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Dry Matter Partitioning in Seedlings and Sprouts of Several Deciduous Broad-leaved Tree Species : with Special Reference to the Functions of Tree Architecture*

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Abstract

The growth characteristics of advance reproduction on the forest floor is an important factor in understanding the natural processes of forest regeneration. In this paper, the growth characteristics of seedlings and sprouts were analyzed for five deciduous broad-leaved tree species. Changes in growth characteristics induced by sprouting, (which modifies internal factors), are discussed from an ecological view point. The dry matter economy and three aspects of tree architecture, hydraulic, supportive and assimilative efficiencies were examined using several simple indices calculated from tree dimensions and dry matter allocation for seedlings and sprouts of *Meliosma myriantha*, *Magnolia obovata*, *Pterocarya rhoifolia*, *Styrax japonicus* and *Styrax Shiraianus*.

Generally, sprouts increased their proportion of non-photosynthetic organs by sacrificing efficiency in matter economy. In particular, small-leaved or sympodial branching species, *S. japonicus*, *S. Shiraianus* and *P. rhoifolia*, modified their growth characteristics by sprouting from the 'waiting' growth (diameter-preferred growth) type to the 'competing' growth (elongation-preferred growth) type. The latter (competing) was observed in the seedlings of the large-leaved and monopodial branching species, *M. myriantha* and *S. obovata*. As a result of this change, small-leaved species and sympodial branching species tended to reduce supportive and assimilative efficiencies through sprouting. These characteristics in sprouts are thought to depend on the role of the original root system of the mother tree.

1. Introduction

In forest regeneration processes, it is advantageous for succeeding regeneration materials such as seeds and seedlings to be constantly present on the forest floor in order to utilize canopy gaps which are less predictable as regeneration sites (Grime, 1979). Of these regeneration materials, 'advance reproduction' established on the

* 伊藤 哲：落葉広葉樹数種における実生および萌芽稚樹の物質分配特性 — 樹形の機能に関連して —

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forest floor is more important in the natural regeneration of many hardwood tree species which produce seeds intermittently (Tryon and Powell, 1984). Moreover, the ability of "advance reproduction" to survive under unfavorable conditions such as inadequate light environment on the forest floor may increase the probability of successful regeneration (Grime, 1979). It is therefore necessary to investigate the growth characteristics of advance reproduction in relation to survivability in order to understand the natural regeneration process of forests.

The growth characteristics of trees should be discussed from the following three ecophysiological view points; physiological activities of plant parts, quantitative allocation characteristics of assimilates to the plant parts (dry matter partitioning) and spatial arrangement of the plant parts (tree architecture). Of these, dry matter allocation and tree architecture are the fundamental components of growth characteristics. Differences in these growth characteristics between species have been discussed in relation to difference in the niche of each species, especially with regard to assimilative architecture (e. g., Fisher 1984) (Shukla and Ramakrishnan, 1986.). Recently, differences in tree architecture within climax forest species of the same niche were also reported for warm-temperate broad-leaved trees (Kohyama, 1987). On the other hand, environmental variations in tree architecture within a species (Kohyama, 1987) and variations due to differences between regeneration types such as seedling, sprouts (Ito *et al.*, 1989) (Ito and Suzaki, 1991) and layering (Higo, 1987) have also been reported. This may be due to the fact that each species basically has its own specific growth characteristics which can adapt to changes in the internal and external environment. The purpose of this study is to compare growth characteristics between seedlings and sprouts which may make the principle contribution to the forest regeneration (Peters and Ohkubo, 1990) in order to investigate changes in growth characteristics induced by sprouting.

Tree architecture has been studied as the manifestation of dry matter production from three angles; hydraulic architecture (Zimmermann, 1978) (Zimmermann, 1983) (Ewers and Zimmermann, 1984), supportive (mechanical stability) architecture (McMahon and Kronauer, 1976) (King, 1981) (King, 1986) and assimilative (light interception) architecture (Fisher, 1984) (Shukla and Ramakrishnan, 1986) (Kohyama, 1987). However, there are few studies which deal these functions synthetically. This paper examines the differences between seedlings and sprouts in terms of these three aspects of tree architecture. This was done by evaluating the above three functions using several simple indices calculated from tree dimensions and weight of each plant part.

