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GROWTH CHARACTERISTICS OF *BETULA ERMANII* IN PARTICULAR REFERENCE TO RESPONSE PATTERNS AT TIMBER LINES

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Introduction

Betula ermanii is broadly distributed from the montane to subalpine zones in Hokkaido⁷⁾. It is also often found in lowlands ; for example, it forms lowland forests along seashore in the northeastern Hokkaido, which has a cool summer climate¹⁸⁾. Moreover, it invades even to *Pinus pumila* zones, although the trees exhibit a shrublike form¹¹⁾.

This broad distribution is likely due to its exceptional ability to resist various severe stresses. The buds and cortex can survive freezing even below -70°C ¹⁵⁾. According to KOIKE⁸⁾, this species is perhaps more adaptive in photosynthetic characteristics to low temperatures than *B. platyphylla* var. *japonica*, which is mainly distributed in lowlands. OKITSU¹¹⁾ investigated *B. ermanii* communities and concluded that sprouting from the stem base could play an important role in the maintenance of communities at forest limits. Such characteristics as mentioned above are likely of benefit in preserving *B. ermanii* communities under severe stresses.

However, there remain many unanswered questions regarding how *B. ermanii* can be distributed at various sites including timber lines. Perhaps the most fundamental question is what type of inherent tree construction enables such a broad distribution. But this question has not been sufficiently analyzed yet.

The *Betula* species has many short shoots bearing pairs of leaves. These leaves and pairs of leaves developing on the proximal end of long shoots are called early leaves because of their early expansion in spring^{3,4,9)}. Further, they are accompanied by few internodes. Therefore, a tree architecture with many short shoots and many early leaves may be one kind of efficient structure for matter production in various sites, including severe stress sites⁴⁾. But the significance of such a tree construction pattern has scarcely been investigated to date.

Therefore, in this paper, a comparative growth analysis of *B. ermanii* saplings growing at 3 different sites (*i. e.* timber lines, open sites in lowlands and shade-suppressed sites in lowlands) was carried out for the purpose of elucidating such questions as mentioned above, with special reference to the tree construction

pattern with short shoots and early leaves.

Materials and Methods

Investigated samples were collected from 3 stands in the Nakagawa Experiment Forest of Hokkaido University : a timber line (600 m above sea level) of Mt. Panke (631.8 m above sea level), and 2 stands in lowland mixed forests (50 m and 110 m above sea level) where many open site and shade-suppressed site saplings



Fig. 1. Study area and 3 stands used for sampling. Square, the Nakagawa Experiment Forest. A, B and C, sampling stands : A, timber line saplings ; B, open site saplings on lowland ; C, open site and shade-suppressed site saplings.

of *B. ermanii* are located. Fig. 1 shows the study area and the 3 stands used for sampling. On Mt. Panke, *Pinus pumila* communities occur above 500–600 m¹⁷⁾, where many shrublike *B. ermanii* saplings often form timber lines with one or another of a few species. The number of sample saplings from the timber line, the open site and the shade-suppressed site were 14, 23 and 10, respectively.

Their aboveground parts were collected and brought to the laboratory for growth analyses. The samples from the timber line were collected from late August to early September of 1989.

The samples from the open sites and the shade-suppressed sites were collected during the same period in 1981, 1985 or 1989.

In the laboratory, tree age, annual growth increments in height and diameter, bifurcation ratio (Rb), short shoot ratio, early leaf ratio and leaf weight ratio (LWR) were estimated for each sample. Rb was estimated by following commonly used formula^{4,13)}.

$$Rb = (\Sigma N - Nl) / (\Sigma N - Nmax),$$

where $\Sigma N = N1 + N2 + \dots + Nk + \dots + Nmax$, and Nk is the number of branches in HORTON'S order¹³⁾ k. Short shoot ratio and early leaf ratio mean the percentage of all terminal shoots which are short shoots and the percentage of all leaves which are early leaves, respectively.

