Explanation of the pictures on Book-cover

The Face (upper-left: extraorgan-freezing of an vegetative bud of Japanese larch tree (longitudinal section).

Middle-left: extraorgan-freezing of a winter leaf bud of mulberry (cross section).

Lower-left: overwintering rhododendrons (-10C, in my garden, 2003)

The reverse

Upper-right: extraorgan-freezing of vegetative bud of Saghalin fir (longitudinal section)

Upper-middle: flowering of the rhododendrons (2003,5: in my garden)
Preface

In a scientific climate dominated by molecular biology, this book is particularly important, providing insight into the evolution and ecology of plant cold hardiness, as well as cryopreservation—a field of study which Dr. Sakai has pioneered. It is very much a personal journey of Dr. Akira Sakai and unlike a dry textbook, is written in an engaging manner by balancing the literature with his experiences and historical perspectives.

Many thanks to Hokkaido University Press for allowing the electronic distribution of this English version and to Mat Uemura (one of Sakai-sensei’s former students) for valuable suggestions and making these arrangements. The expert translation was conducted by Dr. N.P. Sukumaran, a student of cold hardiness in both the USA and Japan. His translator’s notes have been kept (blue notes at the end of each chapter) along with Dr. Sakai’s editorial comments which have been used to revise the text. Thanks also to M.P.M. Nair for digitizing all of the images. I appreciate Gloria Gingera’s work to convert all of the individual files into the more readable book format. This project was funded by a grant from the University of Saskatchewan and Dr. Sakai. The English translation of this book was announced as a part of the CRYO 2009, the 46th Annual Meeting of the Society for Cryobiology, co-chaired by Drs. Seizo Fujikawa, Toru Tamaki and Mat Uemura. The conference was located in Sapporo, Japan with one of the sessions dedicated to Dr. Sakai. At the time of this writing, Dr. Sakai is daily enjoying a beautiful view of his beloved mountain and trees. One of his sons, Dr. Ko Sakai will be showing him the English version of his book on a laptop computer. Thanks, Ko!

I am honoured to call Dr. Sakai one of my mentors, who along with Mrs. Sakai, I came to know well during their one year stay at Oregon State University, coinciding with my first year of a Ph.D. program under Dr. Bud Weiser. Dr. Sakai always used to ask me, “What is your DREAM?”

Dr. Sakai has had many dreams fulfilled, from seeing Halley’s comet to the long term storage of plant germplasm by cryopreservation. Thank you, Dr. Sakai, for all of your many contributions. You have inspired several generations of researchers and your work lives on through them.

Dr. Karen Tanino, Dept. Plant Sciences,
College of Agriculture and Bioresources, University of Saskatchewan
November, 2009
Explanation of Coloured plates

Fig. 1: overwintering hardy rhododendrons in my garden (-10C, 2003 March)
Fig. 2: extraorgan freezing of vegetative bud of mulberry (cross section polarized microscope at -20C)
Fig. 3. extraorgan freezing of vegetative bud of fir (cross section at -20C)
Fig. 4: extraorgan freezing of vegetative bud of Siberian larch (longitudinal section at -20C)
Fig. 5: intraorgan freezing of vegetative bud of Japanese larch (longitudinal section at -20C)
Explanatory of Coloured plates

Fig. 6: extraorgan freezing of vegetative buds of metasequoia (longitudinal section at 20C)

Fig. 7: extraorgan freezing of vegetative bud of Alaskan white spruce (longitudinal section cooled to -70C pictured at -20C)

Fig. 8: upper. Glassy solid of PVS solution when rapidly cooled in liquid nitrogen (transparent)

bottom: Freezing of PVS2 solution when cooled slowly at -70 C (whiten)

Fig. 9: upper left: encapsulated wasabi apical meristem into alginate beads

Recover growth of encapsulated wasabi meristem into beads. They were osmoprotected and dehydrated sufficiently and then rapidly immersed into LN.
AKIRA SAKAI (Career)
1920  Born in Kiyosu Aichi Prefecture Japan
1944  Graduated Dept. of Zoological Science, Hokkaido University
1966  Professor of the Institute of Low Temperature Science, Hokkaido University
1970  Visiting professor of University of Minnesota (Horticulture, Dr. C.J..Weiser lab, one year)
1983  Retired from Hokkaido University, Emeritus professor of Hokkaido University
1984  Visiting professor of Oregon State University (invitation) one year
1987  Visiting professor of West Washington University, Biology one year

Book Publications:
1982  Sakai, A. Plant Cold hardiness and plant adaptation (Gakkai Press Center) (written in Japanese)
1988  Sakai, A. and W. Larcher: Frost survival of plants (written in English), Springer -Verlag
2006  Sakai, A. Cryopreservation of plant germplasm by PVS2-vitirification. My greatest legacy (written in English), self-published.
2009  Sakai, A. Strategy of plant cold temperatures –From Siberian coldest forests to Tropical rain forests (english translation). Internet publication.

Green notes added by Karen Tanino
Accelerated graduation, draft examinations and student mobilization had begun in December 1941, as World War II had started. At that time, I had just returned to college after my long break from studies because of tuberculosis. Because of my poor health, I passed the draft examination with the lowest grade, "Heishu". I wanted very much to appear for the entrance examination for admission to the Faculty of Science, Hokkaido University. Luckily, in the following spring, in April 1942, I could join the Department of Zoology in the Faculty of Science of the University. As the war intensified, I was drafted in March 1944 after a stint of group labor service in Sakhalin in the summer, and spent some time serving in the army at Nagoya. Just before I was to be sent to the front line, the authorities found that there was a surplus of personnel and luckily I was relieved of military service and returned to Sapporo. While I served in the army, a new scholarship system for postgraduate studies had started. But I was not eligible for this. Thus, although I could graduate from the Faculty of Science, I could not continue research and had to return home. During the little more than 2 years that I spent as a student at the Faculty of Science, I had tasted the joy of research work. After the war, I returned to Sapporo, where the food situation was not quite good, to work as an unpaid Laboratory Assistant at the University of Hokkaido, just because I wanted to do research. But after 2 years, at the end June 1948, my tuberculosis returned and I boarded the ship Hikawamaru at the Otaru harbor, seen off by my friends, and headed for my hometown in the outskirts of Nagoya. I feared that this would be the last time I had anything to do with Sapporo and Hokkaido University. After 5 years, luckily, with the kind help of Professor Kiyoshi Aoki, I could return to Hokkaido University with a position at the Institute of Low Temperature Science.

After joining the Institute, I came to know that Dr Tokutaro Hirata, who became principal of the Nagoya Technical College where I had studied during the war, was a pioneer in the science of snow and ice, along with Professor Ukichiro Nakaya of the Institute. When I gave a lecture in an institute in Paris once, a friend told me that "Sakai" meant very cold in French and asked me how it came about that a man named Sakai started research on low temperature. On another occasion, about 15 years ago, a close friend visiting from a research institute of Harbin, China commented, “You have the face of a northern mongoloid, well adapted to cold
climate”. In my long research career, I had to face life-threatening situations and circumstances that forced me to leave research, which was so dear to me. But each time, an unexpected helping hand would save me and I continued my research on plants and low temperature. Thus, I came to believe that I was destined to do some “pioneering work on plants and low temperature” in Sapporo.

While recuperating from tuberculosis, a rose enthusiast had gifted me a few stems of roses. Looking at these roses I fell completely under the spell of their graceful beauty and fragrance. I started to grow roses while recovering from my illness. This association of mine with roses opened up an opportunity to start work on the frost hardiness of mulberries at the request of Professor Aoki after my return to the Institute of Low Temperature Science.

At that time, very little work had been done anywhere on the cold hardiness of plants. Since there were no special facilities, studies on cold resistance were done mainly in cold rooms and outdoors in winter. So, I started increasing my own cold resistance by entering the cold rooms frequently in autumn. The studies on cold hardiness of plants that I started in 1953 and the research on cryopreservation that I started in 1956, earlier than others, continued until my retirement in 1983. I returned in 1988 after a stint [as a visiting professor] at an American university, 5 years after my retirement, and started work with my own funds on the development of technology for long-term storage (at -196°C) of plant genetic resources through vitrification. In this endeavor, I later received the cooperation of more than 10 researchers working at regional experiment stations in Japan and young foreign researchers. With their help, I could continue this work for almost 16 years, until 2004. I am happy that we could substantially achieve the objectives and create this gift for the coming generations. Four of us received the New Technology Award of the Japanese Society for Plant Cell and Molecular Biology for this work, on August 6, 2003.

I feel really fortunate that I could continue my favorite research work and pursue my dreams for 47 years, i.e., during my professional life and after my retirement, until well over 82 years of age, along with many young researchers. I have come to know many things about plants and the forests of this earth, which range from the tropical to the polar regions, came to love plants and flowers, and had the opportunity to meet a number of researchers both from within and outside the
country and learn many things from them. My happiest memories of this long research career are of the times when I entered unknown treasure troves of nature and of the excitement and joy of uncovering new treasures, forgetting everything else.

I owe a great debt to Mr. Jiro Maeda of the Hokkaido University Press for his help in publishing this book. Ms Kyoko Tanaka and Ms Nobuko Itoh read the draft of this book and pointed out deficiencies in explanation, redundancies and parts that were difficult to understand. They have made a great contribution to making these sentences easy to understand. I wish to record my sincere gratitude to Dr Saburo Funakoshi and Dr Mitsuru Saito of the Field Science Center for Northern Biosphere, Hokkaido University (earlier known as Hokkaido Forest Research Experiment Station) who were kind enough to give many detailed suggestions. I wish to thank my colleagues and post-graduate students at the Institute of Low temperature Science, the research fellows who worked with me there, and the more than 10 researchers of my last team who worked with me after my retirement for developing the vitrification technique and raising the technology to level that has been appreciated internationally.

Professor Masami Fukuda of the Institute of Low Temperature Science of Hokkaido University and Yojiro Matsuura of the Forestry and Forest Products Research Institute provided me new materials readily at all times. I learned much from Dr Kihachiro Kikuzawa and Dr Emiko Maruta who encouraged me often. I am very grateful to all of them.

In the end, I would like to dedicate this small book to the late Professor Yasushi Aoki, who gave me the opportunity to do the research, for his continued appreciation and encouragement. I also thank my wife Tazuko who gave unwavering support when I was sickly after I got back to work from my illness and allowed me to concentrate on my research for many years.

Akira Sakai
September 2002

Translator's notes:
1. Words added by the translator for clarity are given in [square brackets]
2. Kindly check parts marked in orange. Their translation is uncertain.

Epiloque
Please correct Prof. Aoki Kiyoshi.

Please correct or added

Epilogue: page 10 8 bottom) Nagakawamaru…Hikawamaru

6L (bottom) Yasushi--Kiyoshi Aoki

Page 3 achieve the objectives and create this gift for the coming generations.
Continued: We (4 people) had received Technical Prize from Japanese Association of Biotechnology on August 6, 2003. page 3 Mitsuru Saito: Hokkaido Forest Research Experiment Station. Page 4 Kiyoshi Aoki.

Page 2 bottom 2002--2003 Thank you, Sakai

Sentence appearing in Chapter 13 supplement:
Very recently, the President of the Japanese Society for Plant Cell and Molecular Biology informed me that our work on “Ultra-low temperature preservation of plant cells, tissues and germplasm (A. Sakai, T. Niino, T. Matsumoto, D. Hirai and N. T. Thinh)” has been recommended for the New Technology Award of the Society for the year 2003.
Strategy of Plant Cold Hardiness

Akira Sakai

Originally published in Japanese, March 2003

Hokkaido University Press, Sapporo, JAPAN

English version distributed online, November 2009

Translated by N.P. Sukumaran, Edited by Karen Tanino
**Strategy of plant cold hardiness**

The global occurrence of cold, frost and snow cover, the major environmental impacts of daily, seasonal and historical microclimates in plants stands and soils are described and related to temperature fluctuations in different plant tissues (Adaptation and evolution of plant cold resistance). This book draws a comprehensive picture of plant cold hardiness to stress biology. This book can be recommended for plant scientists in physiology, botany, ecology and agriculture and forestry as well as for lectures and students for a short, but profound insight into cold stress and related phenomena.

- Siberian forests to tropical rain forests-

I. Plant survival on cold stress

1. Overwintering tree in Sapporo (temperature fluctuations of overwintering stem). Frost cracking of stem, freezing of ground in Hokkaido

2. Existence of water under subzero temperature
   - Avoidance from cold, supercooling, intracellular freezing, extracellular freezing, extraorgan freezing

3. Challenge to survival at deepest temperatures of cold hardy plants on the planet, LN (-196°C), LH (-268°C)-long-term conservation of plant germplasm.

4. Cold hardiness between ecotype in different altitudinal and regional changes in Hokkaido

5. Merit and demerit of snow cover

6. Temperature fluctuations on northern hemisphere historical
   - Acquisition of cold hardiness of Pinaceae (pine, conifers, temperate hardwood, glasses) disappearance, extinction or mitigation for mild climates (Taxodiaceae)
   - Cold hardiness evolution and adaptation during ice age.

7. Strategy of temperate hardy plants.


9. Overwintering of plants at Antarctica. Climates and overwinter

10. Emergence of cold climate in the Northern Hemisphere and changes in the flora
11. The evolution of cold survival strategies of plants in the alpine areas of the tropics
12. Cold survival and overwintering strategies of temperate plants
13. Plants of Antarctica that live in extreme environments

*Supplement:
- A long-term conservation in LN of plant germplasm for future generations.
  1. Seed storage for 1000 years
  2. To develop an efficient and cost-effective protocol for cryopreservation (original).

II. Various forests living at different climates
1. Adaptation from severe cold climates to mild tropical rain forests.
2. East Siberian forests (original).
3. Forests at high altitudes of Himalaya mountains (original).
4. Forests surviving at New Zealand (the southern hemisphere) (original).
5. Tropical rain forests.
6. Tree succession in permafrost on Alaska; Rising forests during the ice age in Japan.
7. Some old-type willows native to tropical and subtropical willows in Asia and Africa. Evolution of willow trees (original).

References
I STRATEGIES OF PLANTS THAT LIVE IN COLD REGIONS

1 How I came to work with trees

It was in 1953 that I returned to the Institute of Low Temperature Science, Hokkaido University after a 5-year fight with tuberculosis. At that time, researchers in the Biology Section, to which I belonged, were working mainly on Cold resistance of insects, freezing behavior of plant and animal cells, and analysis of cooling curves to determine the start of freezing in plant tissues cooled at a constant rate. Research on cold hardiness of mulberry commissioned by the National Sericulture Experiment Station (Kokuritsu Sanshi Shikenjo) had started a year earlier. Professor Yasushi Aoki of the Biology Section was working alone on freezing characteristics of mulberry shoots, by inserting thermocouples into small samples. At that time, the laboratory had no freezer that could cool to $-30^\circ$C, or automatic recorders. Salt water was cooled to about $-20^\circ$C the previous night in a cold room and used as the cooling medium. The scientist would strain his eyes in the dark to read the ammeter every 10 seconds to determine the cooling curves, and use them to analyze the freezing process. Marker pens with oil-based ink and polyethylene bags were also not available, and there were of course no copiers. “Ok, you can help me in my studies on mulberry”, Professor Yasushi Aoki told me, a zoologist, after coming to know that I enjoyed growing roses during my recuperation. At that time, plant researchers who had graduated from Science Departments were mainly working on the cells and tissues of beet, onion, spinach, and other such plants. They almost never considered woody plants like mulberry, with a complex structure, as research material.

I then selected *Yamaguwa* (*Morus bombycis* Koidz.), a wild mulberry of Hokkaido said to be very cold hardy, and several cultivated mulberry varieties of Honshu with relatively low cold hardiness, and decided to examine how low a temperature their shoots could tolerate in different seasons. Almost everyday, I walked about 150m to collect shoots from the mulberry fields of University’s experimental farm located south of a poplar-lined street. [In winter], walking with *Kanjiki* (traditional Japanese snowshoes) on the windy snow covered fields, I often got exhausted on the way. While resting in waist-deep snow, I used to gaze at the overwintering poplar trees standing tall in the wind-blown snowfield and wonder whether they were frozen and how they were withstanding the severe cold. I
wanted to find out the mechanisms and the limits of their cold hardiness. At the same time, my mind was filled with gratefulness and joy because I had somehow regained my health after the long bout of illness, and was doing scientific research again. Initially, I was planning to return to studies on animals, my area of specialization. But this changed completely after working one winter with mulberry. We found that the cortical cells of mulberry shoots were very cold hardy and presented numerous advantages as a material for basic research. These advantages had a major influence on the development of my work and were the reason for some lucky breaks. In the third year after starting the work on mulberry, I could confirm the survival of plants at the temperature of liquid nitrogen (−196°C) and was lucky to be able to open up the new field of cell vitrification while investigating the survival mechanism.

We often refer to “plants” collectively, but there are a great many different kinds of plants. Unlike short-lived herbaceous plants that overwinter buried in snow, woody plants withstand the wind, snow and severe cold. They live long and create forests. I felt a boundless attraction towards them. So, even after completing the research on mulberry, I chose trees as the material for studying cold hardiness.

**Definitions**

How a plant responds and adapts to sub-freezing temperatures differs greatly, depending on the type of the plant and its habitat. Some plants chose to live in places where the temperature does not go below freezing while others avoid being cooled to sub-freezing temperatures by covering the tissues and organs essential for survival. They thus avoid risky chilling by selecting suitable habitats or by covering themselves suitably. This response is called “Cold avoidance”. Quite a few plants allow their body temperatures to go below the freezing point but avoid freezing of their important tissues and organs by various means. This is called “Freezing avoidance”.

When a plant remains viable after exposure to −10°C, for example, for a certain time and subsequent warming, this means that the plant had tolerated this low temperature regardless of whether it froze (extracellular freezing) or did not freeze (freezing avoidance), and we say that it has a cold hardiness of −10°C. But the two mechanisms of survival at −10°C are very different. I have summarized in Fig 1 the different responses of plants to low temperature.
**Winter hardiness**

Winter hardiness is the capacity of a plant to overwinter without getting damaged. Wild plants are winter hardy and therefore rarely get irreparably damaged by overwintering in their natural habitats. However, crop plants sustain various kinds of injury, depending on the species, the region of cultivation and also the weather conditions within the region. In Hokkaido, for instance, when wheat is exposed to strong cooling without snow cover, it dies of freezing (frost injury). In the bitterly cold season, in the absence of snow cover, the ground freezes and plants cannot absorb water through their roots. The stems and leaves dry up and the plants wither (drought injury). When the melting of snow is delayed, certain snow molds caused by psychrophilic (cold loving) bacteria appear (disease injury). Pasture plants in the frozen soil zone (Toudo chitai) experience peculiar types of damage such as the roots being torn because of frost heaving of the ground. Injury from late frost (frost injury), drought injury caused by freezing of soil, snow damage from branches and trunks breaking under the weight of snow, and snow mold and rodent damage to young trees when the melting of snow is delayed, are also major concerns with planted larches and Todomatsu firs.

**Cold hardiness**

Plants that have a high capacity to overwinter (frost hardy) in very cold regions and can withstand the winter drought caused by freezing of the soil are generally called cold hardy plants. But, unlike winter hardiness, this term does not cover the ability to withstand snow damage or snow mold.

**Freezing of cells**

Ice formation inside the cells when a plant is cooled to sub-freezing temperatures is called intracellular freezing. If the ice is formed in the space between the cells during this process it is called extracellular freezing. The cell structure is destroyed and the cell invariably dies when freezing occurs inside a cell. But extracellular freezing does not necessarily lead to cell death. In this book, the word “freezing” when used alone usually refers to extracellular freezing.

**Frost hardiness**

Plants that are adapted to cold regions have mechanisms that prevent intracellular freezing in tissues and organs essential for survival and the ability to tolerate
freezing-induced dehydration caused by extracellular or extra organ freezing when cooled to sub-freezing temperatures. Such ability to withstand freezing is called frost hardiness.

**Measure of frost hardiness**

An index, called “frost hardiness”, is used to numerically express the minimum temperature that a plant can tolerate. To measure frost hardiness, leaves or shoots cooled to about –5°C are brought into contact with ice or frost to induce extracellular freezing. They are then further cooled to different temperatures and thawed. The lowest temperature at which they remain viable, or show 50% survival, is taken as the frost hardiness.

Responses to sub-freezing temperatures

1. Cold Avoidance
   a. Moderation of cooling (covering)
   b. Adoption of suitable habitat
   c. Adoption of suitable life form
   d. Use of the latent heat of freezing

2. Cold Hardiness (Cold Tolerance)
   a) Freezing avoidance
   b) Frost hardiness

   1) Freezing avoidance
   a. Supercooling
   b. Desiccation
   2) Frost hardiness
   a. Extracellular freezing
   b. Extra organ freezing

Fig. 1 Different responses of plants to low temperature

*Translator’s notes:*

1. *Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.*
2. *Words added by the translator for clarity are given in [square brackets]*
3. *The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.*
2 Do trees overwintering in Sapporo freeze?

Around late October, the temperature in Sapporo often goes below freezing early in the morning. Frost desiccated plants show up at this time. Deciduous broad-leaved trees lose their leaves by October end, the annuals go to seed and dry up where they are standing, and perennials sprout rosettes of leaves close to the ground, burying winter buds below the surface to get ready for the winter. Such herbaceous plants will be buried under snow in December and you will see only overwintering shrubs and trees above the snow. Earlier, people thought that trees would not freeze easily because they were covered with a thick bark. The mean temperature of Sapporo in January is about −5°C and the mean daily minimum about −10°C. I therefore examined whether the overwintering trees froze under such weather conditions.

(1) Freezing of trees

It is impossible to know just by looking at an overwintering tree whether it is frozen. So, in December 1965, I conducted some experiments with a Sennoki (Kalopanax pictus (Thunb.) Nakai) tree with trunk diameter 13.5cm growing in the premises of the Institute of Low Temperature Science. Thermocouple junctions were inserted into the center of the trunk and 1cm below the surface on the southern and northern sides of the trunk, at a height of 1m from the ground and the change of trunk temperature recorded during the course of the day. The lowest ambient temperature recorded was −15°C, at dawn on a clear day. At that time, the central part of the trunk of the Sennoki tree was at −13°C. It was a fine clear day throughout and the ambient temperature rose to about 3°C. But the center of the trunk (Fig 2,B) remained frozen. The southern side of the trunk (Fig 2, S) recorded the highest temperature of about 18°C around 13 hours because of the sun shining on that side. But with sunset, which was around 17 hours, the ambient temperature dipped below freezing and the southern side of the trunk started to freeze again. I conducted a similar experiment with a white birch. The surface of the trunk of this tree is white and several layers of thin bark exist just beneath the surface. Because of this, there was almost no increase in temperature within the trunk from the sunshine.

Thus it became clear that the central part of the Sennoki trunk of about 13cm
diameter remained frozen in the severe cold of January and February in Sapporo, that the sunny side of the trunk thawed for a few hours on sunny days, and that the entire trunk again froze when the temperature dropped below freezing in the evening (Fig 3). Trunks of such deciduous trees can survive even when the temperature dips to −20°C in the severely cold season. Many shoots and winter buds can withstand temperatures as low as −30°C or even lower.

I wondered whether the trunks of giant elm trees on the Hokkaido University campus, with diameter exceeding 80cm, also froze. To test this, I drilled a small hole from the northern side of an 86cm diameter trunk, perpendicular to the trunk. The peripheral area of the trunk was frozen and contained a large amount of ice. The central region had a very low water content and no freezing could be confirmed there. But that part also probably remained frozen because its temperature was more or less constant at about −2°C (Fig 2, C) during the severe cold of January and February.

The tree trunks were thus found to freeze much more easily than people had thought earlier. They froze at the relatively high temperature of −0.5 to −3°C. The specific heat becomes almost half after freezing and the tree temperature decreases surprisingly fast although still more slowly than the change in ambient temperature. In a 15cm diameter tree overwintering in an experimental forest of the Kyoto University, in Shibecha in eastern Hokkaido, which is far colder than Sapporo, the central part of the trunk recorded −18°C when the outside temperature dipped to −20°C. From these observations, we can imagine that forests in the interior and eastern parts of Hokkaido where the mean temperature in January is about −10°C, overwinter in a frozen state at a temperature of −10°C or lower. Forest more than 1000m above sea level in the Tohoku region [of Honshu] also probably overwinter in the frozen state in the coldest season.
Fig 2 Change of temperature in trees overwintering in the Hokkaido University campus. S: センノキ (直径 13.5 cm) の幹の南側 (表面から内部 1 cm), N: 同北側, B: 同中心部, C: 直径 86 cm のニレの大木の中心部, A: センノキ幼木 (直径 1 cm), T: 外気温の日周温度変化

图2 北大校内越冬中之木之温度变化。S: センノキ (直径 13.5 cm) の幹の南側 (表面から内部 1 cm), N: 同北側, B: 同中心部, C: 直径 86 cm のニレの大木の中心部, A: センノキ幼木 (直径 1 cm), T: 外気温の日周温度変化

Fig 2  Change of temperature in trees overwintering in the Hokkaido University campus. S and N: Respectively, southern and northern side (1cm below the trunk surface) of a Sennoki trunk of diameter 13.5cm; B: Central part of the same tree trunk; C: Central part of a giant elm trunk of diameter 86cm; A: A young Sennoki tree of diameter 1cm; T: Ambient temperature during a day.

*Abscissa:* Time of day

*Ordinate:* Temperature (°C)
(2) Frost cracking of tree trunks

Frost cracking is the phenomenon where tree trunks exposed to extreme cold develop longitudinal cracks that spread from the interior of the trunk towards the periphery (Fig 4, Left). In the state of Minnesota, the US mid-west, the
temperature goes as low as –30 to –40°C in the coldest season. Many trees growing on the campus of the University of Minnesota show frost cracking, almost like an exhibition on frost cracking. In Hokkaido, frost cracking occurs in many types of trees. But it is particularly frequent in Todomatsu firs (genus Abies)⁹. In the Asahikawa area, about 20% of Todomatsu fir trees have frost cracks*36. Todomatsu fir trees become increasingly prone to frost cracking with increasing trunk diameter. The length of each crack is usually about 1m and most frequently they occur 0.5 to 3m above the ground. Frost cracking is a mechanical injury. So, if the wound heals, the injury does not become fatal. But in some cases, radial cracks (Fig 4, Right bottom) are often present in the interior of the frost-cracked trunks and some of them reach up to the outer bark. When this happens, the utility of the timber is reduced significantly.

*36Classification of needle-leaved trees of the pine family:
The needle-leaved Todomatsu firs that grow naturally in Hokkaido belong to the genus Abies and Akaezomatsu and Ezomatsu are of the genus Picea. They do not belong to the genus Pinus, commonly called pine. Some needle-leaved trees of the major genera of the family Pinaceae are listed below:
Genus Pinus: Akamatsu (P. densiflora), Kuromatsu (P. thunburgii), Haimatsu (P. pumila)
Genus Abies: Momi fir (A. firma), Todomatsu fir (A. sachalinensis), Ooshirabiso (A. mariesii), Urajiromomi (A. homolepis)
Genus Picea: Ezomatsu (P. jezoensis), Akaezomatsu (P. glehnii), White spruce (P. glauca)(Alaska)
Genus Larix: Karamatsu (L. leptolepis), Guimatsu (L. gmelinii), Dahurian larch (L. dahurica)(eastern Siberia)
Genus Tsuga: Tsuga (T. siebokdii), Kometsuga (T. diversifolia))

The mechanism of development of frost cracks has been studied in great detail by Ishida*36. Frost cracking is not confined to a certain region or to certain tree species of a forest. In Todomatsu fir, which is very susceptible to frost cracking, 7-34% of the trees develop cracks. The cracks develop only in some trees and only in certain parts of the trunk. Very few Akaezomatsu and Ezomatsu trees, which belong to the genus Picea, develop frost cracks.
If frost cracking is caused only because of rapid decrease in temperature, we may expect its incidence to show regional variation. But the absence of such regional variation suggests that some trees or parts of trees have some special characteristics conducive to the development of frost cracking. Ishida demonstrated that frost cracking occurred only on trunks having water-filled rot holes (*suishokuzai*) (Fig 4, Right, bottom), where the water content of the trunk was high in a localized manner, and that the larger the water-filled area, the higher was the incidence of frost cracking. Ezomatsu firs have almost no such water-filled rot holes and therefore almost never develop frost cracking. The abnormally large amount of water in the water-filled rot holes of Todomatsu firs comes from holes in the roots and other injured parts and from defective parts of the branches and shoots. Ishida also showed through his experiments with tree logs and disk sections that when the heartwood at the center of the trunk freezes, internal pressure due to expansion develops within it, which affects the width of the cracks. He also showed that if ice is removed from the water-filled rot holes, the width of frost crack is reduced considerably and that the crack completely closes on thawing.

When a 1m long log of diameter 15cm was cooled in a cold room at –16ºC, most of the water in the heartwood froze at –0.5 to –5ºC and this eventually caused frost cracking. About 20h was needed for this to occur. In other words, it appeared that the tree should be exposed to a temperature of about –10ºC or lower for quite a long time for frost cracking to occur.

The Maruyama Park of Sapporo has many 110 year-old planted cedars. About 20% of them have frost cracking. More than half of the 2-3m tall Oshirabiso trees growing near the tree-line, about 1000m above sea level, on Mt Akakura in the Hakkouda mountains were seen to have frost cracks. I also saw many cases of frost cracking at the northern limit of the temperate Tsuga forest near Juno in Alaska. However, there are almost no frost cracks in Ezomatsu trees, which grow at a higher altitude than Todomatsu firs and are found even in the Maritime province of Siberia. I also came across almost no frost cracks among the trees species growing naturally in the sub-arctic interior Alaska and eastern Siberia. This suggests that the spread of tree species prone to frost cracking into the subarctic region is naturally limited and only those resistant to frost cracking thrive in the subarctic zone.
Fig. 4  
Left: A frost cracked *Todomatsu* fir. The crack runs from 1m to 7m above the ground. 
Right, top: Enlarged view of the part marked with a rectangle in the left Fig. 
Right, bottom: Cross sectional surface of the frost cracked trunk. The dark part is the *water-filled rot hole*. Many radial cracks can be seen.

(3) When the ground itself freezes
In Sapporo, there is not much freezing of the ground because of the thick snow cover. But in the Tokachi region of Hokkaido, the ground starts freezing from the surface downward in mid-November. In cold regions where the snow cover is relatively thin, the ground may still be frozen to a depth of more than 70cm in early March. Thawing starts at the surface and gradually advances downward when the spring arrives and most of the frozen ground would thaw by mid-May. Such ground that freezes only in the winter is called “seasonally frozen ground”. It is distinguished from the permafrost found in Alaska and eastern Siberia. In the eastern and interior Hokkaido, where there is not much snowfall, the chilling is quite strong for the latitude and the soil freezes. The mean daily minimum temperature in Obihiro is about –16ºC in January, roughly 7ºC lower than in Sapporo. Because of this, the soil freezes to a depth of 50-60cm when the snow cover is less than 20cm, and the soil temperature in frozen zone is –5 to –10ºC (Fig 5). Once the ground freezes, the plant roots can no longer absorb water. The aerial parts of the plants are deprived of water supply from the roots and experience severe drought. Under this condition, herbaceous plants, which are not very drought hardy, often dry up and die unless they are covered with snow. Freezing injury to the roots and tearing of roots caused by frost heaving of the ground are also common among overwintering plants such as pasture plants, wheat, etc, in regions where the ground freezes.
Fig 5  Snow cover, depth of ground freezing and soil temperature in the Tokachi region of Hokkaido.

Key:
Top Fig: Snow drift (depressed ground)
Abscissa: Nov, Dec, Jan, Feb, Mar, Apr, May
Ordinate (upper): Snow cover (cm)
Ordinate (lower): Depth of frozen ground (cm)

Bottom Fig: Windswept area (hilly ground)
Abscissa, Ordinate (upper) and Ordinate (Lower): Same as in Top Fig.
Ordinate (lower, right): Soil temperature (°C)
Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.
2. Words added by the translator for clarity are given in [square brackets]
3. The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.

Dr. Sakai’s comments:
Part I - Chapter 2
page 4: Tsuga (Sieboldii)
page 5: Oshiraboso (Abies Maiessi Mast)
page 6: chilling ---cold
3 The state of water at subfreezing temperatures

Water is the most important substance for any living organism. The solidifying point (freezing point) of water is a relatively high 0ºC, which is about the middle of the temperature range (-40 to 40ºC) that we normally think of in relation to the life activities of plants. The adaptation of plants to cold and their survival strategies are closely related to the characteristics of aqueous solutions and the change of their phase (freezing or vitrification) at subfreezing temperatures.

(1) Freezing of water

Let us first look at a freezing curve (Fig 6) to understand the freezing of an aqueous solution. A freezing curve is a record of the change in temperature of the substance while cooling, with temperature as the ordinate and time as the abscissa. An aqueous solution does not normally freeze even when cooled to below its freezing point. It continues to cool for some more time and then starts freezing. The latent heat (about 80cal/g) is released at the time of freezing, which raises the temperature sharply to the freezing point. Thus, by looking at a freezing curve we can know exactly when freezing occurred. The phenomenon of an aqueous solution being cooled to a temperature below its freezing point is called supercooling and the temperature at which the supercooled fluid starts freezing is called the supercooling point (SC and S respectively in Fig 6).

The photograph of Fig 7 (Left) is that of an ice crystal formed when a 35% aqueous solution of albumin froze at -3ºC. A nucleus had formed at the center from where the crystal grew. Thus the freezing of an aqueous solution involves two different processes, the formation of an ice nucleus, which gives a start to ice formation, and the growth of the ice nucleus. The growth rate of the ice crystal (GR in Fig 7, Right) is already fairly high close to the freezing point but the temperature favorable for ice nucleation (NR) is considerably lower than the freezing point.

After an aqueous solution starts to freeze, the freezing of water advances with further lowering of the temperature, the solution gradually becomes more concentrated and its freezing point is lowered. At temperatures below the freezing point, the supercooled water and solution have higher vapor pressure than ice at the same temperature and water migrates because of this difference in vapor
pressure. In extra cellular freezing, there is supercooled cell sap within the cell and ice outside the cell, with the cell wall between them. Water migrates from inside the cell to the ice outside (freeze desiccation) because of the difference in vapor pressure (chemical potential).

**Fig 6** A freezing curve of an aqueous solution. S: Supercooling point; SC Extent of supercooling; $\Delta$ Freezing point depression $^{109}$.

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**Key:**

Abscissa: Time

Ordinate: Temperature (°C)

**Upper section, left to right:** Starting temperature of freezing; Freezing point; Melting point

**Lower section:** Liquid; Ice-solution; Solid
Fig 7  Left: A hexagonal crystal formed when a 30% aqueous albumin solution froze at -3°C. A nucleus formed at the center and the crystal grew from there. Right: Change with temperature: the crystal growth rate (GR) and the nucleation rate (NR) of a 50% aqueous solution of polyvinyl pyrrolidone (PVP)°.

Abscissa: Temperature (°C)
Ordinate(Left): Crystal growth rate (mm/min)
Ordinate(Right): Nucleation rate (nuclei/second/cm²)

i Formation of ice nuclei

Water does not start freezing (crystallization of water molecules) easily even when the temperature drops to the subfreezing level, unless there are nuclei; it remains in a supercooled state. In particular, water that is free of impurities can be supercooled to about -40°C. Around this temperature, the water molecules themselves aggregate to form clusters of a certain size, which can act as nuclei for
the growth of ice crystals. Ordinary water that we normally come across is not pure. It contains foreign matter like dust particles, microcrystals, etc. Such foreign particles adsorb water molecules on their surface and promote the formation of ice nuclei. The freezing of water in natural environments is most often induced by such foreign matter.