2. Materials and methods

The forest where materials were sampled is a cool-temperate forest at 1000–1200m above sea level in the Miyazaki Branch of the University Forests, Kyushu University,

located in central Kyushu, Japan (32°30'N, 131°E). The species investigated in this paper were *Meliosma myriantha* Sieb. et Zucc. (awabuki), *Magnolia obovata* Thunb. (hohnoki), *Pterocarya rhoifolia* Sieb. et Zucc. (sawagurumi), *Styrax japonicus* Sieb. et Zucc. (egonoki) and *Styrax Shiraianus* Makino (kohakuunboku). From a conifer-hardwood mixed forest co-dominated by momi (*Abies filma* Sieb. et Zucc.), tsuga (*Tsuga Sieboldii* Carr.) and mizunara (*Quercus crispula* Blume), 5 to 17 individuals of naturally recruited seedlings and sprouts of five species were sampled from 8-10 July 1990 for measurement of tree dimensions. For each individual, tree height (H), basal trunk diameter (D) and two horizontal diameters of crown at right angles (CD_1 and CD_2 , including the maximum diameter) were measured, and basal trunk area (BA) and crown projection area (CA) were calculated. CA was calculated to be an ellipse from two crown diameters, CD_1 and CD_2 . Tree age of all samples were determined in the laboratory from the annual rings at the trunk base. Materials were separated into plant parts and dry weight (85°C, 48hr.) was measured for leaves (WL), stems (WS) and branches (WB). From the data collected above, the following indices were calculated to examine the functions of tree architecture.

1) Leaf mass:basal area ratio (WL/BA), which indicates the hydraulic deficiency (resistivity) where the permeability of unit cross sectional area of a trunk is assumed to be constant (cf. Zimmermann, 1983).

2) Stem density index (WS/D^2H), which indicates supportive efficiency. As D^2H has been recognized as a good indicator of stem volume (Ogawa and Kira, 1977), WS/D^2H corresponds the bulk density of a stem while varying depending on the stem form. Stem strength can be assumed to be generally proportional to bulk density (Panshin and de Zeeuw, 1980).

3) Relative height (H/D), which indicates supportive deficiency. Although the supportive deficiency is correlated to H^3/D^2 (King, 1981), H/D was adopted here for the sake of simplicity.

4) Relative branch mass (WB/WT), where WT is the total mass of the above ground plant part. The relative value of branch mass indicates the assimilative efficiency because branches provide spatial arrangement to photosynthetic organs (Kohyama, 1987).

5) Relative crown area (CA/BA), which indicates the assimilative (light interception) efficiency (Kohyama, 1987).

3. Results and discussion

3.1. Dry matter economy and D-H allometry

Of the five species investigated, *S. japonicus* and *S. Shiraianus* had smaller leaves (2-10 cm long) and showed a sympodial branching pattern in the range of tree size

measured. On the other hand, *M. myriantha* and *M. obovata* had large leaves (10–40 cm long) and a monopodial branching pattern with an orthotropic trunk and plagiotropic lateral branches. *P. rhodfolia* had complex leaves with small leaflets and had a monopodial branching pattern.

Fig. 1 shows changes in the $C:F$ ratio (mass ratio of non-photosynthetic organs to photosynthetic organs) in the aboveground parts of individuals according to age. The $C:F$ ratio affects the productivity and matter economy (Iwaki, 1958). The $C:F$ ratio increased with age in seedlings of all species, and showed a tendency to increase as a result of sprouting. Particularly, *S. japonicus* which has small leaves and the sympodial branching pattern, showed significantly higher $C:F$ ratios in sprouts compared with seedlings. Increased $C:F$ ratios by sprouting was reported not only in several deciduous broad-leaved tree species, including *Quercus mongolica* var. *grosserrata*, *Acer mono* Maxim. and *Tilia japonica* Simonkai (Higo, 1987), but also in *Pasania edulis* Makino, an evergreen broad-leaved tree species (Ito *et al.*, 1989). The high $C:F$ ratio is thought to indicate an inferior matter economy because fewer photosynthetic organs must pay a respiratory cost for a greater proportion of non-photosynthetic organs. The higher $C:F$ ratio in sprouts can be interpreted as the result of a greater proportion of assimilates being allocated to non-photosynthetic organs so as to expand the leaves to more advantageous position supported by reserved sub-

