tetraploid taxon than the Apoi race. Hara (1939, 1959) pointed out that the varieties endemic to Mt. Apoi have generally narrower and more lustrous leaf-lobes than corresponding plants in other districts. Kitamura (1956) regarded these varieties to be the ones deformed in the serpentine area. Leaf blades of the Apoi race of *C. sachalinensis* are narrower and firmer than those of the central Honshu race, and Kitamura's opinion seems to be justified. The point at issue is therefore whether the original tetraploid race of *C. sachalinensis*, which is either the central Honshu race itself or a race the most closely related to it, developed autochthonously in Japan or migrated from adjacent regions.

Before going further, it should be noted that the establishment of the coniferous subalpine belt in the mountains of central Honshu may be ancient. There is ample paleobotanical evidence to demonstrate that the woody floras of Japan in the Miocene and Pliocene periods had close similarities to those of continental eastern Asia and North America (Chaney, 1967; Tanai, 1971; a.o.). According to Tolmachev (1954), the cradle of the montane coniferous vegetation should be looked for most probably in the Pacific parts of Asia and North America and this type of vegetation was formed very early, at least in the Miocene period in the mountains of the temperate zone. This hypothesis was strongly supported by Kornaś (1972) who made an extensive phytogeographical analysis of corresponding taxa of temperate Eurasia and North America. Tanai (1963) clarified the altitudinal differentiation of the Daishima-type flora of the middle Miocene age in southwestern Hokkaido and called attention to the zonal vegetation of that time. These arguments support the view that the coniferous subalpine belt in the mountains of central Honshu, in which the tetraploid central Honshu race of *C. sachalinensis* is now growing luxuriantly, may have been more or

less developed as early as in the Miocene period.

A clue to the probable place of origin of the tetraploid *C. sachalinensis* can be provided by examining the distribution of the tetraploid taxa related to it and their interrelationships. In this connection, plants growing in Japan, Sakhalin, the Kuriles, Kamtchatka and Korea must be observed with special care.

Ten species of *Calamagrostis*, besides *C. sachalinensis*, are distributed in Sakhalin. Four of them seem to be represented only by high-polyploid strains: *C. brachytricha* (Tateoka, 1969), *C. lapponica* (Nygren, 1946), *C. hakonensis* (Tateoka, 1968b) and *C. stricta* (=*C. neglecta*). Although European strains of *C. stricta* are tetraploid (Löve and Löve, 1961), collections from eastern Hokkaido of this species have shown 2n=84 chromosomes (Tateoka, unpublished). Three of the remaining six species may be tetraploid but have morphological features suggestive of their remote relationships to *C. sachalinensis*: *C. epigeios*, *C. monticola* and *C. sesquiflora* (cf. Tateoka, 1954 and 1973b for chromosome counts). The other three species might not be distant phylogenetically from *C. sachalinensis*: *C. deschampsioides*, *C. langsdorffii* and *C. angustifolia*. The chromosome number of *C. angustifolia* is not yet known, and *C. deschampsioides* which is definitely tetraploid (Tateoka, 1973a) is principally an Arctic plant (Tzvelev, 1964). The tetraploid strains of *C. langsdorffii* which may be distributed in Sakhalin (Tateoka, 1974a) have generally bigger culms and leaves than the tetraploids of this species distributed in central Honshu, and the latter are apparently closer to *C. sachalinensis*. It can be said that the tetraploid taxa related to *C. sachalinensis* are scant in Sakhalin. Similarly, in the Kuriles and Kamtchatka, species of *Calamagrostis* are not many, and only *C. deschampsioides* and part of *C. langsdorffii* can be assumed to be the tetraploids more or less related to *C. sachalinensis*.

Species of *Calamagrostis* are also not many in Korea (eight species according to Chung, 1965). *C. sachalinensis* has been enumerated as a plant indigenous to Korea by Lee (1966) but not by Chung (1965). Lee's designation is apparently based on an erroneous record caused by misidentification (cf. Ohwi, 1936). No Korean specimen of this species has been seen. *C. langsdorffii* is also found in Korea, and other species possibly related to *C. sachalinensis* in Korea are *C. paishanensis*, *C. subacrochaeta* and *C. heterogluma*. Chromosome numbers of these plants are unknown.

