Root Development of Sand Dune Plant Community

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Introduction

Most ecological studies of the plant community have been mainly in regard to the terrestrial organ, and studies of the subterranean organ have only rarely been made. All of the responses of plants to soil factors are closely connected with the condition of their root systems, but in the past both botanist and agriculturist in the main have been satisfied with interpreting results by observation of the shoot only. A knowledge of root development and distribution under different natural conditions is not only of much practical value, but also readily leads to numerous scientific applications.

Since the plant community has integrated all the terrestrial and subterranean organs of its habitat, a study of the subterranean organ should not be omitted in the ecological research of the plant community. Early studies of the subterranean organ, by Freidenfeldt (1902), Alten (1909) and Cannon (1911), treated mainly the morphological forms of the root system in relation only to cultivated or useful forest plants, but recent studies of the subterranean organ have been made mainly with respect to wild plants.

Representative studies of the subterranean organ of the herbaceous plants are as follows: studies on the subterranean organ of the prairie plants by Weaver and co-workers (1920, 1922, 1929, 1930, 1935a, 1935b, 1945, 1946a, 1946b, 1949, 1950a, 1950b, 1954, 1958a, 1958b, 1961), those of the moor plants by Metsävaino (1931), and of the desert plants by Cannon (1911).

The above-mentioned studies, which emphasize the biological significance of the root system, treated root morphology in relation to the environment and the adaptation of the subterranean under several environmental conditions. The results of these investigations disclose useful information concerning the morphological characteristics of the subterranean organs, but lack synecological significance, as the majority relate only to the root of an individual plant.

In the present study four analytic habits were used describe the characteristics of the root and rhizome system, namely, root depth, root morphology, root area and vegetative propagation. The characters of the subterranean organ, expressed by the four habits, show the synthetic character of the subterranean organ. This method effectively expresses the details of the subterranean organ and the details of the root system, and makes it possible to treat the characters of the subterranean organ, and to explain the relation between the subterranean organ and the environment.

Sand dune plants and desert plants have been studied by the following investigators: Canon (1911), Yoshii (1910), Waterman (1919), Seifritz (1932), Rawitcher (1948). Salisbury

(1952), Ranwell (1959), Horikawa and Yano (1955), and Howard and Ditmer (1959). The results of their studies indicate that the subterranean organs of sand dune and desert plants are well developed and that all of the plants are tolerant of sand deposit and thus show adaptation to such a habitat. Most of the studies mentioned above, however, dealt only with the adult stage of the selected species in the sand dune habitat, and did not treat all the growing stages of the subterranean organ in the plants.

The present studies were made on the subterranean organs of the plants growing on the Tottori Sand Dune in 1953 (August), 1954 (June) and from 1960 (August) to 1977 (August). The study of the subterranean organ was undertaken with the following objectives: to increase the knowledge of the subterranean habits of dominant and subdominant species growing on the sand dune and to reveal the developmental aspects of each stage of the plant growth.

Method

To obtain samples for this research a modification of the direct or trench method was used (Weaver 1926, Yano 1960a). Classification of the subterranean organ was made on the basis of four analytic habits: root morphology, root depth, root area and vegetative propagation. The first habit represents more strongly genetic characters, but the remaining three are influenced by both genetic and environmetal conditions.

Details of these analytic habits are as follows:

The root morphological habit is classified into the following five types on the basis of the mutual relation between the lateral roots and the tap root. Schema of these types is illustrated in Fig. 1.

I Root morphology (Rm)

A. Monopodial branching

1. Primary

a. With tap root ·· Rm 1

b. With tap and lateral roots ·· Rm 2

2. Secondary

Tap root undeveloped, lateral and adventitious roots well branched and well developed (in some cases a part of the lateral roots develops well and replaces the main root). ·· Rm 3

B. Polytomus branching

C. Fibrous

Tap root disappears and adventitious roots arise from the node on stem or rhizome. ·· Rm 4

D. Fasiculate

Tap root soon disappears and fasiculate roots develop profusely ···· Rm 5

The root depth expresses not only a genetic character but also an adaptation to soil conditions such as soil aeration, water content, and ground water table. This habit was classified into five grades. They are useful for the investigation of subterranean organ in the communities.

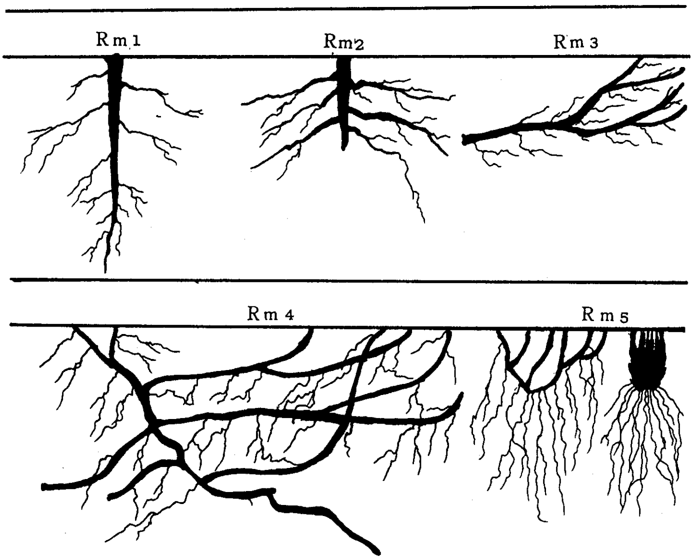

Fig. 1. Schema showing five morphological types (Rm 1—Rm 5)

II Root depth (Rd)

D...Maximum depth of root.

1. D > 100 cm ········· Rd 1
2. 100 ≧ D > 50 cm ········· Rd 2
3. 50 ≧ D > 25 cm ········· Rd 3
4. 25 ≧ D > 10 cm ········· Rd 4
5. 10 ≧ D > 0 cm ········· Rd 5

The root area is classified according to the occupation of the root population in the soil. The character is influenced by the soil structure, water content and ground water table.

III Root area (Ra)

1. Cylindrical
   occupies all the layers of soil. ········· Ra 1
2. A. Obconical
   mainly occupies the upper layers. ········· Ra 2
   B. Fusiform
   mainly occupies the middle layers. ········· Ra 3
   C. Conical
   mainly occupies the lower layers. ········· Ra 4
3. Pan-shaped
   Dense roots cover an area in the upper layers. ········· Ra 5

Most of the plants with rhizomes and stolons have numerous adventitious roots which constitute the main root population in the community. Consequently the vegetative propagation organ from the terrestrial stems is important for the study of the root population.

Vegetative propagation is expressed by the mutual relation among the extension of the population, density of shoot (individual distance), and shoot height. A schema of these habits is shown in Fig. 2.

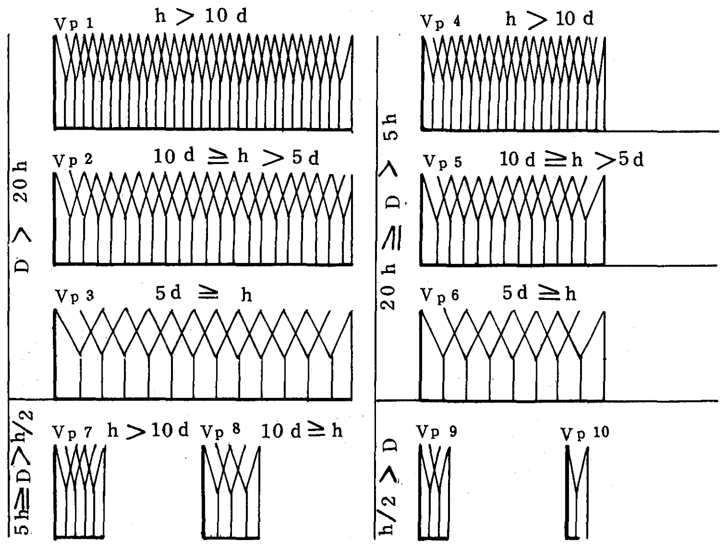

Fig. 2. Schema showing the habits of root vegetative propagation (Vp 1—Vp 10). D : Population diameter. h : Shoot height. d : Individual distance.

Ⅳ Vegetative propagation (Vp)

D...Population diameter. h...Shoot height. d...Individual distance.

1. $D > 20h$
   - $h > 10d$ ········· Vp 1
   - $10d \geqq h > 5d$ ········· Vp 2
   - $5d \geqq h$ ········· Vp 3
2. $20h \geqq D > 5h$
   - $h > 10d$ ········· Vp 4
   - $10d \geqq h > 5d$ ········· Vp 5
   - $5d \geqq h$ ········· Vp 6
3. $5h \geqq D > h/2$
   - $h > 10d$ ········· Vp 7
   - $10d \geqq h$ ········· Vp 8
4. $h/2 \geqq D$ ········· Vp 9
5. Monadic stem (without propagation organ) ········· Vp 10

General description of the habitat

The Tottori Sand Dune is situated at the northern side of Tottori city, and it lies along the beach line of the Japan Sea (Fig. 3).

This sand dune is derived from sand discharged by the Sendai River which flows through the Tottori field. The sand accumulated at the mouth of the river has been carried to land by wind, resulting in the formation of the sand dune. According to a report by Yamana (1955), the old sand dune constructed by the accumlation on the agglomerate layer was sunk into the sea by an earthquake. Later it was covered by fine sand and clay silt loam, and following a volcanic eruption, volcanic ash accumulated on it and sand accumulated again on the volcanic ash. Consequently under this sand dune an unpermlable layer and a volcanic ash layer exist. This sand dune covers an area of 3583.66 ha, including both the Koyama and Hamasaka sand dunes.

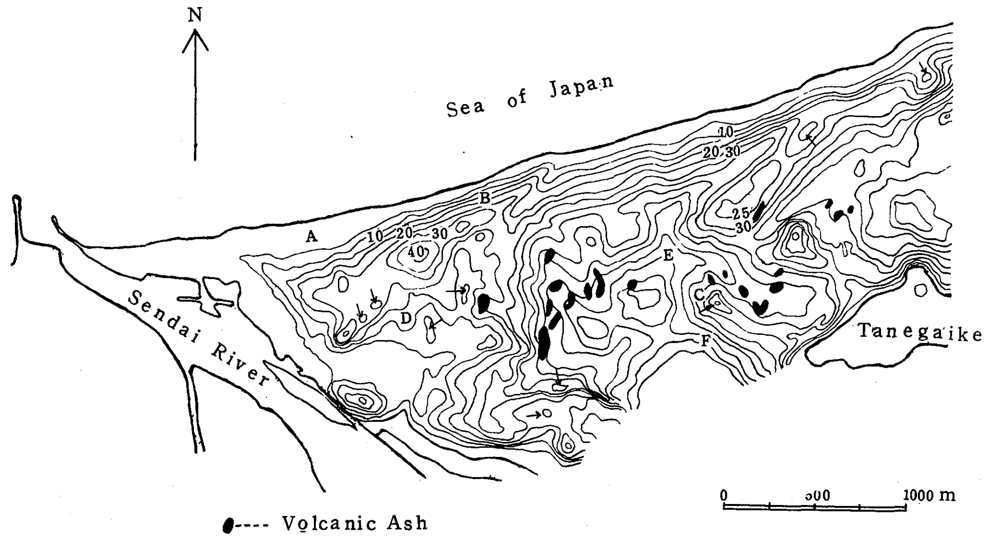

Fig. 3. Topographical map of the Tottori Sand Dune (from Yamana 1955). A, B, C : Accumulating and eroding, eroding, accumulating habitat respectively—unfixed dune. D, E : Semifixed dune. F : Fixed dune.

Factors affecting the habitat

1. Edaphic factor.

According the reports of Hara (1930 and 1932), the soil-composition of the Hamasaka sand dune is as follows: the sand being from 1.0 to 0.5 mm in diameter is 35%; from 0.5 to 0.25 mm is 61.6%; less than 0.25 mm is 3.4%. Consequently this dune is composed mostly of very fine sand from 1.0 to 0.25 mm in diameter. The survey made by the author (1955) in August, showed that the sandy soil was weakly acid ranging from pH 5.0 to 6.0. This result is almost the same as that obtained by Hara (1930 and 1932).

The maximum temperature of the sand dune surface (August 1953) was 53℃. and temperatures at the depth of 0—10 cm and 30 cm were 35℃. and 25℃. respectively. According to a report of Ikeda (1958), the maximum temperature of the sand surface is 58.3℃. and the minimum temperature is 25.8℃. in July, and the temperature of the soil deeper than 50 cm from the surface is hardly influenced by the atmospheric temperature. The seaward sand dune is always influenced by the salt spray and sea water, therefore its soil usually contains a considerable amount of salt.

2. Moisture.

Ikeda (1957) reported that in the area of the sand dune the mean annual precipitation is 2078.9 mm, the mean monthly 173.3 mm and the least precipitation is seen in August, and that Köppen's dry index of this area is 133.3, which shows that the area belongs to the moist climate zone. A result of a survey on water content of the sandy soil made by the author in August 1959, is shown in Table 1. From the result it is clearly seen that the water content in the

Table 1. Water content of sand soil at various depths in the representative habitats

Habitat	Unfixed dune		Semifixed dune	Fixed dune	
Distance from the beach line (m)	40	40—80	500	1000	Average
Community	*Messerschmidia sibirica*	*Wederia prostrata*	*Fimbristylis sericea*	*Imperata cylindrica* var. *koenigii*	
Depth					
0—1 cm	0.6%	0.6%	0.2%	3.0%	1.1%
30 cm	0.9%	0.2%	2.2%	3.7%	1.8%
60 cm	0.2%	1.6%	5.4%	0.4%	1.9%
80 cm	0.4%	1.4%	6.0%	0.2%	2.0%
100 cm	4.2%	2.0%	—	1.2%	2.5%

upper layer of the sand soil is generally less than that in the lower layer.

In an investigation made by the author (Horikawa and Yano 1955) in August 1953, the soil contained no available water in the layer from the surface to 10 cm depth. Hara and Tanaka (1955) pointed out that available water was not contained in sand from 0 to 40 cm in depth after a continued drought of 40 days, and indicated that the sand surface was in a very dry condition.

The seasonal variation of ground water table in the sand dune is shown in Fig. 4 based on unpublished data by Torii.

Generally the higher ground water table is seen from January to May and the lower one from June to December. This fact shows that the edaphic condition is unfavorable for the plant growth in its growing season. Hara (1930 and 1932) and Hara and Tanaka (1955) reported that the ground water table is from 1.5 to 2 m in a flat sand dune, and that even in a sand dune which reaches 30 m above the sea level, it is only 50 cm in a place where the silt loam layer is shallow. In the fixed dune, sand moving is stable and contains fallen leaves or other organic matter; consequently the water content is increased. It is evident that the water content has a close connection with the root development (Kramer 1949 and Weaver 1920), and its conditions in June, July and August greatly influence the growth of sand dune plants.

3. Wind.

One of the greatest factors which infuence the sand dune vegetation is the wind which carries moving sand and salt spray from sea water. The sand dune plants are injured by flying sand and buried or eroded by moving sand. The plants are also injured or sometimes destroyed completely by the salt spray contained in the wind blowing from the sea. The formation and movement of the sand dune are influenced by the wind direction, which is from the south-east in summer and from the north or west in winter. The moving sand accumulats at the leeward of the plant communities and makes a small hummock. In the early stages of sand accumulation, the hummock is small, but it becomes larger with the sand accumulation, and at last it forms an irregular wide dune. Many dune kettles (Dünekessel) are distributed on this sand dune. The windward face of the kettles is subjected to accumulation of sand by wind (from 1 to 2 m in one year), the leeward is subjected to sand erosion, and the

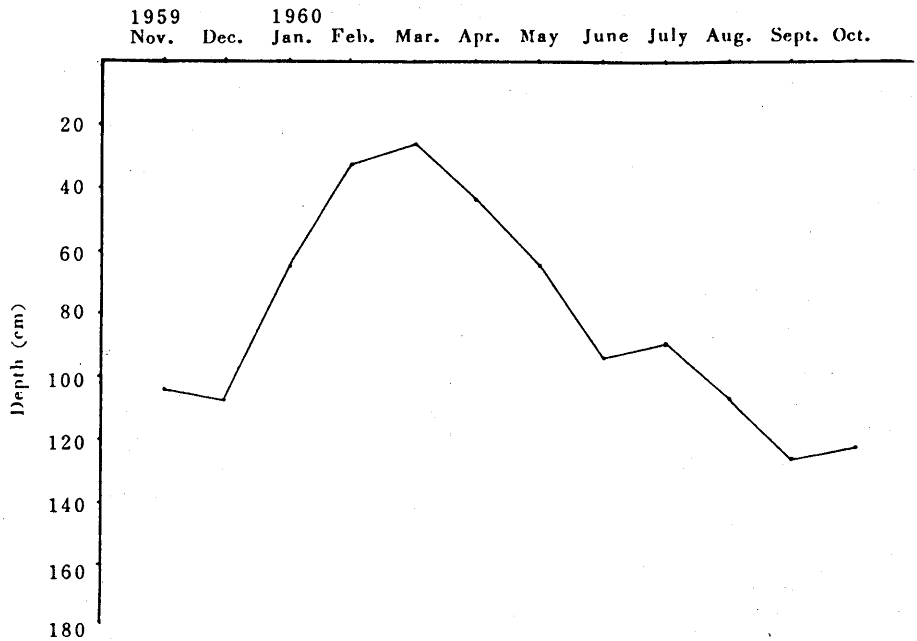

Fig. 4. Graph showing the seasonal variation of ground water table in the Hamasaka sand dune during 1959—1960 (from unpublished data by Torii).

center of the kettles becomes shallow and flat, the ground water table of the center is high and there occur special plant communities consisting not only of sand dune plants but also of other plants.

The sand dune is classified into three dunes on the basis of the degree of sand movement: unfixed, semifixed and fixed dune. The unfixed dune is divided further into three habitats based on the states of sand accumulation and sand erosion, namely, (1) "eroding and accumulating habitat," where sand accumulation and sand erosion occur simultaneously; (2) "eroding habitat," where sand erosion is caused by the main wind in plant growth season; (3) "accumulating habitat," where sand accumulation occurs by the main wind in plant growth season. In the "semifixed dune" the sand accumulation and wind erosion do not exceed 10 cm per year. In the "fixed dune" the sand moving is scarcely seen and this habitat is encountered in the artificial forest, namely, the forest of *Pinus thunbergii* and *Robinia pseudoacasia.* Salisbury (1952) recognized two forms of dunes in the coastal dunes of the British Isles, namely, white and ash sand dunes; in the former, sand movement occurs continuously, but in the latter, sand is stable and contains much organic matter. The unfixed and semifixed dunes mentioned above may correspond to the white sand dune , and the fixed dune to the ash sand dune .

