On the Crown Slenderness in Clones and Seedlings

By Ryookiti Toda

Introduction

When we select elite trees we must put considerable importance on the slenderness of their crowns (Lindquist 1948). Not only is crown slenderness usually correlated with thinner branches which causes better quality timber, but also it seems to be one of the important factors in determining the yield of trees. If the possible number of stems per unit area is fairly proportional to crown slenderness, then we may be able to obtain planting materials that are individually slower-growing, but still on a unit area basis high yielding, by selecting extremely narrow crowned trees among acceptable growth rates. Indeed, for the purpose of obtaining 30 per cent increased yield from the same area, it might be enough to select trees of only 17 per cent decreased crown diameter assuming the height and diameter of stems in average are constant (Toda 1953 a).

On the other hand, Reineke (1933) has found a certain relationship between average stem diameter (D) and the maximum number of stems on a unit area (N), and he showed that the relation could be represented, regardless of the species, by the following formula:

\[ \log N = K - 1.605 \log D \]  
(1)

If it is possible to set the premise that the average crown diameter (S) is the same as the diameter of a circle calculated by dividing the unit area by the number of stems, we can easily get the relation between crown and stem diameters introducing:

\[ N = \text{const} \cdot S^2 \]

into the formula (1). This premise, as will be shown later, seems to be in error, but now we get the following formula by the calculation:

\[ \log S = K_S + 0.803 \log D \]  
(2)

When this formula is plotted on bi-logarithmic section paper, trees of the same genetic quality will be arranged on a straight line which is parallel to other lines plotted for trees with different genetic qualities. So, if this formula would apply to practical materials, the slenderness of crown must be represented by the value of \( K_S \) in the formula (2) or the related value.

Above was the author’s original hypothesis. Starting from this hypothesis, the author tried the measurement in a clone of Cryptomeria, which was propagated by cuttings and was the only real clone available in south-west Japan (Toda 1954). The results showed that the coefficient 0.803 of log D in the formula (2) could not be applied to this material, but the new coefficient 0.51 seemed to be correct. The reason for this disagreement seemed to be due to the fact that the author had set an unsuitable premise when he introduced formula (2) from formula (1). Additional measurements in a natural population of Pinus densiflora and its naturally reproduced second growth (Toda 1954), and the measurements on the elite trees of Cryptomeria selected in the southernmost part of Japan (unpublished), seemed to agree on the above mentioned new coefficient. So the author proposed a numerical value, which was named as “spacing value” and was represented by \( K'_S \) in the following formula (3) as an indication of crown slenderness of a tree.

\[ \frac{K'_S}{100} = \log S - 0.51 (\log D - 1) \]  
(3)

This value was thought to be determined mainly by genetic factors and it may be influenced environmentally (Toda 1954).

Later, the author had an opportunity to study in Denmark at the Hørsholm Arboretum of the Royal Veterinary and Agricultural College where Dr. C. Strøbø Larsen has grown his extensive materials. He has kindly allowed the author to measure his materials and the author is much obliged to him for the allowance and for his kind guidance. The results of these measurements did not support the author’s original hypothesis, still the study showed certain interesting facts which will be reported here. The author also expresses his thanks to all of the staff in the Arboretum for their valuable help and discussions which he appreciates very much.

Materials and Methods

A clone of Larix decidua, “Tinghus” or V. 44, and three other clones and their self-pollinated progenies were selected as material. Forked or extremely abnormal stems were excluded from the material.

Stem diameter was calculated from the girth at a height of 1.2 meter. Thicker stems were measured by means of usual measuring cloth tape and thinner ones by means of thin brass wire and wooden scale. The crown diameter of small trees was measured in four directions directly with a cloth tape. For tall trees the aid of two projectors constructed with a pendulum, mirror and hollow zinc cylinder was required (Toda 1953 b).