**ii  Ice nucleating bacteria**

The ice nucleating capacity of dust particles is not very high (-1 to -10°C). Silver iodide, a well-known ice nucleator causes water to freeze at about -8°C. But ice nucleating bacteria can induce water to freeze at -1 to -3°C. The cloud physicists Schnell and Valli (Vali?) discovered that when a fluid derived from decomposing fallen leaves of alder was added to water droplets, they started freezing at a relatively high temperature and searched the fluid for substances that might be promoting ice nucleation. They found that *Pseudomonas syringae*, a bacterium commonly found on plants, strongly promoted ice nucleation. This epoch-making discovery had a major impact on researchers in the fields of agriculture, pathology and cryobiology. Later, other bacteria were found to have similar properties and the genes concerned with ice nucleation were isolated. Furthermore, the protein involved in ice formation has been prepared in bulk quantities using *E. coli*. It was found that this ice nucleating protein existed on the surface layer of the cell membrane of ice nucleating bacteria and plays the role of a mold on which small seed crystals of ice are gathered. In the Calgary Winter Olympics, held in Canada in 1988, a powder containing ice-nucleating bacteria killed by gamma irradiation was used for inducing snowfall. Ice nucleating proteins have been discovered in many types of plants and insects, apart from bacteria.

**iii  Antifreeze glycoproteins**

The freezing point of human blood serum and the blood serum of ordinary fish is about -0.56°C. The freezing point of sea water in the frozen seas of the Arctic and the Antarctic in the winter comes down to -1.85°C. Fish living in such environments do not freeze even when cooled to -2°C. This is because the blood of fish living in these Polar Regions contains an antifreeze glycoprotein. This protein not only suppresses ice nucleation but also physically inhibits the growth of ice crystals by getting adsorbed on the surface of ice microcrystals that do form. It has
been reported that plants also have this kind of protein, but its role is not very well understood, unlike in fish and insects. Fujikawa and his co-workers have recently found a similar protein in large quantities in the xylem ray cells of trees. Some researchers feel that this protein may have a role in the high level of supercooling shown by these cells.

The formation of ice nuclei and their growth and suppression were conventionally treated as physical phenomena. Now, however, it has been discovered that the living organisms have ice nucleating bacteria, ice nucleating proteins and antifreeze proteins, and that plants, insects, etc overwintering in natural environments adapt on their own to subfreezing temperatures by inducing freezing or sustaining supercooling as needed.

iv Possible states of water

Fig 8 shows the possible states (phases) of water in the subfreezing temperature range. The freezing point of water under a pressure of 1 atmosphere is 0°C. But if the water is pure, it can almost stably supercool to a temperature of up to -40°C. When ice nucleation occurs in this temperature range, the water freezes and releases latent heat, transforming itself into a stable crystalline form.

In a natural environment, the most important requirement for a plant to survive when its temperature drops to subfreezing levels is to avoid intracellular freezing, which is fatal.
Fig 8 Stable and quasi-stable states of water at subfreezing temperatures. Th: Homogeneous nucleation temperature; Tg: Glass transition point; Tm: Melting point\textsuperscript{*22}.

**Key:**

*Left side, top to bottom:*
Ultra-rapid cooling
Amorphous glass
Tg = -134°C

*Middle, top to bottom:*
Supercooling
Quasi-stable
↓ Freezing
Solid
Crystalline

*Right side, top to bottom:*
Maximum density
Liquid
Vitrification of water

What is glass?

Ordinary glass has a complex composition. Its main component is silica (SiO$_2$) and it contains a lot of silicate. The traditional soda lime glass is typical of such glasses. Glass starts to soften at temperatures above 500ºC and its fluidity increases. The glass can then be worked or molded. Glasses differ from other substances in that they change from fluid to an amorphous solid at a certain temperature, called the glass transition point. This solid has a random arrangement of molecules as in fluids but its hardness and cohesive force is similar to those of solids. Ordinary glass is made by first melting it at a temperature above its glass transition point, about 500ºC, and then rapidly cooling at room temperature to below the glass transition point. Therefore, it gets solidified with the random arrangement of molecules of its liquid form.

The lava spewed out from erupting volcanoes cools rapidly and forms a lot of glass. Obsidian is such a natural glass that has been used in various ways by humans since ancient times.

Vitrification of water

Water also changes its phase, from liquid water to solid crystalline ice (freezing) and from liquid water to a glass-like (amorphous) ice (vitrification). The freezing point of water is 0ºC, which is very low compared to the glass transition point (about 500ºC) of soda lime glass, and the crystal growth rate of ice is very high even at temperatures just below 0ºC. Because of this, it is pretty difficult to solidify water into a glass by rapid cooling without freezing it. But Macmillan and Loss successfully vitrified water by rapidly aggregating steam on to a copper sheet cooled with liquid nitrogen. They demonstrated that the transition temperature was about -134ºC. The glass transition point (-134ºC) of ultra-rapidly cooled water is shown in Fig 8.

Vitrification of concentrated aqueous solutions

As I had mentioned earlier, it is difficult to solidify pure water into a glass. In
concentrated aqueous solutions, of sucrose or glycerol for instance, the water molecules do not move around easily because of the high viscosity. In this type of solution, ice nuclei do not form readily and the solutions supercool to very low temperatures. If cooled relatively rapidly, a 70% aqueous sucrose solution supercools to about −50°C, and a 60% aqueous glycerol solution to about −110°C, before they vitrify (Plate 8). This glass transition point differs considerably, depending on the kind of solute and its concentration. When a solution vitrifies, no ice crystals are formed. So, if we vitrify cells before storing them, intracellular freezing can be avoided and the cells can be kept viable at liquid nitrogen temperatures (see Supplementary Discussion 2).

*Translator’s notes:
Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.*
Avoiding injurious intracellular freezing

Seeds and spores capable of withstanding drying do not have freezable water. They can therefore survive exposure to low temperatures no matter how low they are. Many overwintering plants contain 40% or more water, on a fresh weight basis. When such plants are exposed to subfreezing temperatures they become prone to fatal intracellular freezing that destroys cell structure. The prevention of intracellular freezing is thus very critical for surviving the winter. Plants that overwinter in very cold regions have the ability to survive even when the cells are dehydrated by freezing to below –30°C.

(1) Freezing of plants
Even in the warm Honshu region of Japan, on frosty mornings, the leaves of various plants growing along the roadside, and spinach, Komatsuna (Brassica rapa L. var. peruviridis) and radish growing in fields can be seen to freeze, turn dark green, droop and lie on the ground. If you pluck such a leaf at the petiole, wearing a glove to prevent your body heat from thawing it, you can see a number of needle crystals in the intercellular spaces. Soon, the morning sun melts the ice, the cells reabsorb the water, the plants straighten up and the leaves regain the original color. Plants like dahlia and canna, which are not frost tolerant, however, die of freezing and would never stand upright again. Fig. 9 (Left) shows a plant of Himeaoki (Aucuba japonica Thunb. var. Borealis) overwintering in Sapporo. We can see the frozen, now dark green, drooping leaves. These leaves can withstand extracellular freezing up to about to –20°C. Fig. 9 (Right) (see also Plate 1) shows overwintering Hakusan shakunage (Rhododendron catawbiense), its leaves hanging with margins curled inwards because of freezing. When this very hardy American Rhododendron starts freezing, first the petioles droop and with further decrease in temperature, the leaves reduce their width by curling up, becoming cylindrical like a Senbei (rice cracker) roll at about –10°C. Thus, we can approximately estimate the outdoor temperature from the extent of drooping and curling of Shakunage leaves. Through this response, above all, the large leaves of evergreen plants like Shakunage living in mountainous cold areas reduce transpiration loss of moisture, apart from preventing strong cooling through radiative heat loss and a sharp increase of temperature in sunshine. The drooping of the leaves is also effective in preventing accumulation of snow on them and consequent breaking of branches and stems.
Some explanation of the differences between animal cells and plant cells would be appropriate, before describing the freezing of plant cells. The intercellular spaces of land plants are normally filled with air and not fluid, unlike in animals. This is because gas exchange, more than anything else, is essential for plants. Another major difference is that animal cells are naked whereas plant cells have a cell wall outside the cell membrane. Such cells are the units assembled, like bricks, to form stems and trunks.

![Image of frozen leaves](image)

**Fig. 9** Left: Frozen leaves of overwintering *Himeaoiki* (Temperature: -10°C). Right: Frozen leaves of overwintering *Hakusan Shakunage* (Temperature: -10°C). The arrows point to flower buds (Photographed by the author).

(2) Intracellular and intercellular freezing

Let us now see where the ice forms when a plant is cooled. When a small piece of a plant is cooled slowly, ice first forms in the intercellular space outside the cell walls. The inside of the cells rarely freezes even when ice crystals grow outside. It is believed that this is because the cell membrane surrounding the cell allows the easy passage of water but not of ice. This mechanism is particularly well developed in the winter in highly frost resistant cells. If we gradually lower the temperature further while the ice is in contact with the cells, the water present in the cells migrates out through the cell membrane and cell wall, reaches the surface of the
ice and freezes there. Thus, the cells gradually get dehydrated and shrink while the ice crystals outside the cells grow (Fig 10). This type of freezing is called extracellular freezing. Fig 10 shows a cultured cell after extracellular freezing. Cultured cells were immersed in silicone oil after removing the medium and supercooled to about –5°C. Then, ice was brought into contact with cell surfaces to induce extracellular freezing. We can see that the intercellular water has become deposited and frozen outside the cell, forming ice columns. Once extracellular freezing occurs, with further lowering of temperature, the dehydration and shrinking of the cells advance and the concentration of solutes within the cells increases. This makes the contents of the cells more difficult to freeze. Nevertheless, even in extracellular freezing, beyond a certain limit, the mechanical stresses of dehydration and accompanying cell shrinkage can cause freeze damage. The temperature at which freeze damage occurs varies, depending on the plant variety and season. As will be explained later, cells in the woody part (xylem) of the twigs of deciduous broad-leaved trees can supercool stably up to about –30°C in the winter. This is because their cell walls permit the passage of very little water. For extracellular freezing to occur, the water within the cell should pass through the cell membrane and cell wall and be continuously supplied to the ice present outside. The conditions needed for this are that the freezing first occurs outside the cell and that the intercellular space that can accommodate the ice is available.

When the cells are cooled rapidly, freezing starts after the cells are substantially supercooled. So, the freezing also advances into the cells. This type of freezing is called intracellular freezing. Once freezing occurs inside the cells, the cell membranes and microstructure of the cells are destroyed. No living cells can withstand this. Under natural environments, the temperature decreases only about 4-5°C per hour. Therefore, overwintering wild plants almost never experience intracellular freezing.

Overwintering leaves, stems and roots of herbaceous plants; leaves of evergreen trees; and the bark (including the cambium) of branches, and stalks (trunks?) and the roots of deciduous broad-leaved trees, all survive subzero temperatures through extracellular freezing.
Avoiding intracellular freezing through supercooling

Mature leaves of *Shuro* (a type of palm) can supercool stably up to about $-12^\circ$C. Freezing occurs first at around $-5^\circ$C in the parallel veins of the leaves. But this freezing does not advance to the surrounding supercooled mesophyll cells up to about $-10^\circ$C. When cooled to below $-12^\circ$C or so, freezing gradually advances to the mesophyll cells, increasing the freeze damage of these cells.

Supercooling is known to occur in the cold hardy *Shuro* palm leaves distributed in
the subtropical to the temperate zones, *Sasa*, bamboo, leaves and seeds of giant
rosette plants (see I-11), and certain tissues and organs, such as tissues in the
xylem and seeds, of deciduous and evergreen broad-leaved trees. As I had
mentioned earlier, pure water can supercool only up to about –40ºC. In winter,
plant tissues have large amounts of solutes like sugars in their cells, and therefore,
they can supercool to –50ºC or even lower.

In 1955, Aoki*2, *3, from the Institute of Low Temperature Science, [Hokkaido
University, Japan] first reported that xylem tissue (Fig. 11, Left) of the winter
twigs of mulberry trees could be supercooled to at least –20ºC. At that time, his
laboratory did not have the facility to cool to –30ºC. Soon, Professor Aoki left the
institute and the research was discontinued. When I was requested to guide the
research of a graduate student, Quamme, at Weiser’s laboratory at the University
of Minnesota in 1970, Quamme’s research topic was supercooling of apple twigs.
Let me now briefly introduce his research work. Fig. 11 (Right) shows the
differential thermal analysis#1 trace of a small piece from a current year’s apple
twig. Freezing (A) first occurred at around –10ºC in the bark tissue and xylem
vessels. But this freezing did not affect the survival of the shoot. When further
supercooled to about –32ºC#1, another release (D) of latent heat of freezing occurred.
This represents intracellular freezing of the parenchyma in the xylem after being
supercooled to –40ºC. The tissue died of freezing at this temperature. When cooling
was halted at a temperature above –30ºC or so, where the freezing had started#1,
and the specimen warmed, the shoot was fully viable#8. The tissues in the xylem of
winter twigs of apple trees remained supercooled for as long as a month at –30ºC.
But when cooled to below –40ºC, the supercooling broke down and the tissue froze.
The mechanism by which tissues in woody parts are able to remain supercooled at
–30 to –40ºC is not well understood. The probable reasons for the ease with which
such tissues can be supercooled are the fact that cell walls of the xylem ray cells do
not allow easy passage of water which makes it difficult for extracellular freezing
to occur and the very high concentrations of the intracellular fluid because of the
high contents of sugars and proteins. Additional reasons that contribute to the
supercooling could be an absence of ice nucleators that initiate freezing inside the
cells and the presence of special proteins that suppress the growth of ice crystals.

(† Differential thermal analysis: One junction of a thermocouple is inserted into the
specimen (bud or shoot) and the other junction into a similar but dry specimen. The
two specimens are then cooled at the same rate to determine the freezing points of the test specimen from the release of latent heat of freezing. In supercooling and extra organ freezing, which will be explained later, the temperature of the start of freezing at the lower temperature is often the lethal temperature. Thus, this method can be used to determine the frost killing point.

Tissues in the buds and stems of deciduous trees of the cool temperate zone are highly frost hardy and can tolerate temperatures even below –50ºC. But the tissues in their woody parts can survive only up to about –30º to –40ºC, through supercooling. Exceptions are tissues in the xylem of highly frost hardy willows, poplars and white birch. They can survive up to –70ºC. Fujikawa had recently shown the possibility of xylem ray parenchyma of these species surviving up to –70ºC by supercooling.

The work of Quamme et al. confirmed that tissues in the wood of the winter twigs of many temperate deciduous and broad-leaved trees can stably supercool up to –30ºC. This finding evoked great interest globally. When Quamme was preparing a research paper on this finding, I requested him to give the reference of the Japanese papers of Aoki, who had made a similar discovery about 15 years earlier. After my return from USA, I described to Professor Aoki, then working at Sendai, the findings of Dr. Quamme at the University of Minnesota on supercooling. Professor Aoki was very delighted that his findings had been confirmed.

It is difficult to imagine an entire plant of the temperate zone surviving the winter in a supercooled state, unlike an insect. In a large plant, unlike in a small insect, depending on their function, shape and structure, each tissue or organ undergoes extracellular freezing (freezing resistance), supercooling or extra organ freezing (which will be explained later) to avoid intracellular freezing.
Part 2

(4) The overwintering mechanism of buds

i Flower buds of broad-leaved trees

In the mid 1970's, research workers at Weiser's laboratory at the University of Minnesota discovered that florets in overwintering azalea flower buds (Fig 12, Left, F) supercool to below -20°C and that their ability to supercool varied significantly with the season. This finding was made through differential thermal analysis. The scales that covered the bud (OS and IS) and the axis (A) showed...
extracellular freezing at around –10°C. But the 6 florets (F) inside the flower bud succumbed to intracellular freezing one after the other after supercooling to –20°C or lower. Spikes caused by the release of latent heat in this process appeared on the differential thermal analysis trace (Fig. 12, Right, 2). Each spike corresponds to the freezing of one floret. Thus, one could determine the killing points of individual florets by differential thermal analysis. Fig 12 (Right, B) is the differential thermal analysis trace of a flower bud in spring, after overwintering. We can see that the ability of the florets to supercool has been considerably reduced because of the increased water content.

Ishikawa et al. demonstrated that the killing point of Japanese azalea florets varied greatly, depending on the cooling rate. Let us now look at this phenomenon in Sanshuyu, (Cornus officinalis Sieb. et. Zucc.), a plant of the dogwood family, which bears small yellow flowers in early spring. Fig. 13 (Left) is a longitudinal section of a Sanshuyu flower bud. Scales surround a number of florets at the center. In early winter, a tannin-like substance creates a barrier at the boundary between the stem and the flower bud (Fig 13, Left, b) stopping the movement of water and ice from the stem to the flower bud. When such a flower bud is cooled to several degrees below zero, the florets supercool while freezing first occurs within the scales (Fig. 13, Right, B). Once freezing occurs within the scales, the water from the supercooled florets migrates to the scales through the vascular bundles (dotted lines in Fig 13, Left). Because of this, when the temperature dips further, the florets get dehydrated while ice crystals form one after the other in the scales. We can see from Fig. 14 that the water content of the florets (F) is reduced markedly while that of the scales (S) increases correspondingly. For such dehydration to occur in the florets at subzero temperatures, it is essential that freezing first occurs in the scales. Recently, Ishikawa and his coworkers discovered that there was an ice nucleating material in the scales, which therefore freeze first, at relatively high subzero temperatures.

In this freeze-induced dehydration, the freezing point of the florets was lowered by about 9°C and the killing point after supercooling to about –25°C. Fig 13 (Right) is a cross sectional view of a flower bud that had been slowly cooled to –22°C, by lowering the temperature by 5°C daily. Extensive dehydration of the florets and the formation of a large amount of ice (I) in the scales can be seen. Thus, although the florets in the flower bud cannot withstand extracellular freezing, they allow
migration of water to the scales through the vascular bundles, permitting concentration [of the fluid in them] and becoming capable of surviving a low temperature of about –25ºC. Florets are very large compared to cells. So, their dehydration takes a longer time (Fig 14). Because of this, if the flower buds are cooled rapidly, the dehydration of the florets cannot keep pace with the cooling and they are killed by freezing at a relatively high temperature. Thus, the killing point of a flower bud varies considerably depending on the cooling rate.

This type of supercooling, accompanied by dehydration, was unknown until then. Freezing is prevented by this mechanism and survival below –30ºC becomes possible for [vegetative] buds (see Plate 2) and flower buds of broad-leaved trees and of needle-leaved trees (to be discussed later). These are important embryonic organs (Haikikan) having complex differentiated structure with densely packed cells. This is a very clever way of freezing avoidance by plants. We named this mechanism “extra organ freezing”.

Traditionally, cells and tissues that withstand freeze-dehydration by extracellular freezing are called frost hardy. Cells and tissues that cannot survive extracellular freezing but survive subfreezing temperatures by supercooling are, on the other hand, said to survive by “freezing avoidance”. No water migrates outside the cells (into the intercellular space?) in supercooled cells or tissues. If water were to migrate into the intercellular space, extracellular freezing would result. The flower buds of broad-leaved trees that we had discussed earlier and the buds of needle-leaved trees to be discussed later, get dehydrated by allowing the water within them to migrate outside the organ and freeze, very much like in extracellular freezing. These organs withstand such freeze dehydration in a supercooled state up to temperatures as low as –30ºC. As in extracellular freezing, the temperature up to which an organ can withstand extra organ freezing is determined by its resistance to freeze-dehydration. If an organ can withstand severe freeze-dehydration, it can survive cooling to even lower than –70ºC, like the buds of needle-leaved trees of Alaska and Siberia.

As I had explained earlier, several researchers in Weiser’s laboratory at the University of Minnesota studied the supercooling of flower buds through differential thermal analysis in the 1970’s. However, they kept the cooling rate constant, starting the cooling in the morning and ending it in the evening. In this
scheme, the buds were cooled fairly rapidly. Besides, the researchers did not directly observe the frozen buds in a cold room. So, they did not notice the migration of water from the florets to the scales, and the phenomenon was considered merely a case of supercooling of the flower bud. We discovered the mechanism only when we directly observed the frozen flower buds under a microscope in a cold room, in addition to analyzing the phenomenon by the indirect method of differential thermal analysis.

**Fig 12** Left: A longitudinal section of a Japanese azalea flower bud. F: Floret; IS: Inner scale; OS: Outer scale; P: Peduncle; A: Axis of the stem; LB: Leaf bud. Right: Differential thermal analysis traces of azalea flower buds. 1. Freezing (extracellular) of scales, the axis, peduncle, etc. 2. The 7 spikes represent freezing (intracellular) of florets in the flower bud. Cooling rate: 0.14°C per minute

**Key**
- A: March 1
- B: April 16

**Ordinate**: Differential temperature

**Abscissa**: Time (One division = 15 minutes)

**Arrow**: Temperature
Left: A longitudinal section of a flower bud of *Sanshuyu*. The dotted lines indicate vascular bundles.*

Right: Polarized light micrograph showing ice deposited in the scales (B) of a *Sanshuyu* bud cooled slowly to −22°C. I: Ice deposited in the scales (Extra organ freezing); F: Dehydrated floret.

Key (Clock-wise from top right): Florets; Receptacle; Bud; Stem; Barrier; Scales
ii Morphology of the buds of needle-leaved trees

The leaves and shoots of *Todomatsu* fir (*Abies sachalinensis*) and Japanese spruce growing wild in Hokkaido have a frost hardiness of about −70°C. But their vegetative and reproductive buds can withstand a low temperature of only about −40°C. Because of this, buds are the critical parts in the cold survival strategy of needle-leaved trees. In the winter bud of *Todomatsu* fir (Fig 15, Left), a shoot
primordium (P) of size about 1-2mm and the leaf primordia (N) are connected to the stem through an elastic membranous structure called the crown (C). This crown plays a crucial role in overwintering of Todomatsu fir. Among needle-leaved trees of the pine family, such crowns can be found in trees like fir, spruce, Japanese hemlock and larch distributed mostly in the northern region. But the crown is absent in the genus Pinus, Taxodiaceae, Cupressaceae, Taxaceae, etc, which have existed on earth for a very long time. In Sapporo, crown tissue forms in late September in Todomatsu fir buds. The winter buds are complete and ready to overwinter only after the crown is formed.

In the winter buds of Todomatsu fir (Fig 15, Left) the shoot primordium (P) at the center of the bud is surrounded by more than a hundred scales (F), which protect it from drying. In early winter, the outside of the scales is further thickly covered with a whitish resin (Fig 15, Right, R). This resin melts in spring and is absorbed by the plant after the buds open. The number of scales in the winter buds of the Todomatsu fir is greater in colder regions. On the small (about 2mm) shoot primordium of Todomatsu fir buds, the primordia of the shoots and leaves (N) that would emerge in the following spring are all ready in autumn. I once counted the number of leaves on a current year’s twig of an about 2m tall fir in my garden. The 8cm long twig had 205 leaves. This means that the shoot that would emerge with 205 leaves was already preformed in the tiny shoot primordium (P) of the previous year’s winter bud.
iii Extra organ freezing of the buds of needle-leaved trees
When an approximately 2mm long shoot primordium was removed from an overwintering bud of *Urajiromomi* (*Abies homolepis*⁴ and subjected to differential thermal analysis, the primordium froze and died when cooled to below –10°C. Under natural conditions, however, shoot primordia in buds could withstand temperatures even lower than –30°C. To investigate this difference further, we
observed the distribution of ice in the bud under a binocular microscope in a cold room at –15ºC. To our surprise, needle ice crystals (I) were seen growing from the crown tissue downwards, pushing the pith of the stem supporting the bud (Fig 16, Left). The moment I saw this, I understood that water passed from the shoot primordium (P) through the barrier of the crown (C) and got deposited as ice crystals below. As in extracellular freezing, the water in the shoot primordium passed through the membrane structure of the crown, froze outside it, causing freeze-dehydration of the primordium. This suggests that the crown has pores big enough to allow the passage of water but not of ice. Besides this, the crown changed its shape with the lowering of the temperature to form a dome, which increased its surface area and promoted the dehydration of the supercooled shoot primordium (Fig 16, Right). It thus came to light that the buds of *Urajirimomi* cooled to about –30ºC had extensive ice formation beneath the crown (Fig 16, Left) (see Plate 3 also).

(†We needed nearly 1000 more or less uniform buds for the experiments conducted in one winter. For this, 10 Urajiomomi firs growing wild in a mountainous area of Honshu were transplanted in the premises of the Institute [of Low Temperature Science, Sapporo] because it is easy to obtain a large number of buds from this tree).

With the arrival of spring, the ice below the crown melts off, leaving a gap there (Fig 15, Right, A). The size of this gap reflects the size of the ice mass formed in winter and the severity of the cold of the winter that the plant survived. The role of the crown and its morphology in the bud of needle-leaved trees and the significance of the space below it became clear for the first time, through our study described above. Through such microscopic observations and differential thermal analysis, we came to know that the cells constituting the shoot primordia of the buds of needle-leaved trees like *Todomatsu* fir could not survive extracellular freezing, the primordia could survive in a supercooled state even below –30ºC through removal of their water and its freezing outside them*†101, 105. In this case also, it is necessary that ice crystals form beneath the crown first. It is very likely that this area has some ice nucleators, as in the flower bud scales, but this is not yet confirmed.

Next we examined the reproductive buds of larch. Plate 4 is a photograph of a longitudinally cut bud of Siberian larch after it had been cooled slowly to –30ºC. A
large amount of needle crystals can be seen beneath the crown. Plate 5 is a similar photograph of a Japanese larch reproductive bud after it had been cooled rapidly, at the rate of 5ºC per hour. Dehydration of the shoot primordium could not keep up with the rapid rate of cooling and therefore the inside of the shoot primordium froze before it could be sufficiently dehydrated, leading to death.

Plate 6 shows extra organ freezing of a reproductive bud of metasequoia (dawn redwood) of Taxodiaceae. Unlike the needle-leaved trees of the sub-family Abietoideae, the needle-leaved trees of Taxodiaceae do not have a crown. The water in the shoot primordium of the bud gets deposited out as ice in the scales located at the base of the bud.

**Fig 16** Left: Early stage (-12ºC) of extra organ freezing in *Urajiomomi* (*Abies homolepis*). Tashe water in the shoot primordium (P) has deposited out as needle crystals (I) beneath the crown (C), pressing down the pith below them*105*.

Right: A sectional view of a bud showing extra organ freezing at -20ºC. S: Scale; I: Ice deposited beneath the crown; A: Pith of the axis
Extra organ freezing of the buds of needle-leaved trees in Alaska

The buds of the needle-leaved trees of Hokkaido, even when cooled slowly, can withstand cooling to \(-40\) to \(-45^\circ\text{C}\) at the most. I requested a friend at University of Alaska to send to Sapporo by air, shoots of two types of spruce (\textit{Picea}) overwintering in interior Alaska, where the temperature drops below \(-50^\circ\text{C}\). When I examined them, I could see large amounts of ice below the crown the primordia of these buds also, as seen in \textit{Todomatsu} fir. Moreover, the innermost scales also had ice deposited in them (Plate 7). These spruce buds were viable even after cooling to \(-70^\circ\text{C}\). In other words, it became clear that they were capable of withstanding far more intense dehydration than the buds of the needle-leaved trees of Hokkaido.

Among the needle-leaved trees of Pinaceae, those distributed widely in the subarctic to the subalpine parts of the temperate zone, such as the genera \textit{Abies}, \textit{Picea}, \textit{Tsuga} and \textit{Larix}, had appeared relatively recently, compared to genus \textit{Pinus} distributed in the subtropical to the temperate zones. The former had expanded their distribution, adapting to the cold climate of the middle to high latitudes of the northern hemisphere. The characteristic feature of their buds is that the shoot primordia are only about 2mm long, they all have crowns, and they overwinter through extra organ freezing. Contrary to this, in the genus \textit{Pinus}, which is the oldest among the needle-leaved trees of Pinaceae, the primordia of the long buds are very large (1-3cm) compared to those of the above-mentioned needle leaved trees, do not have a crown at the base, and are directly connected to the stem. It has been confirmed that the primordia in the long buds of \textit{Pinus} survive the winter through extracellular freezing. Thus, even among the needle-leaved trees of the family Pinaceae, the mechanism of overwintering of the buds is very different, depending on the morphology and structure of the bud.

(5) Strategies of cells, tissues and organs for withstanding cold

No plant cell can survive intracellular freezing. In this sense, all the strategies of plants for withstanding cold under subzero temperatures can basically be considered as “freezing avoidance”. Internationally, however, the cold resistant cells are broadly classified into two types, cells that can withstand extracellular freezing and those that cannot. The former are called frost hardy cells. According to this classification, if we assume that extra organ freezing is also a type of frost hardiness, since the cells withstand freeze dehydration, the survival
strategies of cells, tissues and organs against cold can be classified as follows:

1) Acquisition of frost hardiness (tolerance of freezing-dehydration)
   a. Extracellular freezing: Herbaceous plants and evergreen leaves, bark tissue of stems, etc of woody plants
   b. Extra organ freezing (supercooling accompanied by dehydration): Winter buds and flower buds of broad-leaved trees, and buds of needle-leaved trees

2) Freezing avoidance
   a. Acquisition of the ability to supercool (supercooling not accompanied by dehydration): Xylem ray parenchyma of broad-leaved trees, palm leaves, Sasa, bamboo etc growing in the subtropics and tropics and leaves of giant rosette plants growing in tropical highlands
   b. Freezing avoidance by acquiring desiccation tolerance (acquisition of high resistance to drying): Seeds, spores, pollen, etc.

Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink and alternatives sometimes given in parenthesis.
   #1 There seems to be some discrepancy between the text and the Fig.
2. Words added by the translator for clarity are given in [square brackets]
3. The translation of the words given in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.

To Dr. Karen Tanino (9.9.2004)
Supercooling on my book published at Hokkaido Univ., I would like to change my comments on supercooling of Salix, Poplar, Betula and dogwood. These xylem parenchyma cells may supercool to about –70C, but not extracellular freezing in winter when cooled slowly. These cells accumulate a lot of anti-freezing proteins or any water soluble proteins, especially in winter season (refer Arakawa, 7IPCHS).
In many cases, I cooled rapidly into LN after prefreezing at different temperatures. This may be different approaches- the size of ice crystal caused frost injuries. I did
not cool very slowly to –70°C. So, I would greatly appreciate it if you could check of winter twigs of xylem parenchyma cells. Dr. Fujikawa researches indicate that these twigs were injured until cooling near –70°C by supercooling.

When rapidly frozen in LN from room temperature, several time, xylem cell membranes were broken and washed several times, the xylem supercooling ability decreased rapidly after washing. Thus, these proteins contained in the cell interior are very important to the supercooling, but not xylem parenchyma cell walls.

The xylem tissues (deep supercooled xylem below –50°C) can supercool when they were re-cooled after re-warming. So, the existence of xylem cell wall may be reason of the deep supercooling xylem parenchyma cells.

Xylem cell walls may not be permeable to water. So, the extracellular freezing may not occur. These facts suggest that water soluble proteins in xylem parenchyma cells may be the main factor for the deep supercooling. In extracellular freezing and or extrafreezing, Ice-sink (extracellular or scale or conifer crown, INA activity is strong, but cell interior primordial tissues do not include INA activity, but antifreezing proteins are included (to be capable to supercool). Sakai 9.9.2004.
5 Exploring the lowest survival temperature of plants

The minimum temperature so far found to occur naturally on earth is –88.3°C, at the Russian Antarctic base Vostok (S latitude 78° 28 min, altitude 3488 m). The minimum temperature recorded (officially recognized) in a region inhabited by people is the –67.8°C recorded in Verkhoyansk, eastern Siberia. The temperature of dry ice (solid carbon dioxide), often used as a coolant, is –78°C and that of liquid nitrogen is –196°C. Liquid helium has a temperature of –269.5°C and the absolute zero, the lowest temperature possible, is –273.16°C. Thus, there are different levels of subfreezing temperature. Around 1953, when I started researching cold hardiness of mulberry, no one knew the lowest temperature that ordinary plants with about 40% water content could survive, although some information was available about extremely dry (water content of a few percent) seeds, pollen and microorganisms, which did not have freezable water.

(1) Willows survived cooling to -196°C

Two years into my research on cold hardiness of plants, in 1955, I could confirm survival of bark cells of winter shoots of mulberry after freezing at –30°C and their viability after cooling to about –90°C with dry ice. Then an idea struck me. When highly frost hardy cells and tissues are freeze-dehydrated by extracellular freezing, the cell [fluids] soon get so concentrated that there is no freezable water left. This highly concentrated tissue might survive even if cooled to the temperature of liquid nitrogen (–196°C) through vitrification. To check this, I first cooled bark tissues of mulberry shoots to different temperatures to freeze-desiccate them to different levels and then cooled them in liquid nitrogen. All the cells of tissues freeze-dehydrated to below –30°C before cooling in liquid nitrogen were found to be alive when thawed at 0°C. However, tissues that had been cooled only to –15 or –20°C before cooling in liquid nitrogen showed considerable damage when thawed under the same conditions. These results seemed to suggest that the cells cooled to –30°C got vitrified during the subsequent rapid cooling in liquid nitrogen and remained viable. However, I could verify only the survival at the cellular level in these experiments with mulberry bark tissue.

I then tried a similar experiment with winter shoots of willow. If the winter shoots of willow survive they would root and develop into trees. I cooled about 15cm long
shoots of Koriyanagi willow (*Salix koriyanagi* Kimura) to -30°C, kept them at that temperature overnight for freezing dehydration and then cooled them rapidly in liquid nitrogen, where they were kept for a day. The shoots were then thawed in air at 0°C and the cuttings planted in a greenhouse. They developed roots and grew normally into willow plants (Fig 17). This was the first time in the world where ordinary plant tissue had regenerated into plants after being cooled to the liquid nitrogen temperature.

Shoots of Onoeyanagi willow (*Salix sachalinensis* Fr. Schmidt) treated in the same way and stored in liquid nitrogen for one year remained alive, developed roots, and grew normally*84, 85. Koriyanagi and Onoeyanagi willow shoots freeze-dehydrated to -30°C and then cooled in liquid helium (about -269°C), which is close to absolute zero, also survived*87. Fig 18 shows an Onoeyanagi willow tree that grew from such a shoot. From the results of these experiments, I developed a method of cryopreserving animal and plant cells and tissues*84, 86. This is a pre-freezing method, where the cells are first freeze-dehydrated by cooling to about –30 to -40°C and then cooled in liquid nitrogen for vitrification. This pre-freezing method opened up a new way of cryopreservation† of animal and plant material.

†Method of cryopreserving animal and plant material: Non-frost hardy cells and tissues of animals and plants are first treated with an antifreeze such as glycerol and DMSO (dimethyl sulfoxide), to increase their freezing resistance to about –30 to -40°C. They are then freeze-dehydrated by lowering the temperature to about –30 to -40°C before cryopreserving in liquid nitrogen).

Fig 19 shows new shoots that grew normally from a winter bud of apple grafted onto a stock*84, 99. The bud had been freeze-dehydrated at -30°C, stored in liquid nitrogen for one year, and thawed at room temperature before grafting. At the USDA ARS Plant Genetic Resource Unit, located in Geneva, New York, they presently have the winter buds of about 2000 apple lines under long-term storage at -150°C, for which they use a modified version of our method. Their final target is to store about 2500 lines by the year 2005. The average survival rate after 5 years of storage is 75%.
A Koriyanagi willow (*Salix koriyanagi* Kimura) plant that grew from a cutting that had been freeze-dehydrated at -30°C, cooled to -196°C and then thawed in air before planting (photographed by the author).
Fig 18 An *Onoeyanagi* willow (*Salix sachalinensis* Fr. Schmidt) that grew from a cutting that had been freeze-dehydrated at -30°C and cooled to about -269°C with liquid helium before planting (photographed by the author in 1963).