Vegetation affected by the habitat

Ranwell (1959) reported that the vegetation of the sand dune varies with the topographical condition. This fact seems to be due to the effect of wind and ground water table, which vary with the topography. The author (Horikawa and Yano 1955) gave an outline of the vegetation on this sand dune in which they recognized four communities dominated respectively by *Carex kobomugi*, *Calystegia soldanella*, *Zoysia macrostachya* and *Ischaemum anthephroides* var. *eriostachyum* on the unfixed dune. Furthermore there were observed *Ischaemum anthephroides* var. *eriostachyum*-*Artemisia princeps* community on the semifixed dune and *Imperata cylindrica* var. *koenigii*-*Paederia scandens* community on the fixed dune. Howerer, as a result of the author's investigation in 1959, it seems that the unfixed dune

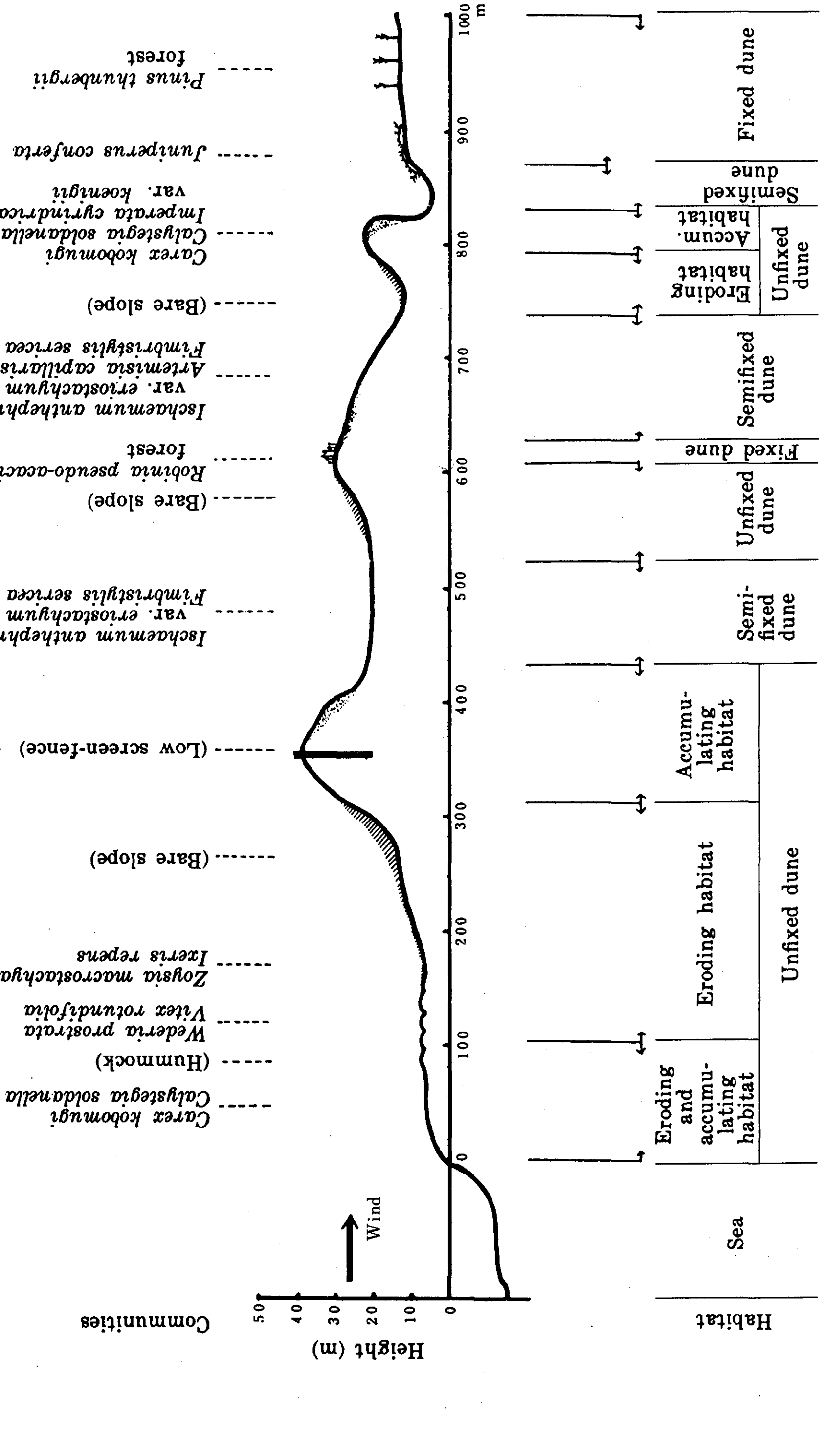

Fig. 5. Diagrammatic profile of the Tottori Sand Dune at a representative site, showing topography and zonation of communities.

should be divided further into three habitats. Researches were again made on the vegetation of each habitat. Fig. 5 shows a topographic profile of the Hamasaka sand dune and several communities developed on the dune.

It may be explained briefly as follows:

1. Unfixed dune.

a. Eroding and accumulating habitat. Eroding and accumulating habitat develops in the area 40—100 m from the beach line and is more strongly influenced by moving sand and salt spray. The vegetation of this habitat is characterized by the *Carex kobomugi* community, *Calystegia soldanella* community, and small community of *Messerschmidia sibirica.* Subdominant species of these communities are *Wederia prostrata, Zoysia macrostachya, Glehnia littoralis,* etc. These communities are remarkably open with low density and a low degree of cover. The *Calystegia soldanella* community is developed near the beach line and is usually a pure community. *Calystegia soldanella* forms flat and wide hummocks on the sand, and individual plants are connected with each other by their rhizomes. The *Carex kobomugi* community develops near the beach line. The components of the community are usually very poor, but occasionally compound some other species. Upper shoots of *Carex kobomugi* are branched sparsely and form small hummocks by means of the sand accumulation. These small hummocks combine with each other to form a flat and large hummock. Individual plants forming a small hummock are connected with each other by the rhizome, and form a small community which arranged like a mosaic. The *Messerschmidia sibirica* community develops near the beach line, and in most cases, the community consists of only one species and is rarely associated with *Carex kobomugi.* The hummocks formed by this plant are small in size and they cannot develop into a large hummock.

b. Eroding habitat. This habitat develops on the windward slope of the dune, and covers the area between 100 and 300 m from the beach line. Most of the habitat is kept bare by wind erosion, especially on the side which suffers violent wind erosion, there develops no community (Fig. 5). However the transitional zone between the eroding and accumlating habitat, and eroding habitat supports some communities which form sand hummocks by sand accumulation, that is, communities of *Zoysia macrostachya, Ixeris repens, Wederia prostrata* and *Vitex rotundifolia.* All of these are usually very poor. In general, their propagative organs are well developed and invade the bare land. They can more or less control the moving sand by means of their vegetative growth, for sand accumulation occurs to the leeward of these communities and various hummocks are made in the habitat. In the early stage of sand accumulation, small hummocks are formed, however, the more the sand accumulation increases, the larger these hummocks become.

c. Accumulating habitat. This habitat occurs between 800 and 1000 m from the beach line, and especially it develops in the leeward slope of a dune kettle. Coastal sand is driven landward by wind; in the leeward of the dune kettle occurs sand accumulation, but in the windward occurs sand erosion. Thus a dune kettle is formed. Points of C_1, C_2 and C_3 in Fig. 6 show the accumulating habitat. At these points, sand accumulation reaches 1 m or more per year, so that plants are damaged by sand accumulation, but the influence of salt spray is rather weak there. C_1, C_2 and C_3 in Fig. 6 show the difference of components of the communi-

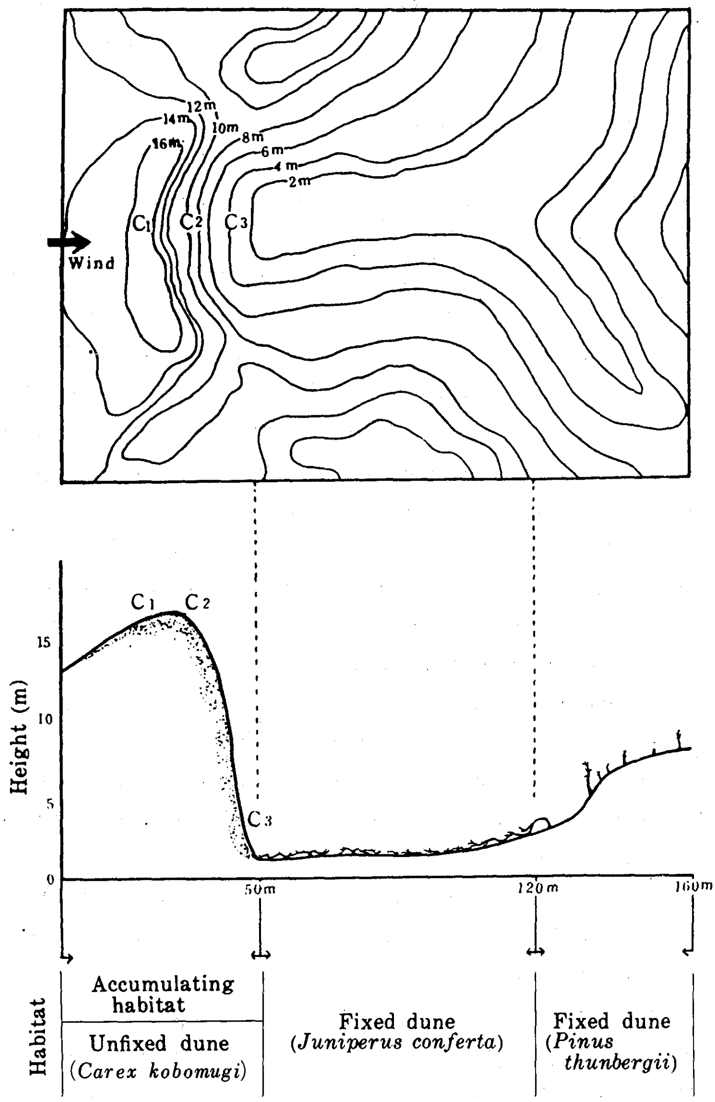

Fig. 6. Diagrammatic profile of a "dune kettle" along its longitudinal axis. C_1, C_2 and C_3 are communities observed by the author.

ties which develop corresponding to varied degrees of sand accumulation.

In the habitat where violent sand accumulation occurs, there develop communities of *Carex kobomugi*, *Imperata cylindrica* var. *koenigii*, and *Calystegia soldanella*. The main components of these communities have a characteristic ability to endure the sand accumulation and to invade the habitat. *Carex kobomugi* and *Imperata cylindrica* var. *koenigii* extend their rhizomes vertically upward and form small communities .

2. Semifixed dune.

A semifixed dune occurs at a distance of 400 m or more from the beach line, and it is on a sand flat where the wind is rather weak and the sand accumulation is slight. Main communities developed in this dune are of *Ischaemum anthephroides* var. *eriostachyum*, *Bulbostylis barbata*, *Ischaemum anthephroides* var. *eriostachyum*-*Artemisia capillaris*, *Fimbristylis* *sericea*, *Linaria japonica* and *Vitex rotundifolia-Artemisia capillaris*. In general, the main species of these communities are less endurable to sand accumulation, and they die when buried by accumulated sand at a depth greater than they can adapt to themselves. Some species, such as *Artemisia capillaris*, *Fimbristylis sericea* and *Indigofera pseudotinctoria*, can endurable only a little sand accumulation.

3. Fixed dune.

This dune is seen 1000 m from the beach line. In natural conditions, the stable habitat seems to develop at far distance from the beach line, however, on this sand dune, the sand moving is stabilized by the artificial forests of *Pinus thunbergii*, *Robinia pseudo-acacia*, etc, so that the stable habitat is seen under these forests. In general, the main species of the communities in this dune have less tolerance against moving sand, although most of them are perennials with rhizomes. *Juniperus conferta*, *Imperata cylindrica* var. *koenigii*, and *Imperata cylindrica* var. *koengii-Artemisia capillaris* communities are observed in this habitat. Other component species of the communities are *Pinus thunbergii*, *Juniperus conferta*, *Imperata cylindrica* var. *koenigii*, *Lespedeza cuneata*, *Indigofera pseudo-tinctoria*, *Dianthus superbus*, *Artemisia princeps*, *Artemisia capillaris*, *Rumex acetosella*, *Hypnum plumaeforme*, *Rhacomitrium canescens*, *Ischaemum anthephroides* var. *eriostachyum*, *Miscanthus sinensis*, *Paederia scandens*, *Potentilla chinensis*, *Luzura capitata*, *Solidago virgaaunea*, *Rosa wichuriana*. *Vitex rotundifolia*, *Calystegia soldanella* and *Carex kobomugi* also occur on the fixed dune, but they have more slender propagative stems on a dune of this type.

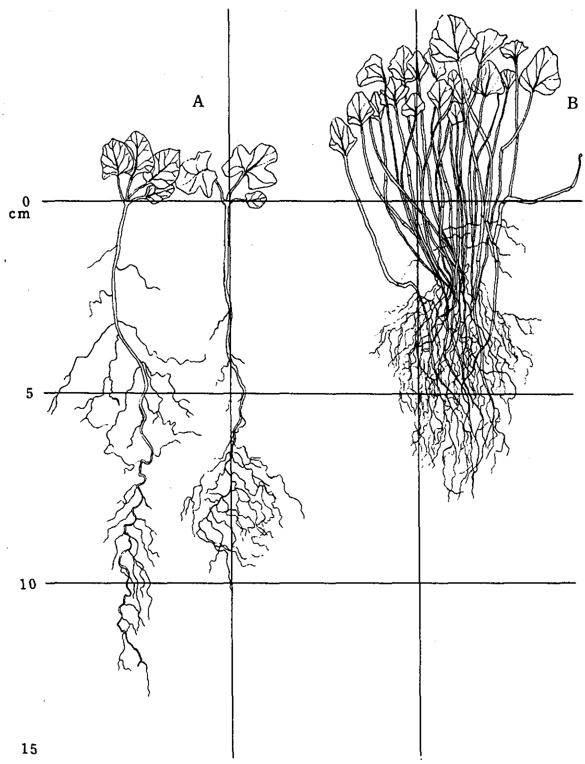

Fig. 7. Root system of *Ixeris repens*.
A. Root system of one-year-old plant
B. Aggregation form.

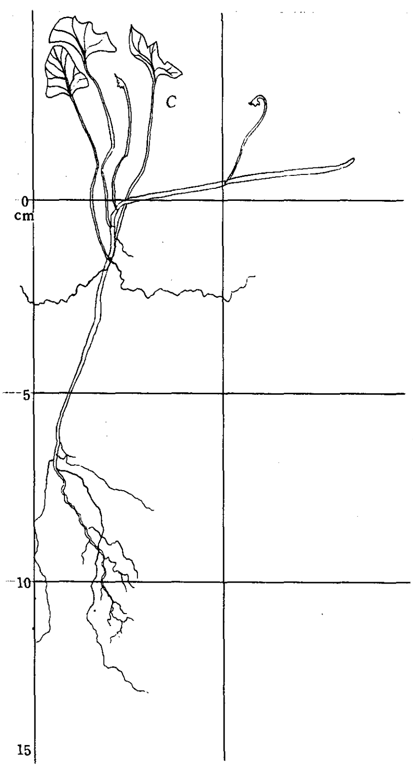

Fig. 8. Root system of two-year-old plant of *Ixeris repens*.

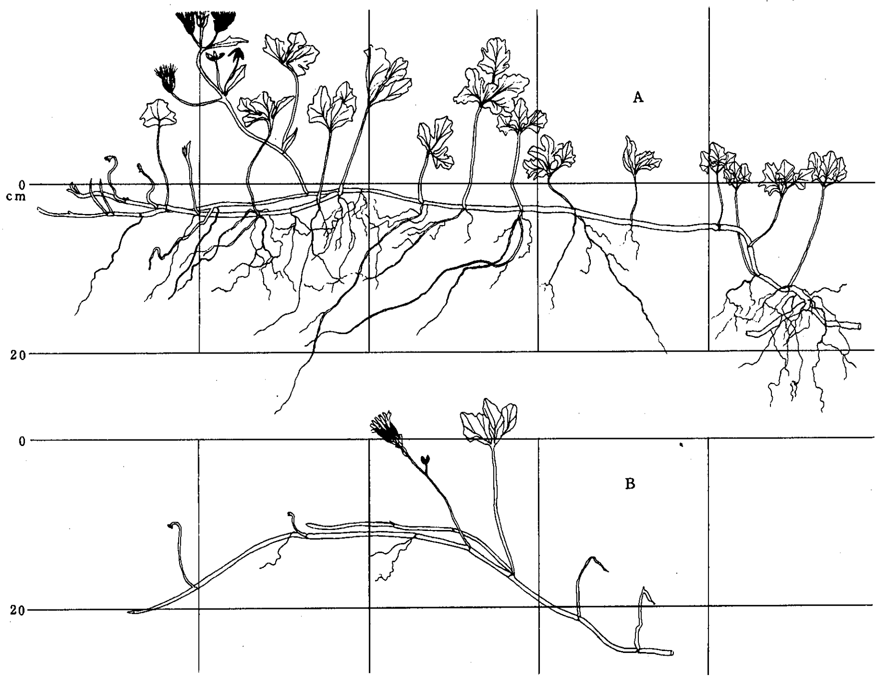

Fig. 9. Root system of *Ixeris repens.*
A . Root system of adult plant.
B . Root system of the eroding habitat.

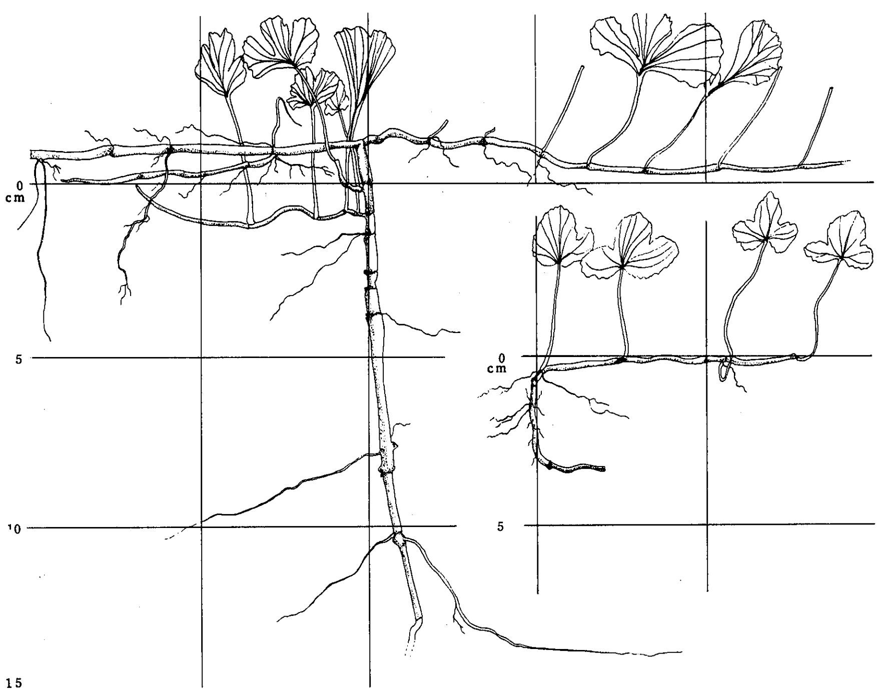

Fig. 10. Root system of *Ixeris repens* on the volcanic ash.

Root system

Studies of the root systems were made concerning dominant and subdominant species in the sand dune plant communities . Description of the root systems of the species studied are as follows:

1. *Ixeris repens* (Figs. 7, 8, 9 and 10)(Table 2).

Table 2. Root development of *Ixeris repens.*
* —spring
* * —summer

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of rhizome in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Length of internode in cm. *	**	Average elongation of rhizome for a year in cm.
1	4—5	4—15	0	5—10	1—1.2	0.02—0.1	5	—	—	5—10
2	10	10—20	10—15	10—20	1.5—3	0.1—0	30	7.35	8.95	20—30
3	10	10—25	10—25	10—25	3.5—4	0.1—1	500	5.1	6.8	30—155

The specimens studied were chosen in the community developed at the unstable habitat, 40—100 m from the coastal line. *Ixeris repens* flowers from July to October, and most of the flowers are fructified on the head and buried in sand soil in that condition. Most of the seeds germinate from June to July. Seedlings aggregated in a group of 16—20 individuals, but within a month aftr germination the plants are reduced to 2 or 3 individuals. The root of a one-year old plant consists of a main root which runs vertically downward and at a depth, of 10 to 15 cm produces numerous fibrous roots. The developmental stages of root system in each estimated age are shown in Table 2. The rhizome and root require about three years to reach full growth. The rhizome of a one-year plant is very short, but a two-year old plant has a longer rhizome which is usually 2.5—4 mm in diameter but in rare cases may be 6.5 mm or more. The rhizome is somewhat soft, succulent and frequently branched. It appears to have an ability of water storage. The rhizomes, which are laid 10—30 cm below the surface, often run obliquely and show scalariform growth in the upper layer. Some of them, however, occasionally run obliquely downward when they are exposed by the erosion of wind. Laterál roots, which are about 0.3 mm in diameter, arise in tufts of 2 or 3 from each node of the rhizome, but are not produced in the portion ranging 20—25 cm from the top of the rhizome. Rootlets are branched from the lateral root and are well extended, forming a cluster.

