THEORETICAL GROWTH EQUATIONS

AND

THEIR APPLICATIONS IN FORESTRY

by

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ABSTRACT

The objective of the present work is twofold, i.e. one of straightening out the cluttering jam of growth equations in search of the most potential one for the growth of trees especially in stem radius, and of applying the theory of growth equation to other important issues of mensuration and forestry to reorganize them into a more rationally-related and interwoven system.

In pursuit of the first objective, numerous growth equations were reviewed in chapter II and classified into four categories, i.e., the empiricals, the quasi-theoreticals, the particular theoreticals and the general theoreticals. In doing so discussion was made as to the superiorities of the theoretical equations over the empirical ones, and of the particular theoreticals over the general ones. However, it was also found that as of today there is no particular theoretical equation expressing the growth of individual trees, and thus it was concluded that the available best for describing the growth of individual trees was the genral theoretical equation. In chapter III, the characteristics of the three general theoretical equations thus chosen, i.e., the Mitscherlich, the logistic and the Gompertz were discussed from an a priori theoretical point of view.

In further pursuit of the most prospective growth equations for trees, the three general theoreticals were

applied to the radial stem growth of 84 white spruce trees in chapter IV. It turned out that although all the equations did not work in application as satisfactorily as expected from the theory, the Mitscherlich revealed the least theoretical discrepancy, while the logistic did the most. The best graphical agreement with the observed growth was attained by the Gompertz, followed by the Mitscherlich, then by the logistic. The easiest to fit was the Mitscherlich, followed by the logistic, then by the Gompertz.

A similar analysis as in chapter IV was conducted with 349 individual growth records of jack pine in chapter V. All the equations worked better with jack pine than with white spruce in every criterion employed. The most remarkable improvement was achieved by the Mitscherlich. It revealed the least theoretical discrepancy, while the logistic did the most as with white spruce. The best graphical agreement with the observed growth was achieved by the Mitscherlich followed by the Gompertz, then by the logistic. The easiest to fit was the Mitscherlich followed by the Gompertz, then by the logistic. As an overall conclusion of chapters IV and V, at the present state of knowledge the best growth equation to describe the growth of trees in stem radius would be the Mitscherlich.

The last two chapter of the present work is devoted to the second objective, i.e., the application of the theory of the growth equation to the other important subjects of mensuration, i.e., the stem taper curve and the height-diameter curve. Assuming that the growth of individual trees in stem diameter and height follows the Mitscherlich equation, a theoretical stem taper curve was derived mathematically. Subsequently it was compared with 50 observed stem taper curves and its theoretical compatibility was discussed. The proposed stem taper curve was also compared with other existing empirical stem taper curves in terms of the goodness of fit to 50 observed taper curves. It turned out that the ten equations compared were separated into five groups singificantly differing from each other, of which the proposed equation fell into the second best group.

Again assuming that the growth of individual trees in stem diameter and height follows the Mitscherlich equation, a height-diameter curve for all-aged stands was derived. Then based on a similar but slightly different assumption, another height-diameter curve for even-aged stand was derived. Both equations are identical in their mathematical appearance but are different in what they mean.

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CHAPTER I

INTRODUCTION

Mensuration, or forest biometrics as is recently called, is a science of means which provides vital statistics concerning the state and structure of trees for the most essential discipline of fores' y, i.e., the management and planning of forested lands. In spite of its time-honored history, most of the mensurational approaches have been rather empirical than theoretical largly due to the complexities and irregularities inevitably involved in any biological phenomena. In other words the history of mensuration was a series of efforts to find hidden uniformity and integrity in what is seemingly random, irregular and arbitrary outcome which individual trees as well as their aggregates demonstrate.

It is generally said that remote sensing and statistical methods are the two major breakthroughs achieved in recent decades in forest biometrics. The former has contributed to the search of uniformity and integrity by providing a literally perspective view of the forested lands, while the latter by providing rational means to process what seems irregular and thus formidable and indigestible data in a logical manner. Unfortunately, however, neither the remote sensing nor the statistical methods constitute the essential core o mensuration. They are simply the means of data collection and data processing respectively that are nonessential to mensuration and can be shared with other discipline of science. This leaves the core still intact and most of the essential parts of mensuration remain rather empirical as ever.