Turning to the plants growing in Japan, a different aspect is found. Sixteen species of *Calamagrostis* besides *C. sachalinensis* are distributed in Japan. Five of them are eliminated from the present account since they have morphological features differing clearly from *C. sachalinensis*: *C. epigeios*, *C. pseudophragmites*, *C. fauriei*, *C. matsumurae* and *C. sesquiflora*. Among the remaining 11 species, one (*C. masamunei*) is still not known cytologically and two (*C. brachytricha* and *C. stricta*) may consist of only high-polyploid strains in Japan (Tateoka, 1969 and unpublished). The rest are composed of four tetraploid species (*C. autumnalis*, *C. nana*, *C. gigas* and *C. adpressiramea*: Tateoka, 1969, 1970b, 1973a, 1973b and Unpub.) and four species which include tetraploids as well as high-polyploids (*C. langsdorffii*, *C. hakonensis*, *C. longiseta* and *C. tashiroi*: Tateoka, 1968b, 1972a, 1974a and Unpub.). These species are not very

different from *C. sachalinensis* morphologically, and thus the tetraploids more or less related to *C. sachalinensis* in Japan amount to eight species, one of which is divided into two subspecies. Fig. 4 shows the geographical distribution of these tetraploid taxa except *C. langsdorffii*, together with that of the two tetraploid races of *C. sachali-nensis*. Cytogeographical studies of *C. langsdorffii* in Japan are now in progress, and the distribution of the tetraploid strains can not yet be delineated though it can be said at this time that the tetraploids are abundant in central Honshu.

The tetraploid taxa appearing in Fig. 4 are all endemic to Japan. Furthermore, they are a little different one another in habitat preference. Taking the taxa occurring in central Honshu, the following situation can be noted. The tetraploid race of *C.*
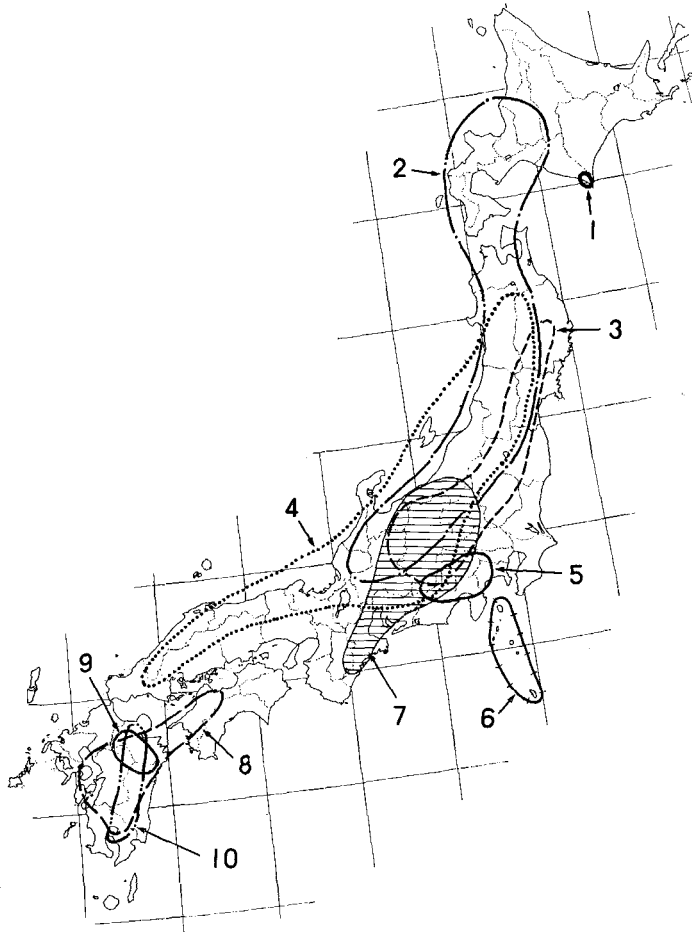


Fig. 4. Outlines of the distribution areas of the tetraploid races of *Calamagrostis sachalinensis* and other tetraploid taxa related to this species. 1: *C. sachalinensis*, Mt. Apoi form; 2: *C. gigas*; 3: *C. nana*; 4: *C. longiseta*; 5: *C. hakonensis*; 6: *C. autumnalis* subsp. *insularis*; 7: *C. sachalinensis*, central Honshu form; 8: *C. tashiroi*; 9: *C. adpressi-ramea*; 10: *C. autumnalis* subsp. *autumnalis*.