Generally the lateral roots are thin, their life is short, and most of them decay in one year. The life of the rhizomes is also short. The root colour is yellow brown, and the rhizome is olive ochre.

The mean length of growth of the rhizome is about 100 cm in a year. The stems and leaves are resistant to the action of salt spray and flying sand . The leaves and petioles decay when the sand accumulation in one year exceeds 10 cm.

The rhizomes which develop in July to June are on an average, 6.5 mm in diameter, 30 cm in length, and those which develop in August to September are 3—5 mm in diameter and 55 cm in length. The life form is G and root types are Rm 5, Rs 5, Rd 4 and Rv 3 on this sand dune.

2. *Calystegia soldanella* (Figs. 11, 12, 13, 14 and 15)(Table 3).

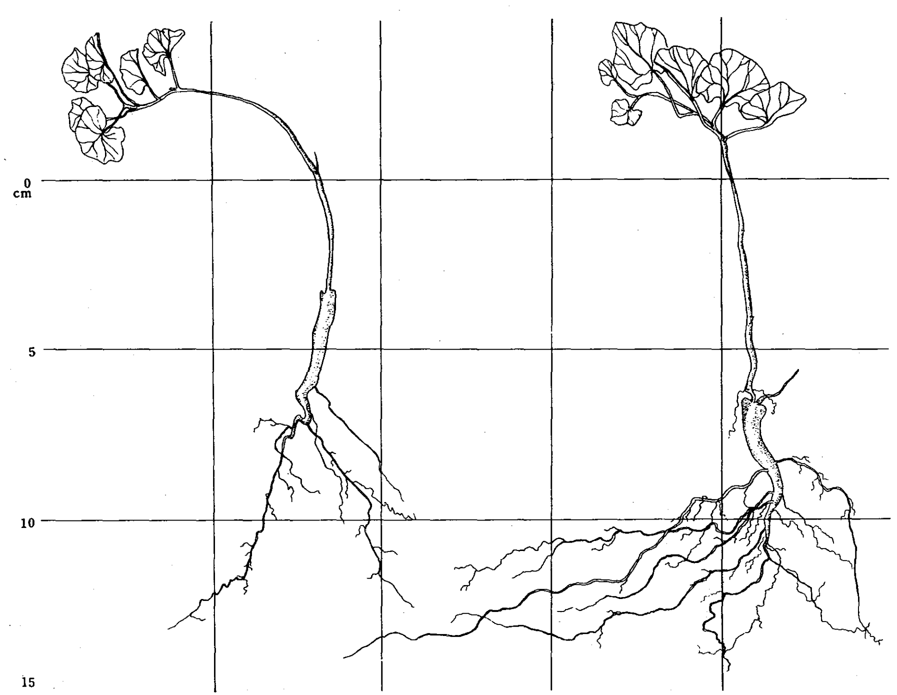

Fig. 11. Root system of *Calystegia soldanella*.
A and B are root system of a one-year-old plants.

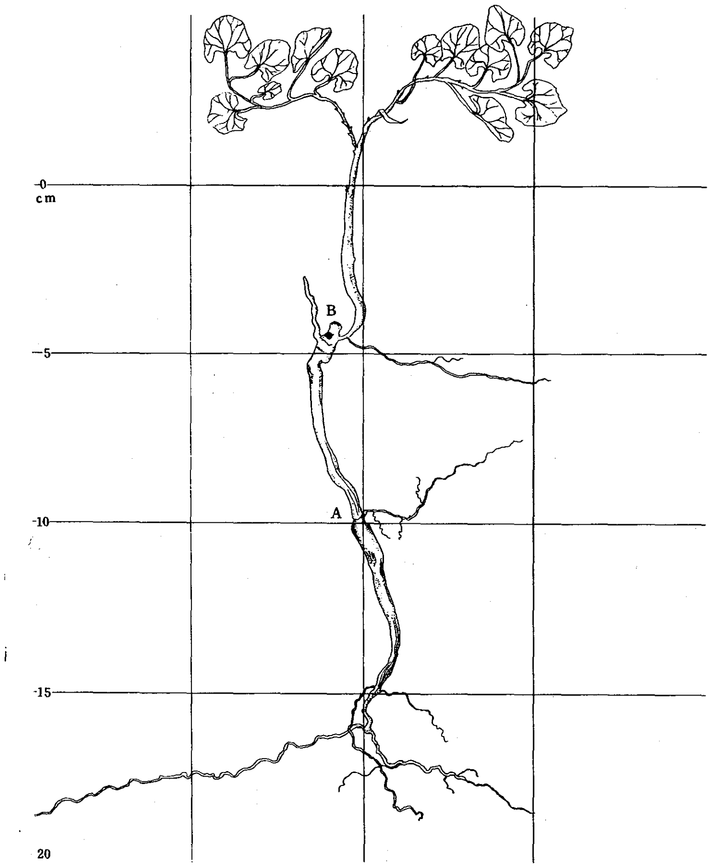

Fig. 12. Root system of a three-year-old plant of *Calystegia soldanella*.
A. Growth point at one year.
B. Growth point at two years.

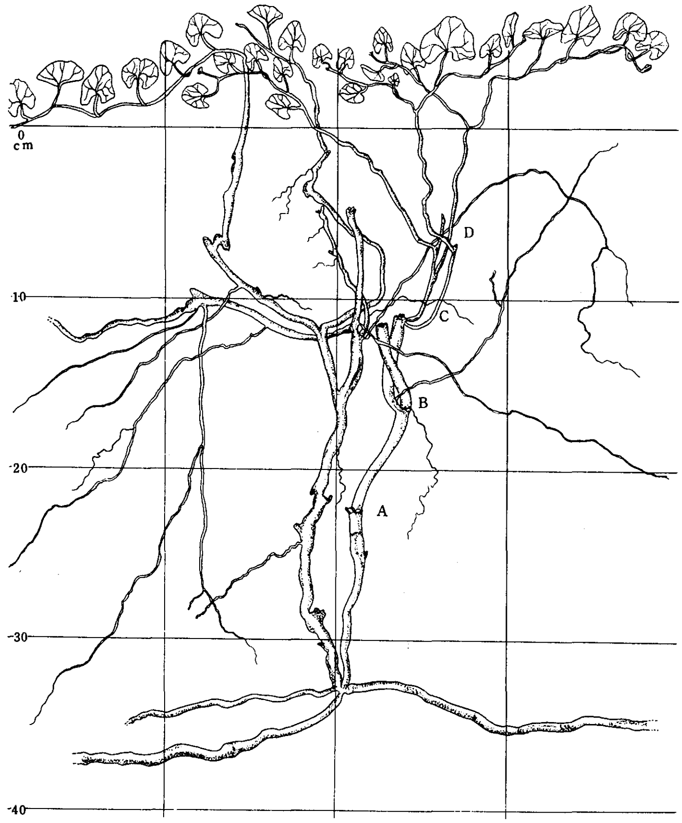

Fig. 13. Root system of a five-year-old plant of *Calystegia soldanella.*
A . Growth point at one year.
B . Growth point at two years.
C . Growth point at three years.
D . Growth point at four years.

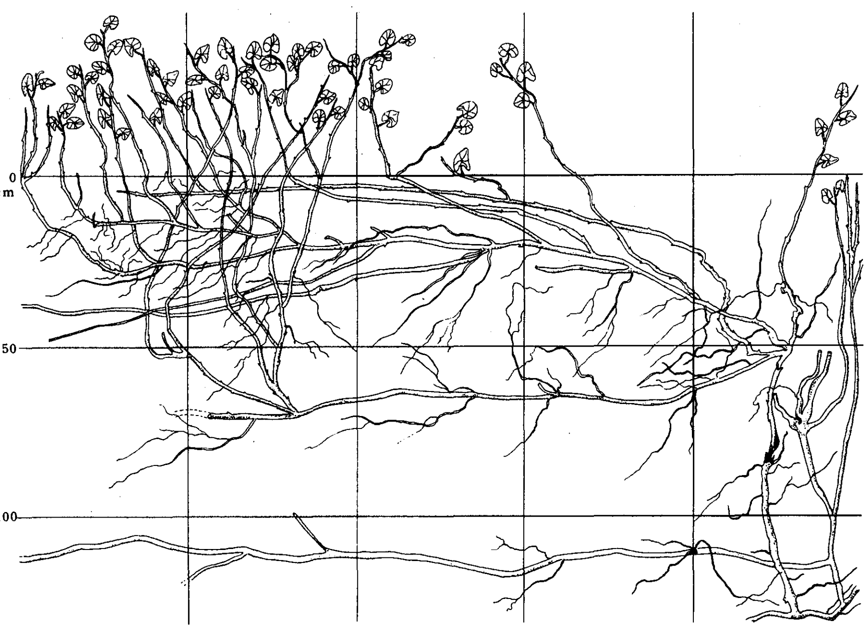

Fig. 14. Root system of adult plant of *Calystegia soldanella.*

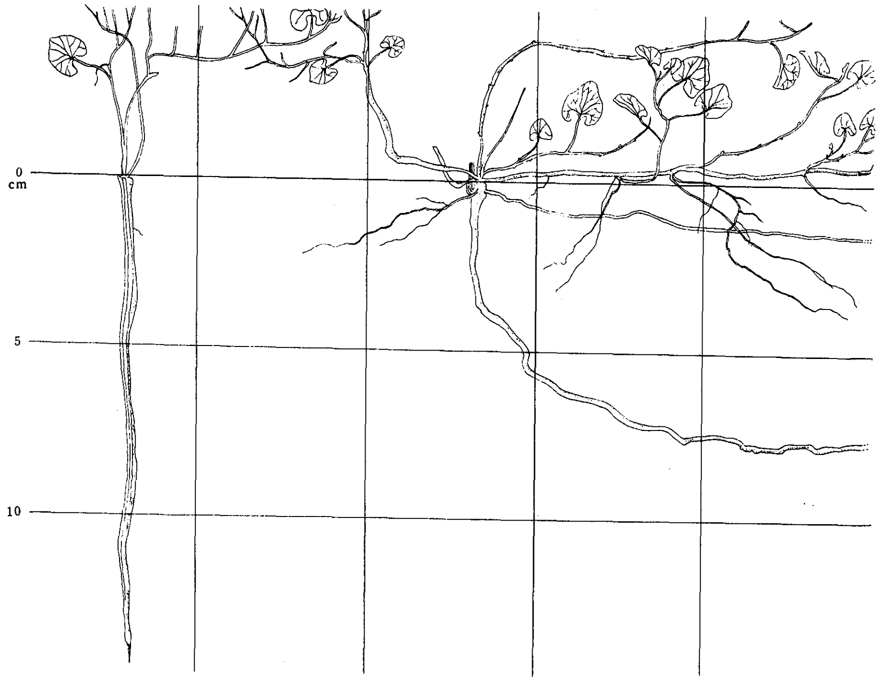

Fig. 15. Root system of *Calystegia soldanella* on the volcanic ash.

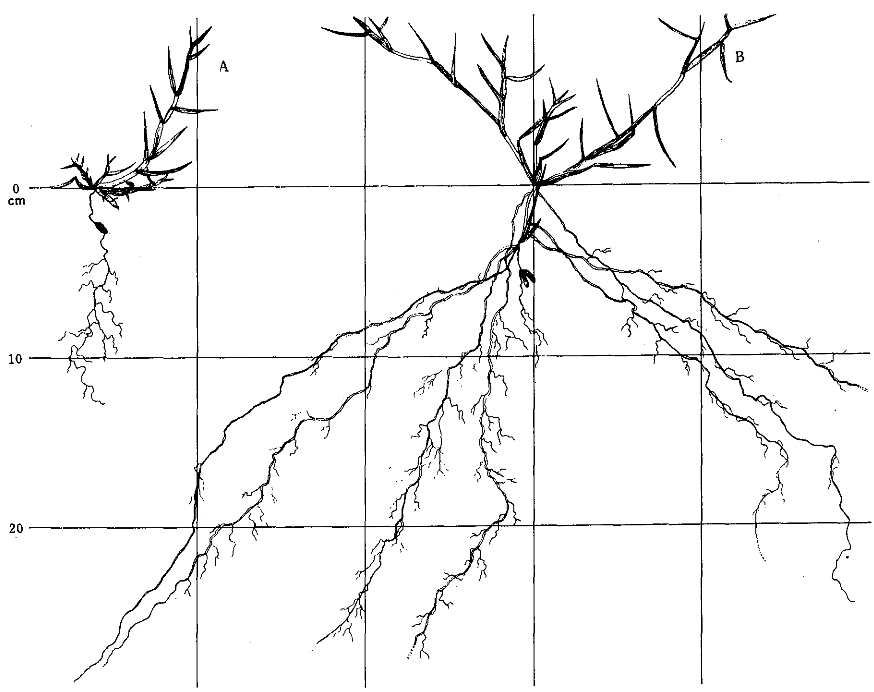

Fig. 16. Root system of *Zoysia macrostachya.*
A . Root system of one-year-old plant.
B . Root system of two-year-old plant.

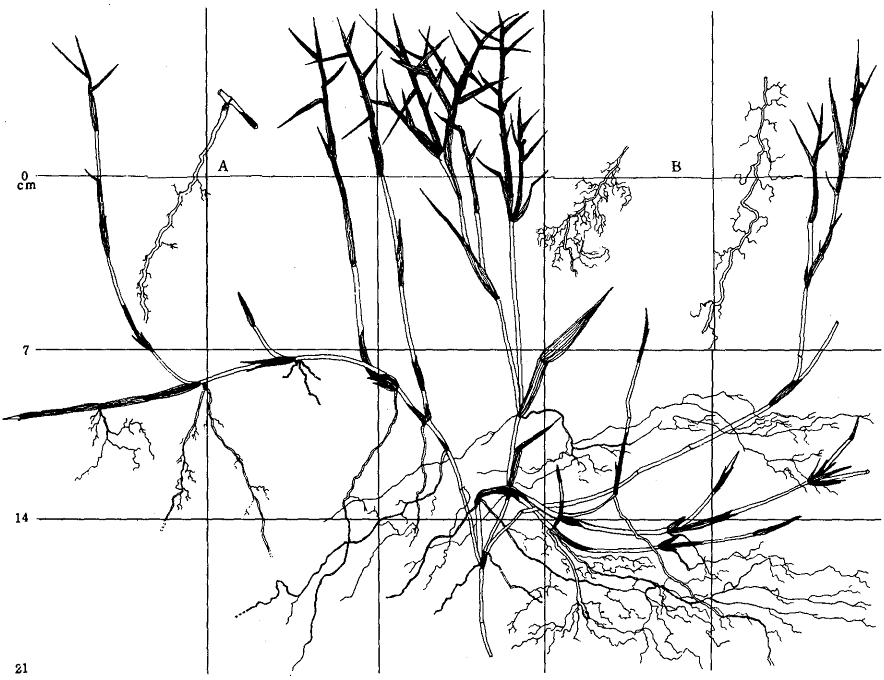

Fig. 17. Root system of three-to four-year-old-plant of *Zoysia macrostachya*.
A. Old lateral root.
B. Young lateral root.

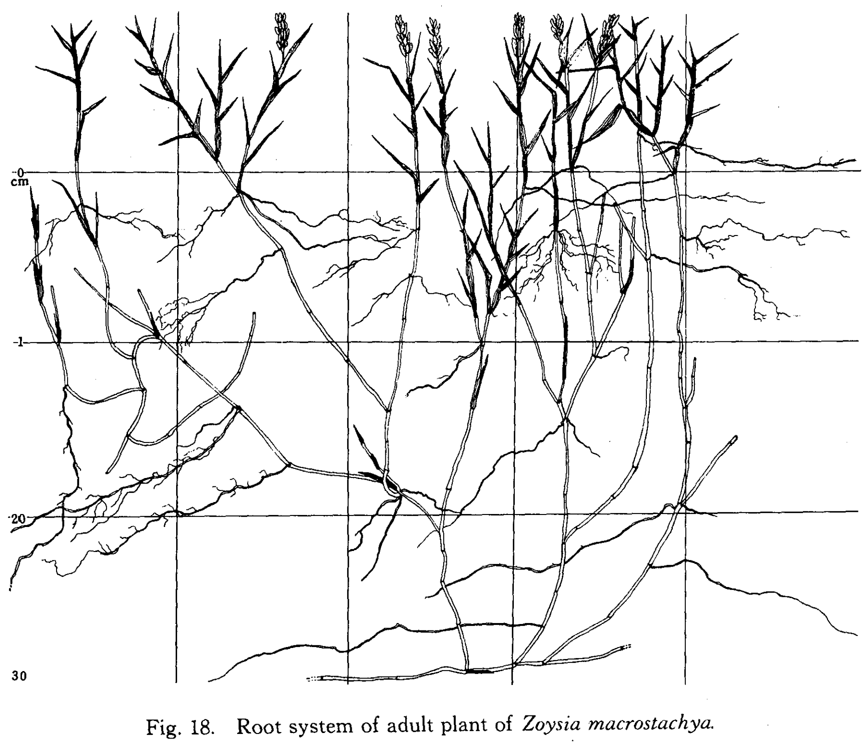

Fig. 18. Root system of adult plant of *Zoysia macrostachya*.

Table 3. Root development of *Calystegia soldanella.*

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of root in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Length of internode in cm.
1	5—6	5—15	20	5—10	1.5—3	0.2—0.3	2	1.24
3	5—6	25	25	10—20	3—4.5	0.2—0.5	5	1.25
4	10	25—30	25—30	10—30	3—5	0.2—2	10—20	2.4
5	10—15	more than 100	30—40	10—40	3—6	4—5	30—40	2.5
6	10—15	more than 100	30—100	10—100	3—6	4—5	100—300	2.5—3

The specimens studied were chosen in the communities developed at an unstable habitat, 40 m from the coastal line, in a floor community of *Pinus thunbergii* forest developed in a stable habitat, and also from the plants growing on volcanic ash. *Calystegia soldanella* is well developed on the semistable habitat. It flowers May to June, and most of the seed as are matured August to September and germinated from April to May. The juvenile plant is 7—10 cm shoot height and the stem is 1.6 mm in diameter. The tap root has a character somewhat succulent and runs vertically downward. It is 3—4.5 mm in diameter, 5—15 cm in length, and 15 cm in depth. Three or four branching roots are branched from the tap root, and lateral roots are branched from the branching roots, but their number is small. The developmental stages of the rhizome and root system at each estimated age shown in Table 4. *Calystegia soldanella* forms its community , which is 2—3 m in diameter, abut 5 years after the germination of a seed. In the plant developed on the unstable habitat, length of the stolones grown in one year is 60—150 cm, in those on the accumulating habitat the stolones develop to the length of 5 m or more in one year. The length of the lateral roots is 15—20 cm. Secondary rhizomes are formed from the stolone, which are buried in the sand , and they run obliquely or vertically upward. The stolone ends sometimes run downward and penetrate the sand soil. The secondary rhizomes are more or less succulent and have a function of water storage. The colour of the young roots is yellow-brown, and the old roots and secondary rhizomes are brown olive. The age of the rhizomes was estimated to be seven or eight years. The specimens in the floor community under *Pinus thunbergii* forest show bad growth (both shoot and root), due to the lack of light and diminution of sand accumulation. The specimens on volcanic ash are poor in development of the tap root because the soil is compact and hard. In winter the leaves decay, and buds grow from the base of leaf-stalk, and they form new stolones. The life form of the adult plant is G or H and root types are Rm 4, Rs 5, Rd 1 and Rv 6 on this sand dune.

3. *Zoysia macrostachya* (Figs. 16, 17 and 18)(Table 4).

The specimens studied were chosen in the community developed on the unstable habitat, 40—100 m from the coastal line. *Zoysia macrostchya* flowers from July to August, and most of the seeds are matured from August to September and germinate from June to July. The juvenile plant has a main root that is 0.2 mm in diameter and 15 cm in length and its course is vertically downward. Two or three lateral roots are branched from the base of stock, and the shoots are 7 cm in length and 1.1 mm, in diameter, short rhizomes run horizontally on the soil

Table 4. Root development of *Zoysia macrostachya*.