H: Cooled in liquid helium
N: Cooled in liquid nitrogen
Fig 19  New shoots that grew in 3 months after grafting of a winter bud of apple on a stock, after pre-freezing to -30°C and storing for 1 year in liquid nitrogen.  S: New shoot that grew from the bud grafted site (circled); D: Stock on which the bud was grafted. 
(2) Experiments on the minimum survival temperature of plants in Alaska

In 1989, I came to know that the noted physiologist and ecologist Dr. Scholander and his co-workers, of University of Alaska working at their polar research laboratory at Point Barrow, had been conducting experiments to find out the minimum temperature that plants could tolerate\(^{119}\). They collected shoots of an Alaskan *Alnus* species and willow in the coldest season from the mountainous region in the northernmost part of Alaska where the temperature drops to about -60ºC, sealed them in glass bottles and carried them in a small aircraft to the Institute of Arctic Biology at Fairbanks. They placed the shoots in liquid oxygen (-183ºC) for 18 hours along with shoots of poplar, white birch and white spruce that they had collected at Fairbanks. After thawing, the shoots were placed in water in a greenhouse for rooting, but all of them were found to have died of freezing. Another group of shoots that had not been cooled in liquid oxygen and were placed in water in a greenhouse for rooting opened their buds normally and grew. From this, they concluded that trees overwintering in northern Alaska could withstand the -60ºC or so that they normally get exposed to but not the temperatures below -180ºC of liquid oxygen or liquid nitrogen, temperatures that do not occur naturally on earth. However, if we recall our experiments with willow described earlier, we can guess that the reason for the death of all the shoots cooled in liquid oxygen (-183ºC) is probably that the temperature of the cuttings in the thermos bottles climbed above -10ºC during the hour or so of the flight from Point Barrow to Fairbanks. Had the liquid oxygen been taken to Point Barrow and the overwintering shoots placed directly in it, they would have definitely survived.

(3) Survival mechanism of cells cooled to -196ºC

With the winter shoots of *Onoeyanagi* willow, which are particularly frost hardy, all the shoots survived and grew normally (Fig 20) when they were freeze-dehydrated by cooling to different temperatures in the range -15 to -70ºC, cooled in liquid nitrogen and thawed at 0ºC in air. Generally, the higher the concentration of the cell [sap], the higher is the freezing resistance of the cell. Therefore, even with only slightly more freezing dehydration, i.e., after pre-freezing at relatively high temperatures, they survive cooling in liquid nitrogen.
The probable reason for the survival of shoots and buds of particularly frost hardy trees at liquid nitrogen temperature after freezing dehydration is that the cell sap concentrated by freezing dehydration vitrifies when cooled in liquid nitrogen.

Hirsh et al. of USA used an electron microscope to examine cells of poplar shoots that had been freeze-dehydrated at -20ºC and then cooled in liquid nitrogen. No ice could be detected electron microscopically. They then measured the glass transition point of the cells and found it to be about -28ºC. It thus became clear that cells that had been pre-frozen at -20ºC and then cooled in liquid nitrogen had vitrified.

No further dehydration occurs in vitrified cells even if the temperature is further lowered and the cells are kept for any length of time at the low temperature. Therefore, they remain viable at liquid nitrogen temperature for a long time.

Hirsch et al. assumed that in extremely frost hardy plants that overwinter in very cold places with temperatures less than -30ºC, the concentration of the cell sap inside the cells would be already quite high because of natural freezing dehydration and that such cells would get easily vitrified when cooled below the transition point. They felt that vitrification of cells was one of the overwintering mechanisms of plants surviving in extremely cold regions.

(4) Residual water content after freezing dehydration

Willows, white birch and many other trees can withstand slow freezing to -70ºC. The Russian researcher A. O. Krasavtsev (1966 Sapporo Congress) had measured the residual water content in cells after about 16h of freezing dehydration of winter shoots, which are highly frost hardy, using a very accurate calorimeter and found that the residual water content was about 24% of the fresh weight in shoots freeze-dehydrated at -10ºC, about 20% at -15ºC, about 15% at -30ºC and about 8% at -70ºC. In the coldest season, when the frost hardiness is maximum, Onoeyanagi willow shoots freeze-dehydrated at temperatures below -15ºC and cooled in liquid nitrogen were all viable when thawed slowly at 0ºC in air, as shown in Fig 19 (Fig 20). From this result, I assumed that about 20% water remaining in the cells freeze-dehydrated at -15ºC vitrified at the liquid nitrogen temperature.
Fig 20  Growth of *Onoeyanagi* willow raised from winter shoots freeze-dehydrated at different temperatures, cooled in liquid nitrogen and thawed at 0°C in air before planting in a greenhouse.
Cold acclimation of temperate plants and their increased frost hardiness

(1) Differences between temperate and tropical plants

In low lying areas of altitudes not more than 1000 m or so in the tropical zone, the temperature remains higher than 25°C during most of the day and even the lowest temperature at night would not be lower than 20°C. Many tropical plants and crops growing in such environments sustain irreversible cold injury if exposed to temperatures of 0 to 13°C for a certain time. Fig 21 shows cold-damaged (darkened) parts of 3-year-old coffee plants (Arabica variety) after exposure to 1°C for 36h. Important tissues and organs, including roots, mature leaves, cambium of stems, apical buds, lateral buds and embryos inside seeds, are the most affected. They cannot recover even when brought back to normal temperatures. The temperature and time required for cold injury to occur varies greatly depending on the type of the plant and the temperature of its growth environment. In the tropics, cold resistant plants grow above an altitude of 2000 m and plants sensitive to low temperature live below this altitude.

Contrary to this, plants growing in temperate and sub-arctic regions, where there is a long cold winter unsuitable for growth and the temperature drops below the freezing point, spend the inhospitable winter season in a dormant state. They have acquired the capacity to tolerate cold, which enables them to survive the sub-freezing temperatures. Temperate plants growing naturally in Sapporo (mean temperature in January is about -5°C) grow actively during the summer growth season, when the mean temperature is about 20°C, and in the dormant period in the winter, they survive a mean temperature of about -5°C (the mean daily minimum temperature is about -9°C). The difference in mean temperature between summer and winter is as much as 25°C. Temperate plants living in such places significantly change their structure and functions as the season changes from summer to winter. They change from a growing to a dormant state and from physiological functions of high temperature to those of low temperature. The plants can reach a high level of cold hardiness only through such changes. The series of changes that take place in the bodies of temperate and sub-arctic plants from summer to winter are called cold acclimation. The opposite change, from the dormant to growing state, takes place during spring. The temperate and sub-arctic plants have expanded the range of temperatures that they can survive and the
area of their distribution by acquiring a capacity to acclimate to cold, which
tropical plants do not have. At the same time, they had to compensate by
sacrificing a considerable amount of growth in order to adapt to the shorter
growing periods and can now live only in areas with a certain period of low
temperature.

**Fig 21** Cold injury in a 3-year-old coffee seedling after exposure to 1°C for 36h.
The damaged parts are indicated in a darker shade and the percentages
represent the extent of damage.
Cold acclimation of temperate deciduous trees

i Short day-induced dormancy of temperate deciduous trees

In the temperate and sub-arctic zones, the length of the day (daylength) (Fig 22) and the temperature change considerably as the season changes from summer to autumn. As the days get shorter, this information is perceived by a protein pigment in the leaf cells called phytochrome, and the growth inhibitor abscisic acid (ABA) is synthesized. Plants stop growing because of the action of ABA, produce winter buds and enter a dormant state. This cessation of growth and entering the dormant state are the initial stages of cold acclimation. For a plant to grow successfully in the temperate or sub-arctic zone it is essential to stop growth, form winter buds and prepare for the winter in good time, before it becomes dangerously cold.

There is a poplar species called black cottonwood (Populus trichocarpa) that is widely distributed from north to south along the west coast of North America, reaching as far north as Anchorage (N latitude about 62°) in Alaska and as far south as California (N latitude 33°) (Fig 23, Left). The time of growth cessation in these poplar trees growing naturally at different locations was studied in detail by preparing rooted cuttings from the trees and planting them at an Institute in a suburb of Boston*77. Growth was found to cease earlier in trees growing at higher latitudes. The poplars of mid-latitudes (N latitude 45-47°, which spans the southern part of the state of Washington to northern Oregon) varied by about 2 months in their time of growth stoppage in spite of the difference in latitude being small. In this range of latitudes, poplar trees grow from coastal plains to mountainous areas with fairly varied topographic and climatic conditions. Researchers then studied the relationship between the time of growth cessation, and winter bud formation, and the length of the frost-free period (growth period) among the poplar trees of this latitude. It was found (Fig 23, Right) that trees from mountainous regions with shorter growth periods stopped growth and formed winter buds earlier in the season. Trees from the coastal area, where the autumn cold arrived much later and the growth period was longer, ceased to grow much later. Thus, even among plants of the same species, the critical daylength that
induces growth cessation is more or less genetically determined so that they stop growing in good time in response to the winter cooling of their natural habitats, according to their climatic and topographic conditions. Apart from the daylength, nighttime cooling acts in a compensatory manner on the time of growth cessation. In other words, night time cooling promotes the synthesis of growth inhibiting hormones that suppress plant growth.

Norway spruce, which grows naturally over a wide area in Europe, stops growing and forms winter buds when the daylength in Norway (N latitude 74°) becomes 21h, which happens in mid-July. The same spruce at N latitude 58° stops growing when the daylength becomes 18h, in early August. For those growing in Austria at N latitude 47°, which is the southern border of the spruce’s natural habitat, the critical daylength is 15h, reached in mid-August. Even at the same latitude, the critical daylength becomes longer with increase in altitude, i.e., the trees stop growing earlier. One interesting point is that inside the arctic circle, the sun does not set until mid-August and therefore the day length is 24h, but the plants living there stop growing by the middle of August. These tundra plants of the high latitude arctic region have been now found to cease growth in response more to night cooling than the daylength.
Fig 22 Change in natural daylength with the seasons at different latitudes.
Sapporo: N latitude about 43°; Yakutsk: N latitude about 63°

Key:
Abscissa: Winter solstice; Spring equinox; Summer solstice; Autumn equinox;
Winter solstice
Ordinate: Daylength
Inside the graph: Sapporo: North latitude
Fig 23 Left: Distribution of poplar (*Populus trichocarpa*) on the west coast of USA. S: Seattle (N Latitude 47°36' N). Right: The relationship between the latitude and time of growth cessation in poplar trees distributed over N latitude 45 to 47°.

**Abscissa:** Growth cessation time: July, August, September, October.

**Ordinate:** Frost-free period (days)

**Inside the Fig:** N Latitude 45 to 47°.

**ii Cold acclimation and biochemical changes in cells**

Temperate and subarctic plants, which spend a long dormant period in winter under low temperatures need to accumulate, before the arrival of the winter, substances necessary for overwintering and for the growth in spring and to develop resistance against the winter cold and dryness. Firstly, when growth ceases in autumn, a large amount of starch is accumulated in the plant body (Fig 24). Also, during autumn to winter, there is active synthesis of ribonucleic acid (RNA) and protein, and the metabolic pattern switches from the growth phase of the summer to the dormant state of winter[^82][^83]. This is accompanied by synthesis and accumulation of sugars at low temperature and changes in the biomembranes (increase in phospholipids and increased unsaturation of membrane lipids)[^135][^136].
Moreover, the structure of the cells also changes greatly during cold acclimation. In the growth phase, the amount of cytoplasm in the cell is small and most of the cell volume is occupied by the vacuole. But in winter, the cells are filled with cytoplasm and nucleoplasm, and the vacuole shrinks. The ultrastructure of the cells also changes. In winter, the cells become capable of tolerating extensive freeze-desiccation and mechanical stress through a series of such changes. The seasonal changes in frost hardiness, osmotic concentration of the cells, and their sugar content are the most striking part of the process of cold acclimation. When plants are exposed to 0°C for two weeks in autumn, the sugar content and osmotic concentration increase remarkably and the frost hardiness also increases correspondingly. The sugar content and osmotic concentration decline in early spring under natural conditions. But if the plants are exposed to low temperature at that time, the sugar content and frost hardiness increase again.

The “wisdom” acquired by plants over their long period of adaptation to changes in the external environment, has been incorporated in their genes as information and is passed on to subsequent generations. A strikingly large number of genes are involved in the series of complex processes of cold acclimation. The identification of these genes, elucidation of the conditions for their expression, and the roles of the proteins involved are important tasks for the future.
Fig 24  Top: Seasonal changes in accumulation of starch in European beech. The starch (dark portion) accumulates before leaf fall in autumn. In winter, the starch changes into sugar at low temperature. The starch content increases again just before opening of the buds in spring.

Key:

Inside the Fig: European beech
Spring: After bud opening; Autumn; Winter

Fig 24  Bottom: Starch accumulated in bark cells of mulberry shoots in late September (photographed by the author).
Fig 25 Seasonal changes in frost resistance, sugar content and osmotic concentration of cells of the bark tissue of *pseudoacacia*. The osmotic concentration is expressed here as the concentration of a salt solution that is isotonic with the cells and frost resistance as the minimum temperature withstood by the plant without frost injury. -20°C L and -30°C L means the sample was transferred to liquid nitrogen from -20 or -30°C. H: Treated at 0°C for 2 weeks\textsuperscript{134}.

*Key:*

*Abscissa:* Time of the year: July, August . . . June

*Ordinate left outer:* Osmotic concentration (M)

*Ordinate left inner:* Frost hardiness (°C)

*Ordinate right:* Sugar content (percent of fresh weight)

*Inside the Fig, clockwise from bottom left:* Frost resistance; Sugar content; Frost resistance; Osmotic concentration
iii Strategies of overwintering plants for preventing moisture loss

Overwintering herbaceous plants without snow cover, evergreen broad-leaved trees and needle-leaved trees are exposed to dry winds and sunlight and lose a lot of moisture. Particularly when the soil is frozen and sufficient water is not supplied to the above-ground plant parts, the water balance of the overwintering plants is disturbed and they suffer drought damage. To prevent this, overwintering plants develop, during cold acclimation, mechanisms that reduce moisture loss from their body surfaces. Evergreen leaves close stomata in winter and develop a cuticle layer on the leaf surface to reduce transpiration to 1/4th to 1/3rd of the summer level. Needle-leaved trees develop a surface cuticle layer on their leaves to suppress cuticular transpiration. Moreover, they close their stomata and solidify (protect?) their surfaces with resin. Overwintering buds of broad-leaved trees are covered with many layers of scales and stipules and their surfaces are further covered with tars and resins. The surfaces of young shoots of broad-leaved trees also get covered with wax or cork layers to prevent moisture loss from their surfaces. Thus, in the process of cold acclimation, plants create mechanisms to reduce moisture loss from their body surfaces, apart from raising the level of desiccation tolerance of the cells, tissues and organs by increasing their freezing resistance.

(3) Cold-induced dormancy and survival strategies of warm-temperate evergreen trees

The northern limit of sub-tropical vegetation in the Japanese archipelago is the Amami Ooshima island located north of Okinawa. Nase, at N latitude 28° (mean temperature in January is about 14°C) on this island is in the frost-free zone. Yakushima and Tanegashima islands, located further north than Amami Ooshima have a January mean temperature of about 10°C and their coasts are frost-free. Kagoshima has a mean temperature of 6.7°C in January, with a mean daily minimum temperature of 2°C, and the temperature frequently falls below zero. For evergreen broad-leaved trees like Tabu (Machilus thunbergii), camphor and Quercus acuta to expand their distribution from frost-free areas, such as Amami Ooshima, mainland Okinawa and Yaeyama islands, towards the north of the southern end of Kyushu, where there is a danger of freezing, it is important to have dormant winter buds and to acquire frost resistance. Yurugi and Nagata have confirmed these aspects. The dormancy of the winter buds of these evergreen
broad-leaved trees is induced when the plants are exposed to low temperatures below 13°C, unlike in deciduous broad-leaved trees in which short days trigger dormancy. Moreover, in these evergreen trees, the dormant period varies depending on the coldness of the winter of their natural habitats, with longer dormant periods in colder locations. As in the deciduous trees, the dormancy breaks only after they are exposed to low temperatures for a certain period of time.

Tabu trees growing south of Amami Ooshima have no dormancy. They have no frost resistance either. When some of these Tabu trees were brought to the Tsu city of Mie prefecture for overwintering, they started to open their buds and to grow in late November (mean temperature 11.7°C). They then died with the arrival of frost. Contrary to this, Tabu (Machilus thunbergii) trees growing naturally in Kagoshima, Tsu, Chiba and Iwate, all entered dormancy in early November in Tsu. In other words, they required a higher temperature for bud opening and the buds did not open in autumn, they opened the following spring under natural conditions.

Apart from warm-temperate evergreen trees, warm-temperate deciduous trees and many needle-leaved trees of Taxodiaceae stop growing when the temperature becomes lower than 13°C or so, and enter dormancy. But the deciduous trees and needle-leaved trees of the cold-temperate and sub-arctic zones stop growing and enter dormancy when the days become short, as mentioned earlier.

(4) Adaptation of alpine plants to different times of thawing

Alpine plants growing in high altitude areas not only have adapted to seasonal changes on global scale but also to topographic differences in the time of thawing, by changing their growth form, and the times of flowering, fruit formation and seed dispersal. In windy places in the alpine zone in Hokkaido (Daisetsuzan), the snow melts in early June and the plants have 120 days of growth period. But in the hollows, the snow melts only in mid-August, leaving only 50 days for growth. Only some mosses and a few graminaceous plants can survive in such snowy fields. Thus, in alpine regions, the length of the growth period depends greatly on the time of snow melting. Therefore, the type of vegetation changes in the following sequence, starting from plants growing in places where the snow melts early: Lichens, dwarf evergreen and deciduous trees, perennial grasses, graminaceous herbs and mosses. Moreover, in response to slight variations in the time of the spring thaw,
each plant alters its time of flowering, number of flowers per plant, amount of nectar and the time of seed dispersal, to suit the temperature required for germination. This is how the plants improve their reproductive success and the survival of their seedlings. It is very interesting that a difference in the time of the spring thaw, a [seemingly small] change in the balance of nature, not only affects the life of living things significantly but also acts as a driving force for creating new relationships among species.59.

(5) Frost hardiness of plants

Before 1960, the frost hardiness of cultivated plants had been studied to some extent both in Japan and other countries, but almost no such studies had been done on wild plants. I wanted to find out the frost hardiness of the major plants of the earth. For this, I decided to measure the frost hardiness of evergreen and deciduous broad-leaved trees and needle-leaved trees (about 250 species growing in Japan, the north American continent, the Southern Hemisphere and the Himalayan region), alpine plants, major flowering plants (like the genera Rhododendron and Camellia, and roses) and bulb plants. It took about 20 years to do this. Only after this comprehensive survey, was the frost hardiness of naturally growing plants understood on a global scale.

Frost hardiness is almost fully determined genetically, depending on the species and on the area of growth, within the same species. But the frost resistance does not increase sufficiently until the plants are exposed to sub-zero temperatures, particularly -3 to -5°C for a certain period of time. Therefore, if you measure the frost resistance of a plant growing in a warm place, you can find out the apparent frost resistance, which depends on the coldness of its natural habitat, but not the maximum frost resistance that the species is capable of attaining. To determine this, it is necessary to measure the frost hardiness of the plant after enhancing its frost hardiness sufficiently by exposing the plant collected in winter to about 0 to -3°C for at least 2 weeks, or to plant it in a cold place and measure its frost hardiness in winter.

i. Frost hardiness of the leaves of evergreen broad-leaved trees and its limitations

Fig 26 shows the frequency distribution of the leaf frost resistance of 90 evergreen
broad-leaved tree species distributed in warm-temperate zones of the world. The leaves of many of these warm-temperate evergreen tall trees have a frost resistance of -7 to -15°C. Evergreen plants with a frost hardiness of -20 to -25°C are limited to bushes like camellia, Japanese spindle trees, Japanese aucuba, and Himeaoki (a sub-species of Aucuba japonica Thunb.) etc. Rhododendron naturally growing on forest floors of temperate mountainous areas is the only evergreen that is frost hardy to below -30°C. From these facts, it may be assumed that the reason why evergreen broad-leaved tall trees are limited to the warm-temperate zones, where the soil does not freeze and the winter cold is not very severe, is that the frost resistance of the cambium of their evergreen leaves, buds and shoots and the winter drought resistance of the leaves are limited.

ii Frost hardiness of warm-temperate evergreen trees and warm-temperate deciduous trees growing naturally in Japan

Let us now compare the frost hardiness of warm-temperate evergreen trees and warm-temperate deciduous trees of the Japanese archipelago. Fig 27 shows the frequency distribution of the frost resistance of the bark tissue (contains the cambium, which is crucial for growth and enlargement of shoots) of winter shoots of 73 species of evergreen trees and deciduous trees distributed in Japan. For sub-tropical evergreen trees like the green island fig, which has spread its distribution from tropical Asia to mainland Okinawa, the low lying frost-free areas of Yakushima and Tanegashima are the northern limits. They have almost no frost hardiness. The major evergreen broad-leaved trees of Japan are camphor, Quercus acuta, Japanese evergreen oak, pasania, camellia and Tabu trees. These trees have spread northward mainly from the Kagoshima prefecture along the warm Pacific coast to the Ibaraki prefecture. Along the Japan Sea coast, the northern limit of these plants is the relatively warm coastal area of the southern Tohoku region where the mean temperature in the coldest month is 1-2°C. In many of these trees, the leaves and shoots have a frost resistance of only about -10 to -13°C.

Contrary to this, deciduous trees like Buna beech, Mizunara (Quercus crisupula) and Japanese zelkova widely distributed in the interior mountainous part of Honshu, the Tohoku region and Hokkaido have a far higher frost hardiness than the evergreen broad-leaved trees, corresponding to the coldness and dryness of the winter. Japanese zelkova and saw tooth oak, whose northern limit is the northern
end of Honshu, and Buna beech, which is found in the southern parts of Hokkaido have a frost hardiness of about -30°C. However, even the deciduous trees, aphanathe oriental elm, Chinese tallow tree (Sapium sebiferum Roxb.) and crape myrtle (Lagerstroemia indica), which are distributed only in the warm-temperate zone, have a frost hardiness of the level of evergreen trees only (-7 to -15°C).

Among the warm-temperate deciduous broad-leaved trees, Dakekanba (Betula ermani Cham.), white birch, Mizunara, Manchurian ash, amur cork tree, Kalponax septemlobus, etc, which have expanded to Hokkaido, further north to Sakhalin, the Maritime Provinces [of Canada] and the northeastern part of China, have an even higher of frost hardiness. In many of these trees, the bark tissue of the shoots can withstand temperatures lower than -70°C and the buds -40 to -50°C. The xylem ray parenchyma (see I-5) can tolerate supercooling to -30 to -40°C at most, but willows, poplars and white birch can withstand supercooling to -70°C, according to recent studies of Fujikawa et al. These warm-temperate deciduous broad-leaved trees are forming mixed forests with sub-arctic needle-leaved trees in Eastern Siberia and Alaska*92, 94.

I had discussed earlier the frost hardiness of the buds of needle-leaved trees growing naturally in Hokkaido, in relation to extra-organ freezing*106. Their leaves and stems were found to have high frost hardiness. For instance, when 3-4 year-old potted trees were placed in a cold room at -30°C for one month, the plants, including the roots, remained quite normal.

iii Frost hardiness of herbaceous plants

I measured the frost resistance of 18 herbaceous species, including common plantain, narrow-leaf plantain, common dandelion, bitter dock and annual blue grass, to compare with deciduous trees growing in and around Sapporo. In these herbs, the frost resistance of the leaves was -10 to -15°C and that of the roots -5 to -7°C. This much of frost hardiness would be sufficient for plants to overwinter under snow cover. The rhizomes of Hamaboutu (Glehnia littoralis Fr. Schmidt) and Hamanninniku (Elymus mollis Trin.) that overwinter in the windy coast [of Hokkaido] could withstand even -15°C*74. Ferns growing on trees and rock walls exposed directly to severe cold had a far higher frost hardiness than the ferns that overwintered on the forest floor under snow cover, and could withstand
temperatures as low as -20°C¹¹⁷.

iv Frost hardiness of alpine plants

In the Daisetuzan area, the first snow usually falls in mid-September. Around that time, *Arctous alpinus* Niedenzu and other plants show fall colors and this is the most beautiful season there. After that, the temperature falls below zero more and more frequently and from October onwards the monthly mean temperature remains below zero. In the alpine regions, generally, there is strong cooling in the early part of the winter, i.e., September and October, with not much snow cover. This makes the soil freeze deeply and the soil temperature drops sharply. In mid-October, the leaves and stems of most of the alpine plants withstand temperatures below -30°C, while their underground parts withstand freezing at temperatures lower than -20°C. We measured the frost hardiness of alpine plants [such as] *Loiseluria procumbens* Desv., diapensia, cowberry, bog bilberry, *Arctous alpinus* Niedenzu, *Kumomayukinoshita* (Saxifraga laciniata Nakai & Takeda) Ezomameyanagi (*Salix nummularia* Andersson ssp. pauciflora) growing on flat windy parts near the Mt. Kurodake Hut in the Daisetsuzan area. Their leaves could withstand temperatures lower than -50°C, stems lower than -30°C, and the underground tissues of many of the plants -25°C. Fig 28 shows the summer and winter frost hardiness of alpine azalea, which overwinters in the European alps.
Fig 26 Frequency distribution of leaf frost hardiness of evergreen broad-leaves trees that grow in warm-temperate zones of the world.

Key:
Abscissa: Frost hardiness (°C)
Ordinate: Frequency (%) 
Inside the Fig: Evergreen leaves
Fig 27 Frequency distribution of frost hardiness of the bark tissue (including the cambium) of the winter shoots of 73 species each of evergreen broad-leaves trees and deciduous broad-leaved trees that grow in Japan. All measurements were made after sufficient exposure of the plants to cold.*102

**Key:**
- **Abscissa:** Frost hardiness (°C)
- **Ordinate:** Frequency (%)
- **Inside the Fig:**
  - Left: Evergreen trees, Bark tissue
  - Right: Deciduous trees, Xylem
  - Cambium
**Fig 28** Summer and winter hardiness of alpine azalea growing in windy areas of European Alps\(^{109}\).

**Key:**

*Clockwise from top left:* Winter; Frost hardiness (°C) of alpine azalea; Summer

**Translator’s notes:**
1. Parts where the source text is ambiguous or apparently needs some modification are marked in *pink* and suggestions are sometimes given in parenthesis.
2. Words added by the translator for clarity are given in *[square brackets]*
3. The translation of the words marked in *orange* is uncertain. The corresponding Japanese words are given phonetically in parenthesis.
Part 1· Chapter 6
page 6: Populus trichocarpa, black cotton wood,
page 6 false acacia-- pseudo acacia
page 7 also get covered parafin or wax
page 8 tabu (Machilus thunbergii), Blue oak---Quercus acuta,
tabunoki tabu trees
page 91line ceder family Taxodiaceae
page 11: Alpine zone in Hokkaido (Daisetsuzan)
page 9 short -- dwarf
page 11 blue oak -- Quercus acuta
page 12 Chinese fallow---Sapiium biferum Roxb.
Crape myrtle -- Lagerstroemia indicae
cyou Mizunara Q. prisupula, Sennoki---Kalopanax septeemlobus
page 13, bottom Urashimatsutsuji---Arctous alpins NiedonZu
page 14 alpine azalea ---Loiseluria procumbens Desv.
How does the winter hardiness of plants increase?

There are two approaches to the study of plant adaptation to environment. One is the physiological approach in which we examine how cells, tissues, and individual plants adapt to the environment of the plant's habitat. The other is the approach of ecological genetics, in which we study how the plants adapt to the environment of their habitat through changes in the genetic makeup of populations, at times sacrificing individual plants in the process. In this latter type of study, large numbers of seeds and shoots (scions for grafting) are sampled from populations of the same species growing in different environments and seedlings and grafted saplings (clones of the parent) are grown by the same method at one location to find out the differences between the regional populations in their adaptability to an environment, in relation to differences in their earlier habitats.

(1) Intra-specific variation in the frost hardiness of *Todo* fir

In many plant species, it is known that individuals naturally growing in colder places have higher frost hardiness. Variation in frost hardiness corresponding to the severity of the cold in their habitats has also been observed between populations of the same species distributed across different climatic zones. These facts suggest the possibility of the severity of the winter cold playing a major role in the evolution of highly frost hardy plants through natural selection. Let us examine this in *Todo* firs (*Abies sachalinensis* Mast.) growing at different altitudes.

To study the variation in frost hardiness of *Todo* firs naturally growing at different altitudes, Eiga*'* collected seeds of 51 trees selected from natural forests at altitudes of 250-1200m in the Daisetsuzan area of Hokkaido. Similarly, he selected 80 elite trees with good natural growth and prepared 1200 grafted saplings from their shoots. 5700 of the seedlings and the grafted saplings were grown at a forest tree breeding center in the outskirts of Sapporo under uniform conditions. After 7 years, their shoots were collected, and cooled to -43°C to see the extent of damage to the bud. He graded the frost damage on a 6-level scale of 0-5 and called the mean score the Frost Damage Index. A small value of this index indicated a low level of frost damage, i.e., high frost hardiness.
I shall present here the results obtained with the grafted saplings. As shown in Fig 29 (Top) in the population from the lowest altitude (311m) there were no individuals with a low Frost Damage Index (high frost hardiness). However, the Frost damage Index showed a normal distribution in the populations from the medium altitudes (about 400 to 550m). The proportion of plants with low frost hardiness decreased, and that with high frost hardiness increased with further increase in altitude. Fig 29 (Bottom) shows that the Frost Damage Index (F) decreased and the variance (V) among individual plants decreased with increase in altitude. It has been observed that the temperature in the Daisetsuzan area decreases with increase in altitude. In short, the mean frost hardiness of the population increased as it got colder with increase in altitude. This suggests a decrease in the proportion of individuals with low frost hardiness and an increase in the proportion of plants with high frost hardiness in the population. Thus, the frost hardiness of the population develops over a long period of time through the selection pressure exerted by the winter cold.

Eiga also studied the regional differences in frost hardiness using seedlings grown from seeds collected from natural Todo fir forests at 6 places in Hokkaido and grafted saplings propagated from such trees. The frost hardiness of Todo firs from the Japan Sea coast, which gets plenty of snow but not much severe cooling, showed a normal distribution, suggesting that cold-mediated natural selection had not advanced much in this population. On the other hand, Todo firs from eastern Hokkaido, which does not get much snow and gets severely cold, showed an L-shaped distribution of cold hardiness with decreased proportion of individual plants with low frost hardiness and increased proportion of plants with high frost hardiness. Fig 31, which is given later, shows the mean frost hardiness of Todo firs from different regions.
Fig 29 Changes with altitude in the Frost Damage Index and its variance in clones of elite Todo fir trees from Daisetsuzan. Top: Proportions of trees with different Frost Damage Index values, at different altitudes. Bottom: Changes with altitude of the Frost Damage Index (F) and its variance (V). The specimens were cooled to −43°C.

Top Fig  Abscissa: Frost Damage Index; Ordinate: Proportion (%)
Bottom Fig  Abscissa: Altitude (m); Ordinate (left): Frost Damage Index. Ordinate (right): Variance
(2) Difference in the winter hardiness of trees in natural Todo fir forests of Hokkaido

Hokkaido can be broadly divided into two climatic zones separated the central mountain backbone that runs in the north-south direction. These are the western Japan Sea coastal area and its hinterland, which gets a lot of snowfall and eastern Hokkaido including the Pacific Sea coast, which is the soil freezing area with relatively less snowfall. Hatakeyama and Eiga undertook population genetics type investigations on natural Todo fir forests of different regions of Hokkaido. To be more specific, they studied how differences in the winter environment of their present habitats (snow cover, period under snow cover, freezing index, which is the cumulative degree-days under sub-zero temperatures, soil freezing, growth period in summer, etc) affected their overwintering characteristics.

Grafted clones were prepared from Todo firs growing in 12 different regions and planted at a Hokkaido forest experiment station at Bibai, an area that receives heavy snowfall, to study the extent of snow damage (breaking of branches under the weight of snow). The snow damage was extensive in Todo firs from eastern Hokkaido, which does not receive much snow. But almost no such damage was seen in the firs from western Hokkaido, which receives lots of snow (see Fig 31·4). Drought damage to shoots and leaves because of the freezing of soil was studied at Akkeshi in eastern Hokkaido. The results were just the opposite of what was seen with snow damage, trees from eastern Hokkaido showing not much damage and those from the Japan Sea coast showing major damage. Fig 31 shows the results obtained by Eiga on 6 traits of Todo firs. We can conclude from these results that the Todo firs from the snowy Japan Sea coast and its hinterland were highly resistant to snow damage, snow mold and rodent damage (the resistance increased with increased duration of snow cover) but had low frost hardiness and winter drought tolerance. Contrary to this, Todo firs from the Pacific coast of eastern Hokkaido, which does not receive much snow and has a very dry and cold winter, had high frost resistance and winter drought tolerance but low resistance to snow damage and snow mold. The Todo firs from these two regions probably differed significantly in the amount of growth and quality of the wood also, apart from the winter hardiness traits discussed above. It thus became clear that in natural Todo fir forests, different selection pressures acted on different populations of the same species, depending on the weather conditions of their habitats, causing differences
in their adaptability to certain environments.

Fig 30 Regional differences in snow damage to *T. d. f. *of Hokkaido. Grafted saplings (clones) were planted in Bibai. The shaded parts in the circles represent the proportion of snow-damaged trees.

A: The boundary that separates the [western] snowy region from the [eastern] region with less snow.

Key (clockwise from bottom left): Kucchan; Iwamizawa; Takikawa; Rumoi; Nayoro; Bifuka; Oomu and Okoppe; Kitami; Akkeshi; Ikeda; Urakawa; Furano.
Ecological variation in winter hardiness of *Todo* firs of Hokkaido because of differences in weather conditions. Distance away from the center of each circle represents higher hardiness, greater delay in bud opening and greater amount of growth. D: The boundary that broadly separates the western region from the eastern region.

**Key:**
1. Frost hardiness
2. Winter drought tolerance
3. Bud opening day
4. Snow damage resistance
5. Snow mold resistance
6. Early stage growth

*Clockwise from left:* Kucchan; Haboro and Rumoi; Saloma; Nemuro and Khushiro; Rikubetsu and Honbetsu; Kamikawa
Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.
2. Words added by the translator for clarity are given in [square brackets]
3. The translation of the words marked in orange is uncertain.
8 Adaptation of plants to special environments and the tradeoffs

(1) Alaskan willows cannot grow in Sapporo

Shoot cuttings were taken in summer from five willow (*Salix alaxensis*) trees, each about 10m tall, growing at Fairbanks (Latitude about 62˚N), Alaska and planted for rooting in Sapporo. Sapporo (Latitude 43˚N) is about 20˚ lower in latitude than Alaska (Fairbanks?) where the sun does not set for many months. Even on summer solstice, the daylength in Sapporo is only about 16h. The willows from Alaska, which were adapted to cease growth when the daylength became 16 hours, stopped growing in Sapporo soon after they opened their buds in May. I continued to nurture the plants for several years. But this trait did not change, the plants remained small at 5-10cm, and eventually dried up and died. Thus, none of the saplings cloned through cuttings from these 5 willows could grow in Sapporo. Balsam poplars from Alaska grew a little when brought to Sapporo. But all the plants remained dwarfs (15-20cm tall) even after 10 years (Fig 32).