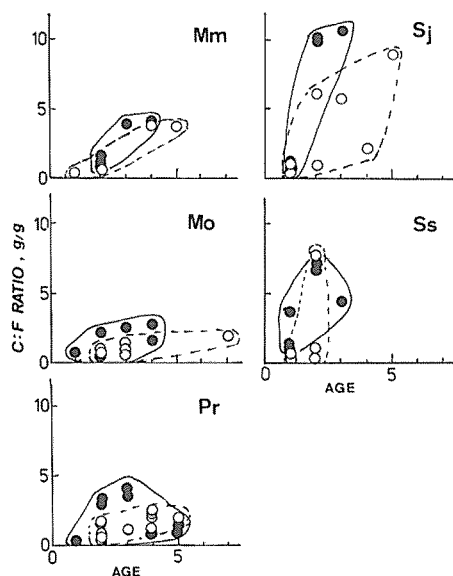


Fig. 1 Relationship between tree age and $C:F$ ratios of seedlings and sprouts in five deciduous broad-leaved tree species, *Meliosma myriantha* (Mm), *Magnolia obovata* (Mo), *Pterocarya rhoifolia* (Pr) *Styrax japonicus* (Sj) and *Styrax Shiraianus* (Ss). Open circles and broken lines indicate seedlings. Closed circles and solid lines indicate sprouts.

Table 1 Allometric relationship between basal trunk diameter (D) and tree height (H) in seedlings and sprouts of five broad-leaved deciduous trees.

Species	Regeneration type	a^*	h	r
<i>Meliosma myriantha</i>	seedlings	0.839	1.715	0.997**
	sprouts	1.030	1.019	0.954**
<i>Magnolia obovata</i>	seedlings	0.954	0.967	0.953**
	sprouts	1.156	0.767	0.732**
<i>Pterocarya rhoifolia</i>	seedlings	0.938	1.027	0.967**
	sprouts	0.760	1.414	0.936**
<i>Styrax japonicus</i>	seedlings	1.077	0.801	0.953**
	sprouts	1.219	1.039	0.972**
<i>Styrax Shiraianus</i>	seedlings	0.961	1.026	0.916**
	sprouts	1.112	1.109	0.945**

* $H = aD^h$; r , correlation coefficient.

** Statistically significant at 0.1% level.

stances in the original root system (Ito *et al.*, 1989).

Fig. 2 and Table 1 show the allometric relationship between basal trunk diameter (D) and tree height (H). The gradients of regression lines in Fig. 2 (coefficients h in Table 1) were larger in sprouts than in seedlings in *S. japonicus* and *S. Shiraianus*. These larger values of h in sprouts indicate that relative height growth rates are greater than relative diameter growth rates, (i. e., elongation-preferred growth characteristics) in sprouts compared with seedlings. This elongation-preferred growth in sprouts was also observed in *P. edulis* (Ito *et al.* 1989). On the other hand, in *M. myriantha* and *M. obovata* which have larger leaves and a monopodial branching pattern, seedlings showed elongation-preferred growth characteristics in contrast to the seedlings of two species with small leaves and sympodial branching. These two species with large leaves and monopodial branching showed less change in growth characteristics when moving from elongation-preferred growth to radial-preferred growth, i. e., relatively small values of coefficient h , as a result of sprouting. However, these change were not clear.