Though implicit in the major parts of the text, the latent objective of the present work is to introduce a theoretical and systematic approach into the mensuration proper. For this purpose the theoretical growth equation was chosen as the nucleus from which a systematic redevelopment of mensuration is to be made. It will be shown in the text that the issue of the growth equation, which has been dealt with to date rather independently as one of the other independent subjects of mensuration, constitute a powerful foundation which binds what are seemingly unrelated subjects of mensuration. Considering the fact that many vital phenomena encountered in mensuration are brought about by the growth of trees, there is no wonder why the subject of growth equation is associated with some of other vital issues of mensuration. In the present work, an extensive and volumenous analysis is made in search of the most powerful growth equation, then its association with the subjects of stem taper curve and height-diameter curve is demonstrated by applying the theory of growth equation to explain why the tapering of tree stems and the height-diameter relationship are shaped as they really are.

In chapter II existing growth equations are reviewed critically so as not only to untangle the cluttering abundance and complexity but also to narrow them down to the most suitable ones for expressing the growth of trees especially in stem radius and diameter. In chapter III, advantages and disadvantages of the three theoretical growth equations chosen in the preceding chapter are discussed on an a priori ground. Then these three equations, i.e., the Mitscherlich, the logistic and the Gompertz equations are applied to the radial stem growth of white spruce [*Picea glauca* (Moench) Voss] to check their feasibility from theoretical as well as from practical points of view. The reason why the radial growth is taken up from among several other measures of tree growth is that it is the only quantity that renders itself to direct, accurate, yet massive measurements. The direct and precise measurement of the other measures such as height, basal area, volume, etc. is extremely difficult and time-consuming if not impossible. Almost similar analysis as in chapter III is conducted in chapter IV with a different tree species, i.e., jack pine (*Pinus banksiana* Lamb.). Jack pine is one of the representative shade-intolerant pioneer species, while white spruce represents shade-tolerant ones. Thus the analyses made in chapters III and IV together give a nearly complete account of the applicabilities of the Mitscherlich, the logistic and the Gompertz equations to the growth of trees in general.

The last two chapters deal with the applications of the growth equation to other subjects of mensuration. In chapter V, assuming that the growth of trees both in height and diameter follows the Mitscherlich equation, which is judged as the most prospective of all in the preceding chapters, a mathematical expression describing the tapering of the stem is derived theoretically. Subsequently, this taper curve is applied to a set of observed taper curves to get a numerical account of the parameters as well as to compare the calculated and the observed taper curves. To check the practical applicability, the proposed taper curve is also compared with various empirical taper curves in terms of the goodness of fit to the observation. The last chapter, i.e., chapter VI is devoted to another application of the growth equation to the other major issue of mensuration, i.e., height-diameter curve. Based on a similar assumption as in the directly preceding chapter, equations describing the height-diameter relationships for even-aged stands and all-aged stands are derived, and then applied to an observed set of height-hiameter relationship.

CHAPTER II

HISTORICAL REVIEW OF THEORETICAL GROWTH EQUATIONS

Introduction

Mathematical expressions describing growth phenomena, i.e. the growth equation, have long been one of the most important and interesting subjects not only in forestry but also in other field of biological science such as demography, population biology, plant and animal physiology, etc. As is often the case with application of mathematics in any other discipline of science, the primary significance of the growth equation in biological science exists in its operational convenience of putting unwieldy masses of numerical data in a concise and perspective view. This condensing function of the growth equation is not only space saving but it also enables us an easy and objective comparison of growth, for example, among different individuals or among different species. In appreciation of these virtures, numerous mathematical equations, both empirical and theoretical, have been presented to date. (e.g. see Shinozaki, 1953; Prodan, 1961). Ironically enough, however, this proliferation of growth equations now makes it almost impossible for us to decide at a glance which one to choose for a specific purpose, and results often in promiscuous use.

The major objective of this chapter is thus to review the existing growth equations to determine their applicability to the growth of trees in stem diameter or radius. Since the growth of trees is one of the most fundamental phenomena in forestry, an appropriate choice of an equation or equations is vital. For example, the growth equation is directly applicable to the forecast of growth and yield which is the most essential objective of the forest planning and management. It also plays a principal role in many stand growth models (e.g. Suzuki, 1966, 1967A, 1967B, 1967C; Umemura & Suzuki, 1974). Once an appropriate growth equation can be chosen, it can further be applied to such growth-related issues as stem taper curves and height-diameter curves as will be shown in the succeeding chapters.