Seedlings of *European Akamatsu (Scotch pine)* brought from north latitude 63˚ were only 20-30cm tall even after several years in Sapporo. But the same species brought from Germany (Latitude 55˚N) grew without any problem in Sapporo. This shows that trees of this species adapted to the long days of high latitudes are specialized and are particularly suited to the high latitude environment. But their adaptability to a range of different environments has decreased and they cannot compete with other tree species under the shorter days of mid-latitudes. Therefore, if the earth were to become cooler in the future, the subarctic needle-leaved trees and deciduous broad-leaved trees that have presently adapted to the daylengths of high latitudes would be unable to spread southwards very much.
Fig 32 A balsam poplar clone from a cutting taken from Fairbanks, Alaska and grown for 10 years in Sapporo. The plant remained only 15-20cm tall. (Photographed by the author).
Why temperate plants are unable to grow in Okinawa

Temperate plants that get cold-acclimated integrate the winter cold into their life cycle. These plants cannot live or grow normally in warm places where the temperature does not go below a certain level because their dormancy is not broken. If we transplant to subtropical Okinawa, Japanese Kuromatsu (*Pinus thunbergii* Par.) or Japanese Akamatsu (*Pinus densiflora*) growing naturally in Honshu, they do not grow beyond a height of 1-2m. Naha, in Okinawa, has a mean temperature of about 16°C and a mean daily minimum temperature of 13.5°C in the month of January, and the temperature goes below 5°C only very rarely. It appears that the dormancy of these trees cannot therefore be broken\(^{120}\). The southern limit of Japan’s temperate deciduous forests is the mountainous area of altitude 300-800m in Yakushima island, which experiences a certain level of chilling in the winter.

When temperate fruit like grapes or pears are to be grown in a subtropical region such as Taiwan or southern Brazil, the dormancy is broken by spraying gibberellin, a plant hormone, or lime nitrogen (which releases ethylene), etc.

Adaptation of *Todo* firs to high altitudes

Kurahashi and Hamaya\(^{61}\) compared, over a period of 7 years, the characteristics of *Todo* fir (populations at different altitudes). For this, they planted seedlings\(^{41}\) of *Todo* fir (*Abies sachalinensis* Mast.) trees growing naturally at different altitudes ranging from 300 to 1600m in a Tokyo University experimental forest in Hokkaido at altitudes different from where they were taken. *Todo* firs are the dominant species in this forest and grow along with Oshida ferns at the altitude of 300-700m. At 700-1000m, *Todo* firs are less common and *Ezo* spruce (*Picea jezoensis* Carr.) and *Chishimazasa* (*Sasa kurilensis*) constitute the dominant vegetation. At the height of about 900m, the forest changes from a *Todo* fir-dominated to an *Ezo* spruce-dominated one. This altitude is also the limit above which there is a significant increase in snow cover and the bamboo on the forest floor changes from *Chimakizasa* (*Sasa paniculate*) to *Chishimazasa* bamboo. Their experiments showed that *Todo* fir seedlings\(^{41}\) from 500-700m, where *Todo* fir is the dominant species had a very high percent germination (percent establishment\(^{3}\))\(^{19}\) and grew well at whichever altitude they were transplanted\(^{19}\) to. But *Todo* fir seedlings\(^{19}\)
taken from a height above 900m showed poor growth in all the sites of transplantation at different altitudes. They had a particularly high rate of death by drying when planted at an altitude below 730m. We can explain this phenomenon as follows. At altitudes above 900m, where the weather is very severe, there is a strong natural selection that pushes the population in a certain direction. Because of this, the traits suited for a high altitude and heavy snow cover environment, such as a short growth period, reduced tree height, increased cold hardiness and increased resistance to snow, are all enhanced. At the same time, the strong selection pressure reduces genetic variability of the population, the population becomes specialized, and adaptability becomes so restricted that they can survive only in high altitudes.

Todo fir populations above the tree line have changed genetically to become bushes, their seeds have almost lost the capacity to germinate, propagate vegetatively, and overwinter under snow cover. When Todo firs from the altitude of 230-430m, which is close to the lower limit of their vertical distribution, were transplanted\textsuperscript{94} to a high altitude of more than 830m, their rate of death by desiccation was very high. In other words, the Todo fir populations growing at low altitudes, near the lower limit of their distribution, have become specialized for low altitudes.

From these facts we can say that Todo fir populations, which are dominant at altitudes of 500-700m, are highly adaptable to both lower and higher altitudes than those of their natural habitats, and thus have a wider choice of habitats. Contrary to this, the populations living at the lower and upper limits of their distribution have suffered a considerable loss of adaptability to other environments, because of very intensive natural selection. The plants adapt in this manner by changing genetically in response to changes in their environment. This is probably the process by which variations that are advantageous in adapting to the environment are selected from among the genetic variations acquired by the plants over a long period of time in the course their adaptation to different environments.

(4) Adaptation of plants to special environments

Some plants survive in the special severe environments of high latitude regions, alpine regions, extremely cold regions, places with heavy snowfall, dry regions, tropical estuaries (mangrove forests) and regions with high soil salinity. These
plants, in the process of acquiring the ability to live in such extreme environments, have specialized by sacrificing the ability to live in normal environments. These populations naturally show very little variation among individuals and have low adaptability to new environments. This, in a way, tells us that these special environments are so inhospitable that plants cannot live in them unless they make such tradeoffs and specialize.

*Translator’s notes:*
*Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.*

#1 *It is not clear whether it was the seeds or the seedlings that were planted at altitudes different from their sources. This has to be clarified. We cannot say “percent germination of seedlings”.*

Dr. Sakai’s comments:
Part I-Chapter 8
Page 1 18 Lines (upper) Yoroppa Akamatsu--European Akamatsu (Scotch pine)
page 2 Japanese Kuromatsu Pinus tunbergii Par.
Japanese Akamatsu Pinus densiflora
Page 3 Chishimazasa Sasa kurilensis
chimakizasa Sasa paniculata
Page 3 Line 4 Ezomatsu --Ezosupruce
9 Advantages and disadvantages of snow cover

(1) Advantages of snow cover

Snow cover is a good thermal insulator because it contains a lot of air and does not move. Plants that overwinter under snow are protected from severe cooling, desiccation and strong light. Overwintering plants select habitats and life forms that utilize the snow cover efficiently to avoid low temperatures and drying. Tall trees that cannot be protected by the snow cover evolve into bushes so that they can avoid low temperatures in the winter by remaining under the snow and expand their range northward and to higher altitudes.

In areas where the soil freezes in the winter, the overwintering plants cannot get sufficient water through their roots. Moreover, [without snow cover] they are exposed to sunlight and strong winds and they experience water deficit. Because of this, even the very cold hardy Haimatsu (Pinus pumila), alpine plants and plants growing in the polar tundra regions can overwinter only under snow cover. The survival of these plants is closely related to the snow cover. The role of the snow cover in protecting plants from severe cold and dryness and in supplying melt water in spring and summer is no small role. The snow cover indeed has a major role in supporting the present vegetation on earth and agriculture.

(2) Disadvantages of the snow cover

Snow cover also has some harmful effects on plants. For example, in areas of heavy snow, the snow cover increases with altitude, which increases the snow pressure. Any tree species that cannot tolerate this pressure gets crushed. Besides this, the temperature near the ground surface under snow cover is always more or less at 0°C, there is little light penetration and it is dark and very humid. Seeds, seedlings and crops overwintering for many months under such conditions are at the risk of infection by snow molds. So, plants cannot survive in heavily snow-covered areas unless they are resistant to snow molds.

For plants in the mountainous areas of mid-latitudes and in alpine regions, which have a lot of snow cover, the annual growth period is determined by the time of spring thaw. So the time of the thaw has a major effect on their distribution and
i Adaptation of plants to snow pressure

The depth of the snow cover decreases with the passage of time. This is because the fresh snow becomes packed snow and its density increases. The density is higher in the lower part of the snow cover. The pressure developed by compaction of the snow cover is called “settling pressure (Chinkoatsu)” or “snow pressure”. The snow pressure causes a strong force to be applied to anything buried in the snow. If this pressure is very large, plants get crushed. Fig 33 shows the relationship between the maximum snow cover measured in a snowy region of Yamagata prefecture with packed snow and the maximum snow pressure. The snow pressure increased with increase in snow cover, becoming about 2 tonnes when the maximum snow cover was 3m. Under 4m of snow it was as much as 2.2 tonnes. Snow pressure is known to cause damage such as trunk deformation (Fig 34), breaking of the trunk, falling of the tree, etc. Plants adapt quite well to such massive pressures.

Mountains on the Japan Sea side of the Tohoku region all get very heavy snow. At 800m above sea level (an area covered by Buna plants, which usually has compacted snow) there is a maximum snow cover of about 3-4m on the average. Haimatsu, Ooshirabiso (Abies mariessi) and Kometsuga (Tsuga diversifolia), the naturally occurring tree species of the Tohoku area, are found at sites with 2-3 m of snow cover. But very few of these species can be found at locations with more than 3-4m of snow. Tall trees cannot survive at higher altitudes with greater snow cover. So, these areas become bush areas with plants like Buna, Miimanara, Miamakaede, Miamahannoki and Takanenanakamado. These bushes overwinter under snow cover, like Chishimazasa (Sasa kurilensis). Thus, the vegetation changes, depending on the thickness of the snow cover.
Fig 33 The relationship between maximum snow cover and maximum snow pressure (Yamagata prefecture).

A snow pressure meter was installed at a height of 1m from the ground. The pressure sensing column (*Juatsuchu*) was 1m long and 10.5cm wide*37.

**Key:**

**Abscissa:** Maximum snow cover (m)

**Ordinate:** Maximum snow pressure (tonnes/m$^2$)

**Inside the graph:** Winter of 1968-69
Fig 34 Deformation of the trunk bases of Japanese cedar (*Cryptomeria japonica*) trees growing on a slope in a heavy snow area (Tokamachi experimental forest). The gradient is about 40°. (photographed by the author).

Japanese cedar trees of the snowy Japan Sea side of the Tohoku region have pliable branches that are attached at obtuse angles. Therefore, the snow that accumulates on the shoots and branches can fall off easily. Contrary to this, the Japanese cedar trees on the Pacific Ocean side have stiffer branches that are attached at acute angles or more or less at right angle to the trunks, which makes it difficult for the snow on the branches to fall off. So, they are very prone to breakage when there is heavy snow load on the tree. Snowfall in the Tokyo region in mid-January 1998 caused the trunks of many snow-covered evergreen broad-leaved trees to split and broke the trunks of many adult Japanese cedars. This was because when the temperature went down to 0 to -1°C, the snow froze to the leaves, making it more difficult for it to fall off. Finally, the trees were unable to
bear the weight and the branches or the trunks split or broke. Snow cover on deciduous trees before leaf fall can cause breaking of branches and trunks even more easily.

ii  Snow resistance of cedars in heavy snow areas

Young Japanese cedar trees fall easily when snow accumulates on them. This is less frequent in taller trees but they develop deformation at the base of the trunk (Fig 34). Such trunk deformation is how the tree copes with snow pressure. If they do not bend, they would sustain fatal damage like breaking or splitting of the trunk. Let me introduce here an interesting study by Takahashi\textsuperscript{125} on recovery from trunk deformation. The resistance of the trunk to snow pressure increases with growth of the tree. With the increased weight of the above-ground parts, a part of the bent trunk touches the ground and rooting occurs there. Soon a prop root develops from the lower part of the bent trunk to support the base of the trunk (Fig 35). The trunk grows rapidly and enlarges after this. It shows eccentric growth, the lower part of the bend showing faster growth than the upper inner part. From the outside, it looks as though the bend at the base is now corrected. With the increase in diameter of the prop root, the above-ground parts start to show better growth. Japanese cedars growing on snowy slopes get stabilized at the base and grow well only after the prop root is developed. However, it takes 30-50 years for these cedars to cope with the snow pressure in this manner.
Fig 35 Recovery from trunk deformation by formation of prop roots in Japanese cedars on snowy slopes\textsuperscript{125}.

K: The projection at the upper end of the base shows where the tree was initially planted.

**Key:**

Immediately after planting  
10 years after planting  
25 years after planting  
←Index of snow pressure→  
50 years after planting  
Mid-line of tree trunk↑  
Prop root  
Planted position↑
iii  Snow mold

Various snow mold pathogens exist in areas with snow cover. Wild plants have acquired resistance to these molds and expanded their distribution to such areas. Snow mold is a disease that is common in graminaceous plants like barley, wheat, pasture grasses, etc. and seeds, seedlings and young trees of wild needle-leaved tree species, which overwinter for 3-4 months under snow. The disease appears often when the spring thaw is delayed. It is clear that some microbes are the cause because in many instances, the disease can be controlled with chemicals. **Sclerotinia borealis**, **Typhula ishikariensis** and **Typhula incarnata** are fungi that cause snow mold in graminaceous crops. They are all saprophytic cold-adapted fungi (basidiomycetes and ascomycetes) that thrive at temperatures close to 0°C under snow cover. There was heavy snow mold damage to mulberry in a field of the Faculty of Agriculture, Hokkaido University in the spring following the winter that I started experiments with mulberry. I cannot forget what I had seen. Most of the elite mulberry lines brought from Honshu had snow mold damage on the stem close to ground level. Because of this, water could not reach the upper parts of the plants and they dried up. In stark contrast to this, the wild mulberry varieties of Hokkaido and some of their hybrids were quite normal. I realized that plants cannot live in heavy snow areas unless they have resistance to snow mold.

iv  Renewal (Koshin) of Ezo spruce on nurse trees

We often come across saplings and young trees of Ezo spruce (**Picea glehnii** (**Picea jezoensis**?) and **Todo** fir (**Abies sachalinensis**)) growing in clusters on fallen decaying parent trees (renewal on nurse trees) (Fig 36). Many young seedlings of Ezo spruce that have germinated on nutrient-rich ground with accumulated decaying fallen leaves die out in a few years because of damage by snow mold and other pathogens during overwintering. The surface of a decaying fallen tree, on the other hand, does not have a thick layer of decaying fallen leaves and therefore is nutrient-poor. Because of this, there are fewer snow molds and other pathogens. Besides, the surface of the fallen tree becomes spongy and has sufficient water, making it a suitable bed for germinating the seeds and nurturing the seedlings. Moreover, young Ezo spruce trees growing on the upper surface of such nurse trees (diameter 40-80cm) have symbiotic ectomcorrhizal fungi on their feeder roots. The fungal hyphae grow deep into the nurse tree trunk, absorb inorganic nutrients like...
nitrogen and phosphate by enzymatic action and supply them to roots of the *Ezo* spruce seedlings*124.

In Hokkaido, good examples of such natural renewal of fallen trees can be seen in places with volcanic sedimentary soils (new (Mijuku) volcanic lapillus) or andesite, slopes of forest paths, moss-covered areas, and areas that had lost the top soil (particularly with mineral soils). All these areas are nutrient-poor, with little accumulation of decomposing fallen leaves and low incidence of harmful diseases. Many needle-leaved species, such as *Pinus* species and *Akaezo* spruce (*Picea jezoensis*) (*Picea glehnii*?), apart from *Ezo* spruce, also have colonized such rather poor environments with the help of symbiosis with ectomycorrhizal fungi. They have become adapted to harsh environments of the sub-alpine and sub-arctic regions also. Even among the broad-leaved trees, it is not uncommon for some of the pioneer species like white birch to have symbiotic relationships with ectomycorrhizal fungi.

![Fig 36 Young *Ezo* spruce trees growing on a nurse tree*124. O: Decaying nurse tree; E: *Ezo* spruce growing anew on the nurse tree.](image)
v  A breeding project for highly winter resistant wheat

For wheat to safely overwinter in the Kitami region [of Hokkaido], which has more snow cover than the Tokachi region, they must have a high level of frost hardiness so that they can withstand the strong cooling before the ground is covered with snow, apart from resistance to 3 types of snow molds seen in that area. Experiments on overwintering of 941 autumn-sown wheat lines gathered from all over the world have been carried out at the Kitami Agricultural Experiment Station over many years. Only about 15% (144 lines) of these showed high a percentage of winter survival. Eventually, 6 lines (about 0.6% of the total number tested) of wheat having high resistance against the 3 snow mold pathogens, high levels of frost hardiness, and the required quality characteristics as a wheat crop were developed through a cleverly designed breeding scheme*1.

(3) Collection and utilization of genetic resources

For breeding wheat varieties with winter hardiness, it is necessary to cultivate numerous wheat lines brought in from abroad for many years under the same conditions to study the genetic characteristics related to overwintering.

The wheat line PI. 17438 from the snow covered area of eastern Turkey showed high resistance against *Typhula ishikariensis* and some wheat lines from Russia, USA and Canada were found to be genetically very frost hardy. After learning about this breeding study of wheat, I came to think that it was very important to collect and preserve genetic resources, evaluate their genetic characteristics by growing them and disclose the findings to the public so that their traits can be utilized.

Parts of interior Hokkaido that receive light snow are the severely cold soil freezing areas. It is very difficult to breed crops that have a high overwintering ability under such severe weather conditions. This again makes us appreciate the toughness and the wonderful environmental adaptability of wild plants that have survived there on their own for such a long time.

Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in
parenthesis.
2. Words added by the translator for clarity are given in [square brackets]
3. The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis
10 Emergence of cold climate in the Northern Hemisphere and changes in the flora

Until about the middle of the Eocene epoch (about 45 million years ago), in early Tertiary, there was an equatorial ocean current that circulated around the globe. Because of this, the warm tropical current was efficiently sent to the Arctic Ocean. Besides, there were no big mountain ranges on earth during that period, which allowed comparatively free heat exchange between north and south. Therefore the temperature difference between the Equator and the poles was not as large as at present. Even within the Arctic Circle, the weather was mild and humid, like eternal spring. Because of such weather conditions, the needle-leaved trees of Taxodiaceae family (like sequoia and metasequoia), which like mild and humid climate, thrived even in the high latitude areas of the Northern Hemisphere.

These trees are the source of the coal now available in these high latitudes. However, in sharp contrast to this, with the emergence of cold dry weather in the Northern Hemisphere in the second half of the Tertiary, the needle-leaves trees of Taxodiaceae, which could not adapt to the new climate, dwindled while needle-leaved trees of Pinaceae (Pinus, Abies, spruce, Larix, etc.) the pine family and deciduous broad-leaved trees that could adapt to the cold climate flourished. It is believed that plants of the Northern Hemisphere acquired adaptability to cold for the first time only after the emergence of this cold dry climate.

(1) A metasequoia fossil forest discovered in a snow field in the Arctic

A fossil forest of several hundred metasequoias was discovered in 1985 in a snowfield in the Axel Heiberg island of Canada (Fig 37). A pilot flying over the area noticed some tree stumps partially exposed above the snow. A number of stumps, about 1m in diameter, about 10m long logs, many leaves, cones and trunks were subsequently discovered in this fossil forest. A survey suggested that there was a fairly dense wetland forest in the area consisting mainly of about 150 year-old deciduous 20-30m tall metasequoia trees. This fossil forest was estimated to be at least 45 million years old, belonging to the early to middle Eocene epoch of the Tertiary (Fig 38). The latitude of the site then was almost the same as now, but the summer temperatures were nearly 20°C higher than today, it is believed. The site is now in the permafrost area and the whole island except the coastal areas is covered with snow. The annual mean temperature is now -14°C and the
summer temperature is 0-3°C. It is believed that the winter at that time was dark most of the time, as it is now, but was misty and cloudy and the temperature of the water of the Arctic Ocean was about 15°C. It is also estimated that the temperature of the Arctic ocean coast rarely dipped below zero, and it never became colder than a few degrees below the freezing point even in the interior⁸.

Apart from the fossil forest of metasequoia, ginko leaves, leaves of birch, alder, willow, and Katsura (Cercidiphyllum), etc, of about 30 deciduous tree genera, and pollen and trunks of conifers of the pine family (especially Larix species) were also found on the Axel Heiberg island. These remains suggest that at that time a forest of deciduous broad-leaved trees with intermixed conifers of the pine family was already present upstream of the metasequoia swamp forest. To survive in the Arctic of that time, where the mild and dark winter persisted for a long time, it was probably more advantageous for the trees to be deciduous, because much energy is consumed for respiration by evergreens. Nevertheless, fossils and trunks of evergreen needle-leaved trees of Pinaceae (pines, spruces and firs) were also discovered in large numbers. It is therefore believed that around that time, in that area, the night temperatures were fairly low already and evergreen needle-leaved trees were also spreading in the Arctic.

It is believed that the among broad-leaved angiosperm trees, the deciduous trees emerged in the early Cretaceous (130 million years ago) of the Mesozoic era, in the evergreen forest belt near the tropics, and that some of these parts had quite dry weather in the relatively cool part of the year⁶. It is likely that the broad-leaved trees that acquired the deciduous trait in this region spread rapidly during the late Cretaceous to the early Tertiary up to the Arctic region, which had dark but mild winters (Fig 39).

According to the American paleontologist Chaney¹¹, needled-leaved trees, mainly of Taxodiaceae, and deciduous broad-leaved trees (circumboreal flora of the Tertiary) were widely distributed in the middle latitudes to the high latitude Arctic region in the Northern Hemisphere and evergreen deciduous trees were probably distributed in the sub-tropical and tropical regions to the south of this, until the early Tertiary period.

Metasequoia and deciduous broad-leaved trees distributed in the high latitude area
of the Northern Hemisphere in the early Tertiary could probably withstand low temperatures of about -10 to -15°C only, reflecting the generally mild climate prevailing at that time. This has been assumed because the sequoias still existing in California can withstand only about -12°C. These are the relics of the evergreen sequoias that were widely distributed around that time in the Arctic areas of Europe.

Fig 37 Left: Axel Heiburg island (arrow) in the high latitude Arctic region of Canada where a fossil forest of metasequoia was discovered.

Key:
Clockwise from bottom left: Canada; Greenland; Ellesmere Island.

Right: A fossil stump (diameter 2.1 m).
Fig 38 Climate change in the Tertiary. The arrow indicates the time to which the discovered metasequoia fossil forest belonged. The ordinate is a temperature index.

**Key:**
- **Abscissa:** Time (million years)
- **Ordinate:** Up arrow: Warm; Down arrow: Cold

**Inside the Fig:**
- ←Tertiary→
- Ice age: Pliocene; Miocene; Oligocene; Eocene; Palaeocene; Cretaceous
- **Slanting arrow (left):** Temperature decline
- **Slanting arrow (right):** Rapid temperature decline
Fig 39 Rapid spread of deciduous broad-leaved trees in the early Cretaceous.

Inside the Fig, clockwise from bottom left:
Evergreen broad-leaved trees; Deciduous broad-leaved trees; Early Cretaceous
The Arctic

Cold temperate zone
Temperate zone  Temperate zone
Warm temperate zone

Tropical zone

Warm temperate zone
Temperate zone  Temperate zone
Cold temperate zone

At the center: Dry climate
(2) Emergence of cold climate in the Tertiary and changes in flora

From the middle of the Eocene epoch of the Tertiary to the end of the Oligocene (about 28 million years ago), the global heat exchange system disappeared and the temperature in the high and middle latitudes decreased by about 10ºC (Fig 38). With this development, apparently, the difference between seasons increased and dryness advanced. Along with this considerable decrease in temperature, the circumboreal flora of the Tertiary, consisting mainly of needle-leaved trees of Taxodiaceae, that were suited to living in the mild and humid climate and were spread up to the Arctic region, were forced to move southward to the middle latitudes. Furthermore, from the second half of the Tertiary period, active mountain building movement pushed up mountain ranges, and the tectonic movements changed the course of oceanic currents and caused regional drying in the interior parts of continents. These changes raised the temperature difference between the equator and the poles sharply, isolated and cooled the Arctic Ocean, and formed the Antarctic ice sheet. With this type of topographical and macroclimatic changes (change from the eternal spring-like mild climate to a continental climate with hot summers and cold and dry winters) the circumboreal plants shifted towards the south and many ancestral plant species became extinct. Most of the needle-leaved trees of Taxodiaceae that could not adapt to the cold and dry climate disappeared almost entirely, with only a few species escaping extinction. These species are now surviving as isolated relicts. Among the needle-leaved trees of the pine family and deciduous broad-leaved trees that survived by adapting to this climate change, many of the ancestral species have now disappeared but new species that adapted to the cold and dry climate have evolved. Under this cold climate, the needle-leaved trees of the pine family and the broad-leaved trees that survived probably acquired the ability to enter into short day-induced dormancy and to acclimate to the cold. The plants that survived this major climate change also withstood the harsh changes in weather, the increased difference between the seasons, and the further lowering of the winter temperature that occurred in the ice age that started about 1.6 million years ago, following the Oligocene epoch, at the end of the Tertiary. It is believed that they then spread rapidly, during the warming phase of the post-glacial age that started about 11 thousand years ago, to the cold-temperate and subarctic zones that were ecologically empty niches until then. This emergence of cold climate requires special mention in the history of environmental adaptation and evolution of plants.
Not many species of deciduous broad-leaved trees survived the cold period of the Tertiary and the ice age of the Quaternary period, and are distributed in the current cold-temperate and subarctic zones. These are from a limited number of genera, such as those of the birch family (about 120 species, including white birch and alder, from different genera), the willow family (about 330 species of willows and poplars), Fagaceae (8 species of the genus *Fagus* and about 50 species of the subgenus *Lepidobalanus* of the genus *Quercus*), the genus *Acer* (115 species), and genus *Ulmus* (18 species) of the elm family (2000 species in total), and genus *Celtis* (70 species). The mulberry family (Moraceae) is a large family that has 75 genera and about 3000 species. But only a few species of the genus *Morus* and a few others are deciduous and distributed in the temperate zone. The about 600 species of the genus *Ficus* and plants of other genera of the mulberry family are evergreen and grow in the tropics. Even among the needle-leaved trees of the pine family, which dominate the subarctic and subalpine regions, the great majority grow in the warm-temperate zone or the temperate zone\(^7\) (see Fig 58 given later). These facts show how difficult it is for tall trees to live in the cold-temperate and subarctic zones.

(3) Distribution of relict species of Taxodiaceae

i  The rise and fall of metasequoia

Recently metasequoia became famous as a living fossil. Fossils of this tree had been found in different parts of Japan and named as *Sequoia japonica*. *Sequoia chinensis* was known from China. Dr. Shigeru Miki, who studied plant fossils, created the new genus *Metasequoia* \(^6\) in 1941 for these fossils because the leaves and cones of sequoias of the Tertiary period of Japan were different from the sequoias currently surviving in the California coast and the deciduous taxodiums still present in southeastern USA. Later, Chaney of USA surveyed the distribution of metasequoia fossils over a large area. It became clear from his study that metasequoia originated from the northern part of the west coast of USA, in the mid-Mesozoic era. Around the end of the Mesozoic and early Tertiary, it spread on a large scale to the arctic region and from there further to Beringia, Japan, Sakhalin, the Maritime Provinces of Canada, and China. In the American continent, metasequoia became extinct before the start of the Pliocene, the last era.
of the Tertiary. A metasequoia fossil forest with 29 stumps belong to the late Pliocene (about 2.5 million years ago) was found in 1967 in the Kita Asakawa river, that runs north of Hachiogi city, Tokyo. It is said that metasequoia became extinct in Japan in the early part of the ice age. *69

During World War II, a joint Sino-American survey of flora was undertaken, mainly in the Szechuan province. In 1945, a forest officer Osen of the Central Plant Research Institute of Chongging, China, while surveying forest resources, knowingly took the difficult course on the southern side of a gorge. While moving along the Matoukei, a tributary of the Yangtze River, he noticed a coniferous tree venerated as a sacred tree near a small shrine of a village. It was a giant tree, about 35m tall with a trunk diameter of about 2.5m. Dr. Hu of Beijing ultimately identified the tree to be the same species as the metasequoia fossils named by Dr. Miki. Soon after this, in 1948, Dr. Hu reported that a living fossil of metasequoia (dawn redwood) had been discovered in China and gave it the scientific name of Metasequoia glyptostroboides Hu & Cheng. *32. This discovery resulted because Osen chose an unexplored difficult path. Currently, metasequoia relics can be seen in the Szechwan province and warm areas of Hubei province (altitude 900-1300m) of China. Metasequoia seeds collected in China were brought to Japan in 1949 via USA. Apart from this, 100 metasequoia seedlings brought from USA were planted in different parts of Japan in 1950. Some were planted to line the entrance of the Mukogawa Women's University, where Professor Miki worked at that time.

**ii Distribution of the relict species of Taxodiaceae**

Many relict species of Taxodiacea that had managed to avoid extinction are distributed in areas still having a Tertiary-like humid mild climate with little seasonal change. These include metasequoia, Cryptostrobus pensilis and Cunninghamia lanceolata, all found in Southwestern China; Taiwania hayata and Cunninghamia lanceolata found in Taiwan; Taxodium distichum in the swamps of Southeastern US, and the coast redwood and giant redwood of California (see Giant Trees, II-8). Relicts of Cryptomeria japonica are found in Japan, those of Yakushima island being the most famous. Natural Cryptomeria japonica forests are found mainly in the moist heavy snow areas on the Japan Sea side, on unstable slopes with not much topsoil, as far north as the Aomori prefecture. The genus Athrotaxis, a very ancient plant of Taxodiacea is closely related to Cryptomeria
japonica. Two relic species of the genus *Athrotaxis* (A. cupressoides Don and A. aelasinoides Don) can still be found near the tree line in the Tasmanian island of Australia, which has a mild Tertiary-like climate. Both the form of the tree and the needle-leaves are very much like those of *Cryptomeria japonica*.

*Translator’s notes:*
1. *Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.*
2. *Words added by the translator for clarity are given in [square brackets]*
3. *The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.*

Dr. Sakai’s suggestions:
Part I · Chapter 10
Page 1 Pine family ---Pinaceae (Pinus, Abies, Spruce, Larix, etc.)
Page 2 16 lines (upper) Karamatse please delete, especially
Leptosperma (delete), especially larch (Larix sp.)
Page 8, 4 lines Athrotaxes, 6 line. The same genus 2 species of Athrotaxes
A. cupressoides Don, A. aelasinoides Don
---
The evolution of cold survival strategies of plants in the alpine areas of the tropics

In the high altitude areas of the tropics, the seasonal change in temperature during a year is not much, but the variation of temperature in a day is quite large and the humidity of the air also changes significantly with that. Even when the daytime is like summer, the night temperature often dips below zero. Plants growing under these relatively mild but peculiar weather conditions on tropical highlands have developed unique methods of avoiding the cold and freezing during the brief nighttime subzero cooling. These plants provide interesting insights into the evolution of cold-survival strategies of plants. I had seen areas covered with clusters of tree ferns at altitudes above 3000m on the outskirts of Bogota (2500m above sea level), a city in Colombia, South America with an eternal spring-like climate and an area in Papua New Guinea with altitude around 3000m.

(1) The weather in the tropical alpine zone

There are many clear days in the tropical highlands, particularly in the dry season, because of which the daily change in temperature and humidity is quite large, and moreover, there is strong UV radiation. The daily mean temperature in tropical highlands at about 4000m in eastern Africa is around 5°C, but the leaves and ground surface, which are exposed to direct sunlight, reach temperatures 10-15°C higher than the ambient. Besides this, around the dawn after a clear night, the temperature dips a few degrees below zero because of radiative cooling. However, it rises quickly after sunrise, the cooling is for a very brief period, and the soil freezes only rarely. Unlike in the mid-latitude alpine areas, there is little snow cover. The cold survival strategies of these plants include covering their buds and stems with leaves, moderating the cooling of buds and flower stalks with the heat released by freezing of fluids in the plant body, and increase the supercooling capacity of the leaves to avoid hazardous freezing.

The alpine region of eastern Africa is generally dry. For instance, the rainfall measured on Mt. Kilimanjaro was 1770mm at about 2800m, and far less above that altitude, being 170mm above 4200m. Plants growing at such heights can utilize a considerable amount of dew every morning and also the frost melt water. Besides, the plants adapt by changing the extent of leaf opening, in response to the
constantly changing intensity of sunlight, temperature and humidity. Generally, the leaves of plants become smaller with increase in altitude. But in the tropical highlands of eastern Africa and South America, there are also giant rosette plants\textsuperscript{14}, which have adapted by increasing their leaf size.

\textbf{(2) The natural range and environmental adaptation of giant rosette plants}

\textbf{i Strategies for moderating the cooling}

Giant rosette plants with 1-5m tall trunks can be seen in the alpine areas (altitude 3500-4500m) above the tree line in eastern Africa (from Ethiopia to Kenya) and the Andes of South America. The majority of these belong to the family Asteraceae (daisy family). Fig 40 shows \textit{Senecio keniodendron} and \textit{Senecio brassica} growing in a valley at about 4500m on Mt. Kenya. Keniodendron has a 2-9m tall trunk and it grows in dense clusters in the alpine region at 3800-4300m, utilizing the moisture in the air. The upper limit of its natural range is almost at the snow line (about 4500m), which is a line drawn connecting places where the snow does not melt even in mid-summer. \textit{Espeletia} of Asteraceae having rosette leaves at the top of a 1-5m tall upright trunk is widely distributed above the tree line also in the Andes. These giant rosette plants are tree-like, with evergreen large, hard and thick leaves that sit at the top of the trunk and prevent strong radiative cooling near the ground surface. The mature, large outer rosette leaves open during the day to increase the temperature within the rosette and promote growth of immature leaves. They close at night to form the so-called “night buds” to prevent the freezing of the growing point of the most important bud. At the center of the rosette, there are many immature leaves that surround the bud. As the outermost leaves get old, the inner leaves take their place one after another. The formation and growth of leaves continues in this manner throughout the year. The old leaves do not fall off but remain hanging, covering the trunk for many years. They form a dense heat insulating layer that protects the trunk (Fig 41). A thin layer of xylem surrounds the trunk. A well-developed pith that retains water is at the center. There is also a well-developed water storage tissue at the top of the pith, just below the rosette leaves. The insulating layer of old leaves covering the trunk softens the decrease in trunk temperature at night and its increase during the day, and thus regulates the water supply from the trunk to the leaves. In fact, if this thermal insulation layer is artificially removed or lost through mountain fires, the water
balance of the plants is disturbed, the leaves start wilting within two weeks, and the plant gradually dies off.

*Senecio brassica* prefers slightly more moist locations. It has recumbent stems that lie above the ground surface or just beneath it. The large rosettes of leaves that this plant produces just above the ground look like giant cabbages. In this plant also, the rosette leaves close at night to protect the growing point inside from strong cooling. Among the lobelias of Campanulaceae, which also have large rosette leaves near the ground, only one species closes its leaves at night. Others keep their leaves open at night. In these latter plants, the rosette has a cup-like shape and contains about 3 liters of fluid. The surface of this fluid freezes at night whereas the fluid at the bottom, near the growing point of the bud does not freeze. This fluid is excreted from the leaf bases and contains a lot of viscous material that prevents evaporation. So, it does not dry up when the temperature rises during the day.

In the giant Lobelia, which also grows in a similar environment, the flower stalk rises from the center of the rosette and bears flowers. The plants flower simultaneously once in a few years and are wind pollinated. A large number of seeds are also dispersed by wind. Wind pollination must have developed in this plant because almost no insects are found above 4000m in the tropics.
Fig 40  Vegetation at the altitude of 4500m on Mt Kenya.