*sachalinensis* is principally a forest dweller in the subalpine belt. *C. nana* occurs on the windy alpine belt. *C. longiseta* mainly grows on alpine or subalpine meadows and is abundant in the areas with heavy snowfalls. *C. gigas* favors more mesic sites on the mountain and subalpine belts than the others. The tetraploid race of *C. hakonensis*, which is luxuriant on Mt. Hakone and vicinity, prefers volcanic soils on the montane belt. *C. autumnalis* subsp. *insularis* is an orophyte on the islands under an oceanic climate. The above situation recalls adaptive radiation of the tetraploid taxa and strongly suggests that they have evolved autochthonously in Japan. It is quite unimaginable that these plants have migrated as a whole from the boreal region.

Another noteworthy fact is that interspecific hybrids of *Calamagrostis* at the tetraploid level are not scarce in the mountains of Japan. As indicated by Nygren (1962), hybridization seems to have played a significant role in the evolution of *Calamagrostis*. Hybrid swarms were discovered between *C. adpressi-ramea* and *C. autumnalis* in Kyushu (Tateoka, 1970a). Tetraploid hybrids of two combinations, *C. sachalinensis* × *C. langsdorffii* and *C. sachalinensis* × *C. longiseta*, have been detected in the Akaishi Range in central Honshu (Tateoka, 1972b and unpublished). Several tetraploid hybrids of *Calamagrostis*, a parent of which is most probably *C. sachalinensis*, have also been discovered in the Hida Range (Tateoka, unpublished). In 1959, Lewis and Epling produced convincing evidence to show that hybrid segregates can develop to a new species without change of chromosome number. Speciation may be more easily achieved in mountain areas than in monotonous lowlands as recently advocated by Takhtajan (1969). There are many examples which suggest that speciation occurred in the uplands of central Honshu (Takahashi, 1971).

The coniferous subalpine woods offer very stable and closed habitats for herbaceous plants in the field layer (Kornaś, 1972). The influence of climatic oscillations during the Pleistocene period may have been the least for this type of vegetation (Uematsu, 1967). Plants migrating from the boreal region during the glacial periods must have been confronted with great difficulties in invading this habitat. It is therefore very unlikely that the tetraploid central Honshu race of *C. sachalinensis* migrated from the north and invaded the coniferous subalpine belt during the glacial periods. The same is not true of the alpine belt which has habitats more mobile and open to the pre-adapted immigrants from other areas.

All the above arguments support the view that the tetraploid *C. sachalinensis* has developed through autochthonous speciation in Japan, possibly in the mountains of central Honshu. As mentioned earlier, this tetraploid taxon must once occupied a vast area extending from Honshu to Hokkaido and may have been split into the present-day two races.

## Polyploidization and Dispersal

As reported in the first paper of this series (Tateoka, 1974b), the majority of existing strains of *C. sachalinensis* belong to a group of hexaploids and octoploids having the apomictic manner of reproduction. Although no decisive answer can be expected

as for the time and place of origin of this apomictic assemblage, it is most likely that its origin was in Japan, because (1) so far as confirmed, the original tetraploid races are not distributed outside of Japan, (2) even if the tetraploid races expanded their range up to the boreal region in the past, the main body of the tetraploids undoubtedly remained in the mountains of Japan which would provide a greater possibility for the origin of a new race, and (3) in Japan are found the most abundant related tetraploid species which might have participated in the origin of the hexaploid and octoploid plants through hybridization.

The distributional expansion of *C. sachalinensis* may have been greatly facilitated by the geneses of the hexaploid and octoploid races accompanied by apomictic seed formation.    Since *C. sachalinensis* is self-incompatible, at least two individuals must go together in case of the sexual tetraploid races when they invade a new area and produce a viable seed.    However, in the case of apomictic races, a group of individuals is not indispensable to produce seeds and even only one individual may be able to colonize successfully.