Moreover, the leaf weight of the preceding year (Wl'), the number of late leaves (*i.e.* all leaves except early leaves, flushing later than early leaves) in the preceding year (Nll') and the annual volumetric increments of aboveground nonphotosynthetic organs (ΔVc) were estimated, and their relationships with one another were analyzed. Wl' was estimated from the relationship between diameter at the lowest raw branch (Dr) and leaf weight in the current year. Nll' was estimated from Wl' and late leaf ratio in the current year, assuming the late leaf ratio of the preceding year and the current year have the same value.

Results and Discussion

1. General description and bifurcation ratio

A general description of the sample saplings of each stand is presented in Table 1. Significantly, the mean height and mean diameter growth increments indicated extremely lower values at the timber line and the shade-suppressed site. Such growth inhibition is considered to be caused directly by the severe stresses.

Table 1. General discription of sample saplings

Site	Sample size	Altitude (m)	Age		Tree Height (m)		Basal diameter (cm)		Height growth increment (cm/yr)	Diameter growth increment (mm/yr)
			Max	Min	Max	Min	Max	Min	Mean (Max-Min)	Mean (Max-Min)
Timber line	14	600	21	9	3.2	1.4	2.7	0.9	16.8 ^{abc} (28.0-10.0)	1.4 ^a (2.7-0.8)
Open	23	50-110	22	3	4.9	0.5	7.0	0.5	31.7 ^{ab} (49.0- 9.8)	3.0 ^{ab} (4.4-1.2)
Shaded	10	50-110	26	5	2.5	0.3	3.4	0.3	11.9 ^{bc} (20.0- 5.3)	1.2 ^b (1.4-0.5)

Values followed by the same letters a and b were significantly different (t-test, p<0.001). Values followed by the same letter c were significantly different (t-test, p<0.05).

But, the Rb values were not significantly different among the samples from the 3 sites (Table 2). Rb values often decrease extremely under suppressed conditions^{4,14,16} ; however such a tendency is not universal. Two types of tree forms (*i. e.* excurrent tree form and decurrent tree form) are recognized in forest trees^{1,3}. And many excurrent growth species maintain high Rb values even under suppressed conditions^{4,5}. The maintainance of such high Rb values is perhaps due to the growth characteristics always constrained by strong apical control^{1,4,5}. It is considered that such strong apical control always inhibits the growth and bifurcation of the lower-positioned shoots, and that overall growth inhibition occurs as a result of simultaneous growth inhibition of the upper-positioned shoots under suppressed conditions. *B. ermanii* also exhibits excurrent tree form. And the Rb values of the saplings investigated at 3 sites can be regarded as high values in comparison with those of forest trees with decurrent growth habits investigated previously^{4,13}. These suggest that *B. ermanii* also has a mode of tree construction always constrained by strong apical control. In other words, the growth inhibition exhibited under severe stresses is perhaps not only the result of severe conditions, but also a reflection of the inherent excurrent growth habit.

Table 2. Bifurcation ratio (Rb)

Site	Sample size	Value of Rb Mean ± SD
Timber line	10	4.19 ± 0.28
Open	10	4.35 ± 0.48
Shaded	10	4.21 ± 0.78

Values at 3 sites were not significantly different (t-test).

2. Short shoot ratio and early leaf ratio

Fig. 2 and Fig. 3 show the results of calculation on short shoot ratio and early

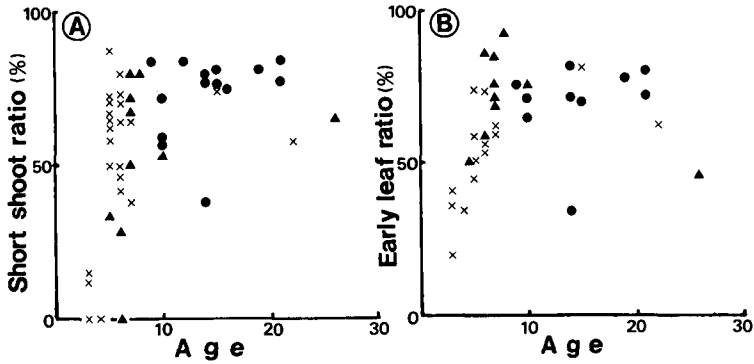


Fig. 2. Short shoot ratio and early leaf ratio (1)
 A, relationship between age and short shoot ratio ; B, relationship between age and early leaf ratio. Circles, timber line saplings ; crosses, open site saplings ; triangles, shade-suppressed saplings.