A: Senecio keniodendron  B: Senecio brassica
ii Cold survival strategy of the flower stalk of Lobelia

The flower stalk of Lobelia telekii rises from the center of the rosette and is a hollow cylinder of diameter 5-8cm and height 2-3m. The outside of the stalk is covered with a blanket of long thin hanging leaves (bracts). Many flowers can be seen between the leaves. Inside the flower stalk, from the ground surface to a height of about 1m is filled with about 50 (57) liters of a highly viscous fluid (Fig 42). This fluid starts freezing at around 0°C while releasing a lot of heat. It maintains the temperature of about 0°C at night also. Air is entrapped in the space
above the fluid. This air warms the upper part of the flowering stalk by convection. The interesting part here is that the fluid inside the stalk starts freezing at around 0°C, without supercooling. This flower stalk grows only during the rainy season when there is not much radiative cooling.

### iii Supercooling ability of the leaves

The large rosette leaves of the giant rosette plants are advantageous for photosynthesis at high altitudes. They also play the important roles of gathering dew and mist efficiently and protecting the growing point and immature leaves. The rosette leaves do not freeze (they supercool) at night even when the temperature goes below zero (Fig 43). The supercooling ability differs depending on the extent of cooling in their natural habitats, which differs depending on the altitude. Plants growing below an altitude of 2850m can supercool to about −7°C, whereas those at 3500m can supercool to about −10°C. It is known that at the even colder higher altitudes, the outer leaves of giant rosette plants freeze because of strong radiative cooling. These leaves have acquired a certain level of frost resistance.
iv Convergent adaptation of giant rosette plants

As described above, the giant rosette plants in the alpine belt of the tropics live, adapting to the sharp temperature changes and the water scarcity in the dry and cold environment, while growing by recycling their water and maintaining water balance through ingenious mechanisms. The wind is not very strong throughout the year in these alpine tropics but both visible sunlight and UV light are strong. So, the leaves of the giant rosette plants are covered with a thick glossy cuticular layer, which is further covered with fine hair or fluff. The leaf angle is regulated during the day according to the ambient humidity to reduce moisture loss.

The giant rosette plants with upright stems in the Andes mostly belong to the genus Espelatia of Asteraceae. Apart from this, there are some plants of Plantaginaceae and Cruciferae. In eastern Africa, plants of the genus Lobelia (Campanulaceae) and the genus Senecio (Asteraceae) are more common. Plants have evolved in this manner to have a similar morphology irrespective the species, over a wide tropical alpine zone, which has large [diurnal] temperature
fluctuations and severe dryness. This appears to be a case of convergent evolution of plants in response to the special climatic conditions of this area. This special morphology and function, and extensive recycling of resources are probably advantageous for life in this special environment.

Plants live in Southern California, Mexico and up to the northern part of South America, and in the low lying deserts and other dry areas of southwestern subtropical Africa in spite of exposure to extreme drying and temperature fluctuations. In these areas also, we can find plants with large leaves borne at the top of upright stems, such as yucca, century plant, Washington palm, aloe, etc.
Fig 43  The ambient temperature at 4200m on Mt Kenya and the temperature of leaves and buds of Senecio*9.

Abscissa: Time of day  Ordinate: Temperature (ºC)

Inside the Fig, from top down:
On Mt Kenya, in the dry season
Ambient temperature
Leaf bud temperature
Leaf temperature
March 26  March 27
(3) **Cold survival strategies of chamaephytes**

In the higher reaches of eastern Africa and the Andes mountain range there are a number of perennial chamaephytes (surface dwelling plants) growing along with the giant rosette plants (Fig 44 B, C and D). Like the tundra plants, these chamaephytes can effectively use the high temperature zone near the ground surface but they are exposed to strong radiative cooling during the night. These are surface-dwelling plants or semi-underground plants and their life forms are a grass-like dense clump of herbaceous stems (B), a rosette (C), or a cushion-like mat (D), or they are woody dwarf plants. All these life forms can effectively use the solar heat near the ground surface. The buds are protected from strong cooling and drying by being within the plants, in the mats, or close to the ground surface. These plants can also utilize dew very effectively. As is common with plants of dry areas, these plants usually have small thick leaves, are resistant to drought, and have some frost resistance. In the tropical alpine area of Venezuela, at an altitude of 4200m, the mean annual temperature is 3ºC and 10cm above the ground the temperature can go as low as about –10ºC. Plants of Asteraceae, Caryophyllaceae and Cruciferae grow there and the leaves and stems of these plants are known to tolerate about –15ºC.

We can now summarize the cold survival strategies of herbaceous plants growing in dry alpine areas of the tropics.

1) **Low temperature avoidance (moderation of cooling)**
   - Protection from cold by insulation of the growing points of buds and the stems.
   - Utilization of heat released when fluid stored inside the flower stalk or the base of rosette leaves freezes.
   - Moderation of radiative cooling by having rosette leaves high above the ground.
   - Adoption of a suitable life form such as the giant rosette form, dense clump form or cushion-like mat form.
   - Emergence of the flower stalk at a suitable time (the rainy season).
   - Selection of a suitable habitat: Slopes with mild weather conditions.

2) **Freezing avoidance – Freezing avoidance by supercooling of rosette leaves**

3) **Acquisition of frost hardiness – [As in] small plants that grow close to the ground surface**
In the tropical alpine regions, plants have adapted to their environment by adopting different life forms and developing their own ingenious cold avoidance and survival strategies to cope with the subzero cooling that occurs briefly at night. However, in an environment with stronger and longer lasting cooling, the protective strategies of the giant rosette plants against cold become inadequate. In such places, plants need to become frost hardy instead.

**Fig 44** Life forms of plants living on Mt Kenya.*

A: Giant rosette  B: Dense clump form of grasses  C: Rosette form  D: Cushion-like mat.

図44 ケニア山に分布する植物の生活形*29．
A：ジャイアント・ロゼット形，B：イネ科植物の叢生型，C：ロゼット形，D：クッション状の群体

Fig 44 Life forms of plants living on Mt Kenya.29

A: Giant rosette  B: Dense clump form of grasses  C: Rosette form  D: Cushion-like mat.
Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.
2. Words added by the translator for clarity are given in [square brackets]
3. The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.
Let us now look at the life and life forms of plants in temperate deciduous forests before summarizing the cold survival and overwintering strategies of temperate plants.

(1) The life and life forms of plants in temperate deciduous forests

i Life in a temperate deciduous forest

Mt. Moiwa (height 530m) is in the southern part of Sapporo city. It has more or less retained its natural forests and was declared a protected site in 1919. The natural vegetation on this mountain consists of temperate deciduous broad-leaved trees. The middle and lower canopy layers of the forest have short trees like *Ookamenoki* (*Viburnum furcatum*) and *Tsuribana* (*Euonymus oxyphyllus*). The forest floor mostly has bamboo grass (*Sasa paniculata*), *Inugaya* (*Cephalotaxus harringtonia*), *Fukkiso* (*Pachysandra terminalis*) and ferns. From mid-April, after melting of the snow, both sides of the hiking paths on the mountain are covered with flowers like *Kibananoamana* (*Gagea lutea*), *Ezoengosaku* (*Corydalis ambigua*), *Enreiso* (*Trillium smallii*) and *Nirinso* (*Anemone flaccida*). Until about the middle of May, when the leaves of the deciduous trees appear in the upper canopy of the forest, plenty of sunlight penetrates to the ground surface. So, plants growing on the forest floor photosynthesize during this period to produce the necessary substances. Soon, new leaves that unfold in the upper canopy block most of the sunlight and allow only a little bit of it to filter down to the ground. Most plants living on the forest floor therefore just manage to survive under low light intensity during the summer. Sunlight shines again on the bamboo grass on the forest floor after a gap of 5 months, when the tree leaves, which dress up the entire mountain in red and yellow autumn colors, fall in mid-October. The bamboo grass assimilates and stores, during this short period before snowfall, the materials and energy needed for overwintering and spring growth. Plants in deciduous forests coexist, sharing the sunlight both spatially and temporally.

ii Classification of life forms and cold hardiness

Plants cannot move about on their own even when exposed to unfavorable
environments. Therefore, they survive by adopting suitable life forms like tall tree, short plant, ground-dwelling plant, or underground plant, etc., taking into account the life, both of summer and winter. In deciduous forests, tall and short trees overwinter while exposed to the winter cold and dryness. But the ground-dwelling plants and underground plants on the forest floor allow their aboveground parts to die out, and survive through their winter buds on the ground surface beneath the snow cover or in the soil.

In 1910, Raunkiaer, a Danish botanist suggested a new way of looking at life forms. His approach gave importance to how plants survive the winter and the dry season, both of which are unfavorable for their life. He classified life forms of plants into 4 categories (Fig 45) on the basis of the height of their winter buds from the ground surface or their depth below the ground. These are 1) Phanerophytes (above ground plants such as tall and short trees that have winter buds high above the ground and survive exposure of the buds to cold and dryness); 2) Chamaephytes (ground-dwelling plants such as bamboo grass, evergreen low bushes, etc in which the aboveground parts do not dry out in the winter); 3) Hemicryptophytes (semi-underground plants like dandelion, *Oomatsuyoi/gusa* (*Oenothera erythrosepala*) and *Azami* (*Cirsium japonicum*) in which most of the shoots above the ground dry out in the winter but the rosette leaves near the ground survive and the winter buds at the center of the rosettes overwinter either on the ground surface or below it); and 4) Cryptophytes (underground plants and aquatic plants, in which all the above ground parts die off in the winter and the winter buds survive underground (on bulbs and rhizomes) or in the water).

Annual herbs dry up after germination and flowering. Their seed formation and the winter hardiness of the seeds alone are important for them. They are therefore not included in this classification. Perennial herbs also produce seeds. But because their underground buds remain viable, they do not die for many years. In this concept, the life forms are classified giving importance to the winter buds and the mechanisms by which the plants withstand the cold and dryness.

The winter temperature near the ground surface where the plant lives is the factor that is closely related to overwintering of surface-dwelling and semi-underground plants. On bare land, on fine days in winter, cold air stagnates near the ground surface because of radiative cooling. This sometimes makes the temperature near
the ground surface a few degrees lower than the ambient temperature measured in a Stevenson screen about 1m above the ground. The soil temperature is fairly higher than the air temperature and does not show much variation, although it is also measured at the ground surface. Because of this, the overwintering ability of winter buds and the underground stems is very much affected by the thickness of the decaying litter layer and the depth from the ground surface or the snow surface. Table 1 shows the minimum temperatures recorded 1cm above the litter layer and the minimum soil temperature measured on the forest floor of the Hokkaido University’s Tomakumai experimental forest. At that site, the soil freezes to a depth of 30-60cm from late November to April end. The thickness of the litter layer varied from place to place in the forest, depending on the type of trees, but it was about 1-5cm. We can see from Table 1 that the minimum temperature on bare land was more than 10ºC lower than in the forest. In soil temperature also, the bare land was a few degrees cooler than the forest.

Fig 45 Life forms as classified by Raunkiaer.

Key: In the Fig, above the ground level line: (Unit: ºC)
Phanerophyte
Chamaephyte
Deciduous
Evergreen
Snow surface
Ground surface
Water surface

Below ground level line, from left to right:
(Annual herb); Hemicryptophyte; Cryptophyte; Aquatic plant
iii Life forms and frost hardiness

From the concept of life forms classified according to the position of winter buds, we can arrive at the hypothesis that plants chose the site of overwintering according the level of frost hardiness of their winter buds (the frost hardiness of the winter buds of plants varies with their site of overwintering). In other words, the lesser the frost hardiness of the winter buds, the safer is the site of overwintering of the plant, with respect to cold and dryness (the safer the overwintering site with respect to cold and dryness, the lesser is the frost hardiness of the winter buds). To verify this hypothesis, we have to simply study the relationship between the low temperature to which the winter bud is exposed and the frost hardiness. Yoshie studied this relationships in 45 plant species of different life forms growing mainly on the forest floor, below deciduous trees in the Tomakomai experimental forest, which has a relatively small snow cover. His studies showed that the rank of the frost hardiness of the winter buds corresponded to the severity of the cold that the plant is exposed to (Fig 46). In other words, the frost hardiness was highest (-25 to –60°C) in aboveground plants, which was followed by surface-dwelling plants (-25 to nearly –60°C), semi-underground plants (about –20°C) and the lowest in underground plants (-5 to –10°C). In one plant species, the part of the stem above the litter layer was more frost hardy than the part below it. In the case of roots, the frost hardiness tended to be higher in parts closer to the ground surface. When he compared the frost hardiness of rhizomes among semi-underground plants growing on the forest floor and those growing on bare land, it was considerably higher in the latter group. In this manner, plants select a suitable life form and habitat to moderate or avoid hazardous low temperatures. Many plants on the forest floor below deciduous trees in the intensely cold Hokkaido overwinter under snow cover unlike tall trees and bushes. These plants have selected the life form and habitat in such a way that they would be covered with snow with certainty in the early stage of winter. The selection of a suitable life form is even more important in the tundra and the alpine areas where the weather is even harsher. Plants living in such places are either underground or surface-dwelling plants. In the tundra, by selecting such advantageous life forms, the plants efficiently produce the necessary materials, utilizing the high temperature zone near the ground surface in the summer and survive the long and severe dryness and low temperatures of the winter even when the snow cover is shallow. Besides, these life forms have the advantage of being able to use the
snowmelt water.

Table 1 The ambient temperature near the ground surface and the soil temperature of different forest floor sites in the Tomakomai experimental forest of Hokkaido University.

<table>
<thead>
<tr>
<th>Trees at the site</th>
<th>Thickness of litter layer (cm)</th>
<th>Minimum temperature 1cm above the litter layer (°C)</th>
<th>Soil temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0 cm</td>
<td>10 cm</td>
</tr>
<tr>
<td>Deciduous broad-leaved trees</td>
<td>2~6</td>
<td>-11.9</td>
<td>-4.5</td>
</tr>
<tr>
<td>Japanese larch</td>
<td>1~3</td>
<td>-12.5</td>
<td>-6.0</td>
</tr>
<tr>
<td>Todo-firs</td>
<td>0.5~1</td>
<td>-13.0</td>
<td>-8.5</td>
</tr>
<tr>
<td>Bare land</td>
<td>---</td>
<td>-24.4</td>
<td>-10.9</td>
</tr>
</tbody>
</table>

The soil freezes to a depth of about 50cm in the Todo-fir forest. The depth of soil freezing depends on the type and thickness of the litter layer. These measurements were made during December 1979 to February 1980.
Fig 46 Frost hardiness of plants in relation to their life forms on the forest floor in a deciduous forest. The specimens were collected in December and the frost hardiness was measured after hardening at −3°C. The black dot on each line represents the mean value. L: Leaf, LB: Winter bud, RH: Rhizome, R: Root*138.

Key:
Abscissa: Frost hardiness (°C)
Ordinate, from top down: Above ground plants (Phanerophytes); Surface-dwelling plants (Chamaephytes); Semi-underground plants (Hemicryptophytes); Underground plants (Cryptophytes)

(2) Cold survival and overwintering strategies of temperate plants

No tall evergreen broad-leaved trees can be found in the cold-temperate zones where the winter is long and severe and the soil remains frozen for a long time. Herbaceous plants and short trees can overwinter in this area only if there is snow cover. Therefore, as discussed earlier, these plants have selected life forms and habitats that enable them to overwinter under snow cover. For plants, it is also very important to overwinter in a suitable developmental stage that has high stress resistance, such as seeds and spores.
Unlike short trees and herbs, the tall deciduous broad-leaved and needle-leaved trees that survive the long severely cold winter, above the snow surface, need to acquire seasonal adaptability through short day-induced dormancy, frost hardiness to lower than –30°C and also winter drought resistance.

Moreover, for woody plants that overwinter in the subarctic regions where the soil and tree trunks freeze for a long time and intense cold and dryness prevail, it becomes necessary to be frost hardy to nearly –70°C, have mechanisms to prevent moisture loss from buds, shoots, and trunks, and have drought resistance. The overwintering strategies (for cold and drought survival) of plants in the cold-temperate regions can be summarized as follows:

1) Low temperature and drought stress avoidance (individual plant level)
   a Spatial avoidance
      · Selection of life forms (above ground, surface-dwelling, semi-underground and underground plants)
      · Selection of habitat (forest floor, bare land, snow-covered area, slopes with milder weather, low lands, areas with suitable soil)
      · Selection of growth form (Evergreen or deciduous†1, annual or perennial)
   b Temporal avoidance
      · Selection of developmental stage for overwintering
      · Formation of seeds or spores and selection of their time of dispersal†2 (strategy for seedling survival)
      · Selection of the time of flowering and fruiting (before or after winter) (improvement of the success rate of multiplication*58, 59, 60)

2) Acquisition of resistance against low temperature and drought stress (at the tissue and organ level) (see I–4 and I–6)
   a Acquisition of frost hardiness (tolerance of freeze dehydration) and its enhancement
      · Extracellular freezing (herbs, and evergreen leaves, cortical tissues, roots, etc of woody plants)
      · Extra-organ freezing (embryonic organs like buds, flower buds, seeds, etc of woody plants)
   b Freezing avoidance
      · Acquisition of supercooling ability (xylem ray tissues of broad-leaved trees, palm
leaves, etc)

· Freezing avoidance through acquisition of drought resistance (acquisition of a high level of drought tolerance – drought tolerant seed, pollen, spores, etc).

3) Individual plant level drought resistance (prevention of moisture loss by covering the winter buds, flower buds, leaves, stems and trunks) and increased capacity of the individual plant for regeneration and renewal after environmental disturbances (floods, typhoons, fire, etc).

4) Genetic adaptation of the species at the population level.
Acquisition of the necessary winter hardiness by the population of each habitat within a species: Ecological genetic differentiation (See I-7 and I–8).

5) Moderation of various stresses by grouping (forests, grasslands and clusters), increased capacity for regeneration and renewal, and environmental adaptation, after environmental disturbance.

†1 Selection of the evergreen or deciduous trait

The cumulative amount of net carbon gained by photosynthesis per leaf can be obtained by subtracting the production cost and maintenance cost (respiration) from the cumulative gross amount of carbon fixed\(^{12, 46}\).

The efficiency of photosynthesis by a leaf declines with time because of physiological aging. Therefore, to maintain a high efficiency of photosynthesis, the plants need to change their leaves at suitable times. The shortest required lifespan of a leaf is the period needed to recover, through photosynthesis, the carbon invested in the production of the leaf.

In the temperate zone, where the winter is cold, the leaves cannot overwinter. Therefore, their lifespan is shortened by necessity. As the time available for growth becomes less, deciduous broad-leaved trees produce thin but functional leaves that lack mechanical strength, concentrate photosynthetic production in the 3-4 month-long summer to utilize the high temperature and strong light, and shed the leaves at the end of summer. On the other hand, the evergreen plants that overwinter, form leaves with complex structure at a high production
cost. But by maintaining a longer lifespan of the leaves, they recover the cost of producing the leaves, over a period of many years. Leaves of evergreen broad-leaved trees photosynthesize throughout the year, but their photosynthetic capacity is low compared to the leaves of deciduous trees. They have better shade tolerance and withstand the cold and dryness better. Generally, in the strategy of selecting the deciduous or evergreen trait, apart from the cost-benefit ratio of investment in leaves, the kind of leaf targeted by the plant, i.e., the long-term strategy of the plant, such as whether to choose leaves with high production efficiency and special resistance to cold and dryness and whether the leaves should be durable, etc. have complex effects. *Kokemomo (Vaccinium vitis-idaea)* distributed widely in alpine areas and the tundra are all evergreen and *Kuromamenoki (V. uliginosum)* are all deciduous. Also, willows, which are extensively distributed all over the world, in the temperate zone, tropical zone and the tundra, are all deciduous.

The time of seed dispersal and the temperature needed for germination

The tall willows of Alaskan forests flower around June 10 and disperse their seeds in early July. The seedlings thus get about 3 months for growth. The seeds dispersed in summer germinate in the temperature range of 5-25°C and they have rather short lives. However, in the tundra near the Arctic Ocean, because of the low temperatures, dwarf willows disperse their seeds sometime during the end of July to early September, providing only a short time for the seedlings to grow after germination. The seeds collected on July 15 germinated normally and developed into seedlings when sown. But when the seeds collected on July 30 were sown, only 42% germinated at 25°C and less than 23% at lower than 20°C. Seeds collected in early September had an even lower germination percentage; they did not germinate at all under natural conditions (soil temperature 5°C). But even with the autumn seed, a considerable number germinated when they were treated in a moist bed at 5°C. The high temperature requirement for germination of the autumn-dispersed seed may be a survival strategy to prevent the seeds germinating in the autumn, so that they can germinate in the following spring. Similar adaptations have been reported in the seeds of white birch of Hokkaido.
Translator’s notes:
Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.

#1 The suggestion that plants almost consciously “choose” a suitable life form and a suitable habitat, which appears at many places in this Chapter needs to be corrected, I believe.
13 **Plants of Antarctica that live in extreme environments**

A continental ice sheet, with an average depth of more than 2500m, covers most of Antarctica. The continent is surrounded by the Antarctic Sea and isolated from other landmasses. Only about 3% of the Antarctic continent is ice-free. Soil, which can retain moisture and nutrients, has not formed even in these exposed parts. The annual precipitation is 200-250mm and very little of it is in the summer. Most of the precipitation falls as snow or ice, which cannot be used by the plants directly. Except in the southwest part of the Antarctic Peninsula (P in Fig 47), the monthly mean temperature does not rise above 0°C even in the warmest season. Besides, the wind is quite strong in Antarctica. For plants to survive in this polar desert, apart from overwintering capacity, they need to have a high ability to photosynthesize near 0°C. Besides, it is important for these plants to find habitats where they can obtain snow melt water. In these environments, wingless insects like springtails and lower animals like rotifers, mites, nematodes, etc, which live in colonies of plants like lichens, liverworts, algae and fungi, form the ecosystem. Seed plants (two kinds of flowering plants) are found only in the southwest part of the Antarctic Peninsula, where the average monthly temperature is above 6°C. At Japan’s Syowa Base on the Antarctic coast (marked with circle in Fig 47), the ground is free of snow cover only for about 2 months. The mean temperature of the warmest month (January) is about -1°C and it is -30°C in the coldest month. The annual precipitation is 200-250 mm.
Fig 47 Distribution (black parts) of Gondwana flora and drifted conglomerates with striae made by glacial movements at the end of the Paleozoic era\textsuperscript{51}. O: Syowa base, P: The Antarctic Peninsula.

**Key:**
- **Center:** Antarctica
- **Inner circle:** Gondwana flora and drifted continental rock
- **Outer circles, clockwise from top left:** South America; Equator; Africa; Madagascar; India; Australia; New Zealand.

(1) **History of Antarctic flora**

Gondwanaland existed during the mid-Paleozoic (about 360 million years ago) to the Jurassic period (150 million years ago) in the middle of the Mesozoic era. It was a combination of the present Antarctica with what are now South America, Africa, India, and Australia. Gondwanaland warmed up and the ice sheet
disappeared during the Mesozoic, following which a dry climate prevailed and amphibians and reptiles thrived. Large tree ferns and needle-leaved trees became abundant. Gondwanaland broke up after entering the Jurassic period. A fragment moved north to become India and another moved east to become Africa. Then, in the following Cretaceous period (130 million years ago), a part that is now South America got detached from Africa and drifted westward to create the Atlantic Ocean. Australia was the last landmass to get separated from the Antarctic continent. It moved northward in the early Tertiary (about 50 million years ago). Gondwanaland thus got separated into pieces, leaving Antarctica and finally reaching the current configuration. The plants that flourished on Gondwanaland during Paleozoic to the Mesozoic era are known as the Gondwana flora. The distribution of Gondwana flora and drifted conglomerates with striae made by glacial movements at the end of the Paleozoic era are shown in Fig 47. Antarctica gained importance in the plant geography after it became known that the current flora on landmasses broken off from Gondwanaland was very similar to one another and that there were a large of number of genera and species distributed only in these areas.

It appears that the Antarctic continent was more or less at its current location and already had glaciers in the early Tertiary. But the Antarctica of that time was not a barren place with only rocks and ice. There was the Antarctic mountain range rising beyond green forests and the mountains had temperate glaciers that shone white when sunlight played on them. It is believed that the scene was similar to current New Zealand or Patagonia in southern Chile. As the temperature declined lower from the Miocene (28 million years ago) onwards in the Tertiary period, many higher plants that had lived in Antarctica until then perished almost completely, it is believed. Maximum development of the Antarctic ice sheet is believed to have occurred at the end of the Tertiary (1.7 million years ago) when the precipitation was still high.

(2) Bryophytes around the Syowa base

About 80% of the bryophytes (liverworts and mosses) of Antarctica are mosses, which have an advanced level of structural differentiation. These bryophytes have the characteristic of having very few species with a majority of them being widely distributed all over the world. This suggests that very few indigenous species had
survived the ice age in Antarctica and that the majority of them had migrated from the surrounding areas to Antarctica when the weather became milder after the ice age.

The most dominant mosses around the Syowa Base are fire moss and Bryum pseudotriquetrum. They form huge, 2-3 cm to as much as 10 cm thick colonies (Fig 48). Around the Syowa Base, the mosses can live only at places where they can utilize snowmelt water. The dense masses of moss that grow like a lawn close to the ground surface is a life form suited for retaining warmth and moisture. The mean temperature at the Syowa Base is about -1°C in January, but the surface temperature of a moss colony can reach 10-20°C on a sunny day. Mosses generally have high drought resistance. But when there is water deficit, their ability to photosynthesize and respire is sharply reduced. Therefore, mosses can live only where water is available. It has been reported that there are moss colonies that are more than a hundred years old around Syowa Base.

Fig 48 Moss colonies near Syowa Base on West Ongle Island (Photographed by Keishi Kanda).
Salix pauciflora, a polar willow grows as a creeper on the ground surface at a windy site near the Mt. Kurodake Hut in the Daisetsuzan area. Clusters of small about 5 mm large round leaves can be seen on the ground surface. But the stems are not usually visible and therefore it does not look like a willow. The thin stems extend along the ground surface in all directions and a 1m long relatively thick root lies horizontally below the ground surface. There are about 120 species of polar and alpine dwarf willows on earth. Salix pauciflora, a willow found only in the Daisetsuzan area, is the only polar willow found in Japan. Its variants are presently distributed in Siberia, the trans-Baikal region and Altai Mountain. Salix pauciflora, along with Pinus pumila, etc. were forced to migrate southwards during the ice age and its relicts are now found at Daisetsuzan.

One day, I felt that if this exceptionally frost hardy willow could overwinter and bear flower buds in a place like Syowa Base in Antarctica it could probably flower too in that barren land. So, after obtaining formal permission, I entrusted some Ezomameyanagi plants, wrapped in sterilized sphagnum moss, to a member of the Antarctic wintering team and requested him to plant it outside the Syowa Base. Not only did these willow plants overwinter under snow for nearly 10 months in a place where the minimum temperature was -25°C, but one of the five plants also flowered naturally. This encouraging news was flashed in various newspapers and by several TV stations at the end of January 1969, under titles like “A willow flowers in barren Antarctica!” (Fig 49). But these willows ultimately died off because in the Antarctic, the summer is only 1-2 months long, with a temperature of only 0°C. Besides, the roots could not grow properly because of insufficient soil and a soil temperature of about 0°C and the plant could not produce enough leaves and buds to continue living in the following summer.
Fig 49 A *Salix pauciflora* willow tree that flowered after overwintering near the Syowa Base in Antarctica (Asahi Shimbun of January 24, 1969) (Courtesy Asahi Shimbun).

**Key:**

*Salix pauciflora* flowers in Antarctica

From Correspondent Takagi at Syowa Base – January 21

*Salix pauciflora* planted at the Syowa Base flowered for the first time.
This was one of the 5 plants that were planted by an expedition member in January last year on the request of Professor Akira Sakai of the Institute of Low Temperature Science, Hokkaido University, who wanted to test whether a very frost hardy plant from Japan could overwinter in Antarctica. The plant is a little more than 10cm tall. We can see the yellowish pistils and the flower petals.

This project started 2 years ago. The willows were brought to Antarctica wrapped in sterilized sphagnum moss so that they would not contaminate the antarctic flora and were planted on moss-covered soil behind a rock. The willows planted a year earlier had all dried up. But this time, they survived the long sun-less winter and one miraculously flowered.

Photograph caption: Salix pauciflora flowers at Syowa Base
Picture sent electronically from the Antarctic research ship Fuji through Kokusai Denshin Denwa (KDD).

(4) Algae living in extreme environments

i Green algae in the Dry Valleys

The summer temperatures in the Dry Valleys, the dry snow-free areas of 78° S latitude remain below zero. It goes to even -15°C in the evening. Besides this, when snow falls, it is either blown away by the wind or sublimated. Therefore, no water is available. But some lichens and green algae were found growing in this polar desert, in spaces a few millimeters below the surface of the sandstone. Around the surface of the sand stone is semi-transparent and porous. So, the sun warms the surface during the day and moreover light and moisture penetrate to several millimeters beneath the surface. This is where the green alga (Hemichloris antartica, of the order Chlorococcum) is found. The space where this algae lives receives only about 0.1% of the light falling on the rock surface. But this much light, the warmth coming from the sun, and the availability of a certain amount of moisture shelter some life forms, protecting them from the extremely dry and cold outside environment.
Life of lichens under extreme conditions

Dry weather prevails during the summer in the snow-free parts of the hilly regions (77° 36’ S Latitude, altitude 1650 m) of South Victoria Land. The maximum temperature during the day is -6°C and the minimum at night is less than -15°C. The German scientist Kappen studied in detail the microclimate, photosynthetic ability, etc. of the lichens of this area. In such high altitude snow-free regions, lichens live where the conditions are somewhat favorable, i.e., sunny locations, places where some summer snow tends to accumulate, small concavities on mild slopes, and the porous parts 5-10 mm beneath the surface of the rock. Although the ambient temperature during the day is below zero (-7 to -10°C), the exposed rock of such sites reaches a maximum temperature of about 5°C because of the sunlight. Thus, the temperature of the places where these lichens live remains above 0°C for several hours during the day and falls to less than -15°C at night (Fig 50). The lichen (Buellia) living at such sites has a black pigment which promotes absorption of radiant energy and also acts to filter out the UV light. The optimum temperature for photosynthesis by these lichen is 2 to 6°C, although it varies depending on the availability of light at the site. The photosynthetic capacity is sharply reduced when the temperature becomes higher than 10°C. It has been confirmed that lichens live on the bare peaks of the Yamato mountains 250 km towards the interior from the Syowa Base.

The surface of the sandstone is porous and transparent, which permits light and moisture to penetrate several millimeters below the surface. The algae and lichens living in surface gaps on such survive for long periods through photosynthesis in the weak light at near-zero temperatures. These habitats, in one of the harshest polar deserts of the earth, provide oases for these algae and lichens. If the planet Mars had had any microorganisms and other lower forms of life in the past, similar sites must have most probably harbored such life.

The role of unmanned Mars probes

It is speculated that probably Mars, like the earth, had life 3 billion years ago. The
major objectives of mars exploration in the early 21st century are to find out: 1) Whether microorganisms are surviving, if not flourishing, on Mars at present; 2) Whether they have all perished; and 3) Whether life ever existed on Mars. Answers to these questions would probably be found in the not very distant future.

Mars is about half the size of earth. The pressure of the atmosphere surrounding mars is about 7 hectopascal. Although we call it “atmosphere” it is 95% CO₂, 3% nitrogen and 0.4% oxygen, with very little moisture. Mars has day and night and four seasons. The surface temperature is always changing. It is -40°C on the average, far lower than the mean surface temperature of the earth, which is 15°C. The polar regions of mars can become as cold as -140°C. This low temperature and the low atmospheric pressure, make the surface of Mars dry and desert-like. However, Mars is believed to have been created by the same forces as the earth. Therefore, it is said that the cold and dry Mars also had permafrost, and that its thickness was about 500m. I wonder whether this underground ice still exists there. Future Mars probes would probably answer this question also.
Fig 50 Microclimate of lichens growing in extreme conditions. Ha: Relative humidity of the air (%), Ta: Air temperature, Tr: Surface temperature of the rock, R: Radiation intensity\textsuperscript{*43}.

**Key:**

*Abscissa:* Time of day  
*Ordinate (left):* Temperature (°C)  
*Ordinate (right, upper):* Relative humidity (%)  
*Ordinate (right, lower):* Radiation intensity  
*Inside the Fig:* Linnaeus Terrace (77° 36' S latitude, 161° E longitude)
Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink and suggestions are sometimes given in parenthesis.
2. The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.

Part I Chapter 13

page 1 16 lines (upper) They can obtain snowmelt water.
In this environments, wingless insects like spring tails mites and
Lower animals like rotifera, mites, nematoda etc, which live in the colonies of
plants like lichens, liver worts, algae and fung, from the
ecosystem.

page 5 16 lines Ezomameyanagi Salix pauciflora Page 5 yellowish

pistils

Thank you Sakai
II FORESTS OF DIFFERENT TEMPERATURE ENVIRONMENTS

1 How forests change from the tropical to the subarctic zone

Forests occupy only about a third of the land area of the earth. But their share of the total plant production on land is 64%. Forests are very efficient production factories of greenery on earth. They not only produce wood but also provide habitats for flora and fauna. Besides, they have huge pools of organic carbon on the ground surface or in the soil, such as the decomposing litter layer on the forest floor. Moreover, forests act as automatic regulators of carbon dioxide concentration [in the atmosphere], contribute to the circulation of water and play a crucial role in maintaining the global environment.

(1) Different temperature zones of the earth

Only about 35% of the land area of the earth is in the frost-free zone (A in Fig 56), where the temperature never goes below 0°C. The remaining 65% of the area is a zone that experiences freezing stress. Within this zone, about 48% of the area has a [mean] minimum annual temperature of –10°C or lower (Fig 56, C). About 25% of this area has a [mean] minimum annual temperature of less than –40°C (Fig 56, D).
Fig 56 Various temperature zones of the earth. A: Frost-free zone, B: Area where the temperature rarely drops below −10°C, C: Area where the mean annual minimum temperature is −10 to −40°C, D: Area where the mean annual minimum temperature is less than −40°C, E: Polar glacier area. The solid line represents a mean annual minimum temperature of −30°C.


Key In the Fig:

Arctic zone
Equator
Antarctica
(2) Changes in forests, from the tropical to the subarctic, caused by changes in the environment

As we move from the equator to the poles, the incident solar energy decreases, the temperature gets lower, the variation in daylength during the year increases, the growth period available to plants decreases and the precipitation decreases. These changes are accompanied by decreases in the height of forest trees, the number of forest canopy layers, plant biomass, i.e., the total weight of plants per unit land area, and the number of tree species, and also by impoverishment of the soil. In this manner, the environment gradually changes from a tropical low stress high energy environment to the high stress low energy environment of the subarctic regions. Forests, where tall trees are the main life form, cope with this change of climate from tropical to subarctic by changing their leaf habit the tree type, while maintaining the necessary amount of photosynthetic production to support the tall tree life form. But they change their leaf habit (evergreen or deciduous) and tree type (broad-leaved or needle-leaved). In other words, they change from evergreen broad-leaved trees to deciduous broad-leaved trees and then to evergreen or deciduous needle-leaved trees. Finally, when not enough production to support the tall tree life form is possible, i.e., from the tree line onwards, the vegetation changes to shrubs and then grasses.