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of root in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Average elongation of rhizome for a year in cm.
1	5—7	15	0—5	5—15	1	0.2	3	4
2	5—7	30	5—20	3—30	1	0.2	20	20
3	10—12	50	20—45	20—30	1—2	0.2—1	30—120	30—60

surface. The developmental stages of the root system at each estimated age are shown in Table 5. Frequently the shoots buried by sand become secondary rhizomes and develop obliquely to the upper layer in branched furcate form. Three or four shoots grow from the base of the stem and enlarge the clone (Fig. 16). In the habitat where the sand accumulation is diminished, the rhizomes run horizontally and form a plain community (Fig. 17). The rhizomes of one-to two-year-old plants produced many rootlets. Plants of three or more years produced coarse roots but few rootlets and root hairs. The colour of the root and rhizome is plate brown. *Zoysia macrostachya* grows the habitat which has sand accumulation of less than 30 cm. The life form is H or G and root types are Rm 4, Rs 5, Rd 2 or Rd 1 and Rv 2 or Rv 3 on sand dune.

4. *Ischaemum anthephroides* var. *eriostachym* (Figs. 19, 20, 21, 22 and 23)(Table 5).

Table 5. Root development of *Ischaemum anthephroides* var. *eriostacyum.*

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of rhizome in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Length of lateral root in cm.	Accumulating sand height in cm.
1	5	7—20	0—1	4—5	1—2	0.2—0.5	5—10	7—8	2
2	10—15	20—30	2—5	5—20	1—2.5	0.2—1	7—12	15	5
3	17	30—40	3—10	5—25	2—2.5	0.2—1.5	13—25	25—60	8
4	20	more than 60	60	5—35	2—2.5	0.2—2	60—120	more than 150	20

The specimens studied were chosen in the community developed in the unstable habitat, 500 m from the coastal line.

Ischaemum anthephroides, on this sand dune, flowers from August to September, and most of the seeds mature from September to October. The juvenile plant has a tap root which, reaches a depth of 20 cm. The lateral root produces two or three branches and the rhizome is very short. The developmental stage of the root system at each estimated age is shown in Table 5.

The adult plant of the *Ischaemum anthephroides* grows in stocklike form with a dense shoot organ. Secondary rhizomes are formed from shoots which are buried by the sand, and numerous adventitious roots are branched from the top of the secondary rhizome. Three to five shoots are produced and grow obliquely to the upper layer, which increases the area of the clone. The rhizomes at a depth of 50 cm or more decline with age and finally decay or lose their absorptive function. Rhizomes occupying the center of a large clone are usually decayed and constitute a dead center. Roots of the adult plant are coarse and have lateral roots

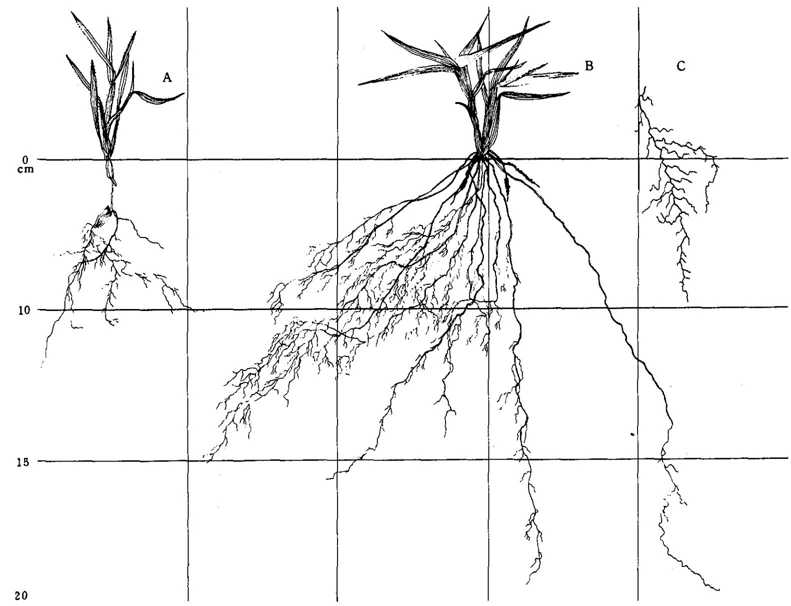

Fig. 19. Root system of *Ischaemum anthephroides* var. *eriostachyum.*
A. Root system of one-year-old plant.
B. Root systej of two-year-old plant.
C. Branching rootlet.

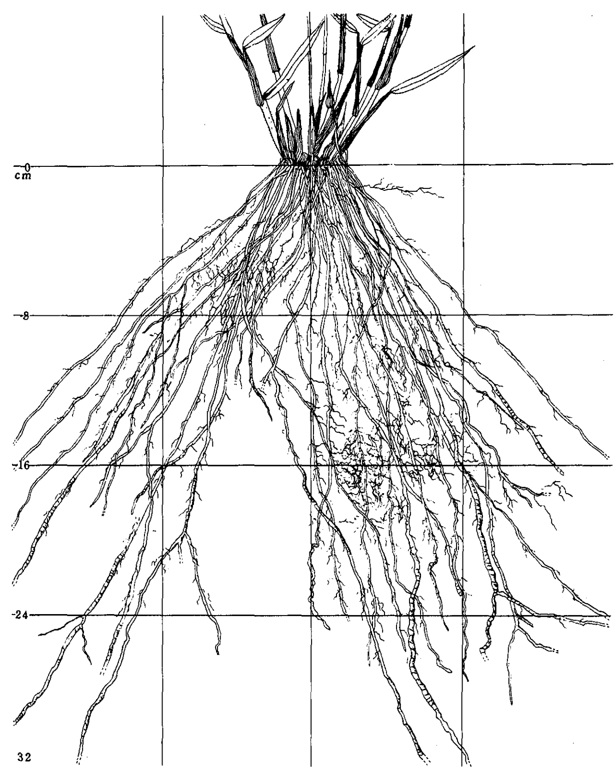

Fig. 20. Root system of three-year-old plant of *Ischaemum anthephroides* var. *eriostachyum.*

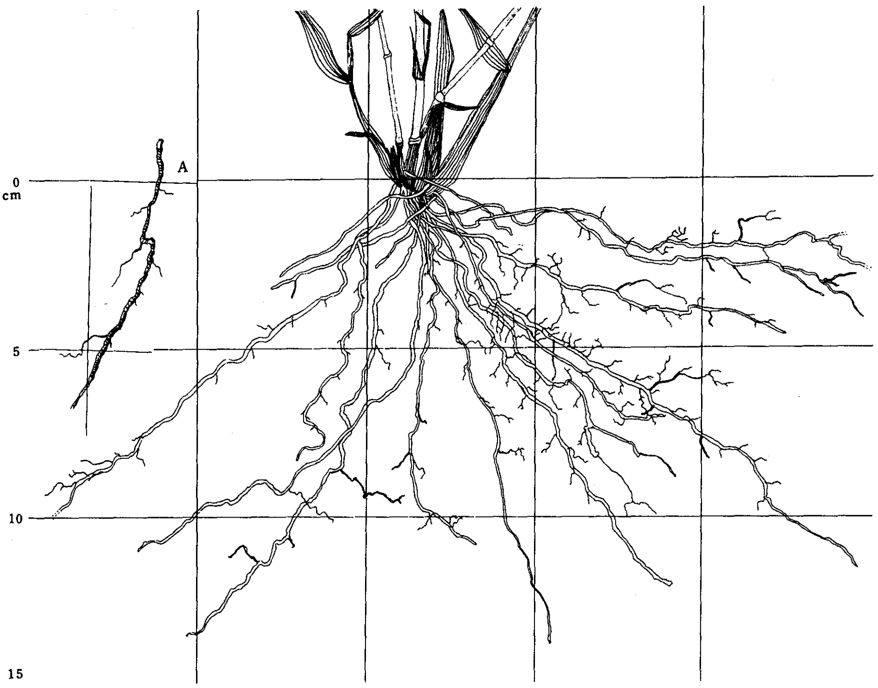

Fig. 21. Root system of *Ischaemum anthephroides* var. *eriostachyum* on volcanic ash.
A. Branching lateral root.

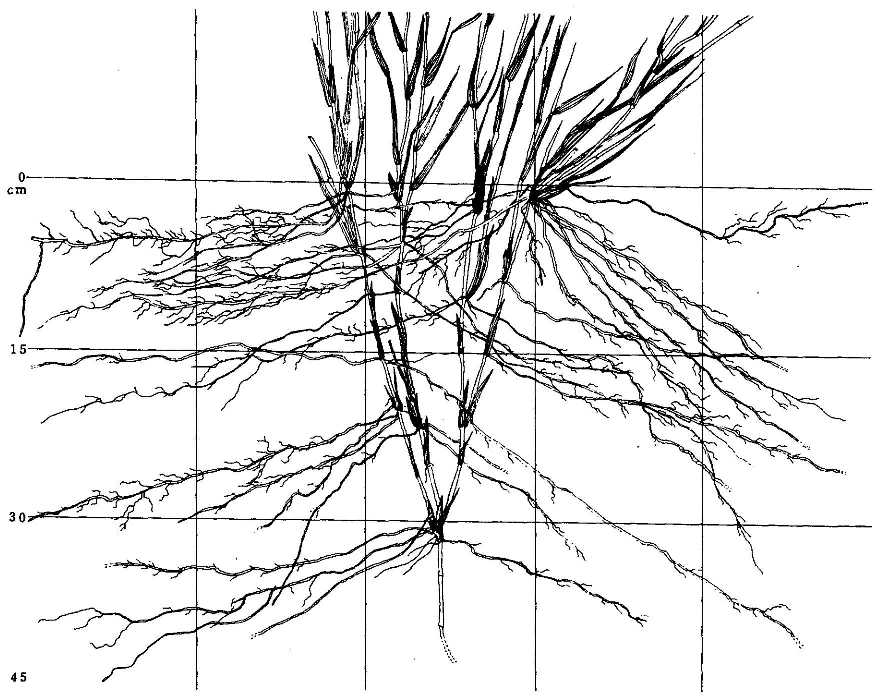

Fig. 22. Root system of adult plant of *Ischaemum anthephroides* var. *eriostachyum* on accumulating habitat.

which are well developed and run horizontally at a depth of 10 cm. The rootlets are distributed mostly from 0 to 25 cm under the soil surface, and are scarce at a depth of more than 25 cm under the surface or near the base of the stem. Most of the roots, which are developed at 40 cm or more under the surface, are decayed and lose their absorptive function. The root suface has many wimples, and in some roots the top part is enlarged and the base is slender. The rootlets are short and swollen. The specimens growing on the volcanic ash have coarse roots with many wimples, and their rootlets are less branched and well crooked. Generally the plant has a strong resistance to sand erosion, and the communities developed in the unstable habitat are sometimes broken down by the wind erosion.

Colour of the root and rhizome is ochre or yellow ochre. The life form is G or H and root types are Rm 5 or Rm 4, Rs 2, and Rv 8 on this sand dune.

5. *Vitex rotundifolia* (Figs. 24, 25, 26, 27 and 28)(Table 6).

Table 6. Root development of *Vitex rotundifolia.*

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Working depth of root in cm.	Diameter of root in mm.	Diameter of community in cm.	Diameter of shoot in mm.	Length of laterel root in cm.	Height of sand accumulation in cm.
1	8—10	15—20	5—15	0.2	1—3	0.7	12—15	1—2
2	—	25	—	—	—	3.5	15—25	—
3	9—10	50	10—30	0.5—1.5	10	3—4	130	5
4	10—12	50—60	10—30	0.5—2.5	25	5.5	180—200	5—7
6	20	more than 90	10—40	0.5—2.5	30—50	7	—	10—15
8—10	20	more than 120	25—90	0.5—2.5	300—400	3—7	—	20—50
20	20	more than 200	—	0.5—4	500—1000	20—35	—	40—100
48—50	20—30	more than 200	—	1.9—5.4	—	50—80	1200—1900	170—200

The specimens studies were chosen in the communities developed in the unstable habitat between 150 and 200 m from the coastal line and also in the stable habitat at 1000 m from the coastal line. *Vitex rotundifolia* flowers July to August, and most of the seeds are matured and fall from September to October. The number of seeds in a sack are 3 to 4, and they fall with the sack. They germinate from June to July. Usually 2 or 3 juvenile plants are aggregated, and their shoots are 2 to 5 cm in length and 0.7 mm in diameter. The tap root is 0.2 mm in diameter, and from 15—20 cm in depth. The lateral roots are only 0.1—0.3 mm in diameter and produced from various locations. The stage of the development of root systems in each estimated age is shown in Table 6. The plants which are four to six years old produce stolones from the base of the stem, and those stolones run horizontally on the sand surface. When the stolones are buried by sand, they are transformed into secondary rhizomes which branch and run obliquely to the upper layer and form a large clone. In a place which has less sand accumulation the stolones elongate horizontally on the sand surface and form a better expanded clone than in a violent habitat. The stolones of ten-year-old plants in the stable

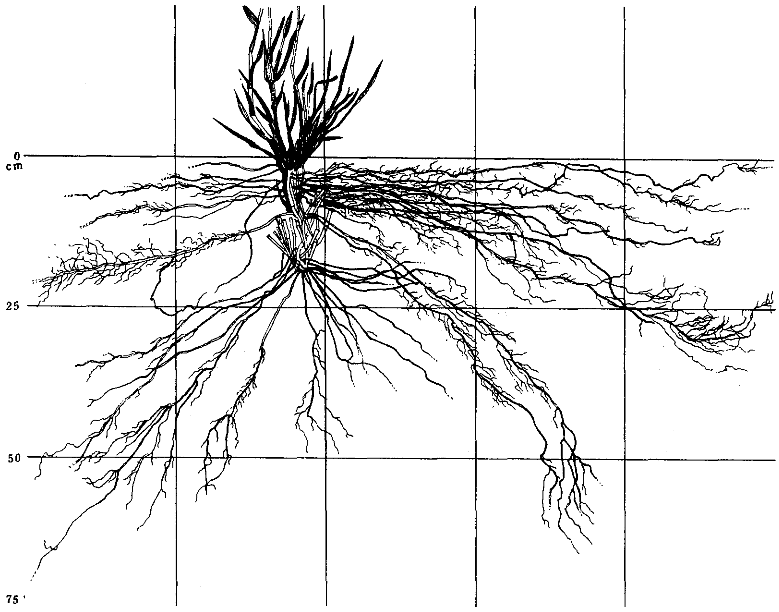

Fig. 23. Root system of adult plant of *Ischaemum anthephroides* var. *eriostchyum* on eroding and accumulating habitat.

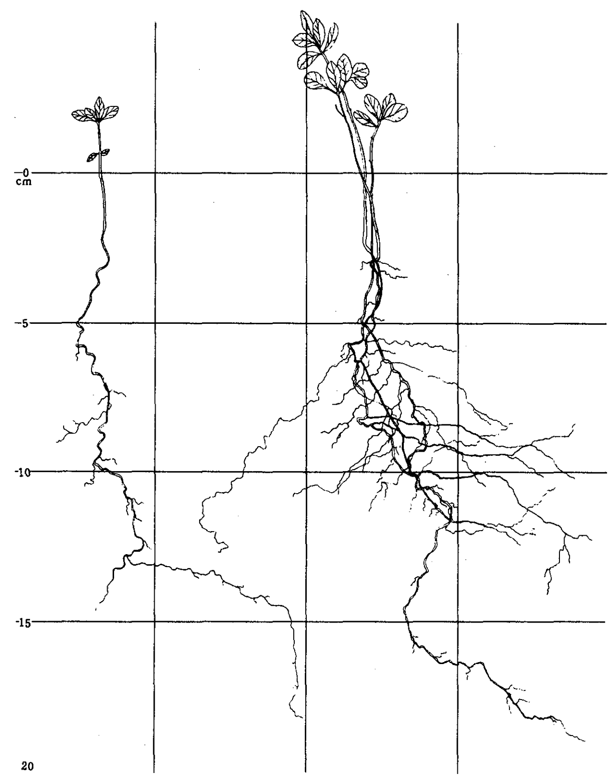

Fig. 24. Root system of one-year-old plant of *Vitex rotundifolia*.

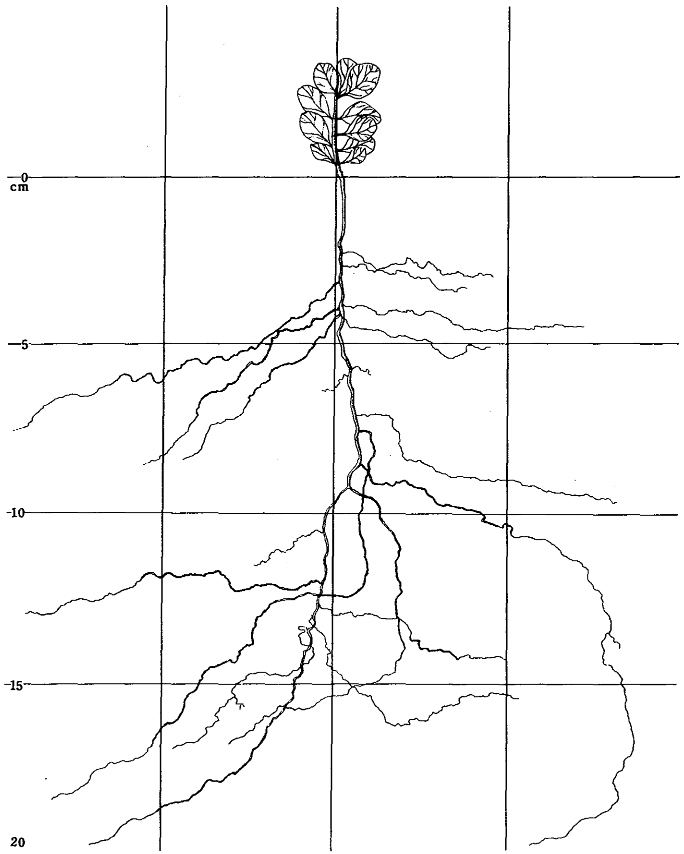

Fig. 25. Root system of three-year-old plant of *Vitex rotundifolia*.

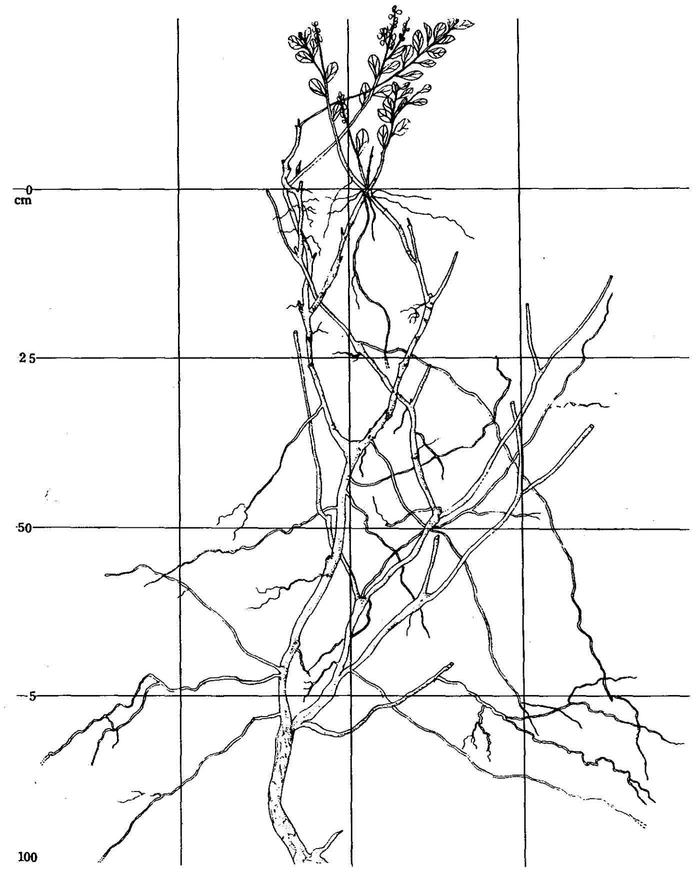

Fig. 26. Root system of adult plant of *Vitex rotundifolia*.