As a matter of fact there exist literally countlessly many growth equations, and it would be impossible to review them all. Thus the scope of the present work is bounded within the domain of rational or theoretical equations. As a matter of fact the cluttering abundance of growth equations is largely attributable to that of experimental or empirical ones, and thus the introduction of this simple criterion of counting those empiricals out reduces drastically the number of equations to be examined.

Moreover, the theoretical equations have many advantages over the empiricals, most of which stem from the theoretical reasoning or the rationale which constitute the basis of the former. First of all, the theoretical reasoning make an equation appealing to our logical thought and easy to comprehend. This applies not only to the equation itself but also to the parameters involved in it. Parameters appearing in the empirical equation are nothing more than mathematical constants, while those in the theoretical equation carry biological significance closely related to the subject. Secondly, the plausibility of the reasoning behind a theoretical equation can be judged either by itself or in comparison with a reality, which makes improvement of the equation possible. Furthermore, the repeated improvement might well lead eventually to the true nature of the growth phenomena, i.e. a law. On the other hand, empirical equations, as Watt (1962) mentioned, are useful for interpolation but little else. Though this mention was made of the use of mathematics in population ecology, the same argument well applies in forestry. Thus examined in the following sections, with a special reference to the applicability to the growth of trees are theoretical equations and those comparable to them. The existing theoretical equations can be classified into six classes by mathematical appearance. They are the exponential, the Mitscherlich, the logistic, the Gompertz, the von Bertalanffy's and the others.

The exponential equation

By far the simplest of all the theoretical growth functions may be the exponential equation. It is based on the assumption that the rate of growth dy/dt of a population or an individual organism at any given time t is proportional to the size y achieved by that time, i.e.

$$\frac{dy}{dt}=ky, \qquad \text{II-1}$$

where k is the intrinsic rate of growth. Integration with respect to time results in the exponential growth equation of the form:

$$y=y_0e^{kt}, \qquad \text{II-2}$$

where y_0 is the initial size. In some cases the exponential curve shows a good agreement with observed growth phenomena so long as its application is limited up to a certain early phase of an entire growth process. However, the exponential curve has no upper limit of growth and thus increases infinitely as time goes on, whereas any actual population or individual organism including trees is regulated by either internal or external or both growth-inhibiting mechanism and doesn't grow infinitely large. This limited applicability, along with the obvious discrepancy from the reality, is the reason why the exponential equation is regarded incomplete. Thus in this thesis as well it is put aside from the major stream of the discussion.

The Mitscherlich equation

This terminology follows the current practice (Suzuki, 1971), but this equation is also known as that of monomolecular chemical reaction. It is based on the assumption that there exists a certain asymptotic limit of growth M and that the rate of growth dy/dt at any given time t is proportional to the difference between the limit M and the size y achieved by that time. In other words the proximity of the size achieved to the limit is postulated as a sole growth inhibitor. This assumption can be formulated in terms of differential equation as follows:

$$\frac{dy}{dt}=k(M-y), \qquad \text{II-3}$$

where k is the intrinsic rate of growth. Integrating Eq. II-3 we get

$$y=M(1-\frac{M-y_o}{M}e^{-kt}), \qquad \text{II-4}$$

where y_o is the initial size. By substituting a single parameter L for the factor $(M-y_o)/M$, Eq. II-4 can be simplified as

$$y=M(1-Le^{-kt}). \qquad \text{II-5}$$

Assuming $y_o=0$, this solution further reduces to

$$y=M(1-e^{-kt}). \qquad \text{II-6}$$

Since Eq. II-5 is more general, it shall be the standard form of the Mitscherlich equation hereafter in the present work. The derivatives, convexity and other major charactericstics of the Mitscherlich equation are tabulated in Table 1, while the general shape of the curve is illustrated in Fig. 1.

As readily seen from the above reasoning, the underlying assumption is of very general nature and consequently the resultant Eq. II-5 or II-6 should be applicable to any growth phenomena; either to the growth of individual organism or to that of population; either to the growth in linear dimension or to that in volumetric dimension. Accordingly it has been applied to a wide variety of growth phenomena as discussed in the following.