One measure used to explain the relationship between climate and the forest belt is the warmth index (WI) suggested by Kira in 1946. This is the accumulated temperature that takes into account the length of the summer growth period and the temperature. To be more specific, 5°C is taken as the minimum temperature needed for plant growth and all the monthly mean temperatures in excess of 5°C are added up for the 12 months of the year. Fig 57 shows the values of WI. According to this concept, a WI of up to 15 fits the arctic tundra. From there, up to WI 45 corresponds to the subarctic forests, 45 to 85 to the cold temperate forests, 85 to 180 to the warm temperate forests, 180 to 240 to the subtropical forests, and more than 240 to tropical forests. In this Fig, the range of temperatures in a year in cities located in the different forest zones is given as the difference between the mean temperature of the warmest and the coldest month. We can see from this Fig that the temperature range during the year sharply increases as we move towards colder regions, from tropical forests (the temperature ranges from 24 to
27°C) to the warm temperate evergreen forests, cold temperate deciduous forests, and subarctic needle-leaved forests. The sharply decreased mean temperature in the winter contributes to the large temperature range in the cold temperate and subarctic regions, more than the change in the high mean temperature in the summer. To be able to survive the long severe winters, plants living in the cold temperate and the subarctic zones*106 have a far higher frost hardiness compared to the evergreen trees in the warm temperate zone. Plants cannot live in those regions unless they are highly frost hardy. Fig 58 shows the number of pine species and their frost hardiness distributed in climatic zones having different WI*76. There are an overwhelmingly large number of the two-needle pine species in the warm temperate zone. Far fewer species are found in the subarctic and subalpine zones where the pines have the very high level of frost hardiness of about –60 to –80°C.
Fig 57  Monthly mean temperature range and the warmth index at locations in different forest zones.

FT: Freezing tolerance, *Southern hemisphere
**Fig 58** The number of pine species and their frost hardiness in climatic zones with different warmth index values*76.

**Key:**

**Abscissa:** Warmth index

**Ordinate:** Range of monthly mean temperature in a year (°C)

In the Fig, upper level, left to right: Arctic tundra; Subarctic needle-leaved forest; Cold temperate deciduous forest; Warm temperate evergreen forest; Subtropical; Tropical

In the Fig, at the bottom of the bars, from left to right:

Syowa base; Barrow (Alaska)
Yakutsk; Fairbanks (Alaska) ← FT: -70°C or lower
Harbin; Montreal; Moscow ← FT: -30°C or lower; Chicago; Sapporo
Tokyo; Pusan; Arco (Italy); Katmandu; Rome; Kunming; Cape town; Christchurch;
Hobart (Tasmania); Punta Arenas (Chile)

Naha
Kuala Lumpur
(3) Characteristics of different forest zones

i  Tropical forests

The area under tropical forests is only about 16% of the land area of the earth. But it is home to more than half of the plant species known to exist on earth. The tropical rain forests have a very stable physical environment. This is the world of evergreen broad-leaved trees. A stable ecosystem has existed here for ages. The tropical rain forests have high temperature and high humidity with little seasonal change. Plants have high productivity and many species coexist in a multi-layered canopy. In such forests, the density of individual tree species is very low. So, the great majority of the flowers are pollinated by animals, like insects and birds. A large variety of living things, including these animals, coexist with very complex interdependence, creating stable ecosystems (see II-5). However, in tropical forests, the leaf litter gets decomposed quickly and not much of it accumulates as a layer on the forest floor. Because of this, the soil is poor in inorganic nutrients. It was recently found that many tall trees of the family Dipterocarpaceae obtain inorganic nutrients like nitrogen and phosphorus through symbiotic relationships of their roots with ectomycorrhizae.

ii  Temperate forests

In the middle to high latitude areas of the Northern Hemisphere, there were major disturbances and destruction of the flora and ecosystems because of big changes in the climate that occurred from the second half of the Tertiary to the Ice Age. Most broad-leaved tree species, which are woody angiosperms, grow in the tropical zone. Only a few groups of tree species spread to the temperate zone after the Ice Age as evergreen or deciduous broad-leaved trees. Unlike the trees in tropical rain forests and subarctic forests, which can get established only in very specific thermal environments, the deciduous trees of the cold temperate forests have adapted to the wide range of temperature conditions of the mid latitudes, where human
habitation is concentrated. Cold temperate deciduous forests consist of groups of tree species belonging to three life forms. The first is that of pioneer species like white birch, Dakekaba (Betula ermani) and alder (Alnus japonica), which depend on wind for the dispersion of their seeds and pollen and colonize newly opened up bare land and recently disturbed areas in no time at all. The second is of trees with insect pollinated flowers like Kaede (Acer sp.), Shinanoki (Tilia japonica) and Mokuren (Magnolia liliflora), which are species of stable forests, and the third is that of tree species that are intermediate between the other two.*45. In the cold temperate deciduous forests of Hokkaido, the ratio of insect pollinated tree species and wind pollinated ones is about 50:50**44, 45. Tropical forests have very diverse tree species. But around any one tree you would hardly find another tree of the same species. On the other hand, in the natural forests of the temperate zone and further north, trees of the same species gather together, forming stands. Besides this, cold temperate deciduous forests have a thick layer of decomposing litter and a high soil temperature in the summer. This speeds up the decomposition of organic matter, which increases soil fertility and allows efficient absorption of inorganic nutrients by the roots.

### iii  Subarctic forests

As we move from the temperate to the subarctic zone, the effect of the arctic air masses of the winter becomes stronger. The winter temperature decreases sharply and the seasonal variation of temperature increases. The winter dryness also becomes more severe. Besides, the soil freezes in the winter. The high latitude subarctic areas have several months of sunless dark season in the winter. The environment becomes increasingly unfavorable for plant growth as we move to the subarctic zone. This limits the number of tree species that can live in such areas. So, stands of a few tree species occupy large areas. Most of the trees of the subarctic zone are wind pollinated, whether they are needle-leaved or deciduous broad-leaved. For instance, in interior Alaska, two types of evergreen needle-leaved trees are dominant. A few white birch and poplar trees, both of which are broad-leaved, are intermixed here and there, to form the subarctic forests. In eastern Siberia, which has the most severe climate on earth, Dahurican larch dominates huge stands of a small number of tree species spread over vast expanses of permafrost area. This needle-leaved tree is a pioneer species with high capacity for individual tree regeneration and natural renewal of the forest. It gets adapted
to the worst geographical conditions and rapidly colonizes an area even after environmental upheavals like forest fires.

In these needle-leaved forests of subarctic and subalpine zones, a thick layer of decomposing litter covers the soil. But the decomposition occurs very slowly because of the low soil temperature and even if the litter is converted to the inorganic form, the nutrients are absorbed by the accumulated decomposing litter layer and do not get leached out easily by precipitation. Therefore, most of the needle-leaved trees have symbiotic ectomycorrhizae on their feeder roots. These mycorrhizae spread their hyphae into the decomposing litter layer and supply to the roots inorganic nutrients, which otherwise the roots cannot absorb, in a form that can be used by the plants\textsuperscript{71, 126}.

iv The reason why needle-leaved trees can live on poor soils

The severely cold and dry subarctic and subalpine zones of the Northern Hemisphere are the world of needle-leaved trees of the pine family. About 760 species of needle-leaved trees, which are gymnosperms, are known to exist on earth. This is a very small number (about 3.7%) compared to angiosperms (240,000 species). But in the subarctic and subalpine forests of the northern hemisphere, the small number of needle-leaved tree species form almost pure stands over vast areas, and in the number of standing trees also they far exceed the deciduous broad-leaved trees, which are angiosperms. In the Northern Hemisphere, about 15 species of needle-leaved trees are found in the subarctic zone and about 40 are found in the subalpine zone. But these are only about 2% and 5% respectively of the total number of needle-leaved tree species (760).

In general, needle-leaved trees can adapt better than broad-leaved trees to unfavorable conditions like infertile land, special soil types, arid land, etc. The evergreen and deciduous broad-leaved trees are more demanding. If the conditions at the site are good, they grow very well and overtake the needle-leaved trees. But they cannot grow when the conditions are poor, and are displaced by needle-leaved trees. For example, we mostly see pines on the ridges of mountains and cliffs of Honshu. This is not because pines like such locations but because these areas are infertile areas and prone to droughts and therefore, broad-leaved trees cannot grow well there, and the pines can thrive. Ectomycorrhizae live
symbiotically on the root hairs of pines and provide to the pines the inorganic
nutrients and water that they absorb through their hyphae that spread through
the infertile soil. In Honshu, when a warm temperate broad-leaved forest (laurel
forest) is deforested randomly and the land becomes barren, Akamatsu (Pinus
densiflora) appears and gets established, covering the mountain. Even in such
Akamatsu covered mountains, after many years, when the fallen leaves
accumulate and the land becomes fertile, the original broad-leaved tree flora starts
reentering the forest.

Leaves of needle-leaved trees have a well-developed structure and functions
adapted to droughts in summer and winter, strong winds and snow cover. In short,
their leaves are thick, with small surface area and their surface cuticular layer
secretes large amounts of wax making itself thick. The stomata are located at the
bottom of depressions on the leaf surface and their surface is covered with wax,
which prevents rapid transpiration from the leaves. This wax reduces the rate of
photosynthesis to about 2/3rds and the transpiration rate to about 1/3rd\textsuperscript{136}.

*Translator’s notes:*

*Words added by the translator for clarity are given in [square brackets]*
Two types of evergreen needle-leaved trees are dominant in the subarctic forests in the permafrost areas of Alaska and Canada. A few deciduous broad-leaved trees like white birch and two types of poplar, are interspersed with the evergreen needle-leaved trees, creating a succession in the forest (shinrin no seni o keisei). Similar subarctic evergreen needled-leaved tree forests exist in Western Siberia where there is no permafrost. But in the permafrost zone of Eastern Siberia, which has a dry continental climate that is the coldest on earth, the deciduous Dahurian larch (Larix dahurica ssp. cajanderi), which can live in a natural environment prone to disturbances, dominates over a large area forming a highly dense forest. In such forests, almost no evergreen needle-leaved tree species other than European red pine (Pinus sylvestris) grows. Also, white birch is the only deciduous tall tree that occurs intermixed with these needle-leaved trees. The subarctic forests of Eastern Siberia that exist in an extreme natural environment and special topographical conditions, maintain a balance with the environment, with only a few tree species and low ecological diversity. This is in stark contrast to tropical rain forests where numerous tree species coexist under a stable tropical environment. If Eastern Siberia gets warmer and its soil gets enriched in the future, increasing the diversity of tree species, the current ecosystem would probably collapse.

Forests of Eastern Siberia, where Dahurian larch dominates, were formed during the postglacial period (11,000 years ago) and are relatively new. At that time, rivers were often flooded and soil and mud got accumulated on the permafrost formed during the Ice Age. Forest trees that had been forced southwards during the last Ice Age (70,000 to 11,000 years ago) moved north again forming new forests. In this region, where a dry climate prevails throughout the year, damage by forest fires is particularly frequent. Dahurian larch and birch are both shade intolerant pioneer species and have a particularly high capacity for recovery and renewal after disturbances like forest fires.

When I surveyed the permafrost regions of Alaska and Eastern Siberia, I noticed that in the interior parts of Eastern Siberia, particularly Yakutsk and the parts east of it, had a larger temperature variation during the year than Alaska or Canada, and that its climate was dry and continental. This can be understood from
the fact that the larch of Eastern Siberia has a bark that is more than twice as thick as in needle-leaved trees of Alaska, to prevent dehydration, and that the soil pH in Eastern Siberia is abnormally high (8-9) as in deserts and arid areas. Compared to interior Eastern Siberia, forests of the permafrost zones in interior Alaska and Canada, where evergreen needle-leaved trees are dominant, are relatively warmer and more humid and may be said to have a coastal climate.

(1) The extreme cold of Eastern Siberia

During the long winters, Eastern Siberia comes under the influence of dry arctic air masses. Because of this, there is not much snow cover and dry weather prevails. The average monthly temperature during December to February is about –40ºC in Yakutsk (N Latitude 62º) and mean the annual temperature is about –10ºC, about the same as at the Syowa Base in Antarctica. The mean of the annual minimum temperature of the past 21 years is about –64ºC, which makes Yakutsk the coldest place on earth. Its winter temperature is about 20ºC lower compared to Western Siberia and interior Alaska, and the climate is very dry. Besides, most of Eastern Siberia has permafrost. In Yakutsk, the permafrost layer is almost 250m deep. This is because Eastern Siberia was not covered by the continental ice sheet during the Ice Age (about 1.6 million years ago), except in the mountainous regions. So, the land was cooled and the permafrost was created. In the summer, from July to August, the temperature is fairly high in Yakutsk. The mean temperature in July is 19.5ºC, about the same as in Sapporo. The annual precipitation is 213mm, comparable to that in the steppes of Central Asia. Almost half of the precipitation falls during the growth period, i.e., July-August. Only about 35mm falls during the winter. The snow cover is about 30cm. It is difficult for us to imagine, from such data, the severity of the cold and dryness. I shall recall here a passage from the book “Oroshiya Kokusui Mutan” by Yasushi Inoue that describes the scary cold weather that the few Japanese seamen had to face when they reached Yakutsk after their ship drifted over, more than 200 years ago. “It was the 9th day of November when 6 Japanese, including Koudayuu (the protagonist), who had set out from the Okhotsk region and reached Yakutsk, a settlement on the banks of river Lena, after passing through endless primeval forests, sometimes on horseback and sometimes on foot. The coldest season had already set in. Koudayuu and his companions realized, for the first time in their lives, that there were different degrees of cold. There were quite a few travelers in the town. All
were wearing many layers of clothes made of animal hide, and fir caps. They also had large cylindrical gloves called *Mufta (Mufuta?)*, made of bearskin and lined with fox fur inside. They walked around placing their gloved hands on their foreheads, exposing their eyes only, as the nose and parts below it were also covered. All these travelers seemed to be accustomed to the cold of this area. Still it was not uncommon to lose an ear, the nose or a finger. Some were walking on a wooden leg with the help of a stick. Some others had faces that looked like one cheek had been scooped out. Such disfigurement from frostbite was seen both among the old and the children, and both men and women. Koudayuu, with firsthand experience of the incredible cold of the area, strictly prohibited his 5 men from going outdoors without a very good reason.”

The winter conditions in Yakutsk 200 years ago would not have been very different from what they are today.

Permafrost is formed by a gradual freezing of the soil from the top down. Therefore, it would appear that the maximum depth of permafrost and the time needed for freezing to reach that depth would be determined by the surface temperature and the thermal conductivity of the frozen soil. According to the calculations of Fukuda\(^26\) based on simple assumptions, if a ground surface temperature corresponding to a mean annual air temperature of \(-3^\circ\text{C}\) were maintained continuously for 1000 to 20,000 years, the permafrost would reach a depth of 200 m. The reason for the wide variation in time required for this is the difference in thermal conductivity of soils. Fig 59 shows a laboratory of the Permafrost Research Institute of Yakutsk, made by scrapping out frozen soil to a depth of about 10-15 m.
Fig 59 An underground laboratory of the Permafrost Research Institute (10–15 m below ground level; the temperature was about −4°C) (photographed by the author).

(2) Forests that coexist with permafrost

First, I would like to explain how Dahurican larch forests were formed. In Eastern Siberia, from the middle of the Ice Age of about 0.2 million years ago, the area under larches of Siberian origin and evergreen needle-leaved trees shrank and these species were forced westwards. It is believed that as the cold and dryness became more intense and the permafrost region expanded, from the second half this Ice Age to the last Ice Age, the Dahurican larch, suited for such extreme weather, evolved and expanded its distribution to Eastern Siberia.

The Yakutsk region is dry throughout the year. The annual precipitation is about 200mm, something like a day’s downpour in Japan in the summer. The roads are dry and the soil is ash-like up to several cm from the surface. Normally, only
grass can grow in such dry areas. Conditions are not suited for the establishment of forests. In spite of this, the taiga, which are Dahurian larch-dominated forests, exist in Eastern Siberia over wide areas spanning 1000 to 2000 km in the north-south direction. The secret lies in the permafrost. If there were no permafrost, the meager rain water and the snowmelt water of spring would have been absorbed deep into the soil in no time, leaving the surface absolutely dry and the area would have become a steppe or a desert. The frozen soil prevents loss of water by seepage. Besides, its loss by evaporation is also prevented in the forests, unlike on bare land. So, the rainwater and snowmelt water are stored in the active layer (thawed layer) of 60-80cm from the surface, which gets thawed in the summer and remains frozen in the winter. The water in this active layer is a reservoir for the Dahurian larch and other flora and the fauna living on the ground surface and underground. In a sense, the permafrost below the active layer is a dead world, whereas the active layer that melts in summer is the source of life and has an abundance of natural blessings. Also, the forest prevents the active layer from becoming abnormally deep and the settling of the ground that occurs when the large underground ice wedges melt (Fig 63). The forests and permafrost of Eastern Siberia have this type of interdependence. It is however, feared that this delicate balance could be disturbed by global warming, forest fires, large-scale felling of forest trees, etc.

(3) Survey of a forest near Lake Saldaha

On August 12, 1972, our survey team reached the shores of lake Saldaha (Suldaha), which is about 350km northeast of Yakutsk. This lake, which is about 4km in diameter, is located at a hilly site between the rivers Lena and Aldan. The lakeshore cliff edge is about 20m above the water level. A forest is established on these cliffs. The lake is about 6m deep. My first impression on entering this pure Dahurian larch forest (Fig 60) on the lakeshore, with its 10m tall trees, was very different from what I had imagined. I had an image of Siberian taiga being a dark dense forest with very tall trees. Although it was mid-August, the forest was bright, like a forest with fresh green spring growth in Hokkaido. There were no mosquitoes or horseflies, perhaps because all insects had already entered diapause. The ground surface had a 5-10cm thick litter layer of fallen larch leaves. Some cowberries, bog bilberries, arctic creeper willows, mosses and lichens covered the surface of the litter layer. A few Siberian irises could also be seen there. To determine the frost hardiness of plant roots near the ground surface, we brought
some of the irises to Sapporo and measured their frost hardiness in winter. We found that the leaves tolerated freezing to –70ºC and the roots to –35ºC. This meant that the roots of these forest floor plants could survive even when the soil temperature dipped below –30ºC.

At 3pm in the afternoon, when the ambient temperature in the forest was 22ºC, the soil temperature measured after removing the several cm thick litter layer was 8.5ºC, which was fairly cold to my touch. The soil was sandy silt and could be easily dug up with a gardening trowel. I lay down on my belly and sampled the soil from every 10cm going down, and measured the soil temperature also. At 70cm from the ground the soil temperature was 0ºC and I encountered a hard frozen soil layer. This meant that the ground in this forest floor had thawed to a depth of about 70cm at the end of August. Roots of the larches were mostly located 10-30cm below the ground, where the soil temperature was a fairly low (4-7ºC). The soil pH was a highly alkaline 8-9, except near the ground surface. Analysis of the soil showed that this high pH was because of large amounts of calcium carbonate present in the soil. As the region receives very little precipitation in the summer, the moisture in the soil does not move downwards. Rather, it moves in the opposite direction, i.e., from the soil to the ground surface where it evaporates. Because of this, large amounts of calcium carbonate accumulate in the middle to upper portion of the thawed active layer. These measurements had been made in mid-August, where the ambient temperature was the highest, the thawed soil layer was the deepest, and the soil was the driest, in that region.

In the second half of May, after the spring thaw, the active layer is probably still very shallow and the soil fairly moist. The roots of Dahurican larch seem to posses a special ability to live in such excessively wet and cold soils. After mid-July, the active layer becomes quite deep, transpiration from the leaves increases and the soils become dry. The Dahurican larches have already stopped growing by this time. Soon, by the end of August, the soil starts freezing again. The Dahurican larches cannot extent their tap roots down more than 50cm or so because of obstruction by the frozen soil. But the lateral roots can become as long as 10m and get entangled with other lateral roots to form a network that supports the aboveground parts of the trees.

To find out the general conditions of this Dahurican larch forest, we measured the
chest height diameter and height of the trees, and took the tree counts at two locations A and B within the forest. We also cut down a few trees to study their growth and age and to cut out discs of the trunk at different heights. At location A, 65% of the trees had a mean height of 8m and mean diameter not more than 8cm. The tree count was 7,600 per ha and the trees were 70-80 years old. At location B, 80% of the trees had a mean height of 5m and diameter not more than 4cm, showing signs of suppressed growth. The tree count was 16,000 per ha and trees were 70-80 years old. A small percentage of trees at location A were very large, with diameter 20-22 cm. It appeared that this forest was one that got renewed after a forest fire 70-80 years ago. In this forest, even trees with the best growth had a tree ring thickness of not more than 2mm, the mean being 1 mm and the minimum 0.06mm. This data suggests the impoverished condition of the environment of these Dahurican larches.

Another surprising finding in this survey was that the proportion of the bark in the cross-sectional area of the trunk was as much as 25-30%, i.e., the bark was extremely thick (Fig 61). This is far higher than the bark ratio of 12% in the needle-leaved trees of the Alaskan permafrost region. This is a sign of the remarkable adaptation of Dahurican larches to the dry climate and forest fires. As in pines of arid areas, the cones of Dahurican larches open only when exposed to high temperatures in a forest fire. Then they disperse a large number of seeds and the forest gets renewed.

I had made these measurements myself, in about 5 hours. During these hours, I got engrossed in my work, like a person uncovering treasures in a treasure trove. When I had finished the observations, two other team members, who were physicists, and the interpreter were already at a supper of fish soup, made from fish caught in the lake and prepared by one of the two Russians who had accompanied us. We chatted happily, looking at the beautiful evening sky. The authorities had unexpectedly granted permission to us to conduct the survey and collect materials. Placing rucksacks full of soil and tree trunk specimens that I had collected, near my pillow, I slept contentedly in a tent in the forest. This was to become my first and last survey of a forest in Eastern Siberia.
Fig 60 A pure Dahurian larch forest near lake Saldaha. The mean tree height is about 10m and the age of the trees about 100 years.
(d) **Characteristic features of forests of Eastern Siberia**

i  **Habitats of Dahurian larch and European red pine**

The active layer is very deep in Eastern Siberia in the sandy soil along the rivers and half way up the slopes. Pure stands of European red pine (*Pinus sylvestris*) can often be found in well-drained sites. Contrary to this, Dahurian larches dominate at the bottom of the slopes and on flat lands where the active layer is not very deep and the drainage is poor. These two kinds of needle-leaved trees occupy different habitats, depending on the depth of the active layer and the drainage and other soil conditions.*
The Dahurican larch of Eastern Siberia has spread to all parts of that area where trees could possibly grow, whether on mountains or in valleys\textsuperscript{10}. Many of these forests have 10-20 m tall trees with chest height diameter 10-40 cm. They have mostly developed after forest fires (Fig 62). The trees in these forests look somewhat malnourished, reflecting the severe and unfavorable climate and soil conditions. When we remember the adverse conditions of Eastern Siberia, such as the complete freezing of the trunks and roots and the inability of roots to absorb water during the 7 months from October through April, the extreme cold of the winter season, the generally dry climate throughout the year, the excessively wet and cold soil during the growth period, and the shortness of the growth period, we come to believe that no trees other than Dahurican larch could have become the dominant species of these forests.

Around the Da Hinggang mountains of inner Mongolia, the Dahurican larch can surpass other species when the soil is excessively moist and cold. But it cannot compete with white birch in well-drained fertile soils. For this reason, these larches are often seen on the northern slopes or at the bottom of southern slopes where the active layer is shallow and the soil temperature is low. Contrary to this, white birch is distributed half way up the south-facing slopes where the active layer is deep and the soil is well-drained\textsuperscript{49}. The Siberian larch (\textit{Larix sibirica}) widely distributed in Western Siberia prefers warmer and better drained land than Dahurican larch. Thus, these two larch species occupy different habitats, depending on the geoclimatic conditions. The Dahurican larch, white birch and European red pine of eastern Siberia are all shade intolerant tree species. They have a high capacity for natural renewal after forest fires (Fig 62).
(ii) Risks faced by overwintering evergreen needle-leaved trees

Spring is the riskiest time for overwintering evergreen needle-leaved trees in the subarctic zone. As spring approaches, the sunlight becomes stronger and the daylength increases. This makes the leaf temperature fairly high. But roots are still frozen and no water is supplied to branches and leaves. At this stage, the needle-leaved trees are forced to make a choice. They could keep the stomata on the leaves closed to prevent moisture loss and not carry out photosynthesis, or open the stomata and photosynthesize, risking moisture loss. Generally, pines keep their stomata closed, while spruces open them and photosynthesize. Larches, which are deciduous trees, completely avoid this serious dilemma. Larches have other
advantages also. Unlike the evergreen needle-leaved trees, they do not have leaves at the time of the spring thaw and therefore, the forest floor is exposed to more sunlight and the snow and frozen soil thaw faster.

(5) **Alasses in forests**

A number of dish-shaped depressions, swamps and lakes of various sizes are scattered in forests on riverside hills along river Lena to the east of the city of Yakutsk. These are called *Alasses* in the Yakut language. In the permafrost region of Eastern Siberia covered with forests and tundra, huge, almost 10m deep, ice wedges in fact exist hidden underground. The locals call them *Edoma* (I in Fig 63). These *Edomas* are frequently found near the estuaries along the coast of the Arctic Sea and at riverside ridges between the rivers Lena and Aldan. Quite a few are found in the forest areas near Lake Saldaha. The *Alasses* of this region are peculiar topographical features formed by the huge underground ice wedges melting when the ground surface is exposed by felling of trees or forest fire and evaporation of the melted water, which causes the ground to sink and form thermokarst depressions (Fig 64). Many of the *Alasses* have water in them and the surrounding areas are used by the Yakut people as pastureland. Lake Saldaha was also probably formed in a similar manner, i.e., a forest fire destroying the vegetation cover, melting of the ground ice, sinking of the ground and accumulation of melt water in the depression. It has no inlet from or outlet to any river. The thawing of ground ice by the sunlight and consequent falling over of trees continues even now near the southern shore of the lake. The *Edomas* are believed to have formed within the permafrost during the Ice Age when there was little vegetation. During the post-glacial age, when the rivers flooded, soil accumulated on the *Edomas* and larch forests grew on it, it is believed\(^\text{26}\).

Lake Saldaha, which is about 6m deep, freezes to a maximum of about 2.5 m from the surface in winter. The water below this ice layer remains unfrozen all year round. Some fish also live there. Since the lake is not connected to any river, these fish were probably brought in by people. Currently, the melting of the ground ice at the lakeshores and the evaporation of water from the lake surface are more or less balanced and the water level remains almost constant. In many other lakes, the evaporation exceeds the melting of ground ice and the water body shrinks every year. Perhaps Lake Saldaha may also one day dry up because of evaporation, it
would be covered by mud and soil and a forest would then reemerge there. Such natural processes have been continuing on an unimaginably vast timescale.

The gigantic masses of ground ice (Edomas) contain plenty of bubbles with a lot of methane gas trapped in them. The Edoma layer is unstable under the current climatic conditions. Probably, with the advancement of global warming, the Edoma layer would melt, and the collapse of the forests, destruction of roads, and the release of methane from the Edomas would emerge as new problems. These possibilities are now being studied in relation to global warming.

(6) Shergin's well

Since ancient times, Yakutsk had scarcity of drinking water in the winter. About 170 years ago, an entrepreneur named Shergin started digging a well with chisels for obtaining drinking water for the winter. After digging about 28 m in about 3 years, he found only permafrost, as hard as cement. He had the well dug to a depth of 116 m in about 10 years. Still there was no water, only frozen soil. Shergin was finally forced to abandon the project as he had run out of funds. A few years after that, Mittendorf, an explorer-scientist found out about this well and measured the soil temperature at different depths. It was -6°C at 30 m and -3°C at 116 m. He then extrapolated the temperature downwards and estimated that the lower limit of the permafrost was about 250 m below the surface. No water was ever to be obtained from this well, but unexpectedly, this Shergin's well provided an opportunity for studying permafrost in Siberia. It was decided to preserve the well under the care of the Russian Academy of Sciences. I visited the well in 1972. I bent forward carefully and peeped into the well. It was about 1 m wide and the frost on the walls was shining white from the light of a naked bulb (Fig 65). The bottom was blurred in the darkness of 116 m below the ground. I heard that water entered this remarkable well during the 1988 flooding of the Yakutsk region and froze it shut.
Fig 63  A larch forest and ice wedges at the shore of Lake Saldaha.

Left: A cross-sectional diagram of the lakeshore. I: Ice wedge, about 40m deep. L: Loam layer. W: lake water. The height of the cliff at the lakeshore from the water is about 20 m.

In the Fig at the bottom: Frozen soil.

Right: A close-up of collapsed ground at the lakeshore. The roots (indicated by the arrow) are about 5m long and near the ground surface. An approximately 1.5 m deep soil layer is present above the ice. The ground has collapsed because of melting of the ice wedge.
Fig 64 Thermokarst depressions caused by melting and evaporation of ice wedges after felling of forest trees. A hexagonal pattern is seen about 3 months after felling of the trees. The ground has sunk by about 1 m. It would reach equilibrium after sinking to about 10 m, but the collapse of the forest continues on the southern slope because of the melting of the exposed ground ice.
Fig 65 Shergin's well (Photographed by the author in 1972).

Translator’s notes:
1. Parts where the source text is ambiguous or apparently needs some modification are marked in pink.
   1# Different times have been specified for ice ages. This is somewhat confusing. Perhaps we should give the names of the different ice ages.
2. Words added by the translator for clarity are given in [square brackets]
3. The translation of the words marked in orange is uncertain. The corresponding Japanese words are given phonetically in parenthesis.
The evergreen forests of New Zealand with their shining glaciers

There are huge continents like Eurasia and North America now in the Northern Hemisphere around the Arctic Sea. The Southern Hemisphere once had Gondwanaland around Antarctica. But from the Jurassic to the early Tertiary (about 50 million years ago), the current continents of Africa, Australia, India and South America got separated from it one after another (see Fig 47). The parts vacated by these land masses became a large ocean in the Southern Hemisphere. Most of the land masses originating in the Southern Hemisphere later became attached, directly or indirectly, to the continents of the north. Nevertheless, the temperate areas of the Southern Hemisphere had long remained isolated from the Northern Hemisphere, and therefore, different species of plants evolved there, under the mild oceanic climate. Thus, the beautiful needle-leaved trees of Pinaceae, such as pines, firs, and spruces, which we in the Northern Hemisphere are familiar with, are not found there. Instead, the Southern Hemisphere has needle-leaved trees of Podocarpaceae some of which we can also see in the warm temperate areas of Japan. Besides this, the beautiful fresh green leaves and fall colours of deciduous broad-leaved trees that we see in the temperate zones of the Northern Hemisphere are almost nonexistent in the south, except for those transplanted from the Northern Hemisphere. The Southern Hemisphere, with its mild oceanic climate, is a world of evergreen trees, the uniformly dark green trees covering the area up to the tree line. The forests are relatively simple, showing very little change with the seasons. They look rather drab compared to the temperate forests of the Northern Hemisphere.

(1) Glaciers and evergreen broad-leaved forests

Around 1975, I came to know that forests of Nothofagus solandri (Fagaceae), an evergreen broad-leaved tree of New Zealand, grew very close to glaciers. In my mind, somehow, glaciers were associated with severe cold and I could not connect them to warm temperate evergreen trees, which cannot withstand much cold. Besides, at that time, very little was known about the frost hardiness of plants in the Southern Hemisphere. I therefore embarked on a study of cold acclimation of plants of the Southern Hemisphere, particularly those originating from Gondwanaland, to compare them with Northern Hemisphere plants. This was a 3-year joint study with Dr. Wardle, a well-known biologist of New Zealand. Firstly,
I studied the climate data of New Zealand and learned about temperate glaciers from my glaciologist colleagues at the Institute of Low Temperature Science.

(2) The climate of New Zealand

Both the South Island of New Zealand (Fig 66) and Tasmania of Australia have high mountain ranges running in the north-south direction close to their western coast. In the winter, strong westerly winds blow against these mountains, bringing as much as 3500-5000 mm of precipitation per year to the area west of the mountain. This falls as snow in the mountainous areas. Besides, the summers are cool and the snow accumulated in the winter does not melt completely, resulting in the formation of glaciers. Unlike in polar glaciers, the temperature of the snow in these temperate glaciers is 0°C. Similar glaciers exist in the central part of southern Chile and in Patagonia, which faces the Pacific Ocean in the Southern Hemisphere. The South Island of New Zealand is located at about the same latitude as the Japanese Archipelago on the other side of the Equator. But the former has glaciers on its backbone mountain and evergreen *Nothofagus solandri* growing even very close to the moraines of the glaciers, where these trees form the tree line (altitude 1000-1200 m) (Fig 67). Near the western coast, there is a warm temperate rain forest, which looks like subtropical forests with its dense growth of evergreen trees and ferns, including a few subtropical tree ferns. Glaciers originating in the mountains cross this forest and run into the sea. This is a scene found nowhere in the mid latitudes of the Northern Hemisphere. But similar landscapes can be seen in Patagonia. The mean temperature in winter is 6.6°C at Hokitika (Fig 66) on the west coast (the January temperature of Kagoshima in southern Japan) and in the summer it is 15°C (July temperature in Kushiro and Nemuro in the eastern tip of Hokkaido). Thus, the temperature difference in a year is only about 8°C. The annual temperature difference is 20°C in Kagoshima and as much as 25°C in Sapporo.
**Fig 66** South Island of New Zealand. M: The dividing mountain range running north south near the west coast. P: The tree line in this area.

**Key:**

*In the Fig, clock-wise from top left:* Hokitika; Christchurch

*In the inset, clock-wise from top left:* Auckland; Rotorua; New Zealand; Christchurch

(3) Cold acclimation of plants of the southern hemisphere

In the first year of our joint research, [shoots of] typical evergreen broad-leaved and needle-leaved trees were collected from different heights in winter, brought to Sapporo, and their frost hardiness measured after exposing to low temperature. From the next year, I requested my collaborator to send shoots from the same trees under cooling at 0°C by air to Sapporo, which took one day. We had also expanded our study to Australian plants. The findings were compiled and published in the international journal, *Ecology*\textsuperscript{103} after 3 years. This paper of ours gave a
Our study showed that temperate trees of the Southern Hemisphere, both needle-leaved and broad-leaved, had a frost hardiness of only about -18 to -20°C. Fig 68 shows the frequency distribution of the frost hardiness of two sets of 30 broad-leaved tree species each. One set (black bars) consisted of evergreen and deciduous trees of the warm temperate and temperate zones of Honshu, Japan and the other set (white bars) consisted of evergreen trees (and a few deciduous trees) from New Zealand, Australia and the south-central region of Chile. We can see that many of the broad-leaved trees from the Southern Hemisphere had a frost hardiness of about -15°C. This is about the same level as in the warm temperate evergreen trees of Honshu. None of the trees from the Southern Hemisphere could tolerate temperatures lower than -25°C, which the cold temperate deciduous trees from Honshu could withstand.

The needle-leaved trees from near the tree line in the Southern Hemisphere had a frost hardiness of about -20°C, about the same as temperate needle-leaved trees, like Cryptomeria japonica, fir and Tsuga growing at about 1000 m on Yakushima Island (in Japan, about 30° N Latitude). These facts suggest that these trees did not evolve in the direction of high frost resistance with the ability to withstand temperatures lower than -25°C, unlike the cold temperate broad-leaved trees and subarctic needle-leaved trees of the Northern Hemisphere. Such high frost resistance is probably not required because the middle and high latitudes of the Southern Hemisphere have an oceanic climate with a small annual temperature difference and no dry intense winter cooling even near the tree line in the interior. Another possible reason could be that the needle-leaved trees of Pinaceae and the temperate deciduous trees of the Northern Hemisphere did not cross the equator to the south and therefore did not interbreed with the trees of the Southern Hemisphere.
(4) Mass planting of pines in the Southern Hemisphere

Needle-leaved trees of Pinaceae have not spread south beyond the equator. The needle-leaved trees of the Southern Hemisphere do not have much commercial value. Because of this, from around the 1930’s, pines were planted on a large scale in the warm temperate zones of New Zealand and Australia. The trees have been improved by many years of breeding and New Zealand and Australia have become sites of huge experiments on pine breeding. They have now become major global producers of pinewood.