Kohyama (1987) examined the significance of architecture and allometry in saplings of warm-temperate rain forest trees and reported as follows. Species with small leaves needed to develop higher orders of branching in order to support the greater number of leaves. Although they expend a greater amount of assimilates than larger-leaved species by allocating dry matter to lateral branches, they are superior in maintaining and expanding an assimilative system at any given height over an extended period. Species with large leaves do not require such a lateral branch system and allocate assimilates to growth in height. He also suggested that the former species are 'pessimistic' about the early formation of a gap and 'choose' to wait on the dark forest floor, and the latter species are 'optimistic' and 'select' growth characteristics to establish ascendancy in sapling competition. Similar results were obtained from five deciduous broad-leaved tree species examined in this study. Further, changes of

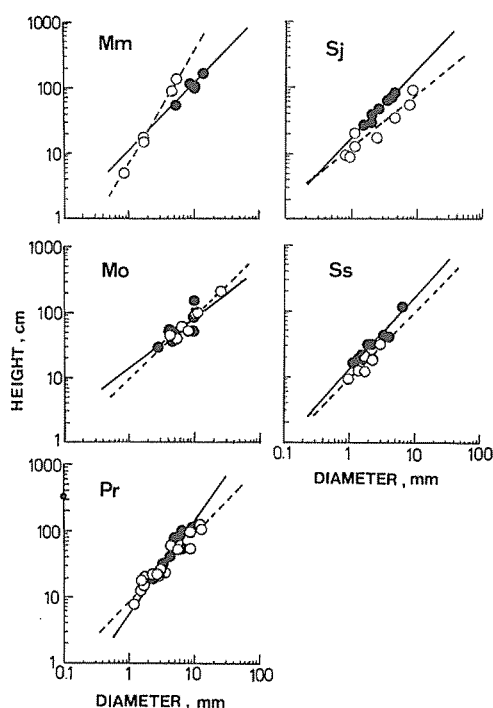


Fig. 2 Allometric relationship between basal trunk diameter (D) and tree height (H) in seedlings and sprouts of five deciduous broad-leaved tree species. Symbols and lines are the same as in Fig. 1.

growth habits induced by sprouting were also observed. From the results obtained from the two small-leaved species, *S. japonicus* and *S. Shiraiianus*, it is thought that seedlings of these species adopt growth characteristics to complete their assimilative structure by sacrificing height growth ('waiting' type), and change to an elongation-preferred growth type ('competing' type) to become ascendant. *P. rhoifolia*, the species with small leaves and a monopodial branching pattern also showed a change in growth characteristics from the 'waiting' type to the 'competing' type in the same way as *S. japonicus* and *S. Shiraiianus*.

3.2. Functional changes in tree architecture

Fig. 3 shows the relationship between tree age and leaf mass/basal area ratio (WL/BA). The values of this index were lower as a result of sprouting, (i.e., hydraulic efficiency was higher), in *S. Shiraiianus*. Values were higher in sprouts than in seedlings, (i. e., hydraulic efficiency was lower), in *P. rhoifolia* as a result of sprouting rather than in seedlings. However, definite tendencies in regard to morphology or branching type were not observed in any group.

Fig. 4 shows the relationship between the age and the stem density index (WS/D^2H)

indicating the supportive efficiency. Seedlings of all sample species except *S. Shiraianus* showed a decline in supportive efficiency with age. In *M. myriantha* and *S. japonicus*, supportive efficiency was lower over the range of age examined in sprouts than in seedlings. Fig. 5 shows the relationship between age and relative height (H/D). Although no particular change in this index was observed with age in seedlings of any species except for *M. myriantha*, conspicuous declines in the supportive efficiency, i. e., increase in relative height, induced by sprouting were observed in the small-leaved species, *S. japonicus*, *S. Shiraianun* and *P. rhoifolia*.

Fig. 6 and 7 show two indices of assimilative efficiency, relative branch mass (WB/WT) and relative crown area (CA/BA), respectively. Generally, the relative branch mass was greater in seedlings than in sprouts, and this tendency was particularly evident in *S. japonicus*. In *M. myriantha*, *S. japonicus* and *S. Shiraianus*, relative crown area also declined as a result of sprouting.

From the above results, it can be concluded that although there was no change in hydraulic efficiency, supportive and assimilative efficiencies declined due to sprouting, and this decline was conspicuous in small-leaved and sympodial branching species.