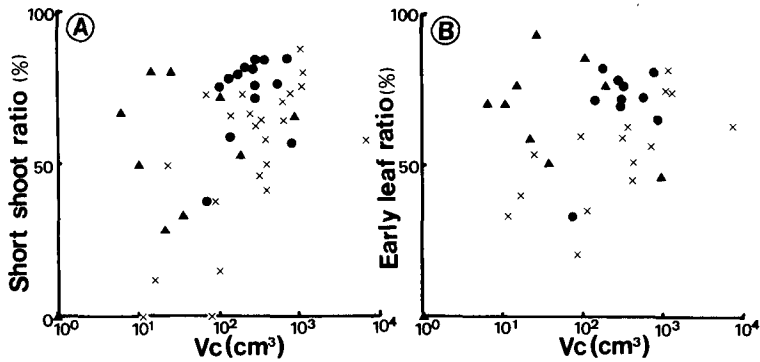


Fig. 3. Short shoot ratio and early leaf ratio (2)
 A, relationship between volume of aboveground nonphotosynthetic organs (Vc) and short shoot ratio ; B, Vc and early leaf ratio. Refer to Fig. 2 for explanation of symbols.

leaf ratio. As shown in Fig. 2, both ratios seem to increase with age in open and shade-suppressed sites. Most older saplings showed higher values at all 3 sites. As shown in Fig. 3, both ratios for timber line saplings and shade-suppressed saplings were higher than for open site saplings, in proportion to the volume of aboveground nonphotosynthetic organs. This suggests that timber line and shade-suppressed saplings exhibit a more effective structure for matter production than open site saplings of the same size, at least with regard to leaf and shoot expansion patterns.

3. Leaf weight ratio

Fig. 4 shows the relationship between age and LWR. On the whole, the LWR values of open site saplings were higher than those of timber line saplings. But this is due mainly to the difference in age between them. The values of open site

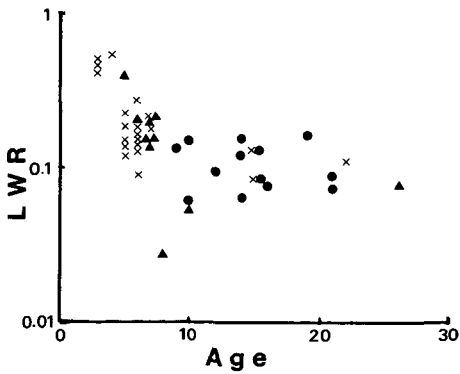


Fig. 4. Relationship between age and leaf weight ratio (LWR). Refer to Fig. 2 for explanation of symbols.

saplings decrease with age and, in consequence, likely become approximately equal to those of timber line saplings. The LWR values of timber line saplings remained nearly constant regardless of their age. The maintenance of such high LWR values is considered to be effective for sustaining life under severe stresses.

4. Production mode of aboveground nonphotosynthetic organs

Fig. 5 shows the relationship between $W1'$ and ΔVc . The ΔVc of open site saplings was nearly in direct proportion to the $W1'$. Such a relationship was recognizable to some extent in the timber line saplings. But the $\Delta Vc/W1'$ values of timber line saplings were extremely lower than for open site saplings. This clearly means that timber line saplings are extremely inhibited in the development of production structures. However, from the viewpoint of the maintenance of production structures, this means that timber line saplings exhibit more efficient responses than open site saplings, because they add less volume of nonphotosynthetic organs to existing structures. In addition, the relatively high $\Delta Vc/W1'$ values in shade-suppressed saplings perhaps reflect the difficulty of sustaining life in shade because of its strong affinity for the sun.