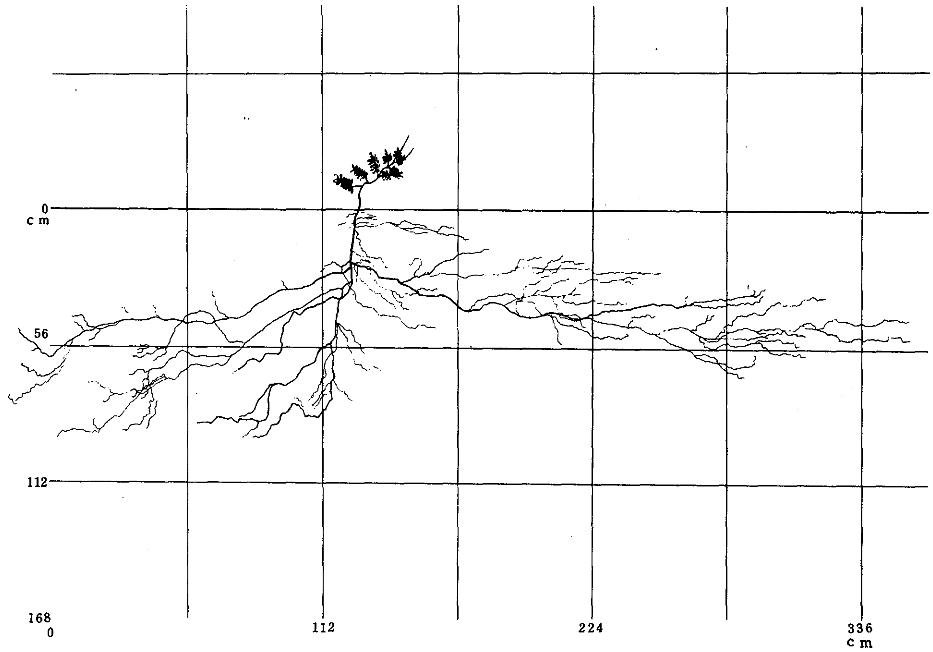

Fig. 27. Root system of a seven-to ten-year-old plants of *Vitex rotundifolia*.

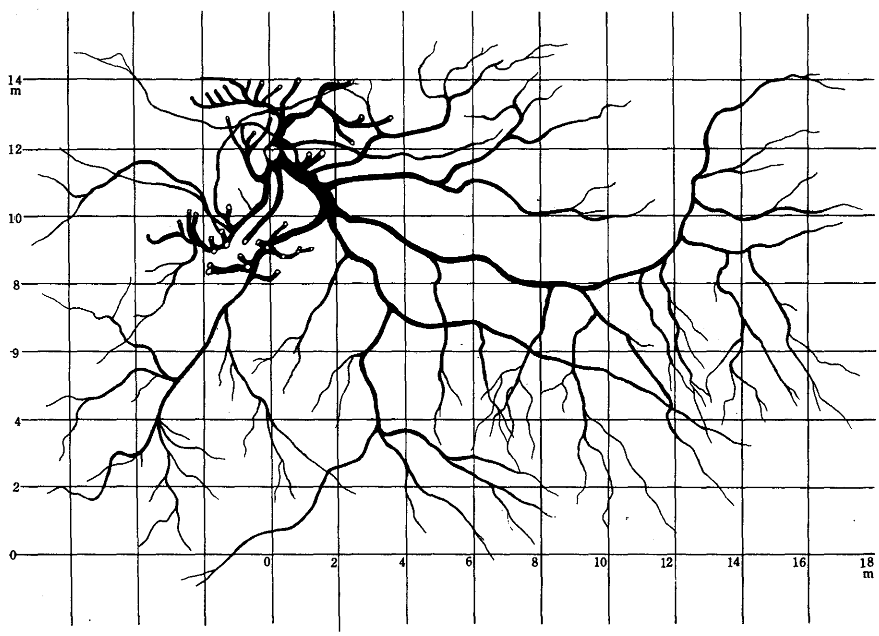

Fig. 28. Horizontal extension of root system of *Vitex rotundifolia* (about fifty years old).

habitat, are elongated to 12 m from the base of the plant; but it is only rare that the length of a stolone becomes 3 or 4 m in the unstable habitat. The tap root is well developed in the early stage, and grows deeper each year but the tap root of a ten-year-old plant ceases elongation and increases in diameter (Fig. 33). The lateral roots develop with the years, and those of a forty-eight-or fifty-year-old plant reach 18—19 m in length (Fig. 28). Adventitious roots are produced from various locations on the secondary rhizome, and most of them run obliquely or vertically downward. Most of the rootlets are poorly branched (Fig. 26). The root and rhizome are lignified and have many longitudinal lines. The colour of the root is grayish red-brown. The plants are resistant to sand accumulation and lying sand. The plants growing in the unstable habitat form a large hummock with a gentle slope. The life form is H or CH, and root types are Rm 4, Rs 3 or Rs 4, Rd 1 and Rv 3 or Rv 6 on this sand dune.

6. *Linaria japonica* (Figs. 29 and 30)(Table 7).

Table 7. Root development of *Linaria japonica*.

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Diameter of shoot in mm.	Working depth of root in cm.	Length of laterel root in cm.	Diameter of root in mm.	Diameter of community in cm.
1	3	8	0.5	3—8	6—7	0.2—0.4	1—2
2	3—4	10—15	1—1.2	3—10	15	0.2—0.8	5
3	5—10	15—20	1—1.5	3—15	55—60	0.2—1	5—7
more than 4	8—30	20—30	3—4	5—20	50—100	0.2—1.5	200

The specimens studied were chosen from a community on the semistable habitat 500 to 800 m from the coastal line. *Linaria japonica* flowers August to October and most of the seeds are matured and fall from August to November. Most of the seeds germinate from May to June. The juvenile plant has shoots 2 cm in length and a succulent root 5—15 cm in length running horizontally below the soil surface. The developmental stage of the root system at each estimated age is shown in Table 7. The succulent roots are branched and developed radially, with many adventitious roots. The adventitious root ran horizontally below the soil surface and elongated 20—30 cm in one year. The root systems of the adult plant reach a depth of 30 cm, and the shoots are sparse. The clone is large, 5—10 m in diameter. The tap root is decayed and furnished with thin lateral roots. The succulent roots develop on the upper layer when they suffer sand accumulation. The colour of the root is yellow ochre. The life form is G or H and root types are Rm 4, Rs 5, Rd 3 and Rv 3 on this sand dune. *Linaria japonica* is endurable to a sand accumulation level of 5—15 cm in one year.

7. *Wederia prostrata* (Figs. 31, 32 and 33)(Table 8).

The specimens studied were chosen in community on the unstable habitat, about 40 m from the coastal line. *Wederia prostrata* flowers from August to September, and the seeds are matured and fall August to November. Most of the seeds germinate in May. The juvenile plant has a tap root 1.5 mm in diameter, which runs vertically downward and reaches a depth of 25 cm. The lateral roots are succulent and produce rootlets from the top. The developmental stage of the root system at each estimated age is shown in Table 8. The stolones are bran-

Table 8. Root development of *Wederia prostrata.*

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of rhizome in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Length of lateral root in cm.	Height of sand accumulation in cm.
1	8	25	—	3—20	—	0.2—1	3	20	2
3	10—12	30—40	—	5—25	3	0.2—3	15—30	50—60	5—10
5	10—15	60	10	5—30	3	0.2—4	30—50	120	10—12
9—10	10—20	200—1600	40—60	5—40	11	5.5	400—500	200—250	20—100

ched from the base of the stem and run horizontally under the soil surface. The stolones, which are buried by the sand, are transformed into secondary rhizomes. The secondary rhizomes are elongated obliquely to the upper layer and extend a clone, the shoots of which are branched from the base of the stem and elongated obliquely upward by sand accumulation. The tap roots branched and run vertically downward. In nine-to ten-year-old plants tap roots are extended to a depth of 160 cm below the surface (Fig. 33). The lateral roots are sparse and less branched. Numerous adventitious roots are branched from the secondary rhizome, and they are frequently distributed near the sand surface. In general, the root sphere is expanded with age by gradual elongation of the stolones. The colour of the root and rhizome is brown olive.

8. *Messerschmidia sibirica* (Figs. 34 and 35)(Table 9).

Table 9. Root development of *Messerschmidia sibirica.*

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of rhizome in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of shoot in mm.	Diameter of community in cm.	Height of sand accumulation in cm.
1	5—6	10—20	10—15	0—15	1—1.5	1—1.5	2—3	1—3
2	10	20—25	20—25	10—25	2—2.5	2—3	5—7	5
5—6	15—20	100	80—100	40—60	6—9	2.5—3.5	300—400	10—15

The specimens studied were chosen in the *Messerschmidia sibirica-Carex kobomugi* community on the unstable habitat, about 40 m from the coastal line. It flowers in July, fructification and fall of the seeds are July to August, and most of the seeds germinate May to June. As the seeds are larger than those of other species, their travelling distance is short. The juvenile plant has a tap root which runs vertically downward and reaches a depth of 20 cm. Three or four shoots are produced from the portion lying 5—7 cm below the surface. The developmental stage of the root system at each estimated age is shown in Table 9. Rhizomes of adult plant are 6—9 mm in diameter and reach a depth of 100 cm. Secondary rhizomes are formed from the stolones, which are buried by the sand. The terrestrial organs are formed from the base of the stem and grow up obliquely.

The plant has an endurance to sand accumulation of even 20 cm in one year, and also to salt spray. The rhizomes run horizontally under the sand surface and are furnished with numerous adventitious buds, their clones are extended. If the plants suffer from wind erosion, the exposed roots are somewhat shrunk, and shoots are brought down to a lower layer of soil. Lateral roots are produced sparsely from rhizomes. They are more or less succulent and

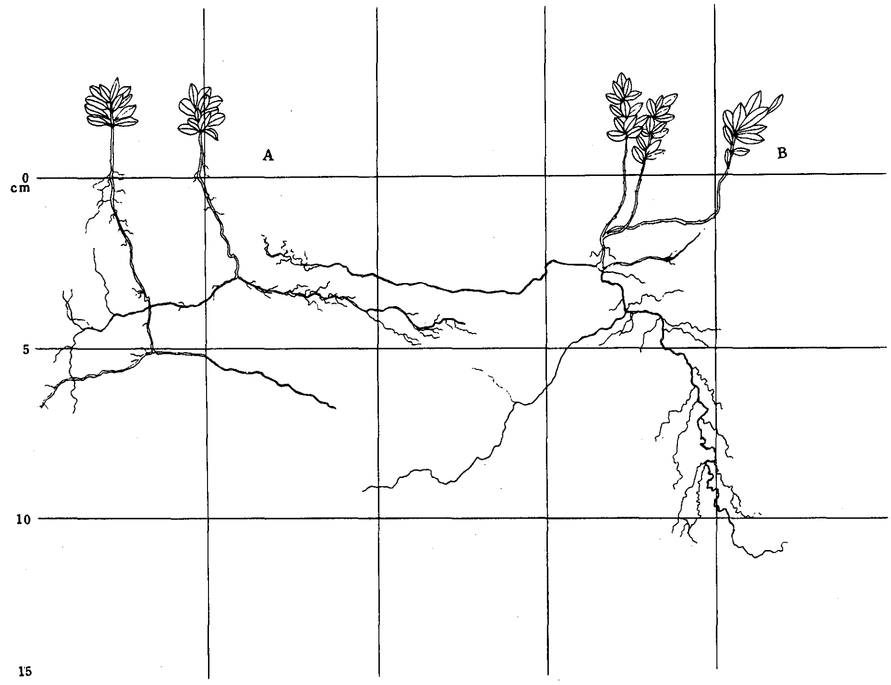

Fig. 29. Root system of *Linaria japonica*.
A. Root system of one-year-old plant.
B. Root system of two-year-old plant.

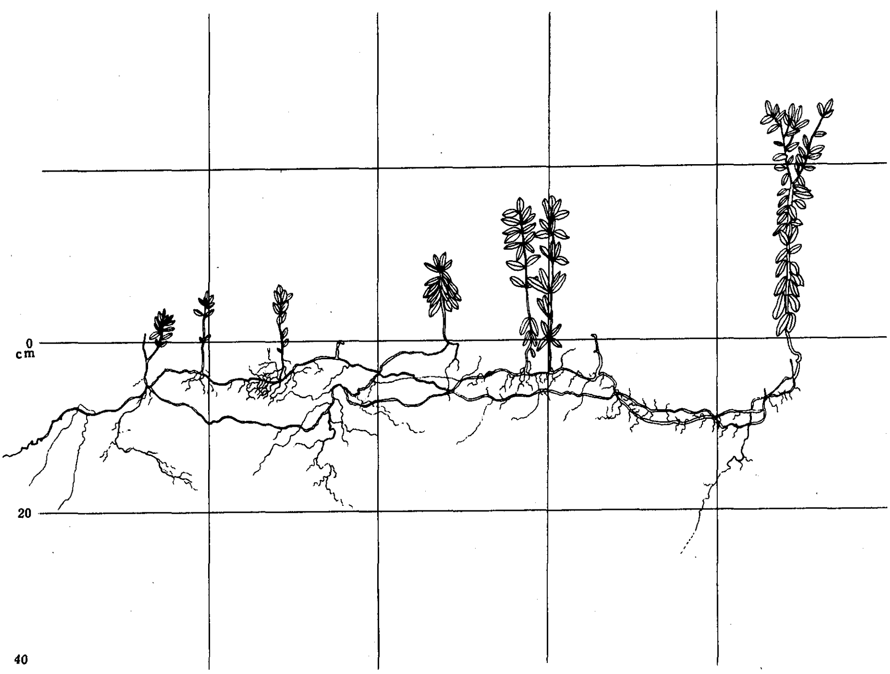

Fig. 30. Root system of adult plant of *Linaria japonica*.

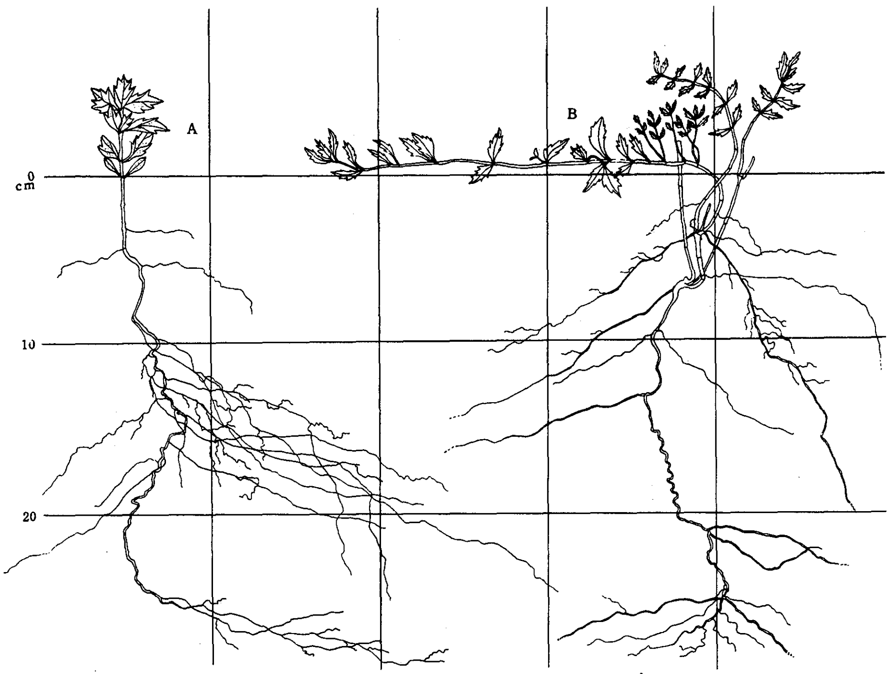

Fig. 31. Root system of *Wederia prostrata*.
A. Root system of one-year-old plant.
B. Root system of two-year-old plant.

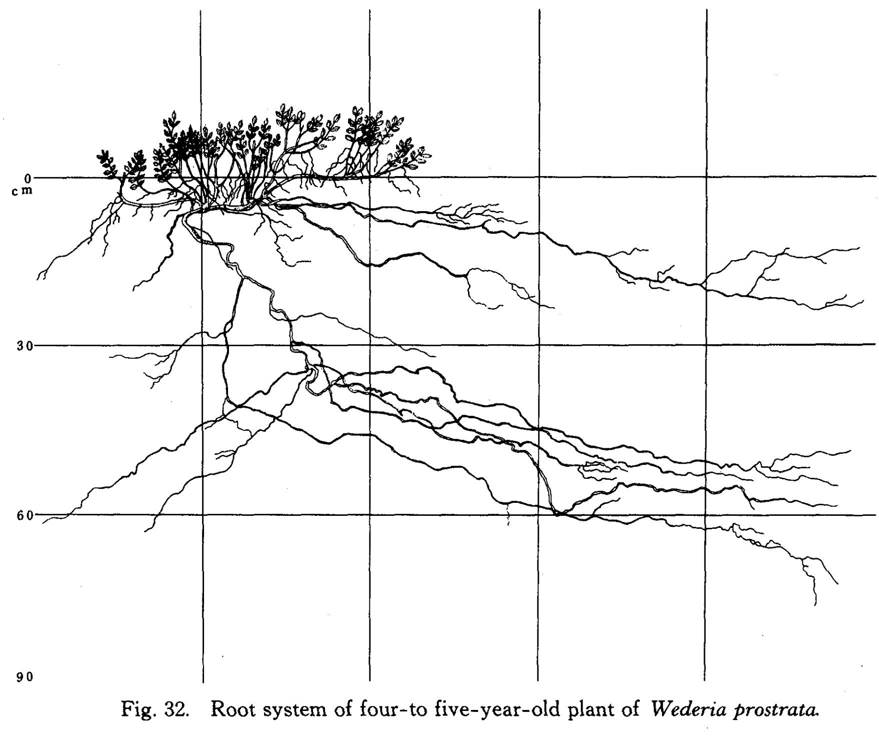

Fig. 32. Root system of four-to five-year-old plant of *Wederia prostrata*.

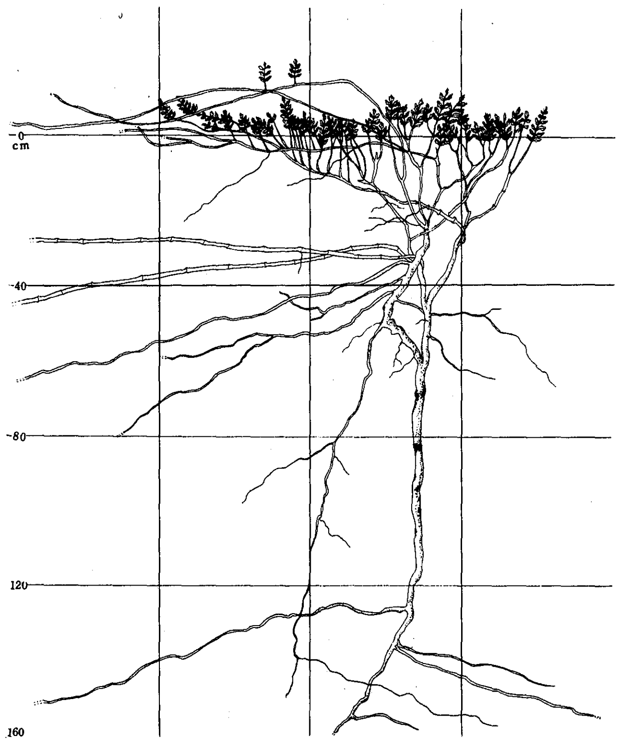

Fig. 33. Root system of adult plant of *Wederia prostrata* (about ten years old).