Annual precipitation in the parts of southeast Australia a little away from the coast is 500-800 mm. In this area, we often see forests of miscellaneous trees, such as naturally growing eucalyptus, acacia, etc, with somewhat poor growth and a height of a few meters only. Some of these forests have been cut down and replanted with pines from the northern Hemisphere, in large-scale experiments.
Pinus radiata was found to be the best suited for these areas. In Australia, where native broad-leaved trees do not grow because of insufficient precipitation, pines from the coastal dry areas of California, which can tolerate aridity and poor soils, were brought in and planted in large numbers in this manner. I was once taken in a helicopter from the capital Canberra to see these plantations. There were endless expanses of neatly laid out pine forests as far as the eye could see. These pines are cut down when they become about 30m tall, which takes 20-30 years. The pinewood is exported to Japan and many other countries. New Zealand and Australia have now become huge experimental farms of pine breeding and clone forestry†, which use conventional crossing and biotechnology for improving the pines and increasing wood production. Another objective is to contribute to ensuring sufficient biomass on earth in the future. One concern here is that we do not know the possible future effects of such large-scale planting of Northern Hemisphere trees in the Southern Hemisphere on the ecosystems of Australia and New Zealand. Finding the conditions under which artificially planted and natural forests can coexist is an important task for the future.

† Clone forestry: After crossing elite trees, lines that show good growth and have high disease resistance are selected. These are then mass-multiplied through tissue culture, allowed to grow into trees and planted as clones. Both conventional breeding through crossing and biotechnology are used in this method, and it yields high quality standardized wood in large quantities.

(5) Christchurch, the flower garden of the world

Christchurch (see Fig 66) is a city with a population of about 300 thousand people, in the South Island of New Zealand. It is a beautiful city, called the “Garden City of the World”, and located at about the same latitude in the Southern Hemisphere as Sapporo is on the other side of the equator. The summer there is cool, the temperature being about 16.5°C (as in Wakkanai at the northern tip of Hokkaido), and the winter is mild at 5.8°C (as in Kochi in southern Japan). It has an eternal spring like climate with an annual temperature difference of about 10.5°C.

The area was a wasteland about 150 years ago. But the new settlers tried their best to create a pleasant environment, like that of Oxford in their home country,
Britain. Spaces where the citizens could relax were created on the banks of the river Avon, which meanders through the center of the city. There are about 600 parks in the city. To mention the trees lining the streets, for instance, about 40,000 trees of 30 species were brought in from all over the world and planted. Many of its citizens have the hobby of gardening. Nearly 40 garden contests are held in this city alone in February, which is the main flowering season. It is like a flower festival of the Southern Hemisphere. It is a paradise of flowers created over many years by citizens who wanted a beautiful city.

The city's dry climate with a cool summer allows white birch, needle-leaved trees of the north, alpine plants and rhododendrons to grow there. Warm weather plants like camellias also grow there because of the mild winter. Thus, a wide variety of plants from both the hemispheres can be grown. It was impressive to see huge giant sequoias, the famous Californian trees, thriving in Christchurch.

*Translator’s notes:*
1. Words added by the translator for clarity are given in [square brackets]

Dr Sakai’s suggestions
p1, dark trees—dark-green trees
non existent —except transplanted from Northern Hemisphere
P.2 Kagoshima (southern part of Japan)
page 3: Kushiro, Nemuro -Eastern tips in Hokkaido
Page 4--Yakushima islnd (in Japan latitude about 30o)
Page 6 Wakkanai Northern tip of Hokkaido
page 6, Kochi--southern part of Japan
Thank you, Sakai
Warm temperate forests of Mother Himalayas with a monsoon climate

The southern slopes of the Himalayan mountain range that runs over a long distance in the east-west direction, northeastern India south of this range, Bhutan and the Yunnan province of China, are rather warm with a small annual temperature difference during the year, something like the eternal spring like climate of the Southern Hemisphere (Fig 69). The temperature of Darjeeling (North Latitude about 27° and altitude 2127m) in northeastern India, famous for its tea production, is about the same as in Christchurch (North Latitude about 43°), New Zealand. Kunming (North Latitude about 25°, altitude about 1800m) in the highlands of Yunnan has a mean temperature of 21°C in the summer and 9.5°C in the winter. Thus, the annual temperature difference is only 11.5°C. The outskirts of Kunming have many evergreen broad-leaved trees that are also found in the warm areas of Japan.

The Indian sub-continent is said to have been formed by fragmentation of Gondwanaland in the Jurassic period (150 million years ago) of the Mesozoic era when a land mass broke off leaving behind the central part that is currently Antarctica. It moved northwards, a few cm each year over a period of 100 million years and collided with the Eurasian continent in the early Tertiary (about 50 million years ago), it is said. As a result, the tropical Tethys Sea that had connected Southeast Asia and England via the Mediterranean Sea disappeared and Tibet and the Himalayas started to rise in its place. Their rise became faster after the Ice Age (about 2 million years ago) of the Quaternary. This long mountain range that lies along the east-west direction blocks the cold waves from the north in the winter. So, the area south of this mountain range came to have a mild climate and quite a bit of rain. But the area north of the Himalayas, where the monsoon cannot reach, became dry. The Indian subcontinent played a major role in transporting plants of Dipterocarpaceae from the south and in the tropical rain forests of Asia.

† Tethys sea: This is a tropical sea that existed between the continent of Laurasia in the north and Gondwanaland in the south, in the area from Southeast Asia to what is currently occupied by the Himalayas, reaching as far as Europe. The current Aral Sea, Caspian Sea and Mediterranean Sea are its remnants. The sedimented remains of organisms that flourished in this shallow tropical sea
turned into the oil deposits of Central Asia and the West Asia.

Fig 69 A map of the area around the Himalayan mountain range

Key:
Clock-wise from top center: Himalayan mountain range; The Tibetan plateau; Mt. Everest; Southwestern (Nansei) Highland; Kunming; Bhutan; Darjeeling; Kathmandu; New Delhi; Shimla; Pakistan

(1) The Southwestern Highland of China

The Southwestern Highland of China is a region that extends from the northwest part of Yunnan Province and southwest of Sichuan Province to the southeastern part of Tibet. The major rivers, Yangtze, Salween and Mekong run from north to south creating gigantic gorges. In this Southwestern Highland, the cold waves from the north are blocked and the winters are mild. During the monsoon, the seasonal winds from the southwest blow into the valley and bring in about 2000mm of precipitation even at 4000m altitude. This is the reason for the existence of forests at this height. The environment of the Southwestern Highland is complex and diverse. Moreover, because it is warm and receives a lot of rain, very diverse
plant and insect life exists there. This is also the place of origin of many plant species of eastern Asia, including rhododendron and rice.

The needle-leaved trees and rhododendrons of the Himalayan region, for instance, have spread from the Southwestern Highland, which is a treasure trove of plant species. For example, about 250 varieties of rhododendron can be found on this highland at a height of about 3000m, whereas the Himalayas have only about 30 varieties. This highland also has about 20 types of needle-leaved firs of Pinaceae, whereas the Himalayas have only one species each of fir, spruce, larch and Tsuga. The leaves of evergreen oaks, Castenopsis sieboldii, Camellia and related species, shine in the sunlight. Therefore, in Japan, they are called “Shoyoji” (trees with shiny leaves). Forests of these trees start from the southern slopes of eastern Himalayas, extend eastwards to the coastal warm areas of the Japanese archipelago, passing through Yunnan and other southern parts of China.

(2) Frost hardiness of Himalayan fir (Abies spectabilis) growing at the tree line

Suburbs of Kathmandu (1337m), the capital of Nepal, have dense forests of trees with shiny leaves. Tsuga and pines become predominant at heights above 2000m in the forests of eastern Himalayas. Himalayan firs form forests at the tree line. Deciduous broad-leaved trees can be found only on the northern slopes, at around 3000m where the soil freezes [in winter]. The Namche bazaar (altitude 3450m) in eastern Himalayas has a mean temperature of -0.3°C in January (the same as in Miyako). Shamboche, located above that (altitude 3900m) is at the tree line. The mean temperature in January is -4°C here (about the same as Karuizawa). This area has many foggy days in winter, and rime ice forms easily on trees because of updrafts. All this seems to suggest that the tree line in the Himalayas is not a very cold place after all. Himalayan fir growing at the tree line is a temperate needle-leaved tree like the firs and Tsuga growing naturally at 1000-1500m in Yakushima Island. So, I guessed that the Himalayan fir would have a frost resistance of only about -20°C. To verify this, I decided to measure the frost resistance, by differential thermal analysis, of buds collected in winter at the tree line.

Around 1978, little was known about the frost hardiness of Himalayan plants. I therefore, embarked on a study of their frost hardiness, together with Dr. Malla, a
renowned biologist of Nepal. In the first survey, in December 1979, we collected plants from different heights, trekking on the mountains for 2 weeks. They were placed in a corrugated cardboard box. These got warmed during the several hours it took for change of flight at the Bangkok airport, which was at more than 30°C even in the winter, and became useless. So, I visited Kathmandu once again after a month and waited there for 2 days to catch a regular flight from Kathmandu to Shampoche, and arrived at the Shampoche airport on a clear day. From there I climbed the steep slope for about 20 minutes, stopping occasionally to catch my breath and reached the Everest View Hotel at the top of the slope. This hotel provided a majestic view of Everest and it was in the midst of a Himalayan fir forest at a height of 3900m (Fig 70). I collected buds of Himalayan fir from this forest and flower buds of about 1m tall rhododendrons from the same forest. I brought the samples to Sapporo in a cool condition, exposed them to -3°C for 2 weeks and carried out differential thermal analysis. I found that the frost killing temperature of the buds of Himalayan fir was -18°C (Fig 71) and that of the *Rhododendron cinnamomeum* flower buds was -17°C. The frost killing temperatures of the buds of Nikko fir (*Abies homolepis*) from the mountainous region of central Honshu and flower buds of *Rhododendron fauriae* from Hokkaido, which were also tested in the same experiment, were both about -30°C. This confirmed my guess that Himalayan fir growing at the tree line in the Himalayas, at a height of 3900m, had about the same level of frost hardiness as firs growing at 1000-1500m in Yakushima Island\textsuperscript{104}. 
Fig 70 The tree line near Shampoche (altitude about 3900m). The Himalayan fir (*Abies spectabilis*) trees are about 8 m tall.
Fig 71  Differential thermal analysis of winter buds of Himalayan fir (Abies spectabilis) and Nikko fir (Abies homolepis) form the mountainous area of Honshu. Measurement was done after exposing the specimens to -3°C for 2 weeks.*104. T: Cooling curve of the bud. Spikes 1-11 represent frost killing temperatures of individual buds. H: Frost killing temperatures of Himalayan fir (1-5), M: Frost killing temperatures of Nikko fir (6-11).

Key:

Abscissa: Time (Each scale division is 30 minutes)

Ordinate: Latent heat of freezing, relative values

Inside the Fig, from left to right: Himalayan fir, Temperature, Nikko fir
(3) A trip to Shimla

I was requested by the National Bureau of Plant Genetic Resources (NPGR) in New Delhi and the Central Potato Research Institute (CPRI) in Shimla to deliver lectures at the end of February 1996, on the preservation of genetic resources in liquid nitrogen. So, I decided to visit Shimla, which I had wanted to do for a long time. After getting out of my hotel in New Delhi before 5 in the morning one day, I boarded the express train, Himalayan Queen, at 6. Around lunch time, the train reached Kalka where I changed to the narrow gage mountain train the track for which had been laid at the time of British rule. The train passed through dry lowland areas with cacti and arrived at Shimla, which still had some snow. I met my friend Dr Sukumaran and his wife, after a gap of 24 years. He, after obtaining his doctorate from the University of Minnesota, had spent one year at our laboratory in the Institute of Low Temperature Science, and returned to India at the end of 1972. Since then he had been doing research work at CPRI, Shimla.

There are virgin forests of deodar cedar (Cedrus deodara), a needle-leaved tree of Pinaceae, within Shimla. This tree is a well-known garden tree in warm areas of Japan. Red-flowered Rhododendron cinnamomeum trees grow on the forest floor. Shimla is a town, on a slope, at a height of 2300m, which was developed as the summer capital of British India. During the day, in late February, the temperature was about 20ºC, but the nights were quite cold and I could not fall asleep easily. I was reminded that after all, this was a hill station built as an escape form the heat of the summer. This town, developed on a slope, has mixed scenery, with a main street with mostly western style buildings and a downtown area that looked more traditionally Indian and Tibetan. Its population was about 70,000 and it was a favorite destination of honeymooners of North India. I could see the silvery white western Himalayas that extended to Pakistan from a hill near a ski slope on the outskirts of Shimla. Shimla falls in the monsoon zone and the rainy season is in July and August.

Mrs. Sukumaran, who hails from Hokkaido, told me, ”Felling of trees is prohibited in Shimla. You cannot cut the tree without special permission even if one of its branches protruded through your window.” During my stay in India I sensed a
general attitude of coexistence of people with animals and plants. Computer network infrastructure was not well developed in India. I had the hard experience of many of my flights being cancelled or delayed by several hours during my two weeks in India. In spite of that, I was deeply impressed by the diversity of peoples, languages, culture, religion and natural environments, the simplicity of the lifestyles of the people, their boundless gentleness towards nature shown through their efforts to live in harmony with all other living things, and their spiritual richness. India, with its diverse climate, is rich in plant genetic resources. The exploration, collection and preservation of plants have been actively pursued since ancient times.

(4) Mother Himalayas with its monsoon climate

In the summer, moist air blows into the subcontinent from the Indian Ocean and hits the Himalayan mountain range, which spans a long distance from west to east. This creates a very strong ascending airflow near the Himalayan Mountains of India and Nepal. The monsoon further advances to the east and northeast, riding on the strong jet stream. This brings monsoon rains to South Asia and the whole of Southeast Asia and the so-called Baiu (the rainy season) in the Japanese archipelago. Without the Himalayas, the monsoon would have reached only the southern part of India and the biodiversity of the forest flora and rice cultivation in Southeast Asia and the monsoon zones of the rest of Asia would have been very different from what it is today.

This monsoon climate extends to the Swat Himalayas at the western end of the Himalayan mountain range. The high Hindu Kush mountain acts as a divider near the international border between Pakistan and Afghanistan, with a Mediterranean climate with dry summers and wet winters to the west of it. By the way, the plants distributed in Japan and China (the Sino-Japanese floristic region) are found growing naturally on the southern slope of the Himalayas (the Himalayan corridor) up to its western end, in a band-like distribution. There are three types of cedar: one can be seen around Shimla. The other two types are seen in the coastal regions of North Africa, Lebanon and Syria, all of which have a Mediterranean climate.
Dr Sakai’s suggestions

Chapter 4: Himaラヤスギ  Cedrus deodora
himalayan spruce Abies spectabilis  urajiromomì: Abies homolepis,
hokusansyakunage R. fauriae  himarayashakunage R. cinamomeum
Sakai
5 Tropical rain forests with high biodiversity that never faced cold weather

Tropical rain forests are forests that have evolved in hot and humid environments with little seasonal change, where the growing conditions are stable and high production is possible throughout the year. Characteristic of tropical rain forests are giant trees that are sometimes as tall as 70m and other tall evergreen broad-leaved trees that form a complex multi-storied structure, and the coexistence of the diverse tree species and other living organisms, each in its own niche. Although tree species of tropical rain forests have a high production capacity, they depend on symbiotic relationships with ectomycorrhizae for obtaining inorganic nutrients needed to support such high production\(^7\). The area covered by tropical rain forests is only about 16% of the total land area of the earth. But they are packed with more than half of the known plant species. The tropical rainy zone is a paradise for evergreen broad-leaved trees.

(1) High biodiversity in tropical forests

The tropical zones of Central and South America and Africa, unlike other tropical zones, have a few months of dry period each year and clear-cut seasons, as in Thailand and Myanmar. However, in the Malay Peninsula, Sumatra and Borneo, which are almost directly at the Equator, have little variation in precipitation round the year. There are tropical rain forests in the low altitude areas below 1000m in Southeast Asia, where tall trees belonging to Dipterocarpaceae constitute the main flora. These Asian Dipterocarpaceae plants came in on the Indian subcontinent, which carried them from the Gondwanaland, and they spread over Asia. The tropical rain forest of Lambir National Park of about 52 hectares in Borneo is said to have about 1200 tree species. In comparison to this, the temperate Fagaceae forest around Kyoto has about 50 species and the almost natural mixed forest of needle-leaved and broad-leaved trees near the Tokyo University Experimental Forest in Hokkaido, has about 40 species. We can see that tropical rain forests have 20-30 times more tree species than temperate forests of the same land area. Why is it that so many different tree species can grow together in a rain forest? Firstly, there is the high level of incident solar energy. Also, the huge tall trees that reach a height of 50-70m allow the development of a complex multistoried structure (Fig 72) below their crowns and the members of each level show advanced ecological segregation\(^55, 56\). In such forests, it is important for
plants to grow fast so that they can get their share of the available light. There must be stiff competition through acquisition of special germination characteristics. But if competitive success alone was involved, only the efficient ones should have survived and driven away the other species. Thus, we cannot explain the high diversity of tree species in tropical rain forests in terms of the canopy heights and the number of stories alone.

Tropical rain forests characteristically have many different tree species, but the frequency of each species is very low. High species diversity and low frequency of individual species are two sides of the same coin. Under such conditions, the plants need effective multiplication systems for maintaining groups of scattered individuals of a species, and interdependence with other plant and animal species plays an important role. Many complex aspects have to be studied to clarify these relationships. These include the time of flowering of each species in the Dipterocarpaceae forest, pollinating behavior of insects, interdependence of plants with insects and other animals and the kinds of insects living in the forest.

In 1982, Erwin lifted a sprayer to the crown of a tree in a tropical rain forest of Cuba with the help of a pulley and sprayed Surin E to collect the insects available there. Only 2% of the insects collected were known species. The following year, Erwin confirmed this in the tropical forest of Amazon. It thus became clear that a huge number of so far unknown insect species live in the tropical forest canopies. Erwin’s report triggered similar studies in other tropical forests, which yielded similar results. This work has opened the door to an unknown world and new field of study called Canopy Ecology. The forest canopy at a height of 70m from the ground gets the maximum sunlight. The productivity is highest, and the ecosystem must be the most diverse. But no one had noticed it because of the height.
The fact that Dipterocarpaceae forest trees flower on an approximately 5-year cycle was known from the quantities of seed and fruit that fell down. Professor Tamiji Inoue and his team from Kyoto University fashioned observation towers and hanging bridges and climbed up to the top of the canopy of the forest of the Lambir National Park in Sarawak, Borneo, to observe flowering. There was no flowering for 4 years. But finally, in March 1996, they observed flowering for the first time, and it continued up to July. They subsequently clarified the time of flowering, interrelationships between plants and insects, and pollination by insects and animals in about 500 species. In the forest surveyed by them, even among the
Dipterocarpaceae trees, which were the largest in number, only about 2 trees of each species flowered in a 100m$^2$ area. The approximately 1200 tree species of the forest did not all flower simultaneously in the 4-month long flowering season; they appeared to flower in a certain sequence. A surprising fact was that the trees of the same species flowered in a synchronized manner. For instance, even if there were only a single tree in a 1km$^2$ area, it would flower at the same time as other trees of the same species. This was probably because pollination cannot occur if they were to flower at different times and there would be no progeny. Flowers of some trees opened during the day. But most flowers opened in the evening and dropped in the morning, lasting only for a short time. The pollinating insects visited the flowers when they were open, whether at day or night, to transfer the pollen. Insects did the pollination in about 80% of the cases, and the rest was done by birds and mammals. Among the insects, the most common pollinator was sawfly, which accounted for about 50% of the pollinations, followed by beetles, about 20%. It is not an easy task to stay awake all night and make observations at the height of the canopy, collect the insects that fly into the canopy, identify them and confirm that they actually did the pollination. During this simultaneous flowering, 402 tree species belonging to 189 genera of 65 families were seen by about 35 researchers to flower at the same time. Out of these, the pollinators of 141 species have been identified$^{141}$.

Tropical rain forests have high diversity of tree species but very low frequency of trees of any one species. For all these tree species to survive, they must produce seeds and leave progeny. It was a mystery why they had to flower at the same time and in 5-cycles. During simultaneous flowering, all buds become flowers and no new leaves at all are formed. According to Professor Inoue, trees invest a lot of energy for bearing large numbers of flowers in this infertile tropical forest with not much humus in the soil. Therefore, they probably store nutrients for 5 years (it is not known in what form) and produce a large number of flowers for 3-4 months once in 5 years. Probably, these many flowers are required to attract the insects. Once flowering occurs, large numbers of bees and other insects arrive there, feed on the nectar and pollen and multiply. At this stage, bees divide their hives. After this, the bees live on meager resources until the next flowering 5 years later. The massive simultaneous flowering, once in 5 years, appears to be a Festival of Reproduction for both the plants and the insects. The details of the life of the pollinating insects, which is synchronized with the flowering cycle, are
gradually being understood. In places like tropical rain forests, where there is little seasonal change, there are a very limited number of environmental cues that can trigger flowering, and afford the opportunity for exchange of genes. In January 1996, days with a minimum temperature of less than 20°C continued for a week. This abnormal low temperature occurred because of strong radiative cooling during a long span of clear weather caused by the El Niño phenomenon. It would be interesting to speculate that this low temperature became a trigger for the simultaneous flowering of the trees of the tropical rain forest that had never known such cold weather. But observations over a longer period would be needed to verify this.

The energetic studies of Professor Inoue and his team had shown that a tremendously large number of insect species, nearly 100 of bees alone, existed along with the 1200 tree species in this forest. Even the relationship between the plants and the bees itself appears to be very complex. After the flowering, the trees would produce fruit simultaneously, around October, and the animals would gather from over a wide area to consume these fruits. Newspapers of September 7, 1997 had this report: “A small plane with 10 persons on board, including two Japanese, had crashed after hitting a hill inside the Lambir National Forest, near Miri, Sarawak State, Malaysia at 7:44 PM on September 6, killing everyone on board. Professor Tamiji Inoue (49) of the Center for Ecological Research of Kyoto University was among them”. The next day’s papers carried the confirmation by Kyoto University officials that Professor Inoue had indeed died. Professor Inoue met with sudden death in the Lambir forest, the very land that he had been studying, just before the trees would bear fruit in October.

Pollen has to be dispersed for plants to survive. How they survive in different parts depends on whether the pollen is randomly dispersed as in wind-pollinated plants or whether it is carried to appropriate places by animals following certain rules. Needle-leaved trees, which are gymnosperms, are wind-pollinated. But most angiosperms have advertising devices called flowers to attract insects, which transfer the pollen. This system was perfected around the second half of the Cretaceous Period of the Mesozoic Era (about 100 to 80 million years ago). The emergence of insects, flying insects in particular, and adaptation of the angiosperm flowers for pollination by them were the prerequisites for this to happen. These developments enabled a rapid increase in the variety of angiosperms and a spurt of
diversification and differentiation of species. This is because a kind of contractual relationship had been established between flowers and insects. Birds and mammals were almost non-existent at that time. When they appeared later, they mainly played a role in dispersing the seeds. For monkeys, which emerged after the birds during the Oligocene (about 30 million years ago) of the Tertiary, finding tasty fruit (the hard seeds are dispersed with the feces *(Shushokugata)*) became a means of survival.

I cannot forget these words of professor Inoue: “Rain forests, which hold such diverse life forms, are so valuable because only there can we perceive the history of co-evolution of living organisms during the last 100 million years”. I sincerely pray for the peace of his soul.

At the time of simultaneous flowering of the forest trees of Lambir, studies were undertaken on 64 species of wild fruit dispersed through frugivory *(Shushokugata)*, including mango and durian. The day-foraging primates of the forest that used to disperse the seeds of these fruits had already been eliminated by humans. So the fruits were rotting where they had fallen or their seeds were eaten by animals other than those that had originally dispersed them. So, the forest had already lost the seed dispersers needed for maintaining it. Thus, even though the biodiversity of trees is still maintained, the network of living organisms that created this diversity does not function any more and the forest is well on its way to becoming a relic forest. Tropical forests can remain stable only when a wide variety of animals and plants form complex ecosystems.

(3) **Mount Kinabalu**

Mt. Kinabalu (altitude 4100m) *(Fig 73)* in [Malaysia] the highest peak in Southeast Asia, is located near the Equator (about N Latitude 5) at the northeastern end of the island of Borneo, which was once a part of Sundaland. The mountain is rich in plant diversity and has a very diverse flora, besides having many primitive angiosperms. It is the center of differentiation of the evergreen genera, *Castanopsis*, *Pasania*, *Castanea* *(Kurigashi Zoku)* and *Quercus* of Fagaceae. Side by side with these plants of the Northern Hemisphere, the needle-leaved trees and angiosperms of the Myrtaceae from the Southern Hemisphere also grow there.
Many groups of plants can coexist in tropical mountainous regions because the temperature and moisture conditions are mild and seasonal changes are small. Because of this, even incompletely differentiated species can survive without being eliminated by competition. As a person studying cold adaptation of plants, I wanted to see such a forest where living organisms coexisted in the environment in this manner. So, in 1980, 3 years before my retirement, I climbed Mt. Wilhlem (4510m) (Fig 73) of Papua New Guinea, a high mountain in the tropics. A local person guided me up to its tree line (about 3500m), where there was a glacial lake. I surveyed the area for 3 days on my own. The night before I left the mountain, I stood wearing winter clothing under a clear starry sky to experience the cold of the tropical highlands. There was extensive frosting, the frost shining white. The minimum temperature was -1°C.

In early February of 1997, I had received an invitation from Dr Emiko Maruta of Toho University. She asked me whether I could accompany her to Mt. Kinabalu of Borneo in late March of that year, as she wanted to study the frost resistance of alpine plants of that region. I decided to climb up to the rest house at Pana Laban near the tree line, at an altitude of 3350m, to commemorate my 77th birthday. We boarded a direct flight that operated only once a week, from Narita airport to Kota Kinabalu airport. From Kota Kinabalu, it took us about an hour and a half by car to reach the Kinabalu Mountain Reception Office. The Sabah State where Kota Kinabalu is located has a rich natural environment. The protection and management of nature were well-organized. Plenty of provisions of all sorts were also available.
Fig 73 Sundaland. The stippled area is the part that had become land during the Ice Age because of regression of the sea level. K: Mt Kinabalu, L: Wallace's line, W: Mt Wilhelm in New Guinea. The arrow indicates the path through which Khasya Pine (Pinus khasya) migrated south during the Ice Age.

Key:
Abscissa: East Longitude
Ordinate: North Latitude
In the inset: Sundaland
In the Fig, left to right: Khasya pine; Borneo; Philippines; Wallace's lin
Mt. Kinabalu has the least rainfall in March. So, that seemed to be the best time for climbing. I got a shock when I looked around at the lowland oak forests near the Reception Office at the height of 1650m (mean temperature 19.9ºC) of Mt. Kinabalu because many of the trees were putting out new shoots. It looked like spring. At the height of 3000m also many plants had new shoots. I had thought that plants grew following their own internal growth rhythms in the tropics because there were no seasons. At the front of the Reception Office, I met Professor Kihachiro Kikuzawa of Kyoto University, who was studying the phenology of leaves there. I was meeting him after a long time and he was kind enough to introduce me to the forest vegetation around there.

On the first night, after having dinner at the top-class restaurant near the Reception Office, I returned to the Rest House and tried to sleep wearing a lot of clothes. But the single light blanket was not warm enough and the cold kept me awake almost the whole night. The day time was comfortable at about 25ºC but at night the temperature dips below 10ºC at the height of 1600m even though it was in the tropical zone. This night time cooling was probably the reason why the warm temperate evergreen montane oak forest was existing around the foothills of Mt Kinabalu, instead of the tall trees of Dipterocarpaceae which generally form tropical rain forests. I did not find a single Nothofagus solandri, an evergreen tree of the Southern Hemisphere belonging to Fagaceae, so many of which I had seen in Papua New Guinea. After this montane oak forest, we passed by groves of bamboo and thick clusters of ferns in the moss-covered forest (cloud forest), where the tree trunks were covered with mosses, ferns and orchids. and climbed to about 2700m. There, the vegetation changed abruptly. We entered a serpentinite area with a yellowish brown soil. The conifer Dacrydium and flowers of Leptospermum of Myrtaceae, which are common in the Southern Hemisphere, became more predominant. Here and there we noticed flowers of the tropical (Rhododendron bireya) and orchids. Gradually, from around a height of 2900m, we could see the summit of Mt Kinabalu towering above the forest. At even higher altitudes, beyond 3000m, we entered an area of huge exposed granite rocks and sedimemted Ice Age rocks. Gradually, it became harder to breath. The area had well-developed rock vegetation, with trees a few meters in height. Soon, we could see the beautiful Pana Laban rest house (3350m) which sits at the tree line. We had started climbing
at 8 in the morning. It took 6 hours and a half to finally reach our destination, at 2:30PM. From the rest house we could get a panoramic view of summit made up of exposed granitic rocks shining white. The rock surface was shining because it was covered with thin ice (Fig 74).

From here, towards the summit of the mountain, in cracks in the rock, mud in depressions and other places where water might accumulate, some boreal plants, Deschampia, Gentiana scabra Var. Buergeri, Ranunculus, Potentilla, Eleocharis congesta and dwarf forms of Leptospermum of the Southern Hemisphere were growing in clusters. I was particularly interested to know how much of freezing the dwarf and cushion plants I saw near the summit could withstand on clear nights when the temperature would dip below zero. According to the weather data measured regularly at 3780m*50, in March, the mean temperature (in the Stevenson screen) is 10.3°C and the average daily minimum temperature is 3.3°C. This mean temperature of 10.3°C is close to that recorded in July near the Hakuun hut (2000m) in Daisetsuzan, Hokkaido. I therefore guessed that the plants growing in the altitude range 3780m to 4100m (top of the mountain) could probably withstand -7 to -10°C, like alpine plants of Daisetsuzan in summer. If the plants in the dormant state are acclimated to low temperature of 0 to -3°C for one week, they would probably withstand -15 to -20°C. This was likely to be the maximum frost hardiness of these plants growing in this alpine region of the tropics.

After returning to Sapporo, I learned from Professor Seigo Higashi of Hokkaido University that no ants lived at a height above Pana Laban on that mountain. No bees were found in a survey*59 of insect pollinators of alpine plants in the high ranges of Mt Kinabalu. The low temperature is probably restricting the movement of bees. This area seems to have no summer season, with the maximum day temperature being only 7 to 10°C. Small insects of the order Diptera, like flies, drone flies (Eristalis tenax), Yuriska, etc play the role of pollinators in this region.
ii  **El Niño and large scale drying up of plants near the tree line on Mt Kinabalu**

Around Christmas in 1997, the sea surface temperature offshore of Peru in South America rose and the local fishermen exclaimed that “El Nino” had arrived. The sea water around the equator that gets warmed and becomes lighter is usually carried westward along the Equator by the trade winds and builds up in the Western Pacific, around Indonesia, Borneo and New Guinea. Because of this, the sea level in that area rises by a few tens of centimeters compared to the South American coast. The sea water temperature also rises. Ascending air flow develops over this warm sea surface, which brings rains to the Malay Peninsula, Indonesia, Borneo, New Guinea, etc. even in the winter, allowing the tropical rain forests to thrive. However, if the trade winds become weak for some reason, they
cannot confine the warm water to the Western Pacific and the bulk of the warm water spreads eastwards creating El Niño. The ascending air flow that develops over the warm sea surface brings rain shifts from the Western Pacific to its central part. One of the effects of this El Nino was the very much reduced precipitation in Indonesia, New Guinea and the northern part of Australia, creating drought. Particularly in New Guinea, almost no rain fell from February 1997. A drought, which they had not seen for the last 100 years, prevailed. Kalimantan, which is under Indonesian control, in the Borneo Island, and Sumatra had many forest fires one after another, creating a major environmental problem in Southeast Asia. We heard that many plants that we had seen along the tree line near Pana Laban on Mt Kinabalu dried up and died in large numbers because of an abnormal drought that persisted for 4 months from December 1997. I was very surprised that even the vegetation above the tree line in this tropical zone was affected in a significant way by the abnormal weather caused by El Niño.

iii A canopy walkway

The Poring hot spring (altitude 500m) is located east of Kinabalu National Park. It had been developed by the Japanese army during World War II. Near this hot spring, there is a hanging bridge (Fig 75) that is about 200m long and is anchored at a height of about 40m to almost 70m tall Dipterocarpaceae trees. Thus, one can walk through the forest canopy. This walkway is used by tourists. While walking on it, one can observe the animals and insects that live in the canopy. It is at such a height that if you look down, you may become weak-kneed with fear. Earlier, visitors could not see the flowers in the tree crowns from close up. But this walkway has made it possible to study at close hand the status of flowering, the insects and animals that help in pollination, attractants released by the opening flowers, ascending and descending air flows in the forest, the microclimate, and the behavior of birds, insects and animals. I understand that very interesting discoveries are being made one after another. Presently, observations and research on tree canopies are being actively carried out not only in the tropics but also in temperate forests (for instance, at the Tomakomai Experimental Forest of Hokkaido University).
(4) Sundaland

The Sundaland Sea of Southeast Asia (Fig 73) is about 100m deep. Sundaland, which includes the current Indonesian Peninsula, Malay Peninsula, Sumatra, Java, and a part of the Philippines, had formed many times during the ice ages because of lowering of the sea level (by about 180m during the last Ice Age). Around the end of the Tertiary period, most of New Guinea Island came up above the sea level due to regression and further the Arafura Sea (see A in Fig 73) between New Guinea and Australia became land during the Ice Age. Moreover, the area connecting to the southern part of New Guinea via the Malay Peninsula, Sumatra, Java, and the Greater Sunda and Lesser Sunda islands became a highland providing a route of exchange between Indo-Malaysian and Australian floras. The plants of the Northern Hemisphere spread southward through these passages. For example, the Rhododendron moved south from the Yunnan Province of China and got differentiated to produce Rhododendron bireya, which spread to New
Guinea and even up to the Fiji islands. The evergreen oak forests (broad-leaved forests) found widely in the warm temperate zone of Asia are also widespread in the Malay Peninsula and New Guinea, forming tropical montane oak forests there. At the same time, the needle-leaved trees of the Southern Hemisphere, from Australia and New Guinea also moved along this passage to the Malay Peninsula and Thailand. Sundaland also played a major role in the migration and spread of the Mongoloid race.

The Wallace’s line (see L in Fig 73), which is famous in biogeography, is a borderline that separates the Indo-Malaysian flora and fauna from the Australian ones. This line goes northward through the narrow but deep strait between the Bali Island and Lombok Island.

Translator’s notes:
1. Words added by the translator for clarity are given in [square brackets]
2. Kindly check parts marked in orange. Their translation is uncertain.

