Comparative Life History of Five Hokkaido
Polystichum Ferns with Reference to
Leaf Development in Relation to
Altitudinal Distribution

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The temperate ferns Polystichum craspedosorum, P. retroso-paleaceum, P. tripteran, P. braunii and P. microchlamys are distributed widely in Hokkaido: on 13 Hokkaido mountains their average altitudinal distributions are 450, 479, 570, 689 and 964 m above
sea level, respectively. The developmental stage of the sporophytic leaf is expressed by
the “number of venation” (NV, the number of veins branching from the midrib of the
leaf), which, in Polystichum ferns, is itself a qualitative expression of the phase-change
from sterile to fertile leaf production and is more discriminatory than leaf area, length
or dry weight. Usually, the developmental stage structure of the fertile leaf expressed
by NV in the five Polystichum ferns showed a normal distribution. Among the four
Polystichum ferns that grow in the forest understory of Hokkaido’s cool temperate
regions, a good correlation was found between the mean altitude of vertical distribution
and the maximum NV of the leaf ($r = -0.993$) and the initiation of maturity in the
relative developmental stage ($r = 0.991$) of the ferns. Polystichum craspedosorum found
on cliffs, however, matures at much earlier stage and has the smallest maximum NV. In
the developmental stage expressed by the NV, the initiation of fertility and maximum
NV seem to be correlated with altitudinal distribution and habitat in populations of
Polystichum ferns in Hokkaido.

Key words: Altitudinal distribution — Comparative life history — Maximum NV — Polystichum — Relative developmental stage.

The life cycle of ferns is characterized by the development of the simple prothal-
lium into the distinctive sporophyte. Although numerous investigations related to
morphological characteristics of ferns have been reported, field study of the life history
characteristics of fern populations, including gametophytic generation, has only just
begun (Farrar, 1978; Cousens, 1979; Schneller, 1979; Sato, 1984).

Recent studies have clarified the differences in the eco-physiological features of
gametophytes and sporophytes; in particular, the wintering capacity of gametophytes
is much harder than that of sporophytes (Farrar, 1978; Sato and Sakai, 1980, 1981a, b; Sato, 1982a, 1983a). Consequently, it has been suggested that in colder regions, there is a wider potential distribution of gametophytes than of sporophytes; so far,
however, there is very little evidence as to the survival of only prothallium in sites where sporophytes' development cannot be permitted (Pickett, 1914; Page, 1979).

In order to elucidate the adaptive strategy of the life cycle of ferns in their different distributional areas, we intend first of all to pay attention to the developmental stage structure of the sporophyte populations of Polystichum ferns, with reference to leaf development. In this report, a new measurement for the qualitative and quantitative leaf development using vein complexity of the leaf will be first proposed. Correlations will then be evaluated between vein complexity, initiation of maturity in the relative developmental stage and the maximum developmental stage, and the altitudinal distribution of Polystichum fern populations in Hokkaido, the northernmost island of Japan.

Materials and Methods

Polystichum ferns are distributed widely in the temperate and subtropical regions of the world and consist of more than 200 species, more than 23 species of which have found in Japan (Tagawa, 1959). Polystichum craspedosorum is distributed widely from Ryukyu to Hokkaido, yet it rarely occurs on the rocky cliffs and slopes of the deciduous forests in Hokkaido. P. retroso-paleaceum is distributed from Honshu to Hokkaido, mainly in temperate regions of Japan; it can be found in Hokkaido on the rather humid deciduous forest floor. P. tripteran is commonly distributed throughout the Japanese Archipelago; it can be found on the rather humid deciduous forest floor in the cool temperate regions and also in the Cryptomeria forests developed in warm temperate regions of Japan. P. braunii is distributed from central Honshu to Hokkaido, in the cool temperate and subalpine regions; it can be commonly found on the forest floor and rocky slopes in the deciduous forests of Hokkaido. P. micro-chlamys is also distributed from central Honshu to Hokkaido, in the subalpine regions and sometimes in the cool temperate regions; it is found rarely on the rocky slopes and in the understory of the subalpine forests in Hokkaido (Tagawa, 1959; Sato, 1982b).

Both the horizontal and altitudinal distributions of these five Polystichum ferns were studied at 488 locations and on 13 mountains in Hokkaido during the period from April 1977 to March 1983 (Fig. 1).

The developmental stage of the leaf is expressed by the number of venation (NV, the number of veins branching from the midrib of the leaf). This is one of the methods which quantitatively represent the developmental process of the leaf as well as the sporophyte. The propriety of adoption of NV has been tested by the following procedures.

1. Measurements have been made of NV, dry weight, area and length of each of a number of sterile and fertile leaves. 2. The ranges of variability of sterile and fertile leaves regarding each of the above four characters have been examined; i.e., if a simple model using an arbitrary value is adopted, the figures, such as 1-5 in sterile leaves and 3-8 in fertile leaves, are obtained. 3. The extent of the overlap between the ranges recognized in sterile and fertile leaves and the total range in each character