Fig. 6 presents the relationship between $N11'$ and ΔVc . ΔVc was approximately in direct proportion to $N11'$, at the timber line as well as in open sites. In

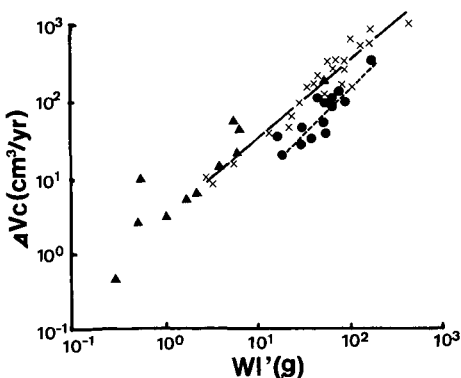


Fig. 5. Relationship between estimated leaf weight in the preceding year ($W1'$) and estimated annual growth increment of aboveground nonphotosynthetic organs (ΔVc). Solid regression line, open site saplings (regression equation, $\log(\Delta Vc) = 0.437 + 1.047 \cdot \log(W1')$; $r = 0.96$); broken regression line, timber line saplings (regression equation, $\log(\Delta Vc) = -0.03 + 1.100 \cdot \log(W1')$; $r = 0.86$). Refer to Fig. 2 for explanation of symbols.

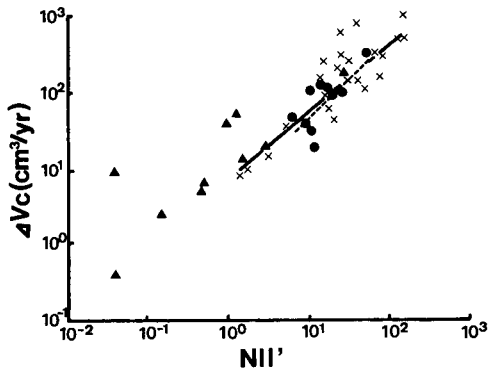


Fig. 6. Relationship between estimated number of late leaves in the preceding year (NII') and ΔVc . Solid regression line, open site saplings (regression equation, $\log(\Delta Vc) = 0.876 + 0.900 \cdot \log(NII')$; $r = 0.87$); broken regression line, timber line saplings (regression equation, $\log(\Delta Vc) = 0.623 + 1.040 \cdot \log(NII')$; $r = 0.75$). Refer to Fig. 2 for explanation of symbols.

addition, the regression equation for timber line saplings was virtually the same as for open site saplings. These suggest that annual volume increments of aboveground nonphotosynthetic organs were caused not by amount of leaves but by that of late leaves. In other words, these may mean that increase in number of early leaves does not cause an increase in the volume of aboveground nonphotosynthetic organs. Thus, early leaves, and therefore short shoots bearing early leaves only, are considered efficient organs for the construction of an accommodative production structure under severe conditions. Maintenance of high LWR values at timber lines mentioned above is likely due to such a growth habit. In the case of shade-suppressed saplings, a few were found to have extremely high $\Delta Vc/NII'$ values. Whether or not these values are due merely to an overestimation on small saplings with a small number of leaves is a question for future investigation.

General Discussion

From the results of this investigation, it may be concluded that *B. ermanii* has a tree construction habit characterized by overall growth inhibition under severe stresses. And such growth habits are perhaps constrained by the inherent mode of branching, characterized by strong apical control. Moreover, such growth habits most likely prove efficient in maintaining the trees and the communities under various severe sites.