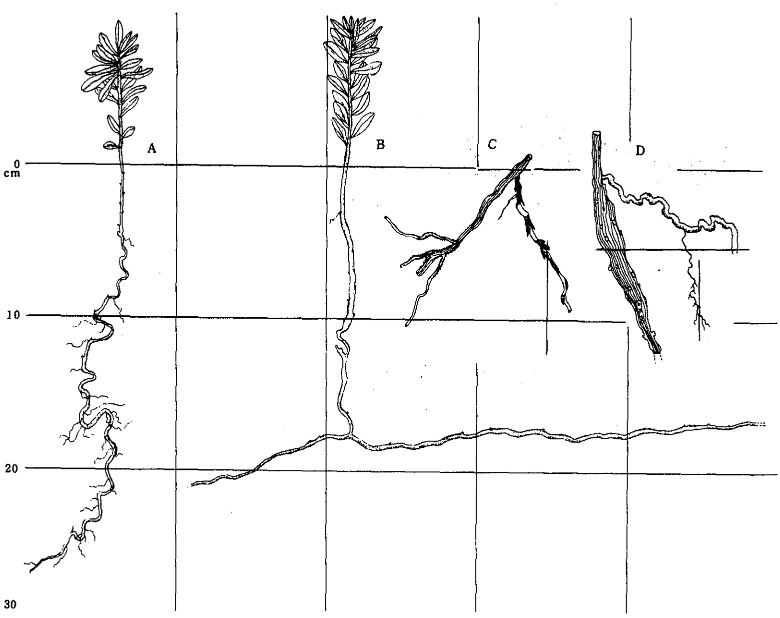

Fig. 34. Root system of *Messerschmidia sibirica.*
A. Root system of two-year-old plant.
B. Root system of three-year-old plant.
C, D. Nodule of root.

can hardly be distinguished from the rhizomes. Adventitious roots 1.5 mm in diameter are sparsely produced from the secondary root, and they run horizontally or obliquely downward. The roots and rhizomes have many wrinkles and are curved here and there. The secondary rhizome has many nodule-like scars of leaf stalks on several places. In parts of the root are spindle-like appendages 8 cm in length and 8 mm in diameter. The colour of the root and rhizome is blackish brown. The life form is G and root types are Rm 4, Rs 3, Rd 1 and Rv 4 on this sand dune.

9. *Glehnia littoralis* (Figs. 36, 37, 38 and 39)(Table 10).

Table 10. Root.development of *Glehmia littoralis*.

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of root in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of shoot in mm.	Diameter of community in cm.	Length of rhizome in cm.
1	10	15	5	3—15	1.5	1.5	4	3—5
2	10	25	5	5—20	3	6	4—5	3—5
5—6	15—20	130	7—15	20—30	4—7	21.5	20	15

The specimens studied were chosen from a community developed in both the unstable habitat, and the semistable habitat about 40 m from the coastal line. Most *Glehnia littoralis* flowers in July, and fructification and falling occur from July to August. Seeds are more or less buried by sand, as in aggregated fruits. Most of the seeds germinate from May to June. The juvenile plant has a tap root which runs vertically downward. The top of the root is a little curved and reaches a depth of 15 cm from the sand surface. The stage of root development at each estimated age is shown in Table 10. The stem is very short and very succulent in its base. The tap roots of the three-to five-year-old plants produce 2 to 5 branches at the top, and reach a depth of 100 cm. The bark of root has numerous lateral lines 3—4 mm wide, and it also has many nodules. The rootlets are produced from the tap root. The tap root is quite succulent, and has a function of water storage. The lateral roots are well developed in three-year or older plants, and run horizontally or obliquely downward. The rootlets are branched from the short secondary rhizome, tap root and lateral root are 0.2—0.3 cm in length. The plants are endurable to the sand accumulation of 3—15 cm in one year. In plants which suffer no sand accumulation, the stems do not elongate. The tap roots which grow in the volcanic ash (hard pan) run horizontally at a depth of 10—35 cm, and more or less penetrate into the hard pan of the volcanic ash. The rhizomes and roots are well endurable to the violent sand erosion. The colour of the rhizomes and roots is alizarine pink, and partially dull orange. The life form is H or G and root types are Rm 1, Rs 1, and Rv 9 or Rv 10 on this sand dune.

10. *Carex kobomugi* (Figs. 40, 41 and 42)(Table 11).

The specimens studied were chosen from communities in unstable, semistable and stable habitats, 40—100 m from the coastal line. *Carex kobomugi* flowers from July to August, and fruits from August to September. The seeds fall from September to October. Most of the spikes are buried in sand soil in that condition. Most of the seeds germinate from May to July. In general, the juvenile plants grow in open communities of *Ixeris repens* and *Zoysia*

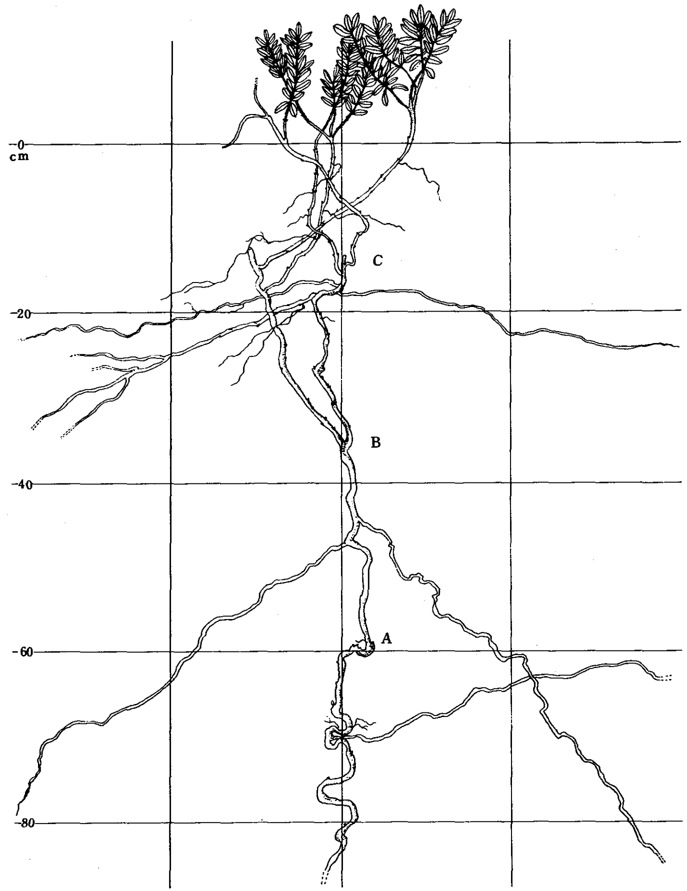

Fig. 35. Root system of adult plant of *Messerschmidia sibirica.* A, B and C showing the sand suface when covered by sand.

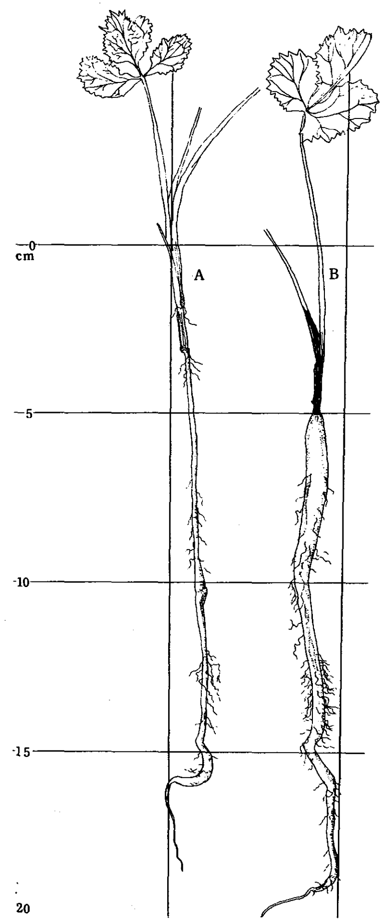

Fig. 36. Root system of *Glehnia littoralis.*
A. Root system of one-year-old plant.
B. Root system of two-year-old plant.

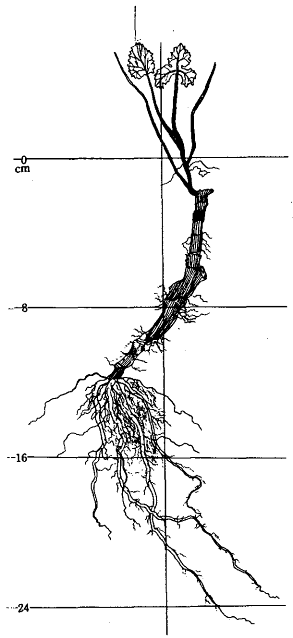

Fig. 37. Root system of cut back tap root of *Glehnia littoralis.*

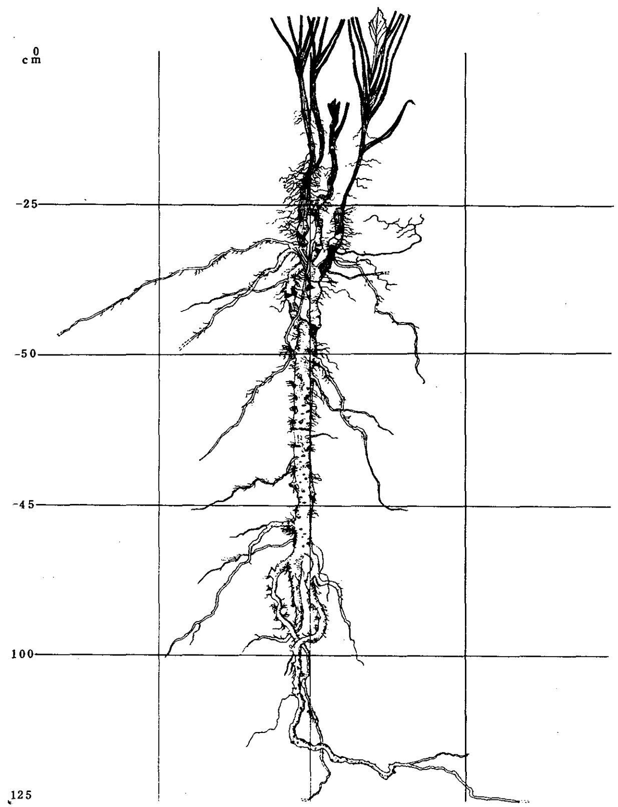

Fig. 38. Root system of adult plant of *Glehnia littoralis.*

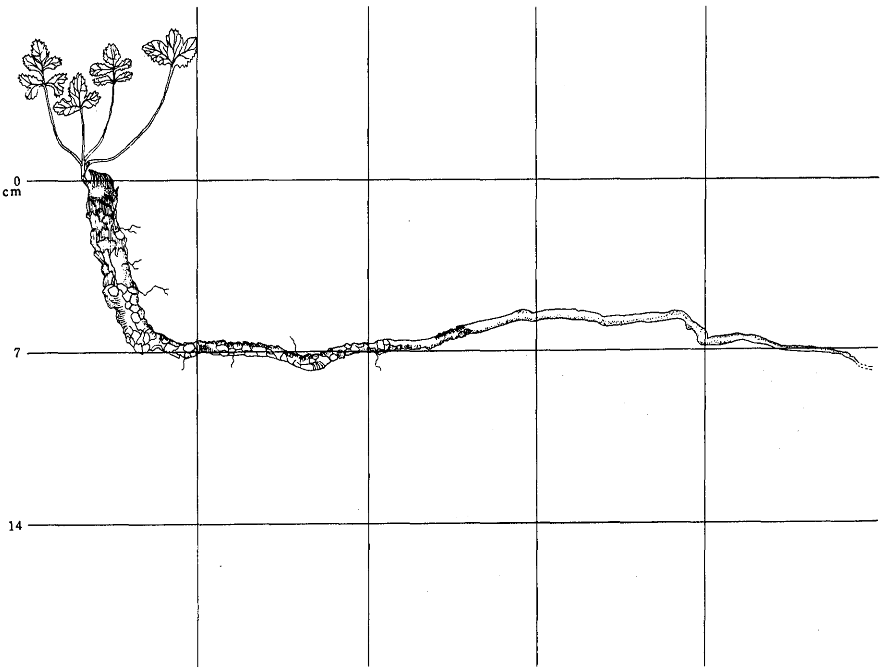

Fig. 39. Root system of *Glehnia litorallis* on volcanic ash.

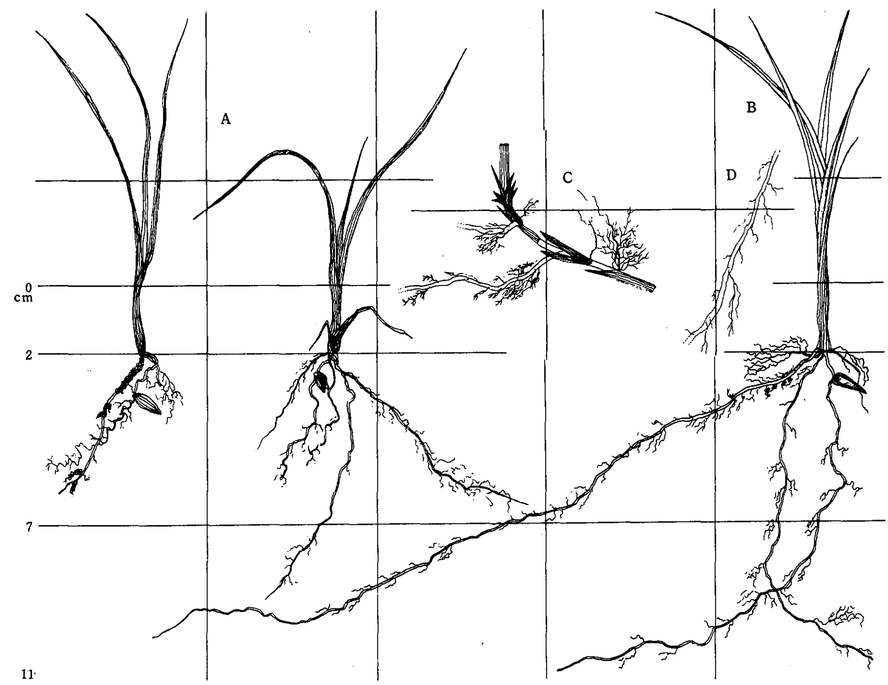

Fig. 40. Root system of *Carex kobomugi.*
A and B are root system of one-year-nld plant.
C and D are rootlets.

Table 11. Root development of *Carex kobomugi*.

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Depth of root in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Height of sand accumulation in cm.
1	5—15	10—15	—	3—10	—	0.5	5	0—3
2	20	30—40	15—20	5—20	2	0.2—0.5	10—20	3—15

macrostachya, and are rarely seen in an unstable habitat. The juvenile plants are about 5 cm in length, and their main roots run vertically to a depth of 10 to 15 cm. The stage of root development at each estimated age is shown in Table 11. The plants become adult in about three years, and they form a community. The rhizomes which are developed in eroding and accumulating and eroding habitats run horizontally or obliquely downward 10—30 cm from the sand surface, and they are branched from several places. Three or four aggregated shoots are produced from the top of the rhizome, and they run obliquely upward and put out a clone. The rhizomes of the plants which grow in the accumulating habitat run vertically upward and cannot extend a clone. The rhizomes are branched at several places, and the branching nodes are plump-like nodules, covered with leaf sheaths. The rhizomes are somewhat thin and seem not to be effective as water storage organs. The lateral roots produced from the nodes of rhizomes are 180—250 cm in length, and run horizontally or obliquely downward, occupying an area 20—40 cm below the surface. The roots are well branched, with rootlets in clusters. The rootlets are net-like, and most of them are distributed near the surface. The root area covers a wide range in the under suface, and this is convenient to absorb the water in the upper layer. The colour of the roots is yellow-brown, and that of the rhizomes is brown.

Carex kobomugi is resistant to sand accumulation but it cannot endure sand erosion. Many plants were of served which had died because of sand erosion. The rhizomes have a vigorous ability of vegetative propagation and also have an ability to stabilize moving sand. The life form is G or H (if the life form is H, most of the buds are decayed) and root types are Rm 4, Rs 3, Rd 1 and Rv 2 or Rv 3 on this sand dund.

11. *Fimbristylis sericea* (Figs. 43 and 44)(Table 12).

Table 12. Root development of *Fimbristylis sericea*.

Estimated age in yers	Shoot height in cm.	Maximum depth of root in cm.	Working depth of root in cm.	Diameter of rhizome in mm.	Diameter of root in mm.	Diameter of community in cm.	Length of rhizome in cm.
1	2—3.5	10—15	1—10	—	0.2—0.3	2	—
3—4	5—7	25	3—15	6.5	0.2—0.5	13	2—2.5
6—8	5—12	60—70	3—30	2.5—6.5	0.2—0.5	25	2.5—7

The specimens studied were chosen from communities developed in both the semistable and stable habitats 200—500 m and 500—800 m respectively from the coastal line. *Fimbristylis sericea* flowers from July to September, and fruiting and falling of seeds are from August to October. Most of the seeds germinate in June. The tap roots of the juvenile plants run vertical-

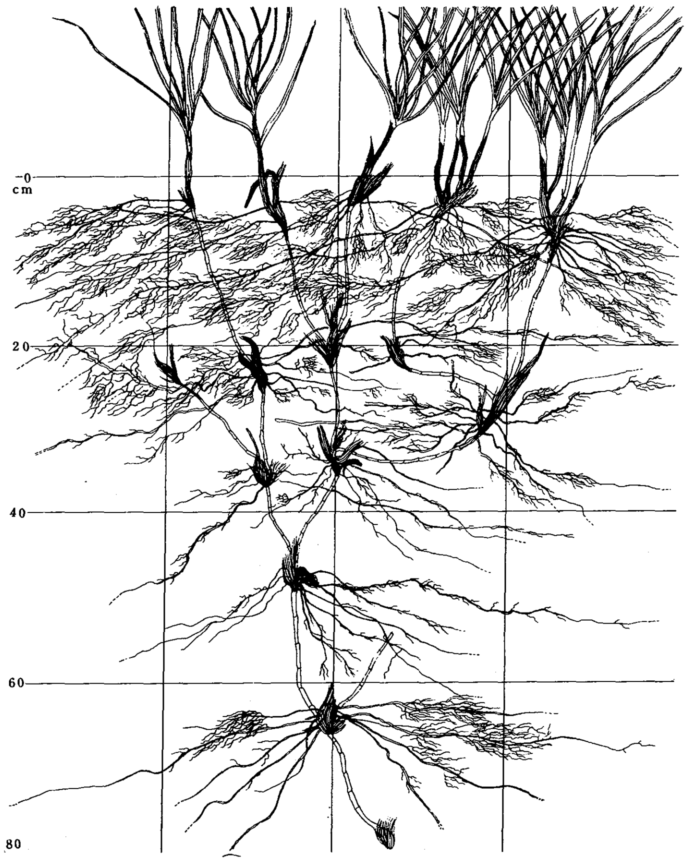

Fig. 41. Root system of adult plant of *Carex kobomugi* on unstable habitat.

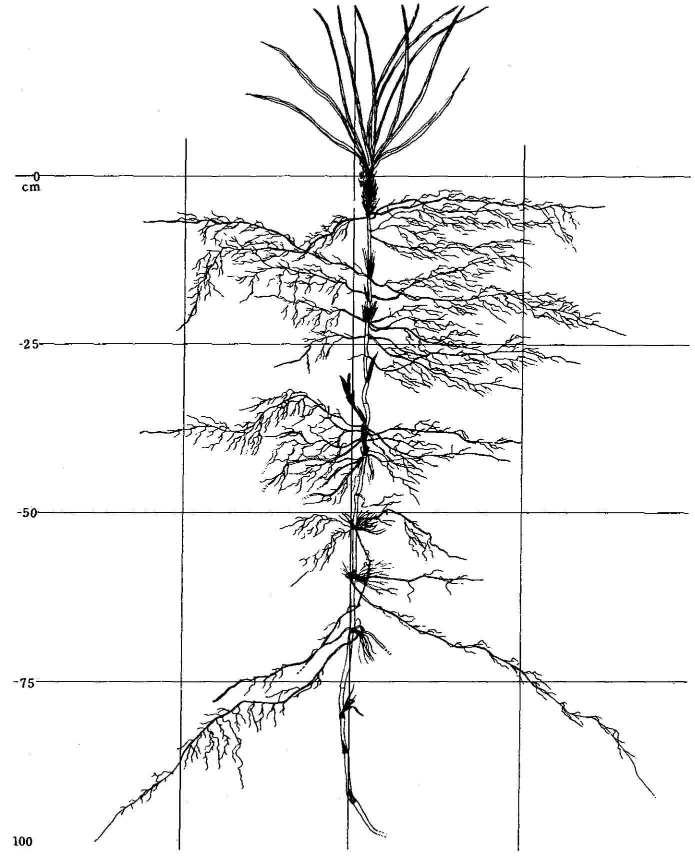

Fig. 42. Root system of *Carex kobomugi* on accumulating habitat.