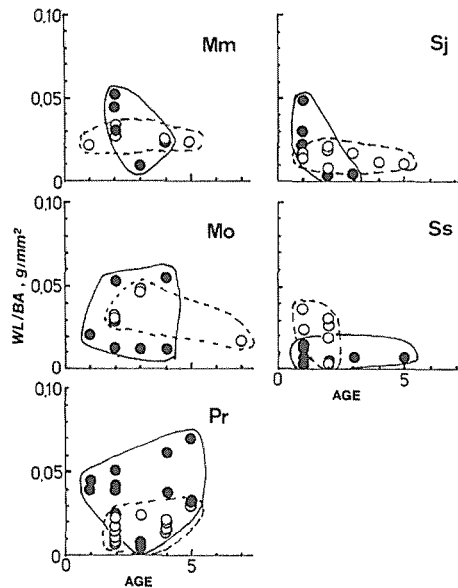


Fig. 3 Relationship between tree age and the leaf mass : basal area ratio (WL/BA) in seedlings and sprouts of five deciduous broad-leaved tree species. Symbols and lines are the same as in Fig. 1.

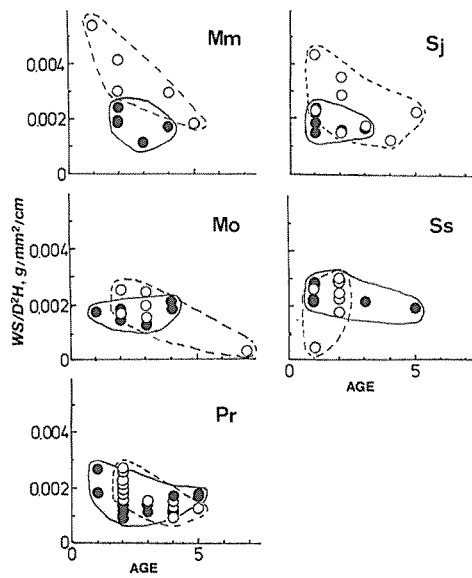


Fig. 4 Relationship between tree age and the stem density index (WS/D^2H) in seedlings and sprouts of five deciduous broad-leaved tree species. Symbols and lines are the same as in Fig. 1.

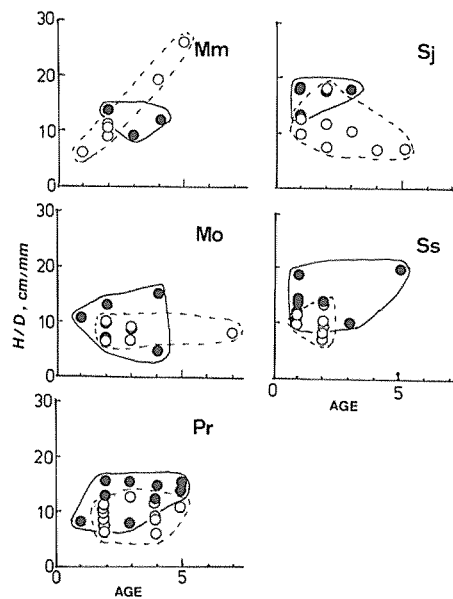


Fig. 5 Relationship between tree age and the relative height (H/D) in seedlings and sprouts of five deciduous broad-leaved tree species. Symbols and lines are the same as in Fig. 1.

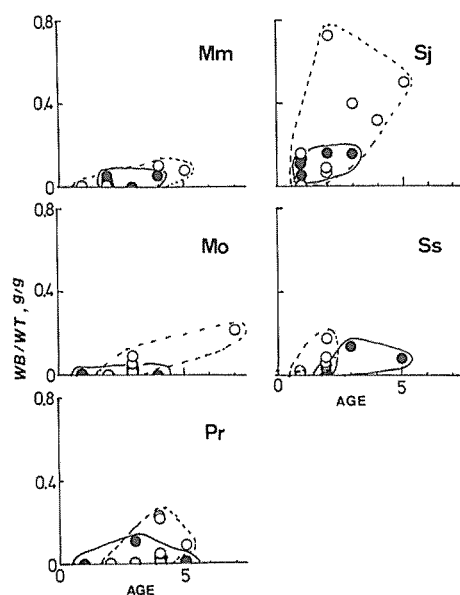


Fig. 6 Relationship between tree age and the relative branch mass (WB/WT) in seedlings and sprouts of five deciduous broad-leaved tree species. Symbols and lines are the same as in Fig. 1.