As suggested by OKITSU¹¹⁾, sprouting from the stem base likely plays an important role in the maintenance of *B. ermanii* communities at forest limits. Indeed, sprouting itself is a response pattern against the inhibition of matter production. However, such a response may also result from the overall tree growth inhibition mentioned above. Sprouting was not found in the timber line saplings investigated. But sprouting could occur easily at forest limits from the standpoint of matter production, because the stresses there are not more severe than at timber lines. Moreover, it is thought that such stress tolerant habits enable the distribution above forest limits, because such a growth mode, characterized by the overall growth inhibition, enable preferential utilization of slight

assimilation products under severe conditions, for the maintenance of existing production structure.

To understand the growth characteristic of *B. ermanii*, it is also important to pay attention to the fact that this species exhibits typical sun-loving and early successional habits. The branching pattern characterized by many short shoots with high Rb values is useful not only for tolerance to severe stresses as mentioned above, but also for supporting sun-loving and early successional behavior, because such branching habits allow for the accelerated vertical development of the production structure in open sites³⁾. After all, it is assumed that *B. ermanii* has two contradistinctive habits (*i. e.* sun-loving and early successional habits and stress tolerant habits), both constrained by an inherent tree construction mode characterized by strong apical control.

From a few investigations of tree construction mode, FUJIMOTO³⁾ has classified the life types of cool-temperate and subarctic tall trees into the *Populus* type and the *Ulmus* type, as shown in Table 3. This classification was thought out with special reference to the GRIME's classification (*i. e.* the triangle theory)⁶⁾, although there is an extreme difference of view concerning to 'non'-competitive strategies between the two classifications. Fig. 7 shows the relationship between them.

FUJIMOTO's classification may simplify the task of understanding the growth characteristics of *B. ermanii*. This species exhibit excurrent growth form. Further, subarctic evergreen conifers (*e. g.* *Abies* and *Picea*) also exhibit an excurrent growth habit and, in consequence, exhibit stress tolerant response patterns^{3,5)}. Moreover, due to their excurrent growth habit, subarctic evergreen conifers also show sun-loving behavior to some extent, as an inherent feature^{3,5)}. These mean that the growth pattern of *B. ermanii* is similar to those of subarctic evergreen conifers, in spite of various ecological difference between them. In other words, *B. ermanii* and subarctic evergreen conifers are perhaps distributed

Table 3. Two life types of cool-temperate and subarctic tall trees^{3, 4)}

	<i>Populus</i> type	<i>Ulmus</i> type
Original life strategy	Noncompetitive and Nonsedentary (or Nomadic ²⁾)	Competitive and Sedentary
Mode of tree construction	Excurrent ¹⁾	Decurrent ¹⁾
Apical control ¹⁾	Always strong	Weak, especially in shade
Stress tolerance	High	Relatively low
Affinity for the sun	High in potential	Low in potential
Shade tolerance	High in potential	Low in potential
Mode of competition	Scramble one ^{1 0)}	Contest one ^{1 0)}
Corresponding taxon	<i>Betula, Populus,</i> <i>Conifers, etc.</i>	<i>Acer, Quercus,</i> <i>Ulmus, etc.</i>

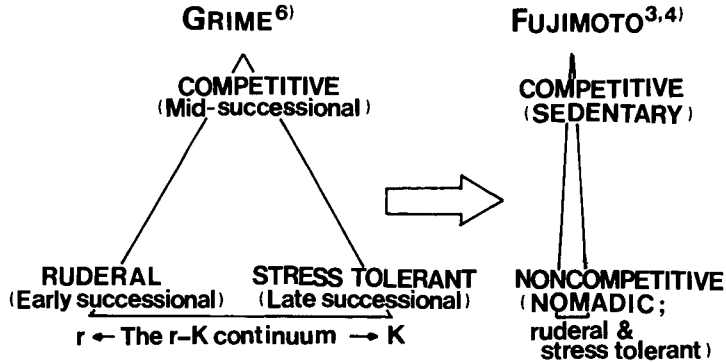


Fig. 7. Relationship between the Grime's theory and the classification shown in Table 3.