Results and Discussions

1. Examination of previous formula

Results from V. 44 are shown in Fig. 1. In this figure it is clearly observed that the clone did not follow an inclination of 0.51 which had been calculated from the clone of Cryptomeria. It seems to show an inclination of about 0.6 which seems to agree with the other measured larch clones show in Fig. 2, but the exact value of the inclination is not calculated here because the variation within the clone is too great as will be discussed later. Naturally, the clone of Cryptomeria has been propagated by cuttings and the trees are standing on their own roots, while the clones of larch by grafting. So the difference between them may be due to the different methods of propagation. But, at present, we have no means to make it clear if it really depends on the propagating methods or not, so it may be safer to consider that the difference in inclination is due to the difference in specific nature. It seems to be natural that the difference which can be found between species can also be found to some extent between different races and so on within a species, because in both cases differences of characters are due to the different genetic nature. So we inevitably reach the conclusion that there is no

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Fig. 1. — Relation between stem and crown diameters of V. 44, a clone of Larix decidua, and its self-pollinated progeny. It is clearly observed that the clone forms a steeper line than that of Cryptomeria (log S = K + 0.32 log D). Also it is characteristic that seedlings appear in a much higher position on the left side and approach gradually to the clone. Unexpectedly wide variation in the clone also offers a problem.

Fig. 2. — Relation between stem and crown diameters of three larch clones and their self-pollinated progenies. All of them show the same tendency as the clone V. 44.

general coefficient for log D in the Formula (2) nor the "spacing value" represented by $K_s$ in the formula (3).

In the previous report (Toda 1954) the author developed two different conceptions, i.e. the "crown projection area" and the "occupation area" of a tree to explain the reason for the discrepancy between the coefficients in the formulas (2) and (3). The "occupation area" is an abstract conception and it means the area really belonging to a certain tree and not to another, and might be calculated from the maximum number of trees on a unit area. If Rennek's formula were surely correct for most tree species, the diameter of the "occupation area" could quite satisfy the formula (2) for most tree species and varieties. But, the "crown projection area" is not the same as "occupation area". It is well known that when a stand is young the banches of neighboring trees deeply cross with each other, while in older stands we can easily find broken canopy even in a relatively dense stand. In other words, the crown projection area is much larger than the occupation area in younger trees, and on the contrary in older trees it becomes smaller than the latter. So, it is quite natural that we find the inclination of the straight line which represents the relation between the stem and crown diameters being less steep. It is also quite possible that the different species or even the different genotypes within a species will show a different inclination of the line, because the relation between the occupation area and the crown projection area may be different according to the different genetic constitutions of the materials.

What is important for us is not the crown projection area but the occupation area which is directly concerned with the number of stems on a unit area. But, at present, we are not in a situation to determine the occupation area directly for each single tree; we do not even know if it is possible or not. Nevertheless it seems, that the width of the crown projection area has a definite influence upon the occupation area thus it may be possible to calculate the latter from the former. This seems to be the task of a further study along these lines.

2. Juvenility in the crown slenderness

In figures 1 and 2, we easily become aware of the fact that there are considerable differences between clones and their self-pollinated progenies. When the trees are smaller, seedlings have much broader crowns than grafts, and this difference becomes smaller and smaller when the trees grow. In Fig. 1, we can see that both grafts and seedlings have shown nearly the same crown diameter when the stem diameter has reached about 10 centimeters. Unfortunately, we cannot know what it becomes when they grow up farther, as we have no bigger materials, but by using measurements from two older trees of open pollinated progenies of the same clone, we can guess that seedlings and grafts will make very similar development afterwards. It is well known that seedling trees show various phenomena of juvenility when they are young, while grafted trees do not show the same character as seedlings of the same size. This difference of crown slenderness may also be an expression of juvenility.

3. Variation within the same clone

On the other hand, the most important result of the present study seems to be the demonstration of quite large
variances in the clone materials. As far as judged on the figures, it is very evident that clones have shown nearly as much variance in their crown slenderness as the seedlings, especially in V. 44. If the crown slenderness is really a genetic character, and the author believes that it is, seedlings must show much larger variance than clones. According to general opinion, we can formulate the constitution of variance in seedlings and in clones as follows:

\[
\text{Variance in seedlings} = \text{genetic} + \text{environmental} + \text{measurement error}.
\]

\[
\text{Variance in a clone} = \text{environmental} + \text{measurement error}.
\]

Although an exact analysis of variance is impossible as the observation has not been designed for that purpose, each component of variance will be examined approximately in the following paragraphs.