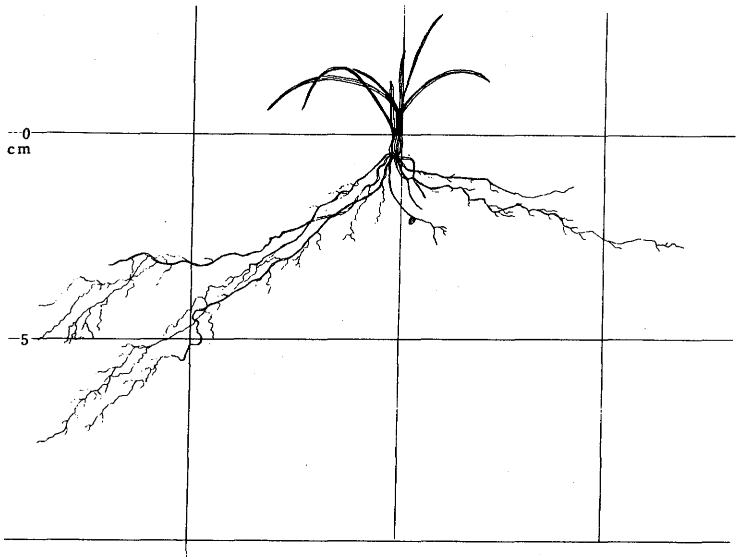

Fig. 43. Root system of one-year-old plant of *Fimbristylis sericea.*

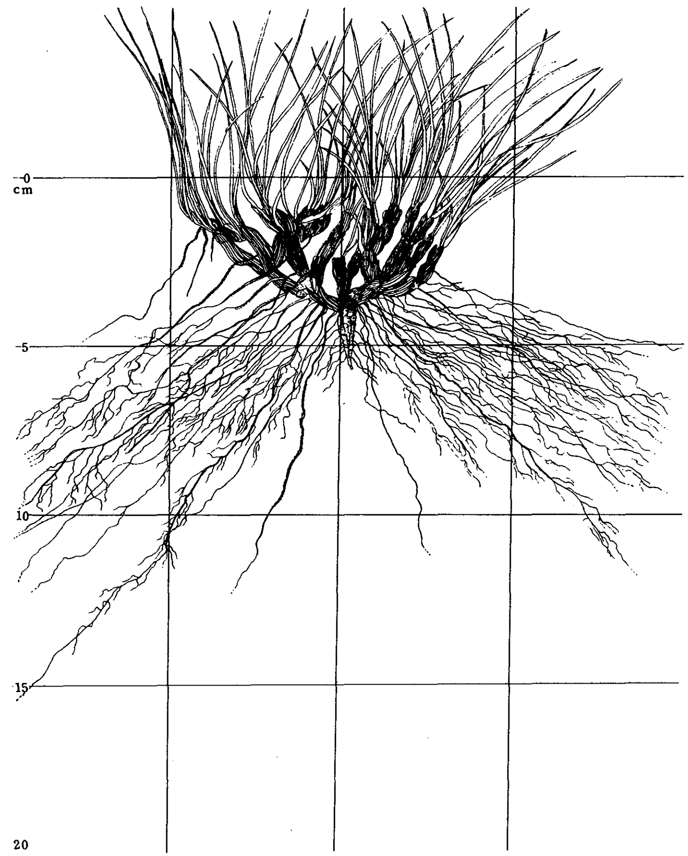

Fig. 44. Root system of adult plant of *Fimbristylis sericea.*

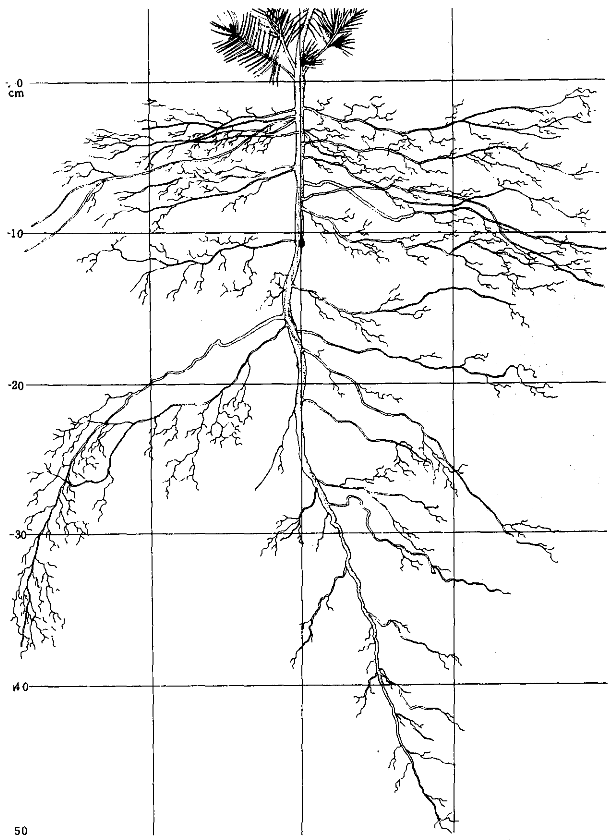

Fig. 45. Root system of young plant of *Juniperus conferta.*

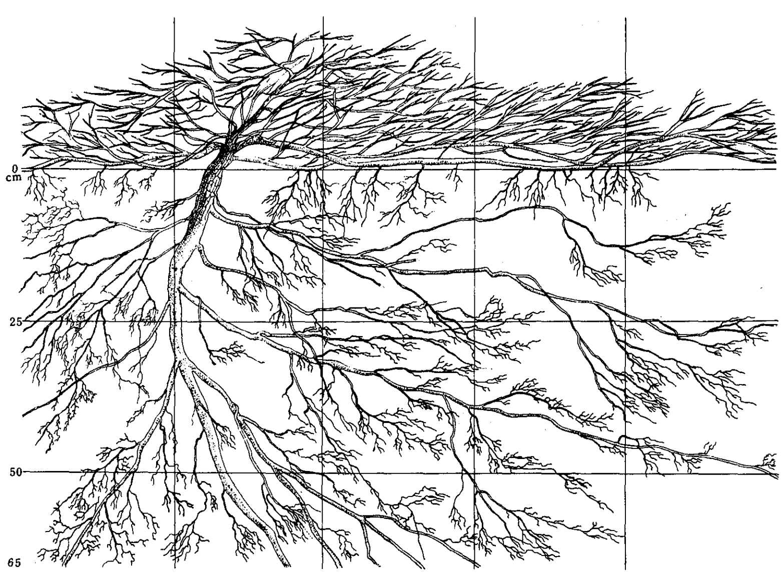

Fig. 46. Root system of adult plant of *Juniperus conferta.*

ly downward, and reach depth of 15 cm. From the lateral roots are produced rootlets which are 10—15 cm in length and run obliquely downward. The developmental stage of the root systems at each estimated age is shown in Table 12.

The terrestrial organs which are 2 or more years old are branched by the influence of sand accumulation, and are transformed into secondary rhizomes which run horizontally or obliquely upward. The stem is very short, ranging from 5 to 7.5 mm in diameter, and 7 to 10 cm in length. The rhizome has many scales which are made by the leaf base on the rhizome node. The lateral roots are coarse and fibrous, and they are produced in aggregation from the base of the stem. The roots are well curved, and run obliquely downward at an angle of 20—30 degrees to the sand surface, up to a depth of 60—70 cm. Rootlets arise from the curve-points of the root, and are usually 1 to 3 cm in length. Most of the root systems are at a depth of 3 to 30 cm below the surface. In a community composed of six year or older plants, a dead center is formed in the middle of the community, and the edge of the community is developed like a ring. The colour of the roots is brown. The life form is H, and root types are Rm 4, Rs 2, Rd 3 and Rv 8 on this sand dune.

12. *Juniperus conferta* (Figs. 45 and 46).

The specimens studied were chosen from a community developed in the stable habitat, about 1000 m from the coastal line, and included another specimen which had been cultivated in a nursery of Hiroshima University. Most of the plants are dominant in the stable habitat where there is less or none movement of sand . The terrestrial organs of two-or three-year-old plants are 5—10 cm in height, and 3 mm in diameter at the base. The tap roots are well extended, only rarely branched, and the lateral roots run horizontally or obliquely downward. Most of the root systems are far below the surface. Shoots of six-year-old plants are 20—50 cm in height; their basal part is 23 mm in diameter and runs horizontally on the sand surface. Secondary rhizomes are formed from the terrestrial organs, which are buried by sand accumulation, and they are furnished with numerous rootlets at several places. The tap roots run vertically downward, to a depth limit of 160 cm and have two or three branches. The tap root depth of the ten year or older plants, is 2 m or more. The lateral roots are 0.52 mm in diameter, curve gently and run obliquely downward. Most of the lateral roots in the lower layer run obliquely with sharpen angles than these in the upper layer. The rootlets are 1 to 2 cm in length and 0.2 mm in diameter. They have an obtuse top and have two or three branches. The colour of the root is dark violet red. The roots of communities of five-or six-years olds are 2—3 m, and those of ten year olds are 6—10 m in diameter. The terrestrial organs run obliquely upward when they suffer from sand accumulation. They are usually branched densely and have a remarkable function to stabilize the sand dune. The life form is CH, and root types are Rm 2, Rs 2, Rd 1 Rv 2 on this sand dune.

Biological spectra of the subterranean organ

Characteristics of the subterranean organ of the sand dune plants were classified on the basis of four analytic habits, and the relation between these characteristics and dune habitats are summarized as follows:

1. Root depth (Fig. 47)

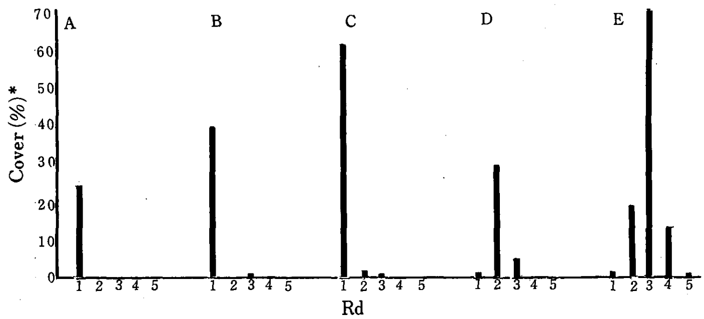

Fig. 47. Biological spectra of the subterranen organ in sand dune plant with respect to the root depth (Rd). A, B, C : Accumulating and eroding, eroding, accumulating habitat respectively. D : Semifixed dune. E : Fixed dune.

Generally speaking, the root system of the sand dune plants is remarkable for its root depth. Most of them in the unfixed dune belong to Rd 1. In the semifixed dune, most plants belong to Rd 2 and few to Rd 3. In the fixed dune, most plants belong to Rd 2 and Rd 3, the latter to a higher degree. From these results, it is clear that Rd 1 is characteristic for the unfixed dune, Rd 3, Rd 2 and Rd 4 for the semifixed and fixed dune. In other words, most of the plants growing in the unfixed dune are deeply rooted whereas those in the semifixed and fixed dune are shallowly rooted. It seems evident that the deeply rooted species have an advantage and the shallower rooted species are at a disadvantage in the drought period.

The working range of the representative species in various habitats are shown in Fig. 48.

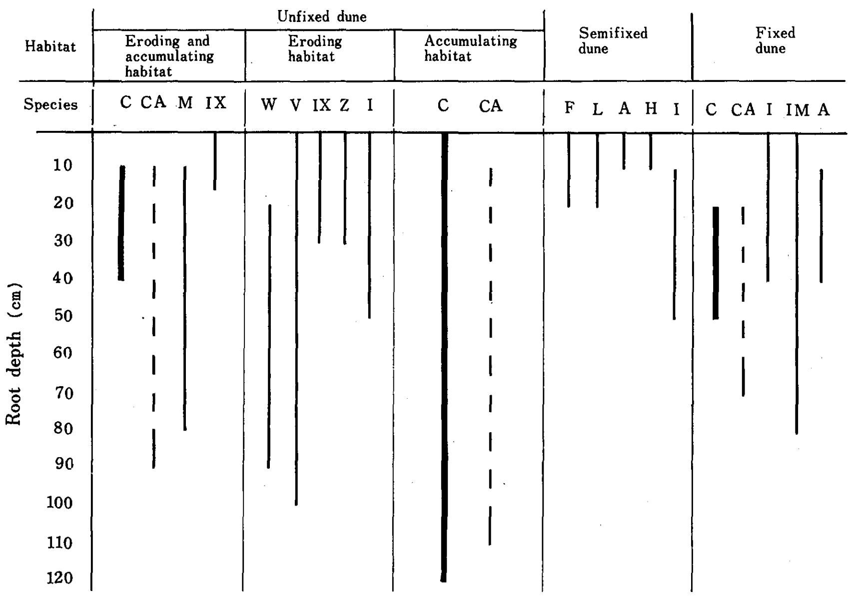

Fig. 48. Working ranges of the root system of the representative species in various sand dune habitats.

C : *Calystegia soldanella*
M : *Messerschmidia sibirica*
V : *Vitex rotundifolia*
F : *Fimbristylis sericea*
I : *Ischaemum anthephroides* var. *eriostachyum*
IM : *Imperata cylindrica* var. *koenigii*
A : *Artemisia capillaris*
CA : *Carex kobomugi*
W : *Wederia prostrata*
IX : *Ixeris repens*
L : *Linaria japonica*
Z : *Zoysia macrostachya*
H : *Heteropappus arenarius*

Calystegia soldanella shows different working ranges corresponding to various habitats. In the accumulating habitat it is widest. The same fact is seen in *Carex kobomugi.* In general, the communities which are developed in the unfixed dune have a wide working range, and communities in the semifixed dune have a narrow working range.

2. Root morphology (Fig. 49).

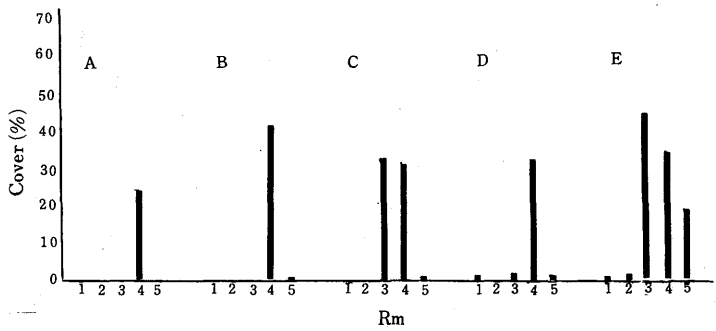

Fig. 49. Biological spectra of the subterranean organ in sand dune plants with respect to the root morphology (Rm). A, B, C : Accumulating and eroding, eroding, accumulating habitat respectively-unfixed dune. D : Semifixed dune. E : Fixed dune.

In general, the root morphology, both in the eroding and accumulating and in the eroding habitat, belongs to Rm 3 or Rm 4, and in the accumulating habitat, belongs to Rm 3 or Rm 4. In the semifixd dune and fixed dune, it belongs to Rm 3, Rm 4 or Rm 5, and occasionally to Rm 1 or Rm 2. These results show that most of the species growing in the unfixed dune have rhizomes and stolones and are endurable to sand accumulation, and that most of the species in the semifixed dune and fixed dune have well-developed tap and lateral roots.

3. Root area (Fig. 50).

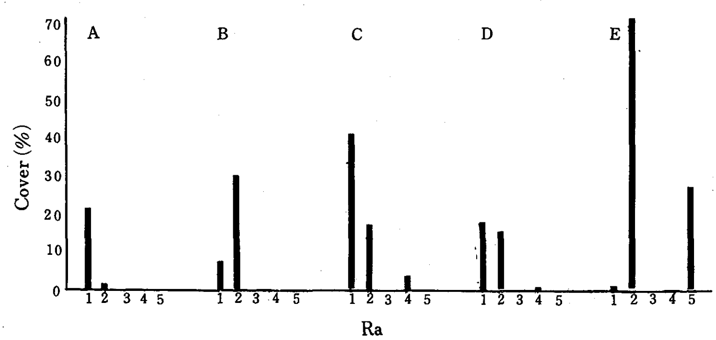

Fig. 50. Biological spectra of the subterranean organ in sand dune plant with respect to the root area. A, B, C : Accumulating and eroding, eroding, accumulating habitat respectively—unfixed dune. D : Semifixed. E : Fixed dune.

In general, most of the species belong to Ra 1 or Ra 2 in the unfixed dune, and this is true also in the semifixed dune. In the fixed dune, most of the species belong to Ra 2 or Ra 5. These results show that most plants in the unfixed dune have roots distributed homogenously from the upper to the lower layers and that those in the fixed dune have many rootlets distributed in the upper layer. The former is adapted to absorb the water in all the layers of soil and the latter in the upper layer.

4. Vegetative propagation (Fig. 51).

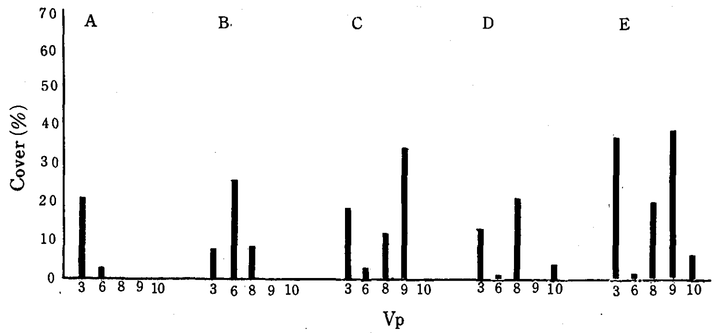

Fig. 51. Biological species of the subterranean organ in sand dune plants with respect to the vegetative propagation. A, B, C : Accumulating and eroding, eroding, accumulating habitat respectively—unfixed dune. D : Semifixed dune. E : Fixed dune.

With regard to the vegetative propagation, the species in the eroding and accumulating habitat belong to Vp 3 or Vp 6. This indicates that the species have well-developed rhizomes and form large communities. In the eroding habitat, most of the species belong to Vp 6, Vp 8 or Vp 3. This fact indicates that these species form smaller communities than those in the eroding and accumulating habitat. In the accumulating habitat, most of the species belong to Vp 9, Vp 3 or Vp 8, and they form much smaller communities than in the other habitats. In the semifixed dune Vp 8, Vp 3 and Vp 10 are predominant, and in the fixed dune, Vp 9, Vp 3, Vp 8, Vp 10 and Vp 6. Thus it is clear that propagative ability decreases from the unfixed to the fixed dune.

5. Subterranean organ forms (Figs. 52 and 53).

To express the synthetic characteristic of the subterranean organ, the author tried to design the subterranean organ forms from the combination of the above four analytic habits. In previous reports, the author has already determined the subterranean organ forms by this method in regard to the moor communities (Horikawa and Yano 1959) and grassland communities (Yano 1960). Subterranean organ forms of the sand dune plant communities are classified into seven forms and eight subforms as shown in Fig. 52 and Table 13.

Form I. The species belonging to this form grow in the unfixed dune, and their tap roots are well developed. The tap roots are succulent and the lateral roots do not extend much. The root area is narrow and confined to a deeper layer. *Glehnia littoralis* is a representative of this form.

Form II. The only species *Juniperus conferta* belongs to this form. In a plant growing in the fixed dune its tap and lateral roots are well developed, and the root area is comparatively expanded. Its stolons are transformed into secondary rhizomes by sand accumulation and produce numerous adventitious roots, which display a remarkable function of stabilizing the sand movement.