According to Yule (1925), Verhulst proposed as early as in 1847 a differential equation and its solution of similar significance as II-3, II-4 respectively to descirbe the growth of human population.

Mitscherlich (1919), to whom the present terminology of the equation apparently owes, formulated an equation to describe plants' response to environmental growth factors,

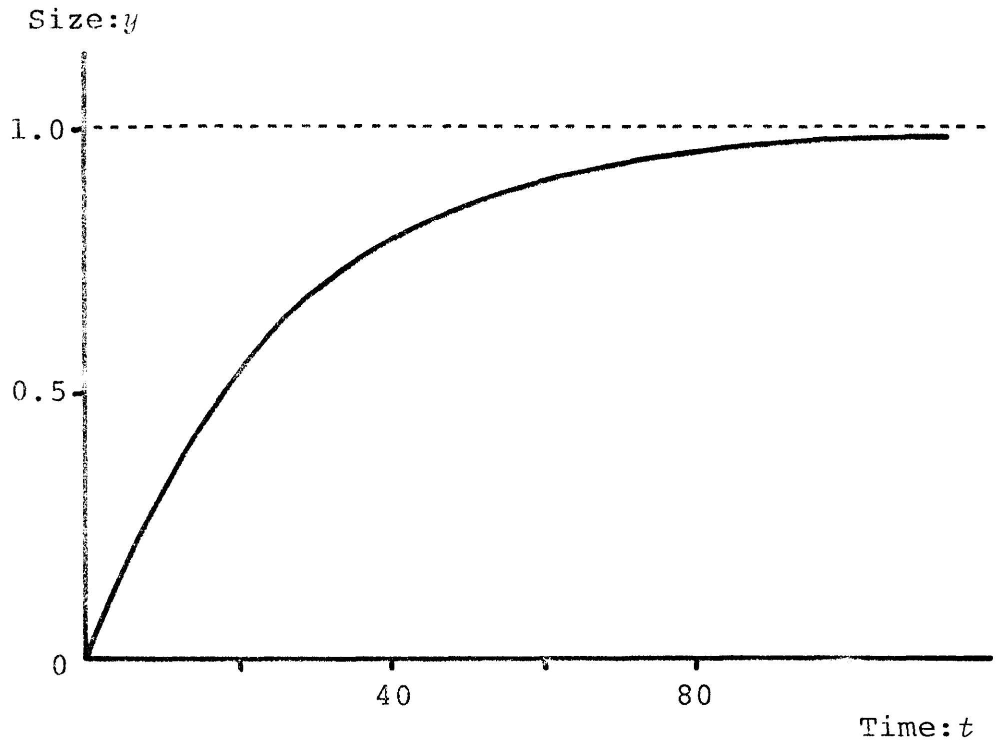


Figure 1. The Mitscherlich curve.

$y = M(1 - Le^{-kt})$: $M = 1.0$, $L = 1.0$, $k = 0.04$, with the broken line denoting asymptote.

which is presently known as the law of diminishing return. The equation Mitscherlich originally presented was of the form:

$$y=A\,(1-e^{c_1 x_1})\,(1-e^{c_2 x_2})\ldots, \qquad \text{II-7}$$

in which y denotes yield, and x_1, x_2, ... amounts of factors controlling the growth. Apparently Mitscherlich's original aim was to express plants' response to fertilizers, but not to describe plant growth as a function of time. However, if we consider time as a single most significant growth factor, the above equation reduces to Eq. II-6. It should be noted that the yield or size y is given in weight in this case.

In 1920 Pütter proposed an equation of the same significance as Eq. II-5 to descirbe the linear growth of individual organisms (after Weymouth et al., 1931). Weymouth (1923) applied this equation to describe the linear growth in shell size of the pismo clam, but he later (Weymouth et al., loc. cit.) turned it off claiming that the equation, being devoid of inflection, had been unsatisfactory to describe at least the linear growth of the clam.

Based on his extensive collection of growth data, Brody (1923) claimed that the entire growth process of animals could be broken up into a self-accelerating phase and a self-inhibiting one, and proposed the Mitscherlich equation for the latter. Then he (1945) successfully applied the equation to the extrauterin growth in weight of a large variety of animals ranging from such farm animals as the cattle, horse, swine etc. to small experimental animals as the guinea pig, mouse, etc.