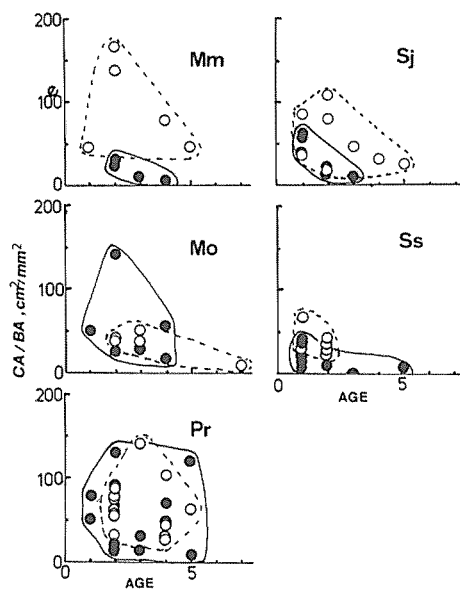


Fig. 7 Relationship between tree age and the relative crown area (CA/BA) in seedlings and sprouts of five deciduous broad-leaved tree species. Symbols and lines are the same as in Fig. 1.

4. Conclusions

In this paper, I examined the differences in growth characteristics of the advance reproduction of seedlings and sprouts, and obtained results indicating that sprouts increased their proportion of non-photosynthetic organ weight by sacrificing efficiency of the matter economy. In particular, small-leaved or sympodial branching species changed growth characteristics by sprouting from the 'waiting' growth type to the 'competing' growth type. The 'competing' growth type was observed in large-leaved and monopodial branching species. As a result of this change, these three species tended to decline in supportive and assimilative efficiencies. These characteristics of sprouts are thought to be supported by the role of the original root system of sprouts, and may be among the features of sprouts (an 'emergence' form) which flushes when the mother tree is damaged (Zimmermann and Brown, 1971).

Although no clear difference in hydraulic efficiency between seedlings and sprouts was observed in the results, a smaller leaf specific resistance to water flow was obtained in sprouts compared with normally grown shoots in *Eucalyptus globulus* (Ito and Suzaki, 1990). In the comparison between seedlings and sprouts of *P. edulis* established after clear-cut, the leaf specific resistance was also smaller in sprouts which had an original stump root system than in seedlings (unpublished data). Moreover, higher photosynthetic activity in sprouts than in seedlings was reported in *P. edulis* (Ito and Suzaki, 1989). It is therefore necessary to analyze the architecture of sprouts by evaluating the role of the original root system and physiological characteristics such as the permeability of conducting organs and photosynthetic activity. In this paper, changes in growth characteristics induced by sprouting were examined. However, these characteristics are affected by changes in external environment such as light, soil moisture, etc. These problems have not been clarified here and require further research.

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落葉広葉樹数種における実生および萌芽稚樹の 物質分配特性

— 樹形の機能に関連して —

伊 藤 哲

要 約

森林の更新過程を解明する上では、前生樹の生育特性の把握が重要である。本研究では、森林の更新過程に大きく寄与していると考えられる実生稚樹および萌芽稚樹の物質分配特性を比較し、萌芽という現象に伴う内的要因の変化により、個体の生育特性がどのように変化しているかを解析した。エゴノキ、コハクウンボク、アワブキ、ホオノキおよびサワルグミについて、個体の各器官の量的分配とサイズから簡単な指数を用いて、水分通導、支持および同化という樹形の3機能を評価し、樹種毎に実生および萌芽稚樹における樹形の生態的意義の比較を行った。

一般に、萌芽では実生と比較して物質経済の有利性を犠牲にしながら非同化器官の比率を増加させる傾向がみられた。特に小型葉で仮軸分枝型の種であるエゴノキおよびコハクウンボクの実生では、大型葉・単軸分枝型の種であるアワブキおよびホオノキに比べて、同化効率と支持効率が高い“待機型（肥大優先型）”の生育特性を持っており、萌芽することによって、大型葉・単軸型の種の樹形でみられた同化・支持効率の低い“競争型（伸長優先型）”へ生育様式を移行させていることが明らかとなった。これらの結果は、萌芽の母樹の既存の根系の働きに支持されているものと考えられた。