As the same method has been used in both of the two materials, the measurement error must be the same for each single measurement. But, there is one question about this component, that, as grafts and seedlings have shown different crown types, the accuracy of the single measurement as an estimate of "crown diameter" may show different values according to the different types of trees. So the author calculated the standard deviation of "single measurement" to mean crown diameter of each tree, and found that they are a little larger in the clone than in the seedlings. As shown in Fig. 3, the standard deviation of "single measurement" can be estimated roughly as 0.08 in clone and 0.075 in seedlings, which are nearly equivalent to logarithmic values of 0.035 and 0.03. As the crown diameter was calculated as the mean value of four measurements, the standard error of each mean crown diameter must be 0.035/\sqrt{4} for the clone and 0.03/\sqrt{4} for the seedlings, and this makes the variances about 3 \times 10^{-4} and 2 \times 10^{-4} respectively. Here, surely, larger variance is introduced in clonal material by measurement error, but the relative amount of the variance is, as shown later, less than one half of the total variance, so the difference between them cannot explain so large a variance in the clone.

The total variance can be estimated from the range of distribution (Snedecor 1952). The maximum range of distribution can be measured in Fig. 1 and we get a value of approximately 0.12 of logarithmic value for both the clone V. 44 and its progeny. About 1/4.5 of the distribution range, i.e. about 0.027, can be estimated as the standard deviation of crown diameter in logarithmic value. We get, therefore, as the total variance about 7 \times 10^{-4} for both of the materials. It means that more than one half of the total variance must have been derived from another factor or factors than measurement error, and the difference in the measurement error between the two groups does not mean very much.

As to the variance caused by environmental fluctuation it is very difficult to discuss it in detail. But, we can surely guess that the site quality, in usual meaning, does not affect crown slenderness very much because (i) various groups planted on different sites follow the same general tendencies, (ii) both bigger and smaller individuals of the same group as well as the transplanted and non-transplanted groups of the same origin show quite the same range of variation and have essentially the same tendency. In other words, the vigor of the growth seems to have no correlation with the crown slenderness.

The most important environmental influence which affects the crown slenderness must be the competition between neighbouring individuals, and among the materials shown in Fig. 1, S. 648, of which some individuals show an extremely poor crown development, is the only case in which the severe competition has taken place. We can also observe the influence of artificial pruning in V. 418 in Fig. 2, which cause a considerable decrease of crown diameter. But, trees of most other groups are growing freely.

Among graftings, V. 44—43 (not top-grafted) was transplanted when the trees reached a rather large dimension, still the range of distribution for them is not different than the other groups from the same clone.

Of course, we cannot know thoroughly about the environment and its effect, but as far as judged from the knowledge available at present, it is nearly impossible to explain the whole residual variance by the environmental fluctuation. On the other hand, when we suppose that the environmental influence is really so big, then it is very difficult to expect that the seedlings show so small a genetic variation even when they are self-pollinated progeny. It is natural to suppose that a quantitative character of this kind is controlled by a polygene system, so in a cross-pollinating plant like larch it is quite difficult to imagine a tree possessing a high degree of homozygocity.

On the other hand, it is well known that some grafts often grow just like branches while the other grafts of the same clone grow upright as normal stems. We can force these branch type grafts to grow upright with the aid of supporting sticks but still for many years we can recognize them by more or less crooked stem, asymmetrical branch habit or not round shape of stem section. Unfortunately, the author has failed to classify all of his materials from the viewpoint of this normality, but still he has tried this in a smaller part of his material and has got the results shown in Fig. 4. It is quite evident that the abnormality of growing habit affects very much the increase in crown diameter, and the difference between normal and abnormal groups is larger than that due to the direct effect of a crooked stem. We can very roughly estimate the variance caused by this abnormality as nearly the same amount as the residual variance other than the measurement error. Of course, the abnormality is transitional from the normal to the extreme, so it seems to be impossible to exclude all abnormal individuals from a group of clonal trees in trying to eliminate the variance due to abnormality. So, we cannot get the exact value of variance due to the environmental fluctuation.
Fig. 4. — Crown slenderness in normal and abnormal stems classified for some of the V. 44. More or less crooked stem, unsymmetrical branch habit and not round shape of stem section indicate the abnormality.

But, what is the nature of this abnormality? Is it genetic variation? Of course, no, it cannot be considered as genetic because every individual within a clone must have the same genetic quality except some somatic mutants which is rather rare in its occurrence. Then, is it due to the influence of environmental fluctuation? It is rather difficult to answer this question, but the environment in usual meaning seems to have no effect on this phenomenon. It is difficult to explain from the environmental difference why some grafts do grow like branches while others grow upright.