The first mention concerning the application of the Mitscherlich equation to tree growth was made by Meyer (1940). He referred to the usage of the similar equation as II-6 in forestry to express the height growth of trees as a function of time.

It is interesting to note that Khilmi (1957) derived a Mitscherlich equation for the volumetric growth of forest stands through an entirely different line of reasoning from the one given earlier in this section. He reasoned that the per-hectare volumetric growth of stands consist of the difference between the solar energy input and a part of it consumed for physiological maintenance. As is readily envisaged, this assumption resulted in a differential equation quite similar in formal appearance to Eq. II-3, which yielded a solution almost identical with II-4 or II-5. He applied this equation to the growth of even-aged single-species stands of pine, spruce and oak. Although he reported a satisfactory agreement with the observed growths, Khilmi's equation doesn't apply to the entire process of stand growth. The reasoning underlying the equation logically makes it applicable only after the crown closure.

The first application of the Mitscherlich equation to the diameter growth of trees was made by Suzuki (1961). He found empirically that the mean diameter growth of several individual trees results in a straight line on a difference diagram, in which the mean diameter at age t+1 is plotted against those at age t. Subsequently he showed this straight line relationship is mathematically equivalent to the Mitscherlich equation. Obviously in this case, the equation descirbes growth in linear dimension. The same equation proposed by Khilmi (ibid.) gives volumetric growth also in linear dimension, since it is given on per-hectare basis. Takeuchi (1979) pointed out the significance of this coincidence of different phenomena being expressed by the same equation when reduced to the same dimension.

To check the descriptive and forecasting power of the Mitcherlich equation, Nagumo and Sato (1965) applied it to the growth of trees in stem height and diameter as well as in stem volume converted into linear dimension by taking its cubic root. Their conclusion: the fit was satisfactory, but the prediction based on this equation reliable only for several years ahead.

The logistic equation

The logistic equation is also known by several other names as Verhulst's equation, Robertson's equation, autocatalytic equation etc. It is based on a general assumption that the rate of growth dy/dt at any given time t is proportional not only to the difference between the maximum achievable size C and the current one y, but also to the current size itself. In terms of differential equation, this assumption is equivalent to

$$\frac{dy}{dt}=ly\,(C-y)\,, \qquad \text{II-8}$$

where l is the intrinsic rate of growth. The solution of the above equation is given by

$$y = \frac{C}{1+e^{a-bt}}, \qquad \text{II-9}$$

where a and b are newly introduced parameters related to the initial size y_o and the rate constant l respectively. The exact mathematical relationship between these new parameters and the original ones is given in Table 1 along with other important characteristics of the equation. The general shape of the logistic curve is shown in Fig. 2. The most marked graphical difference from the Mitscherlich is that the logistic has a inflection, while the former doesn't, appearing exactly midway of the entire growth process. As with the Mitscherlich equation, the notation and expression of what is generally termed the logistic equation varies from one author to another. However, since all the other forms of mathematical expressions can be reduced to form II-9 through proper transformation, Eq. II-9 shall be the standard form henceforth in the present work unless otherwise mentioned.

According to Yule (1925) the logistic equation was first proposed by the same person who proposed the Mitscherlich equation first. Namely, based on the similar logic as the one given just above, Verhulst (1938, 1945) proposed a differential equation along with its solution, each equivalent to II-8 and II-9 respectively, to descirbe the human population growth. Not only he proposed it but also applied it to the observed population growth of some European countries.

The fact that the logistic equation is the best known growth function today may be most attributable to