The FUJIMOTO's classification accepts GRIME's Competitive strategy. But Grime's two contradistinctive strategies (*i. e.* the Ruderal strategy and the Stress tolerant strategy) are merely interpreted as two types of behavior which the *Populus* type (*i. e.* the Noncompetitive and Nomadic strategists) opportunistically exhibits.

to various severe sites and from subarctic and subalpine zones by means of the same response mode constrained by similar tree construction patterns.

Both the sun-loving behavior and the stress tolerant behavior can be regarded as noncompetitive behavior, because both are deeply related to growth sites characterized by weak competition pressure^{3,6)}; 'competition' here is defined as 'contest competition'¹⁰⁾. This means that *B. ermanii* is a noncompetitive strategist as shown in Table 3. According to such an interpretation, its growth characteristics, including not only sun-loving but also stress tolerant behavior, might appear noncontradictory and easy to understand.

If required, the *Populus* type can be divided into two subtypes³⁾: the *Betula* type which often exhibits shade intolerant and early successional behavior, and the *Abies* type which often exhibits shade tolerant and late successional behavior. According to such a classification, *Betula ermanii* could be included in the *Betula* type because of its pronounced sun-loving habit. But these two subtypes are merely categories for comparison. In truth, it is thought that actual models of both the *Betula* and the *Abies* types cannot be discovered.

One of the most important features of the *Populus* type is its nomadic habit (*i. e.* nonsedentary habit)⁴⁾, as shown in Table 3 and Fig. 7. The *populus* type maybe exhibits opportunistically two contradistinctive types of behavior (*i. e.* sun-loving and early successional behavior, and stress tolerant behavior often related to late successional behavior) and, in consequence, its distribution range is unrestricted, as 'nomads' in the sociological sense²⁾. The conclusion may be suggested that *B. ermanii* also exhibits such a nomadic strategy, therefore allowing it to be distributed broadly, including at timber lines.

However, many unsolved problems surely remain. For example, to under-

stand fully the growth characteristics of *B. ermanii*, it is necessary to analyze the mode of dry matter production in detail. Such analyses were scarcely performed in this investigation ; therefore, such analyses are important subjects for future investigation.

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Summary

A growth analysis was carried out on *Betula ermanii* saplings growing at 3 sites. The summary of this investigation is as follows.

(1) Timber line saplings and shade-suppressed saplings displayed very much lower growth increment values than open site saplings. But they indicated difurcation ratio values as high as open site saplings. This suggests that their extreme growth inhibition is caused not only by severe stresses, but is also a reflection of their own inherent growth habit characterized by strong apical control.

(2) Timber line saplings and shade-suppressed saplings showed higher short shoot and early leaf ratios than the same volume of open site saplings. This demonstrates that *B. ermanii* could construct an efficient structure for matter production under severe conditions.

(3) The LWR values of timber line saplings were approximately equal to those for open site saplings of nearly the same age. Moreover, these values were constant regardless of age. Therefore, timber line saplings perhaps maintain efficient structure for matter production for a long period.

(4) The $\Delta Vc/Wl'$ ratio of timber line saplings was very much lower than that for open site saplings. It appears that such extreme growth inhibition is not only the result of severe conditions, but is also an efficient response for matter production at timber lines.

(5) The $\Delta Vc/Nll'$ ratio of timber line saplings was approximately equal to that of open site saplings. Moreover, ΔVc was approximately in direct proportion to Nll' both in open site saplings and timber line saplings. These suggest that early leaves do not cause an increase in the volume of aboveground nonphotosynthetic organs. This likely means that early leaves and short shoots are efficient organs for matter production under severe sites, such as timber lines.

(6) This investigation reach the conclusion that *B. ermanii* has a tree construction habit (*i. e.* the excurrent growth habit) characterized by overall growth inhibition under severe conditions, and that its broad distribution is due to this

inherent tree construction habit as well as their sun-loving nature.

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