SCHAFALTZKY DE MUCKADELL (1954) has recently published his study on the juvenile form of beech trees, in which he states that grafts made from lower, leaf-retaining epicormics keep their withered leaves through winter while those from higher, leaf-shedding epicormics or from the top branches of the same tree shed their leaves. He also made an observation that these characters have been kept unchanged during three years on each group of grafted trees. Here we can see an example that individuals within a clone may react differently to the same environment according to their inner nature, but not genetic. In the present material of the larch, the matter seems to be very similar to SCHAFALTZKY’s beech, although the phenomenon in the former seems to have no relation to juvenility.

A Japanese forest owner MAGOTA HOKUDA, who has grown several clones of Cryptomeria from selected old trees, once told about his experience: that the first cuttings of Cryptomeria collected on the top of old trees not only had been difficult to root but also grew very abnormally. After several repeated vegetative propagations, however, he observed that both the rooting capacity and normal growth habit were recovered (Toda 1953 a). His son has also told the author that twigs collected on the lower part of the crown show the tendency to root better but often fail to grow normally, on the other hand, twigs collected on the upper part of the crown are difficult to root but grow more normally. The author himself also had the same experience with some material.

All these facts seem to show the presence of a long durable aftereffect of the nature of the scion wood, which is determined by the developmental stage or physiological condition in each part of a tree. Even after a considerably long period of independent life of cuttings or grafts, this effect can determine the different ways an individual plant responds. Variation in clonal material may include this kind of variance, which cannot be considered as due to the environmental influence in the present vegetative generation.

No doubt the clonal test is still the easiest and shortest way to estimate the genetic character of a tree (SYRACH LANDEN 1947, TODA 1953 a), but we must be always careful about the fact that it may include some factor of non-genetic but inner variation. It must, therefore, be kept in mind that the results from a clonal test have no more value than that of an approximate estimation. The degree of adaptability of this estimation will differ very much according to the kind of material.

Summary

In the formula which shows the relationship between stem (D) and crown (S) diameters of a tree:

\[ \log S = K_S + C \log D \]

it became clear that there is no constant value of C through different species. Accordingly, we cannot employ the „spacing value“, which has been previously proposed by the author as the method of description of crown slenderness of a tree.

Self-pollinated seedlings have, when they are young, much broader crowns compared with the mother clone, and the difference between them becomes smaller and smaller when they grow. This difference of crown slenderness seems to be an expression of juvenility.

Unexpectedly large variance was found within the same clone. The nature of this variance was discussed and it became clear that the abnormality of growth habit was correlated with the increased crown diameter. This abnormality does not seem to be caused by environmental influence in usual meaning but to be due to the inner nature of scion wood used. Variation within a clone may always include such non-genetic inner variation; so the clonal test must be considered as of approximate value.

Zusammenfassung

Titel der Arbeit: Über die Kronenschlanckheit bei Klonen und Sämlingen.

Es wird festgestellt, daß in der Formel

\[ \log S = K_S + C \log D \]

die den Zusammenhang zwischen Stamm- (D) und Kronendurchmesser (S) eines Baumes erfaßt, für die verschiedenen Species kein konstanter Wert für C angenommen werden kann. Demnach können wir nicht den „spacing value“ verwenden, der früher vom Autor als geeignet für die Kronenschlanckheit vorgeschlagen worden war.

Sämlinge aus Selbstung besitzen in der Jugend sehr viel breitere Kronen, verglichen mit den Mutterkronen. Dieser Unterschied wird aber mit fortschreitendem Wachstum der Sämlinge kleiner. Er scheint ein Ausdruck jugendlichen Wachstums zu sein.

Résumé

Titre de l'article: La finesse des cimes dans les clones et dans les semis. —

Dans la formule log S = K · C + C log D qui donne la relation entre le diamètre du tronc (D) et celui de la cime (S) d’un arbre, on constate que C n’a pas une valeur con-
stante pour différentes essences. Donc nous ne pouvons appliquer le “spacing value” qui a été proposé auparavant par l’auteur comme caractéristique de la finesse de la cime d’un arbre.

Les semis issus d’autofécondation sont pendant leur jeune-

euse une clime beaucoup plus large, comparée avec celle du clone maternel. Cette différence diminue avec l’âge des semis. Elle paraît être un caractère de la croissance juvénile.