Dr. Sakai’s revisions:
Chapter 5
p.188. kinpouge Ranunculus; kijimushiro, Potentilla, komesusuki: deschampsia:
Dacrydium, conifer; leptospermum; Akou Ficus Wightiana matebashii
Pasania:
shii Castanopsis, konarazoku Quercus, oak
Willows that grow naturally in the tropics but still remember the cold

(1) Characteristics of willows as pioneer species

Willows have developed nearly 400 species through polyploidy (up to pentaploid) and repeated crossing. They have spread over a wide area ranging from the temperate zone to the subarctic zone of the Northern Hemisphere, as a pioneer species mainly associated with rivers. The name *Salix* of the genus comes from Celtic language in which “Sa” means near and “Lis” means water. Moreover, willows have differentiated into more than 100 dwarf species that creep on the ground and extended their range to the tundra of the far north and alpine areas. A surprising fact about willows is that a group of willows having traits that are believed to be ancestral have crossed the high barrier to distribution and reached tropical areas with high temperatures and little seasonal change. They have established themselves in the tropical regions of Asia that have a dry season, Africa, and even South America. Few people in Japan know that willows grow fairly widely in the tropics also. These willows have survived in the tropical or subtropical lowlands for several thousand to tens of thousand years but still latently retain the frost hardiness that they had acquired thousands of years ago. They show a fairly high level of frost hardiness when exposed to low temperatures.

Willows are the first trees to flower, in early spring. The seeds set early, a large number of the light seeds get dispersed widely and colonize newly created bare land. Moreover, willows have a high capacity for rooting and regeneration. For example, a broken twig can regenerate a new tree at a spot on the river bank to which it has drifted. Willows can also establish well on mud-covered land left after flooding. They have insect-pollinated flowers with nectar glands, unlike many other pioneer deciduous broad-leaved trees such as white birch and poplar, which are wind-pollinated. The willows have spread not only in the Northern Hemisphere but also in the tropics and in the Southern Hemisphere, in close association with rivers, while maintaining their unique style.

(2) How I came to study willows

Around 1960, I could confirm that the temperate willows growing naturally in
Japan, including *Yamayanagi* (*Salix sieboldiana*), which grows in Kyushu, could all withstand -70°C if exposed to cold and could survive liquid nitrogen temperature (-196°C) if cooled first to -30°C. I then had a strong desire to find out how much freezing the willows growing naturally in the tropical and subtropical regions could withstand. To obtain the winter shoots of these willows, I sent out about 50 letters to acquaintances and botanical gardens abroad. This was in 1965. The first to arrive was Bonapland willow (*Salix bonplandiana*) from the late Dr. Eiji Matsuda, who was a close friend of mine and a renowned botanist working in Mexico. He wrote that this willow was distributed from Mexico to Argentina in South America. After that, *Salix tetrasperma* samples arrived one after the other from forest research stations of India and Pakistan. I came to know from scientific papers of India that only this species of willow was widely distributed in the tropical and subtropical lowlands (up to 1000m above sea level) of Pakistan, India, Myanmar and Thailand, along the rivers. I also came to know that the high altitude areas (above 1000m) and the northern temperate zones of India and Pakistan had many temperate willows found widely in Europe, Russia and West Asia. Another willow species, *Salix safsaf*, arrived from the African countries, Egypt, Sudan, Angola, and South Africa (Pretonia). Presently, we can see this willow growing along rivers in Iran and warm parts of southern Iraq. It had probably moved south along the rivers in the huge gorges of Africa and spread to the southern end of Africa and to Angola in western Africa while differentiating into new species. Willows are believed to have originated in the Northern Hemisphere, as can be seen from the fact that no willow species are found in New Zealand or Australia. Nevertheless, I came to know that some special willows that are different from the temperate willows of the Northern Hemisphere are growing in the tropical and subtropical regions of Asia, Africa and South America.

I decided to prepare cuttings from these willow twigs that I was gifted and grow them into saplings for use in experiments. I visited Professor Alika Kimura of Tohoku University, an international expert on willows, taking some of these willow shoots with me. Professor Kimura was very happy to see these willow samples. He commented that the scales on the buds of these willows would not be fused but free and overlapped like a roof tile, on the adaxial side, the side facing the shoot. Professor Kimura had reviewed the classification of willows in 1928 from the standpoint that once the scales got fused they would not become the free
type again. According to his classification, willows with free scales (Fig 76) belonged to the polystemious subgenus Protitea having primitive characteristics and those with the fused scales were the new true willows of the subgenus Eutitea (Euitea?), which were widely distributed in the temperate zone. After hearing this, I checked the bud scales of the willows that I received from India, Africa and South America. All were primitive willows with free scales. Many of these willows had the basic chromosome number of 2n=38.

I grew these willows that I had gathered from different parts of Asia and Africa, along with temperate willows, for 3 years in a greenhouse (minimum temperature maintained at 10°C, natural daylength of Sapporo). The temperate willows all stopped growing and entered dormancy when the days became short in autumn, shed leaves, and remained leafless for 3-4 months. Contrary to this, the tropical willows did not shed their leaves at the higher than 10°C temperatures under the natural daylength, and continued to grow. Only once a year, in the winter, they stopped growing for 1-2 weeks. They shed their old leaves after opening new buds and then continued to grow. In other words, these willows were not the type that entered dormancy or shed their leaves, depending on the temperature or daylength.

These willows were planted outdoors in Sapporo. Their mature shoots were tested for frost hardiness after the plants were well-exposed to the cold climate in autumn. The willows from subtropical areas of India and Africa where the winter temperature never went below 10°C had a freezing tolerance of about -20°C\textsuperscript{100,107}. But I could not verify before my retirement in 1983 whether these willows growing naturally near the Equator could actually withstand subzero temperatures.

Before my retirement, I gifted these potted saplings of primitive willows from Asia and Africa to the Tohoku University Botanical Garden through Professor Kimura. He was very happy to have them. He said that it was the only live collection in Japan of willows with primitive characteristics. The willow Salix mucronata found in the southernmost part of South Africa was in this collection. This willow had a special significance for Professor Kimura. This was the willow that he had identified, in his younger days, to have primitive characteristics, from dried samples that he received from a friend in USA. That had led him to classify willows into two subgenera in 1928, one primitive and the other the true willow. “I am

100,107
seeing a living sample of this willow for the first time!”, he exclaimed when I took a living plant of this willow to him. Professor Kimura passed away in 1996 at the ripe age of 96. I had heard that he continued to collect willows up to his 90th year.

![Diagram of willow bud scales](image)

**Fig 76**  原始的な形質をもつヤナギ（A）と真性のヤナギ（B）の芽の腹部りん片．A：りん片がDの部位で重ね合わさり，癒着していない，B：りん片が癒着して袋状になっている

The list of plants indeed had *Salix tetrasperma*. This is the same species as the willow distributed widely in India and Thailand. Following a map of this botanical garden, I finally stood in front of two giant trees. They were undoubtedly *Salix tetrasperma* and the label (Fig 77) said that they had been

(3) An encounter with willows in the Bogor Botanical Garden

In early October, 1995, I had a chance to give a seminar on liquid nitrogen storage of genetic resources, at the Research Center for Biotechnology, Indonesian Institute of Sciences. The first thing I did after reaching Bogor was to visit the Bogor Botanical Garden to see if there were any tropical willows there. This Botanical Garden was established in 1860 by the Dutch. It is internationally known for its collection of tropical plants from all over the world.

The list of plants indeed had *Salix tetrasperma*. This is the same species as the willow distributed widely in India and Thailand. Following a map of this botanical garden, I finally stood in front of two giant trees. They were undoubtedly *Salix tetrasperma* and the label (Fig 77) said that they had been
brought from Sumatra. Each tree was about 40m tall with a chest height diameter of about 1m. Many new shoots were coming out from the base of the trunk. There was a pond very close to these trees, which probably supported these willows for many years, because willows planted at two other locations [in the garden] did not exist anymore. After seeing these giant willows, I felt a kind of excitement that I had not felt for some time and happily spent almost 3 hours sitting beside them. If these trees had been planted at the time when the botanical garden was established, they must have been about 180 years old. After seeing these giant willows, I once again fell under their spell.

In 1996, the following year, I collected shoots of *Salix tetrasperma* (Fig 78) growing naturally along rivers in the ancient cities of Ayudhya and Chiang Mai north of Bangkok. I found that in these locations, the willows shed their leaves at the end of December in the dry season (November to April) and unfold new leaves in the middle of January. When I visited the Bogor Botanical Garden again, I obtained special permission from the Director to collect several shoots with buds, growing on the trunk near the ground.

I requested Mr. Toshikazu Matsumoto of the Shimane Agricultural Experiment Station at Izumo to plant these willow cuttings in a greenhouse, move them outdoors, make observations, and conduct tests on frost hardiness. At Izumo, the temperate willows growing outdoors shed their leaves in December. But the tropical willows retained their green leaves even up to the end of December and continued growing. But the tips of the shoots died off because of strong frosting in January. This suggested that tropical willows did not shed their leaves or enter dormancy when the days became short and the temperature low in autumn. I then requested Mr. Matsumoto to freeze some samples after exposing the overwintering shoots to 0°C for two weeks at the end of January. The willow from Ayudhya (N Latitude about 12° and mean temperature in January 26°C) of Thailand withstood -7 to -10°C and opened its buds and continued growth afterwards. Similarly, the willows from Chiang Mai (N Latitude about 18°, altitude 313m, mean January temperature 21°C and daily average minimum temperature 13°C) withstood freezing up to -15°C. The willows from Bogor (originally from Sumatra) showed poor growth and had weak shoots but tolerated freezing to -5°C. We may interpret these results as follows: Although these tropical willows had been growing for many generations close to the Equator, they
have retained the frost resistance that they had acquired when they were growing in warm temperate areas a long time ago. When exposed to near-zero temperatures, they express this capacity to some extent. Contrary to this, deciduous Dipterocarpaceae trees, which are representative of tropical rain forests, could not withstand freezing at all when their shoots were tested in the leaf shedding season. When the shoots of *Ficus whightiana*, another tree that had moved north from the tropical zone to Okinawa, were exposed to cold and then frozen, after the leaves had been shed in the winter, they died of freezing at -5°C.

From the findings of these experiments, I had speculated as follows about the primitive *Salix tetrasperma* trees presently found widely distributed in the tropical lowlands of East Asia. Compared to the high vitality of willows of the temperate zone, these primitive willows did not have sufficient competitiveness to be able to spread to the temperate zone of the Northern Hemisphere, and remained limited to warm temperate areas of subtropical Asia, as relics. They probably moved further south during the Ice Age, lost their capacity to enter dormancy, and spread along the rivers in tropical areas that had a dry season. Most probably, many other willow species that had also moved south during the Ice Age, moved back to the temperate zone or high altitudes in search of suitable temperatures when it became warmer once again. Only this species (*Salix tetrasperma*) of willow remained in the tropical regions with a dry season and the subtropical regions of East Asia where it spread along the rivers. In Southwest Asia, *Salix safsaf* having primitive traits and growing in Iran and southern parts of Iraq spread south from West Asia to Africa passing through the huge gorges of Africa. *Salix safsaf* gave rise to many species and spread along the rivers up to the southern tip of Africa and Angola, in southwestern Africa. Interestingly, *Salix acmophylla*, which has traits intermediate between the willow of India and the willows of West Asia and Africa, grow in the area (in southern Afghanistan and West Asia) about midway between these two regions. *Salix bonplandiana* that grows in Mexico in the North American continent has moved down to South America.

*Salix chaenomeloides* is the only primitive willow species that grows naturally in Japan. The northern limit of its distribution is the northern part of the Miyagi Prefecture. Two or three types of willows with primitive traits are known to grow naturally in Taiwan. *Chosenia bracteosa* Nakai and *Toisusu urbaniana* Kimura are ancestral willows belonging to Salicaceae, but they do not belong to the genus
Salix. These ancient willows have lost their nectar glands and have wind-pollinated flowers. They are distributed in central Honshu, Hokkaido and cool parts of East Asia. As in the tropical willows, these willows have the free bud scales that are not fused on the adaxial side and have the basic chromosome number of 2n=38.

A few years back, Dr Azuma Takayuki (currently at the Botanical Garden of the Hokkaido University), then working at Professor Ohashi’s Laboratory at the Biological Institute, Graduate School of Science, Tohoku University, obtained results after DNA analysis that suggested that willows with primitive characteristics and the basic number of chromosomes that were distributed in the early tropics (earlier in the tropics?) had differentiated as species relatively more recently (about 0.36 million years ago onwards, around the middle of the Ice Age) than assumed. The differentiation of spin-off traits did not occur during the creation of these species, but it is interesting to speculate that this differentiation created an opportunity for willows to lose their cold-induced or short day-induced dormancy, and spread to new areas along the rivers of tropical lowlands, escaping from the cold.

In any case, willows now occur in environments with different temperature conditions on earth, including the temperate zone, polar regions, alpine areas and the tropical zone, mainly along rivers. It is indeed a superstar among woody plants. Weeping willows (Salix babylonica), which are very vigorous trees of the Northern Hemisphere, had been planted in various parts of South Africa for controlling soil erosion along rivers. According to a recent news item, small branches of this willow that drifted downstream have taken root, threatening the survival of indigenous willows, which have less vitality.
Salix tetrasperma trees (from Sumatra) growing in the Bogor Botanical Garden, Indonesia. Their height is about 40 m and chest height diameter about 1 m (Photographed by the author).
Fig 78  

Salix tetrasperma growing naturally in Ayudhya about 8km north of Bangkok. These willows are basically tall trees but remain shrub-like because they are trimmed once or twice a year to provide feed for cattle (Photographed by the author).

Translator’s notes:
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2. Parts of the source text that are ambiguous and require some modification are marked in pink and alternatives are sometimes given in parenthesis.
3. Kindly check parts marked in orange. Their translation is uncertain.

Chapter 6
Dr Sakai’s suggestions
marubaynagi: Salix chaenomeloides Kimura; keshowyanagi: Chosenia bracteosa Nakai; oobayanagi: Toisusu Urbaniana Kimura
Please add part II-Chapter 6,
Page 7, 6Line (upper) Africa (refers: Sakai and Larcher 1987, fig.7.40, page 233)
Page 8, 6line (upper) Weeping willows (Salix babylonica) thank you very much, Sakai
Changing rules of nature

Although individual trees are fixed to the ground and do not move, forest vegetation has seen migrations, successions, and rise and fall with the changing environment and climate. The changes with time in forest colonies, i.e., forest successions, are changes in forest flora on a time scale of several hundred years or a few thousand to a few hundred thousand years at the most. Contrary to this, there are geohistorical changes that take place over a much longer timescale. In a broader sense, succession means change in the dominant species. The history of evolution of living things over a period of 3000 million years on the stage of this earth is, in a way, a story of large-scale changes of the dominant species.

Climate change and changes in forest vegetation

Migration of forests in the ice ages

The period from about 1.6 million years ago to the present is known as the Quaternary Period. The Quaternary is divided into the Pleistocene (the ice ages) that lasted from 1.6 million years ago to about 11,000 years ago and the current Post-Glacial Age. During the Pleistocene, there were at least 4 ice ages with interglacial ages between them. The last Ice Age started about 70,000 years ago and ended 11,000 years ago. In the coldest period of the last Ice Age, the sea level is said to have been about 100m lower than now globally and temperature lower by about 7°C. A lowering of the annual temperature by 7°C would mean that the annual mean temperature of Tokyo, which is presently about 15°C, would become 7.8°C, which is the current mean temperature in Sapporo. Sapporo would have had an annual mean temperature of the present Western Siberia, about 0°C. The temperature changes by about 6°C for every 1000 m of altitude. Therefore, in the coldest period, the vegetation of mountainous regions must have moved down by more than 1000 m. It has been estimated that at that time, most of the interior of Hokkaido was a tundra with open forests here and there. It is believed that during the coldest part of the last Ice Age, warm temperate evergreen broad-leaved forests of Japan had disappeared from Honshu, except from some parts of the warm Pacific Coast. The interior parts of the Tohoku region and Chubu region were probably covered with subarctic needle-leaved forests. Fossils of northern needle-leaved trees like Picea jezoensis, Abies mariessi and Larix leptolepis have
been discovered from the soil stratum belonging to the last Ice Age, in Ekoda, Tokyo\textsuperscript{128}. In this sequence of repeated ice ages and interglacial ages, some plants survived by expanding their range northwards or southwards in search of suitable temperatures. But in places where mountain ranges run east-west, such as the Alps of Europe, their southward migration was blocked and many of the species became extinct.

After the end of the last Ice Age, the ambient temperature rose gradually while undergoing repeated fluctuations, and in the warmest post-glacial time (the hipsisamar \textit{(hypsithermal?)} interval of about 6300 years ago) the temperature is said to have been about 3°C higher than now. In Japan, during the warming phase after the Ice Age, Japanese beech \textit{(Fagus crenata)} trees rapidly spread towards the snow-covered areas of the north and reached the northern end of Honshu from the Wakasa Bay in about 3500 years. This type of shifting of forests in response to change in the ambient temperature is a very slow process. On the other hand, when a forest recedes because of a reduction in temperature, some areas with favorable conditions remain as refuges. Groups of plants that survive there during the harsh inhospitable period start multiplying when the temperature increases. They gradually expand their ranges through seed dispersal, and the refuges eventually get connected. The plants that survived can spread very rapidly in this manner, it is believed.

Trees are fixed to the ground and cannot move by themselves. But groups of trees that exist in forest communities disperse a very large number of seeds \textit{[over a wide area]}\textsuperscript{\textdagger}. If we assume an average lifespan of 250 years for a tree, there will be 4 generations in 1000 years and 20 in 5000 years. The seeds become the progeny after being subjected to the natural selection pressure of climate change. Forests move considerable distances towards favorable temperatures in this manner over long periods of time.

\textbf{ii Mountain vegetation that became extinct}

Slopes of mountains of the Tohoku region facing the Japan Sea are all areas with heavy snow cover. The deepest snow cover is 3-4 m on the average in areas above 800 m. As we move higher, Japanese beech trees that constitute the upper storey of the forest become shorter and their frequency also becomes less. At the same
time, ground-hugging shrubs such as *Fagus crenata*, *Miamanara* (*Quercus magnolica* var. *undulatifolia*), *Alnus maximowiczii*, *Miamakaide*, *Sorbus sambucifolia* and *Sasa kurilensis* appear in the lower storey. There are no needle-leaved trees at all in this area at heights where one would expect to see them. Such areas are called the pseudoalpine zones. Until recently it was thought that needle-leaved trees did not exist here because their growth was inhibited by the snow pressure in these heavy snow cover areas.

In 1982, after studying the Japanese beeches on Mt. Naeba, Kaji confirmed that during the warm post-glacial age, the forest vegetation had extended to 200-400m higher than its present range and proposed the following hypothesis about the pseudoalpine zone: During the post-glacial warm period, the montane forest vegetation belt climbed up on the mountain in search of suitable temperatures. During this time, when the lower limit of the needle-leaved tree belt became higher than the height of a particular mountain, that vegetation disappeared. On such mountains, therefore, when the vegetation moved down during a cool period that followed the warm period it lacked the species that had been pushed out. However, if the mountain was sufficiently tall, it did not lack the upper part of the vegetation and the vegetation sequence of the warm period descended almost intact. Kaji assumed that *Abies mariessi* was the species that the pseudoalpine zone of this area was lacking, studied its distribution in great detail from the flora of that area and the literature, etc and proved the above hypothesis. He thought that forests of bushy trees created by reduction in the height of trees had expanded their range during the post-glacial warm phase to the spaces thus created. He also clarified that such pseudoalpine zones were not limited to heavy snow cover areas but were also found on the Appalachian Mountains in Eastern USA.

(2) **Succession in the Alaskan forest and formation of permafrost**

Plant succession is one of the major concepts in ecology. It is the change in flora with time. For example, if we stop weeding in an upland field or a paddy field, miscellaneous plants would grow all over it in no time. In the following year, tall grasses that are often found on the sides of roads would become dominant. Within 4-5 years, graminaceous plants like *Miscanthicus sinensis* and *Imperata cylindrica* take over. Soon we will have a thicket of assorted trees. In short, one plant community is taken over by a group of other plants and eventually a stable climax
A colony of plants is established. It is difficult for higher plants to cope with fast changing environments by modifying their forms and functions. Instead, they change through succession of plant communities.

Fairbanks and its surroundings in interior Alaska are located in a transitional zone [on the edge] of the permafrost area. The southern slopes of hills and places close to rivers in that area have forests of 10-20 m tall (with chest height diameter about 20-30 cm) broad-leaved trees like white birch, poplar and white spruce (*Picea glauca*, a relative of *Picea jezoensis*). In those areas, the soil temperature is high, and the soil thaws to a considerable depth, is well-drained and fertile. Contrary to this, on the northern slopes of the hills and on the plains, permafrost table exists quite close to the ground surface. Therefore, the soil temperature is about 0ºC, the water drainage is poor and the ground surface is covered with sphagnum moss. These areas have wetland forests of bushy (2-3 m tall) black spruce (*Picea mariana*) trees. Thus, by looking at the vegetation we can determine whether permafrost exists below.

In interior Alaska, the succession of forests, i.e., willows -> poplars -> the evergreen needle-leaved white spruce (climax forest) -> black spruce (a wetland climax forest) continues. In the sandy soils of the flood plains created in the spring, firstly, willows, which are the earliest to flower and set seed, disperse a large number of seeds and occupy the virgin land (Fig 79). Soon, other trees like poplars make their entry. But willows are particularly hardy on the unstable land along the riverbanks. Even when the ground surface is covered many times with sand and mud, they easily extend their roots from their stems and continue to grow there.

After 10-15 years, the litter of willows accumulates, nutrients accumulate, and the land becomes stable. In about 20 years, poplars surpass the willows in height and it becomes a poplar forest. The willows, which have a shorter lifespan, disappear in this process. Shade tolerant conifers like white spruce that had a meager existence on the forest floor below the poplars start growing faster as the soil becomes enriched with large amounts of poplar litter. In about 100 years, when the white spruces become taller than the poplars, the poplars, which cannot grow in the shade, get reduced in number and gradually disappear, allowing the needle-leaved trees to dominate the forest. Thus, it takes about 250 years for a white spruce forest to get established naturally on virgin land. The ground thaws fast and to a
great depth on the southern slopes and riverbanks in summer, and the soils are warm, nutrient-rich and well drained. White spruce is dominant in such places. This is the climax of the succession (Fig 80).

On the plains, however, the situation on the ground changes altogether after the leaves of the conifers cover the surface. In fact, a thick layer of three kinds of mosses covers the ground. Once this happens, the heat above the ground is not easily transmitted to the underground parts and the soil frozen in the winter does not thaw even up to autumn. Soon, fresh freezing occurs from the ground surface downwards and the seasonally frozen soil connects to the already frozen soil and becomes part of the permafrost. When soil that never melts during the whole of the year is once formed near the ground surface, the drainage becomes poor and white spruce, which likes well-drained soils, declines. In its place, sphagnum moss and a wetland forest of short black spruce trees that can grow well on poorly drained soils (Fig 81) are established. Fig 82 is a diagram showing the succession of the vegetation. The black spruce forest is the climax community of succession in such poorly drained plains and northern slopes. In the permafrost zones of Alaska and Canada, this type of segregation of tree species occurs, depending on the depth of the seasonal melting layer.

Forest fires are frequent in interior Alaska, which is quite dry in the summer. When a wetland forest gets burnt in this manner, the surface vegetation burns and the melting layer becomes deeper. The inorganic nutrient content of the soil also increases which triggers a new succession. Black spruce opens its cones only when exposed to forest fires. It then disperses a large amount of seed. Flooding of the river banks and forest fires play important roles in renewing the succession of plants in the permafrost zones of Alaska and Canada.

In the forests of Alaska, the plants that thrive at a certain time create through their activities an environment that is not suitable for their own survival and always provide, instead, soil for other plants that would follow. Succession of plant communities occurs in this manner.
Fig 79  A cluster of willow seedlings on a flood plain along a riverbank. (Photographed by the author, 1974).

Fig 80  A white spruce forest established near a large river. (Photographed by the author).
Fig 81 A wetland forest of black spruce (On the outskirts of Inuvik, Canada).
A diagram of succession of forests in Alaska\textsuperscript{129}.

**Key:**
*In the Fig, from left to right:* Permafrost; Wetland forest; Black spruce; White spruce; Balsam poplar; Willow; Water level of the river.

(3) **Geohistorical succession of dominant species**

Succession is, in a way, a change in the dominant species. The history of evolution of living organisms on this earth over a period of 3000 million years can be viewed as a history of grand successions of dominant species. At one time, fish were dominant. Then it was the turn of reptiles, then mammals, and now humans who are also mammals. There is no doubt indeed that continuous change is the true state of nature. The human race too would be no exception. All the activities being undertaken for promoting human prosperity would themselves create an environment unsuited for our survival. When a time comes when humans can no longer biologically adapt to a global environment that they themselves have
changed, they may have to give up their dominant position to another species that would then take the lead. It would be inexcusable if humans become aware of this reality only when it is already too late. We must understand how crucial the global environment is for the survival of humans. It is sad to note that chemical substances synthesized by humans lower the immunological potential and reproductive capacity of humans and their progeny. It is truly regrettable that environmental degradation is bringing a large number of species, which have evolved over millions of years, to the brink of extinction. It would of course take a lot of time to regenerate the natural environment already degraded by humans over a long period of time. But I sincerely feel that we all should do whatever we can for restoring the natural environment.

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Dr. Sakai’s suggestions

page 207: Chigaya Imperata; susuki Miscanthus sinensis
Giant trees of the world that have lived for 2500 years

(1) The lifespan of plants and animals

A major difference between plants and animals is that plants cannot move around while animals can. This is closely related to how their bodies are made and their lifespan. Unlike plants, animals cannot synthesize the food they need. So, they have to move around and hunt other living things for food. Therefore, in higher mammals, nerve and muscle cells are particularly well developed so that they can execute complex movements efficiently. Moreover, their body temperature is maintained at a certain high level so that they can move fast. Their energy consumption is 30 times that of heterothermal animals. Apparently, mammals have opted for a shorter life and high expenditure of energy for fast movement of their bodies.

Plants, on the other hand, get established at a suitable place with sufficient water, light and inorganic nutrients, produce seed, and continue to produce progeny. Trees in particular make their bodies very large in search of sunlight and appear to have chosen the strategy of living longer. Plant cells are surrounded by hard strong cell walls. The cell walls are particularly well developed in trees. The cells, each surrounded by a hard cell wall, arrange themselves like laid bricks during the growth of the tree. The apical meristems of buds are involved in the elongation of shoots and trunk and another meristematic tissue called cambium located between the bark and the xylem takes part in the thickening of the trunk. In the trunks of trees, only the cells near these growing points are alive. This is very convenient for support because the energy requirement for respiration is very much reduced. The stems and shoots are made of not easily digestible macromolecular compounds like cellulose and lignin. Besides, they also contain substances like tannin, which protect trees from insect damage. Leaves also contain various substances like tannins and alkaloids that protect them from insects. Because of such protective measures, the proportion consumed by animals is not more than a small percentage of the net production of trees. Trees are thus a difficult to use food resource for animals. We may say that this is the reason why the earth still has a green cover.

Cells are similar in different parts of plants and they are totipotent. So, if we take
out a cell and culture it under suitable artificial conditions, we can regenerate a plant. In particular, we can produce genetically identical clones vegetatively in large numbers through aseptic culturing of the apical meristems (growing points). Thus, plants and animals are very different in the way their bodies are organized and also with regard to the concept of individual longevity.

Unlike animals, plants can continue to live for fairly long periods of time if they do not encounter natural calamities and if they are located in a favorable place. Besides, *Katsura* tree (*Cercidiphyllum japonicum*) and many other trees have the property that when the tree becomes old, many suckers grow from the base of the trunk, at the ground surface or near it, which grow taking nutrients from the trunk of the parent tree. These soon become independent trees growing near the parent tree. So, although many individual trees have lifespans, some appear to grow continuously and do not seem to have individual lifespans.

![Young *Katsura* trees (*Cercidiphyllum japonicum*) growing near the parent tree, utilizing nutrients from the old and decaying parent tree (Photographed by the author on Mt. Moiwa). N: Independent trees near the parent tree. O: Roots that absorb nutrients from the old decaying parent tree.](image)
There are a number of giant trees in California believed to be 2000-3000 years old. Yakushima island in Japan has some giant Sugi cedars \((\text{Cryptomeria japonica})\) like the “Jomon Sugi” that are several thousand years old according to some reports. However, many of the giant cedars of Yakushima are partly broken by storms, etc, the upper parts of their trunks had been cut off earlier by people, and the remaining bases of the trunks are now becoming hollow. In any case, if they have lived for a few thousand years, they must have experienced a number of typhoons, lightning strikes, forest fires, land slides and other such natural disasters. It is certain that the area where these giant trees are growing had relatively few natural calamities, rich soil and plentiful water. Tropical rain forests that have high productivity and few typhoons have many giant trees. But it is difficult to determine their age because trees in tropical rain forests do not have distinct tree rings. However, because of the high temperature and humidity, energy consumption for respiration would be high and these giant trees are likely to be only about 100-300 years old. It seems that warm temperate coniferous forests of middle latitudes have many giant trees that are taller than those of tropical forests.

The western coast of USA has a Mediterranean climate, dry in summer with a lot of rain in the winter. Normally, the rainy season continues from mid-October to March, with very little rain from April to late October. During the summer, the dry season, the grass on the ground looks brown and almost dried up. Herbaceous plants germinate in late autumn after the start of the rainy season and the mountains and fields turn green all over and misty with rain. On this West Coast, from California in USA to Vancouver in Canada, from the coast to the hills, a temperate needle-leaved tree belt consisting mainly of Douglas firs \((\text{Pseudotsuga menziesii} \text{ (Mirb) Franco})\) exists. The winter here, which is the rainy season, is mild and there is no strong cooling. In the summer, when the climate is dry, mist provides the moisture and snow-melt water supports the forests.

Stands of 60-70 m tall giant Douglas firs can be seen in the states of Oregon and Washington, which are north of California but have mild winters, and on the Vancouver island of Canada (50° N Latitude), which is more northern than
The forests of 70-100 m tall evergreen broad-leaved eucalyptus trees are also famous. Thus, if we exclude the tropical forests, giant trees are mostly found in areas with Mediterranean climate. In regions where the summers are dry and winters rainy, there are perhaps fewer tree diseases and less rotting of trunks than in areas with warm and moist monsoon climate. Apart from this the mild winter of Mediterranean climate and absence of strong cooling that might cause trunk freezing are also advantageous for trees. In places where strong cooling occurs in winter, trees have to stop growing early and prepare for the winter, sacrificing quite a bit of growth. I believe that these are the reasons for there being many giant trees in regions with Mediterranean climate.

In places like Hokkaido, where the summer temperatures are relatively low and the winters are severely cold, trees rarely become taller than 40 m. The oldest *Mizunara* tree (*Quercus mangolica*) recorded at the Hokkaido Experimental Forest of Tokyo University was 614 years old and the oldest *Akaezomatsu* spruce (*Picea glehnii*) tree recorded at the Teshio Experimental Forest of Hokkaido University was 625 years old. This tree was 40m tall and had a trunk diameter of 1m. Seattle on the western coast of USA, which has a mild winter, has an Olympic National Park (Latitude about 48ºN) which is at about the same latitude as the central and southern Sakhalin islands. The Sitka spruce trees in the temperate rain forest in this park are 90m tall with trunk diameter 4m and girth as much as 13m. We cannot find such giant trees anywhere in Hokkaido, which has severe winters.

**Giant trees of the world and the General Sherman tree**

The Yosemite National Park is located about 200 km east of San Francisco. Some distance southeast of Yosemite, there is a Sequoia National Park. A giant sequoia tree in this park, named General Sherman, has a maximum trunk diameter at the ground level of 12.3 m, girth at ground level 32.8 m, height 82 m, estimated age 2500 years, and estimated weight of 1250 tons. This is the largest tree in the world (Fig 84). Unlike the aged cedars of Yakushima, these giant sequoias are alive up to the tips of their trunks and continue to grow even now. Because of the dry climate of the summer, there are no mosses, lichens and algae attached to the trunks of these trees, which are red in colour.
The giant sequoias do not have a tap root that goes deep into the ground. Nor do they have plank roots, which tropical trees use to support themselves. Instead, the trunk has many round buttressing bulges at the ground level that are connected to the roots spreading near the ground surface (Fig 85). Many of these giant sequoias are found on mountains, such as on the western slopes of the Sierra Nevada, which have a comparatively large annual precipitation (1500 mm). Almost all of this precipitation falls as snow in the winter (snow cover 3m) with almost no rainfall in the summer. The giant sequoias living in this region are on mild slopes of basins where the snow-melt water stored in the soil can be used even in summer. They are thus well-adapted to face the dry climate and forest fires.

This area is subjected to forest fires caused by lightning at the rate of about once in 20 years. Sequoias have an approximately 60 cm thick inner bark inside the outer bark that peels off easily. This inner bark does not contain any easily combustible resins. So it remains more or less intact even when the outer bark is scorched by lightning. The inner bark and the regions inside it contain various chemicals like tannins that prevent insect damage and fungal rots.

Another interesting feature is that like in the pines and eucalyptus in dry areas, the cones are tightly sealed with resin and do not open unless they are heated in a fire. So, unless there is a forest fire, the cones remain attached to the branches unopened for almost 20 years. Even if the cones open and the seeds get dispersed, they cannot germinate unless the humus layer accumulated on the ground surface is burned by a fire and the seeds reach the ground and get covered with soil.

General Sherman, the largest tree in the world, has luckily survived for the past 25 centuries, withstanding repeated forest fires and avoiding insect damage and fungal attack. But this tree also will fall some day after losing its balance like many other giant trees. Factors that can disturb the balance include damage to the roots, forest fires, changes in the surrounding environments (paving of roads and people walking on the ground around the tree), strong winds, abnormal snow cover, earthquake and climate change, and also a combination of some of these factors.
Fig 84 General Sherman, a giant sequoia tree. Height: 82m, girth at ground level: 32.8m, estimated age: 2500 years. (Photographed by M.P.M. Nair, 2000).
(4) Giant trees and annual herbs

The strategy of surviving as a giant tree was beneficial when the climate was mild and stable, as in the period up to the early Tertiary. The large bodies of these trees confer another advantage; they provide the ability to survive environmental changes and to withstand natural disasters better. However, when major environmental changes that cannot be coped with occur, they becomes extinct or remain as relics in well-provided special environments, because they have fewer chances of producing progeny that can adapt to the new environment. The current giant sequoia stands of California cannot compete with the highly competitive needle-leaved trees of the genus *Abies* under natural conditions. So, they are protected and maintained in a National Park.

Changes in the natural environment over a long period of time constitute natural history. The long-lived giant trees are time capsules that have survived with a
record of such changes in their trunks. Thus, they are very precious monitors of natural history.

The annual herbs are a stark contrast to these giant trees. They have short lives and have spread their range to drylands and cold areas where trees cannot grow. Unlike trees, the annual herbs disperse a large number of seeds every year. While some giant trees complete one generation in 3000 years, the annuals have 3000 generations during the same period. By continuing to disperse large numbers of seeds with rich genetic variation every year, they can adapt rapidly to environmental change. The biggest strength of short-lived herbs is the swiftness with which they can adapt to environmental changes. This is even truer for microorganisms with generation times of hours or days.

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Dr Sakai’s suggestions for Chapter 8:
Chapter 8 Fig. 83, Cercidiphyllum japonicum Sieb.net Zucc.
Douglas fir (Pseudotsuga Carr.)
Please correct Chapter 8, Line 3 (upper) Page 3: Pseudotsuga menziesii (Mirb) Franco, thank you, Sakai