Form III. The species belonging to this form have a well-developed tap root in the early stage of growth, but in the adult stage, the tap root is stunted and lateral roots develop well. The primary rhizomes are generally undeveloped or lacking. In the accumulated sand, however, the terrestrial organs run obliquely upward and form secondary rhizomes, which have numerous adventitious roots. In general, the length of the secondary rhizome is short. *In-*

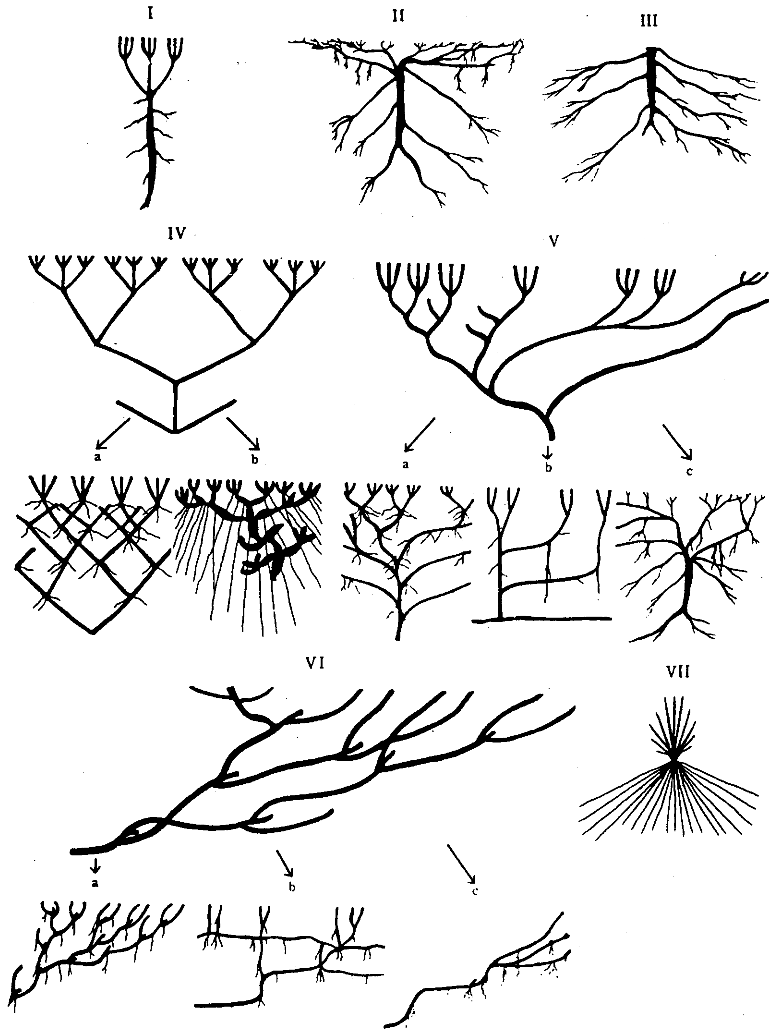

Fig. 52. Schema showing the subterranean organ forms in sand dune plants.

Form	Subform	Representative species
I		*Glehnia littoralis*
II		*Juniperus conferta*
III		*Erigeron canadensis*
IV	IVa	*Ischaemum anthephroides* var. *eriostachyum*
	IVb	*Fimbristylis sericea*
V	Va	*Carex kobomugi*
	Vb	*Messerschmidia sibirica*
	Vc	*Wederia prostrata*
VI	VIa	*Calystegia soldanella*
	VIb	*Linaria japonica*
	VIc	*Ixeris repens*
VII		*Bulbostylis barbata*

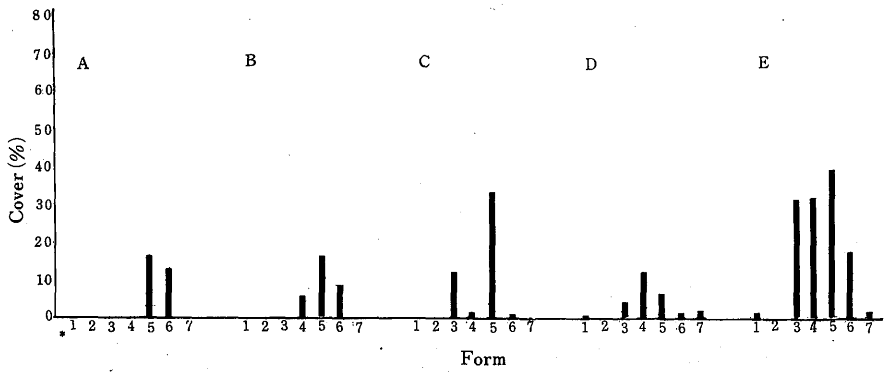

Fig. 53. Biological spectra of the subterranean organ forms in sand dune plants. A, B, C : Accumulating and eroding, eroding, accumulating habitat respectively—unfixed dune. D : Semi-fixed dune. E : Fixed dune.
[7] The numbers of form correspond to the Roman numbers in text.

Table 13. Synthesis of subterranean organ forms in sand dune plants

Rm	Ra	Form	Rd	Vp	Subform	Species
1	1	I	1	9 or 10	—	*Glehnis littoralis*
2	2	II	1	2	—	*Juniperus conferta*
3	2	III	4	9 or 10	—	*Heteroppapus arenarius* *Inaigofera pseudo-tincoria* *Artemisia capillaris* *Erigeron canadensis* *Potentilla chinensis* *Oenothera lamarckiana*
4	2	IV	2	8	IVa	*Ischaemum anthephroides* Var. *eriostachyum*
			3	8 or 9	IVb	*Fimbristylis sericea*
	3	V	1	2 or 3	Va	*Carex kobomugi*
				3	Vb	*Messerschmidia sibirica*
				3 or 6	Vc	*Vitex rotundifolia*
	5	VI	1	3 or 6	VIa	*Calystegia soldanella*
			3	3 or 6	VIb	*Linaria japonica*
				3	VIc	*Ixeris repens*
5	2	VII	4	10 or 8	—	*Bulbostylis barbata*

digofera pseudo-tioctoria, *Artemisia capillaris* and *Erigeron canadensis* are representative members of this form.

Form IV. In this form the tap root disappears sooner or later, and the lateral roots or rhizomes develop strongly. This form is divided into the following two subforms based on characteristics of root depth and propagation.

Subform IV a. The rhizomes are vigorous, running obliquely upward in the accumulated sand, and the clone is strongly expanded. Species belonging to this subform are *Ischaemum anthephroides* var. *eriostachyum*, *Ammrphira breviligulata*, etc.

Subform IV. b. The rhizomes are short and thick, running horizontally or obliquely upward. The roots are hairy, bearing numerous rootlets. This subform is represented by *Fimbristylis sericea*, *Luzura capitata*, etc.

Form V. Plants of this form have usually well-developed rhizomes and stolones. A tap root also is seen in some species. This form is divided into three subforms as follows:

Subform V a. The rhizomes run horizontally or obliquely upward, and frequently produce numerous rootlets arising from the lateral roots. the species belonging to this subform is *Carex kobomugi*.

Subform V b. The rhizomes are more or less succulent and run horizontally or obliquely upward. Lateral roots are few, and rootlets are absent. A species belonging to this form is *Messerschmidia sibirica*.

Subform V c. Secondary rhizomes develop from the stolones in accumulated sand. They are thick and lignified, some are semi-ligneous. The secondary rhizomes run horizontally or obliquely upward and produce sparsely branched adventitious roots. The tap lateral roots are well developed. Species belonging to this subform are *Vitex rotundifolia* and *Wederia prostrata*.

Form VI. The tap root develops only in the early stage and disappears as the plant becomes older. The rhizomes are well developed and vegetative propagation is frequent. The rhizomes with their stair-like extensions, have a great endurance to sand accumulation. In general, the roots are sparsely branched. This form is divided into the following three subforms:

Subform VI a. Secondary rhizomes having a great expansibility develop from the stolone by sand accumulation. Numerous adventitious roots are produced from the secondary rhizomes, and they have an endurance to deep sand accumulation. The species belonging to this subform is *Calystegia soldanella*.

Subform VI b. Morphological differences between root and rhizomes cannot be readily detected. The roots are succulent and rootlets. The rhizomes produce numerous adventitious roots and shoots, and the vegetative propagation is frequently seen. The terrestrial organs are tolerable to some sand accumulation. The species belonging to this subform is *Linaria japonica*.

Subform VI c. The rhizomes are succulent and have sparsely branched rootlets. They are distributed in the upper layer of the sand soil. Vegetative propagation is vigorous. Species belonging to this subform is *Ixeris repens*.

Form VII. The species which belong to this form are mainly annual plants. They have no rhizomes but have tap roots and well-developed lateral roots. Some species have prostrate stems derived from the sand movement, and from them numerous adventitious roots extend. Species belonging to this form are *Digitaria adscendens*, *Bulbostylis barbata*, etc.

Relations between the above-mentioned subterranean organ forms and dunes are shown in Fig. 53. Most of the species in the unfixed dune belong to Forms V or VI, as examples of which *Carex kobomugi*, *Wederia prostrata*, *Messerschmidia sibirica*, *Calystegia soldanella* and *Ischaemum anthephroides* var. *eriostachyum* are cited. They tolerate violent sand accumulation. Consequently, they may be noted as typical specimens of the sand dune plants. In the semifixed dunes, most of the species belong to Form V, IV, III or VII. These species *Ischaemum anthephroides* var. *eriostachyum*. *Carex kobomugi*, *Vitex rotundifolia*, *Imperata cylindrica* var. *koenigii*, *Erigeron canadensis* and *Bulbostylis barbata*. Some of the species are strongly tolerant to sand accumulation, drought salt spray, but others are not.

Summary

Root Development of Sand Dune Plant Community

Norimichi Yano

The author studied, in 1953, 1954, 1959 and 1960—1975, the root system of the sand dune plant communities of the Tottori Sand Dune, which lies along the beach line of the Japan sea in Southwest Honshu.

1. The sand dune was divided into three dunes based on the sand movement and the topographical conditions, that is, unfixed, semifixed and fixed dunes. The unfixed dune was further divided into three habitats based on the states of sand accumulation and erosion, namely, eroding and accumulating, eroding, and accumulating habitats.

2. The subterranean organs were analyzed on the basis of four analytic habits: root depth, root morphology, root area, and vegetative propagation.

3. The root depth was divided into five types. In the unfixed dune , most of the species belong to Type 1 (deeply rooted) in the semifixed dune, to Type 2 (somewhat deeply rooted), and in the fixed dune, to Types 2, 3 or 4 (shallowly rooted). The root depth type of the sand dune plants changes from deeply rooted to shallowly rooted with the stabilization of the moving sand. It is a remarkable fact that the juvenile plant has a well-developed root system which can grow rapidly.

4. The root morphological character was divided into five types. In the eroding and accumulating habitat, Type 4 (main root disappears and a long rhizome arises from a node on the stem) in the accumulating habitat, Type 3 (in some case a part of the lateral root develops vigorously and grows into a main root), and Type 4 in the semifixed dune, Types 4,3,5 (main root disappears and fasciculate roots develop copiously), and Type 1 (with main root) and in the fixed dune, Types 3, 4, 5, 2 (with main and lateral roots) and 1 are recognized.

The number of plants with rhizomes decreases in direct proportion to the increase of stabilization of the moving sand.

5. The root area was classified in to five types. In the unfixed dune, Types 1 (occupies all the layers) and 2 (mainly occupies the upper layers) are conspicuous in the fixed dune, Types 2, 5 (occupies the upper layers with dense roots) and 1 are observed. It can be said that in the unfixed dune, species with a deep and wide root area, and in the fixed dune, those with a shallow and narrow root area are dominant.

6. With respect to vegetative propagation nine types were recognized. In the unfixed dune (accumulating and eroding, eroding dunes), Types 3 and 6 in the semifixed dune, Types 8, 3 and 10 and in the fixed dune, Types 9, 3, 8 and 10 mainly occur. In brief, in the unfixed dune, most of the component species have well-developed rhizomes and usually form a large community, but in the fixed dune they have undeveloped rhizomes and form only a small

community.

7. Seven forms and eight subforms are synthesized from combinations of four analytic habits. Representative plants in these forms are as follows: Form I: *Glehnia littoralis*, Form II: *Juniperus conferta*, Form III: *Artemisia capillaris*, Form IV: *Ischaemum anthephroides* var. *eriostachyum* (Subform a: *Ischaemum anthephroides* var. *eriostachyum*, Subform b: *Fimbristylis sericea*), Form V: *Carex kobomugi* (Subform a: *Carex kobomugi*, Subform b: *Messerschmidia sibirica*,Subform c: *Vitex rotundifolia*), Form VI: *Calystegia soldanella*(Subform a: *Calystegia soldanella*, Subform b: *Linaria japonica*, Subform c: *Ixeris repens*), Form VII: *Bulbostylis barbata*.

There is a close relation between the occurrence of these forms and the degree of sand movement. Namely, in the eroding and accumulating habitat, Forms V and VI, in the eroding habitat, Forms V and III, in the accumulating habitat, Forms V and III, in the semifixed dune, Forms IV, V and III, and in the fixed dune, Form V, IV, III, VI, VII and I occur. In general, the species in the unfixed dune are tolerant to sand accumulation, and those in the fixed dune show a poor tolerance to sand accumulation.

8. In the unfixed dune, hummocks are frequently formed by the plant clone. These hummocks are constructed by the extension of numerous roots, rhizomes, and secondary rhizomes, which are buried by sand. The processes of the hummock formation differs among the species, and the destruction of the hummock begins when the elevation of a hummock arrives at a certain height (1 or 1.5 m).

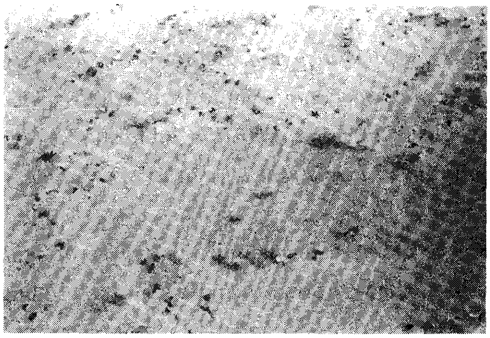

Fig. 1. *Ixeris repens* community on the unfixed dune.

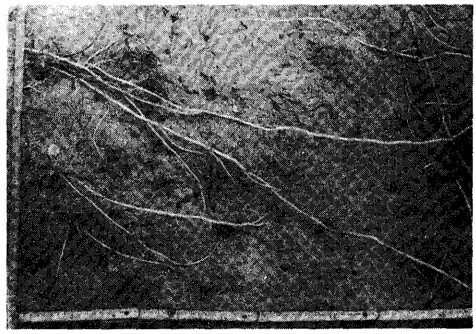

Fig.2. Rhizome of *Ixeris repens* community.

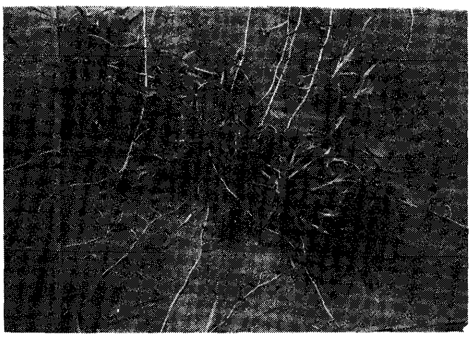

Fig. 3. Rhizome of *Ixeris repens*-*Carex kobomugi* community.

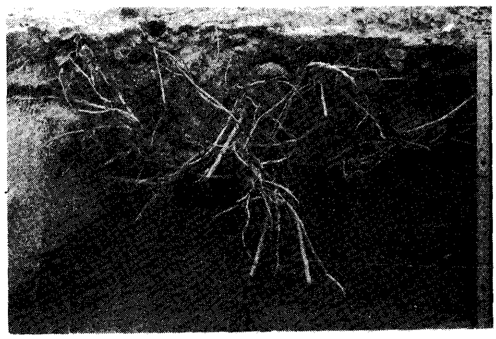

Fig. 4. Rhizome of *Calystegia soldanella* community.

Fig. 5. Rhizome and root of *Zoysia macrostachya* on the accumulating habitat.

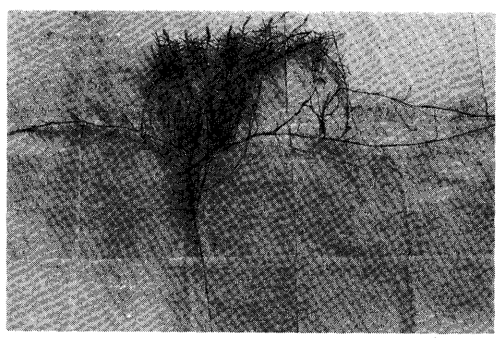

Fig. 6. Rhizome and root of *Zoysia macrostachya* on the semfixed dune.

Explanation of Plates

Plate II

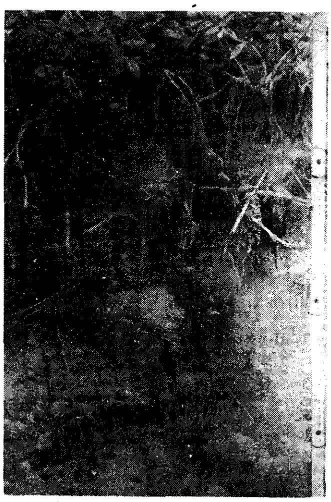

Fig. 7. Rhizome and root of *Wederia prostrata* on the accumulating habitat.

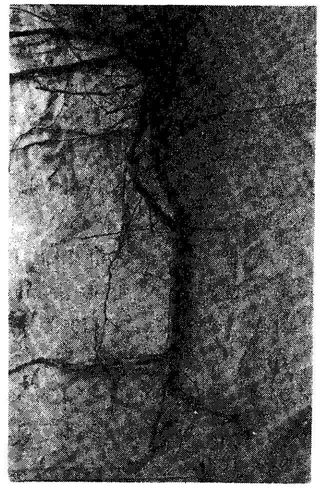

Fig. 8. Tap and lateral root of *Wederia prostrata* on the accumulating habitat.

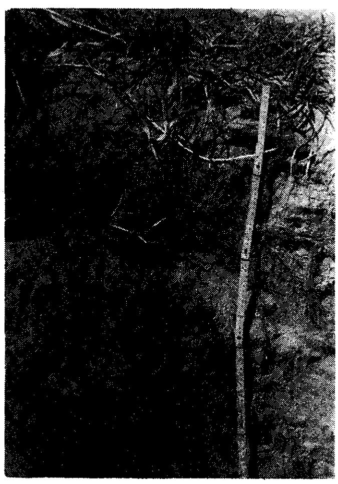

Fig. 9. Rhizome and root of *Carex kobomugi* community on thf accumulating habitat.

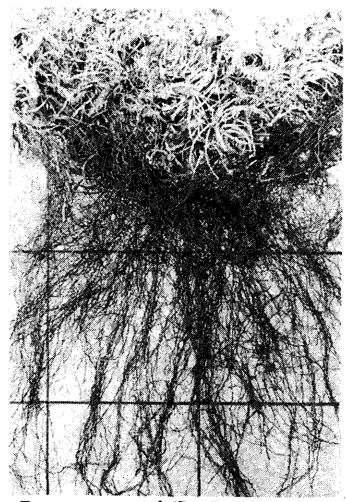

Fig. 10. Root system of *Fimbristylis sericea* on the semifixed dune.

Fig. 11. Rhizome and root of *Ischaemum anthephroides* var. *eriostachyum* on the semifixed dune.

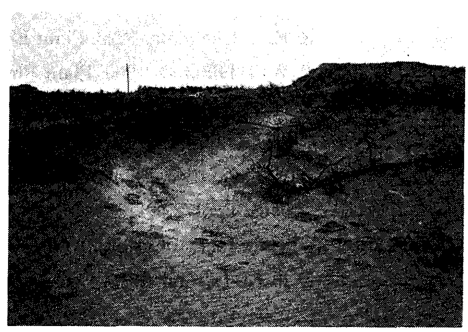

Fig. 12. Rhizome of *Vitex rotundifolia* on the semifixed dune.

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