D’une manière surprenante, on constate une grande variation entre les plants d’un même clone. La nature de cette variation est discutée et on montre que les anomalies de port sont liées à l’augmentation du diamètre des cimes. Ces anomalies ne paraissent pas être causées par le milieu

dans le sens usuel, mais par la nature du bois employé

pour scion. La variation à l’intérieur du même clone peut toujours comprendre de telles variations internes non génétiques; donc les résultats d’un test de clones doivent être considérés comme approximatifs.

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Rassenbildung und Bestandesanerkennung

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Bei der Diskussion um die forstliche Saatgutsetzungs-

gbung (ANONYMUS) taucht immer wieder die Frage auf, wie man sich die Ausbildung von Rassen unserer Holzarten vorzustellen hat, die schließlich der Hauptgegenstand der Saatgutsetzungsgebungen sind, und welche Schlußfolgerungen für letztere aus den Ergebnissen dieser Überlegungen zu ziehen sind. Im nachfolgenden soll versucht werden, eine einigermaßen befriedigende Antwort auf diese Frage zu geben. Um nun hier nicht neue Unklarheiten zu schaffen, ist es zuvor notwendig, die zu verwendenden Begriffe ab-

zugrenzen und zu definieren.

1. Definitionen

1.1. Die Population

Dieser Begriff wurde ursprünglich gleichzeitig etwa mit „Bevölkerung“ gebraucht, hat aber im Laufe der Zeit eine völlig andere Bedeutung erhalten. So bezeichnet man bei-
speisweise in der Terminologie der Statistik ein nach

irgendem oder mehreren Merkmalen zu ordnendes Kol-

lektiv, so etwa schon die Produktion einer Maschine an Ni-

geln, als Population. Allerdings hieraus erheilt, daß für unsere Zwecke klare Definitionen erforderlich sind. Wir wollen eine solche zunächst für die „Artpopulation“ geben. Diese soll die Gesamtheit der lebenden Individuen einer Art um-

fassen, z. B. der Art Picea abies. Zum Zweck soll die „Teil-

population“, im folgenden kurz „Population“ genannt, defi-

niert werden, als zusammenfassende Bezeichnung aller In-

dividuen der Artpopulation, welche innerhalb der Grenzen

eines natürlich oder willkürlich begrenzten Areals vor-

kommen.

1.2. Rasse und Sorte

Unter Rasse soll zunächst eine Population verstanden werden, die sich in einem oder mehreren Merkmalen von

einer anderen Population der gleichen Art unterscheidet. Nur liegt es auf der Hand, daß man diese Unterscheidung nicht auf dem Erscheinungsbild der Population aufbauen kann, das benagt schon die Bedeutung des Wortes Rasse im täglichen Sprachgebrauch, sondern ausschließlich auf Unterschieden in der genetischen Konstitution der zu ver-

gleichenden Populationen, die man als Rassen derselben Art auffassen will. Diese aber, der „Genotyp“, ist für das Individuum gebildet durch die Summe der sein Erschei-

nungsbild bestimmenden Erbanlagen und für die Popula-

tion als Summe der beteiligten Individuen und damit der Summe aller Erbanlagen der letzteren. Dementsprechend wollen wir von „Rassen“ sprechen, wenn mindestens zwei Populationen der gleichen Art vorliegen, deren Genhäufig-

keiten sichere Unterschiede aufweisen. Im Gegensatz zur Population muß hier jedoch die Einschränkung gemacht werden, daß man eine willkürlich oder nach irgendeinem Prinzip herausgegriffene Anzahl von Individuen einer Art-

population nicht als Rasse bezeichnen kann. Sollten sich zwischen den Genhäufigkeiten zweier auf diese Art gebil-

deten Teilpopulationen, etwa nach künstlicher Auslese, Unterschiede zeigen, so sollte man von „Sorten“ sprechen. Der Begriff Rasse schließt nämlich die natürliche Entste-

hung der Genhäufigkeitsdifferenzen ein.)

Eine Rasse ist demnach durchaus nicht etwa eine gene-

tisch einheitliche Population, wie man es manchmal ange-

geben findet.

(*) Es ist klar, daß diese Definition des Sortenbegriffes dann unzweckmäßig ist, wenn man daran denkt, mit der Definition der „Sorte“ alle Möglichkeiten zu erschöpfen, die dem Züchter zu deren Schaffung zur Verfügung stehen. Hier geht es aber ledig-

lich um die Abgrenzung der Rasse gegenüber Populationen, deren Genfrequenzen durch künstlichen Eingriff — Selektion — bewußt verändert wurden.