It is likely that the northward migration of *C. sachalinensis* was greatly accelerated by the climatic oscillations during the Pleistocene period.    The lowered climate and expanded lands in the glacial epochs may have opened habitats suitable for this species in the lowlands of the temperate zone.    When the climate became warmer in the inter- glacial epochs, the strains inhabiting the lowlands must have been forced to migrate
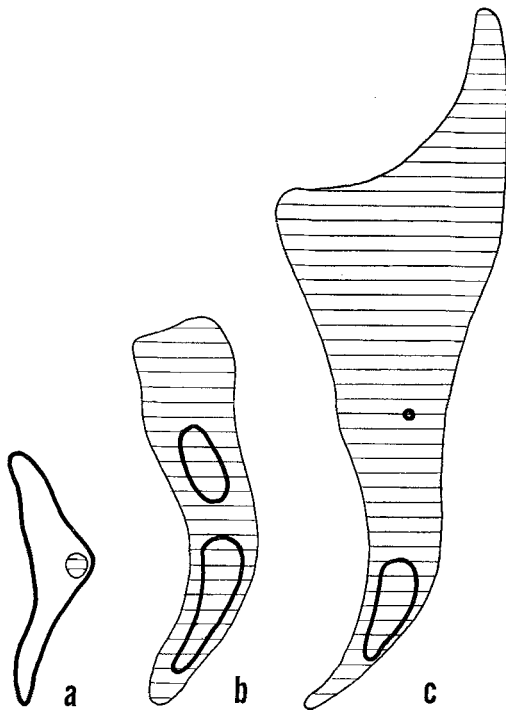


Fig. 5.   Schematic drawing of three distribution patterns.   Distribution areas of the tetraploids are represented by the enclosures with broad lines and those of the high-polyploids by hatched enclosures.   Further explanation in text.

to more northern areas or to the mountains.    Therefore, the northward migration of
*C. sachalinensis* from the temperate montane areas may have been facilitated in both
the glacial epochs and the interglacial epochs.

Fig. 5 is a hypothetic representation of a process leading to the formation of the
present distribution of *C. sachalinensis*.    Fig 5a was prepared on the basis of the actual
example, the distribution of the tetraploids and the hexaploids of *Calamagrostis
longiseta*.    The tetraploids have a wide range (from Hachimantai in Pref. Iwate to
Mt. Takadake in Pref. Yamaguchi; cf. Fig. 4), while the hexaploids have been found
only in the Akaishi Range of central Honshu (Tateoka, unpublished).    Fig. 5c is a
schematic representation of the distribution of the tetraploids and the high-polyploids
of *C. sachalinensis* based on the data reported in the first paper of this series (cf. Fig.
1).    The distribution patterns indicated in Figs. 5a and c can be regarded to be two
extremes interconnected by a supposed intermediate pattern appearing in Fig. 5b.
Starting from the pattern of 5a, the distributional expansion of the high-polyploids
and the partition and reduction of the range of the tetraploids lead to the pattern of
5c via 5b.    A historical transition more or less related to the above assumption would
lie behind the present distribution of *C. sachalinensis*.


## Conclusion

The working hypothesis deduced from the above discussions is that *Calamagrostis
sachalinensis* originated in the mountains of Japan from some ancestors, which came
Japan in the Neogene period or earlier, and the present range of this species extending
from Japan to Sakhalin and Kamtchatka was established mainly by the northward
migration from the southern montane areas to the northern lowlands.    The usual
interpretation for the derivation of the boreal — montane distribution, which postulates
the migration from the north to the south, can hardly be applicable to *C. sachalinensis*,
considering the internal structure of this species and the phytogeographical attributes
of related taxa.

As mentioned in the introduction of this paper, various taxa have a distribution
comparable to that of *C. sachalinensis*.    Also, there are a number of plants in which
distribution deviates but partly corresponds to that of *C. sachalinensis* (cf. Fukuoka,
1965; Kawano, 1971; Koyama *et al.*, 1971; Asano, 1972).    It is apparent that the
distribution of these plants should be examined from a standpoint free from any bias
that exaggerates one-sidedly the migration from the north to the south.    It is also
apparent that the studies incorporated with cytogeographical and cytoecological
approaches are desirable to be extended to these plants.

As early as in 1949, Maekawa pointed out that the starting point of the modern
flora of Japan might be in the Oligocene period.    In 1960, Tolmachev emphasized the
importance of the role of autochthonous development in the formation of the high-
mountain floras in low and middle latitudes.    The conclusion of the present work is
essentially in conformity with these opinions.

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