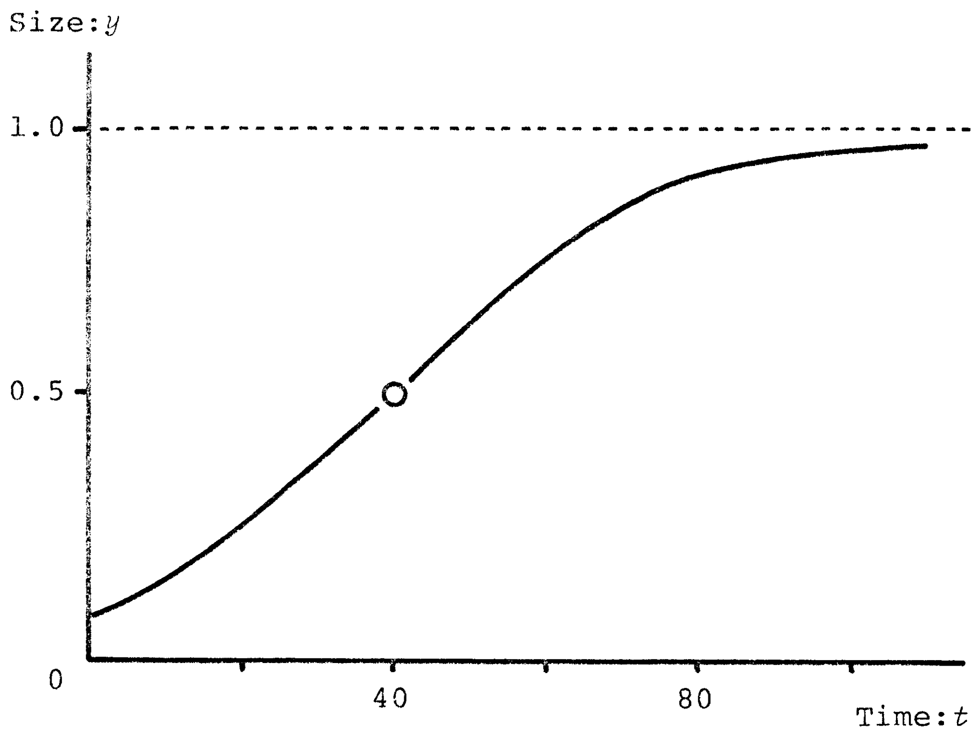


Figure 2. The logistic curve.

$y = C/(1 + e^{a-bt})$: $a = 2.4$, $b = 0.06$, $C = 1.0$, with the circle denoting the point of inflection and the broken line asymptote.

Pearl and Reed (1920), who renewed the same logic and an equation of similar significance as Verhulst's, and then applied it successfully to the observed population growth of the United States. Subsequently the senior author (1924) applied the logistic equation to the population growth of various countries all over the world, in which the equation revealed a remarkably good agreement with the observations as to make the author claim "the logistic law of growth". Apparently, this evoked an onset of applications of the logistic to a great variety of phenomena ranging from population growth of other species than human being to growth of individual organisms. Just to mention a few, Gause (1934) applied the logistic to the population growth of an infusorian.

According to Lotka (1924) the first application of the logistic equation to the growth of individuals was made by Robertson (1908), who applied it to the growth in weight of rats.

As an example of its application to individual plant growth, it suffices to quote Reed and Holland (1919) who fitted the equation to the growth in height of sunflower. Unfortunately, however, the author couldn't find any example of its application to the diameter or radial growth of trees. However, considering from the very general assumption underlying the logictic equation, it is also difficult to find a reason why not it is applicable to the growth of trees.

The Gompertz equation

This equation, apparently named after the person who first proposed it, is based on the assumption that the rate of growth dy/dt at any given time t is proportional to the current size y and the logarithmic difference between the maximum achievable size A and the current size, i.e. in terms of differential equation:

$$\frac{dy}{dt}=qy(lnA-lny), \qquad \text{II-10}$$

where q is the intrinsic rate of growth. Upon integration, Eq. II-10 results in a solution of the form:

$$y=Ae^{-e^{p-qt}}, \qquad \text{II-11}$$

where p is a newly introduced parameter related to the initial size y_o. The exact parametric relationship is given in Table 1 along with other mathematical characteristics of the Gompertz equation. The general shape of the Gompertz curve is shown in Fig. 3. Like the logistic, the Gompertz has an inflection, but it appears at a different position, i.e. approximately at the first one-third of the entire growth process.

As with the Mitsherlich and the logistic, there are several other expressions for the Gompertz equation. Since most of them reduce to form II-11 when subjected to suitable transformation, Eq. II-11 shall be the standard form for the Gompertz in the present work.

As mentioned earlier this equation was first proposed by Gompertz (1825, according to Winsor, 1932) for a purpose other than the growth function, i.e. a mortality

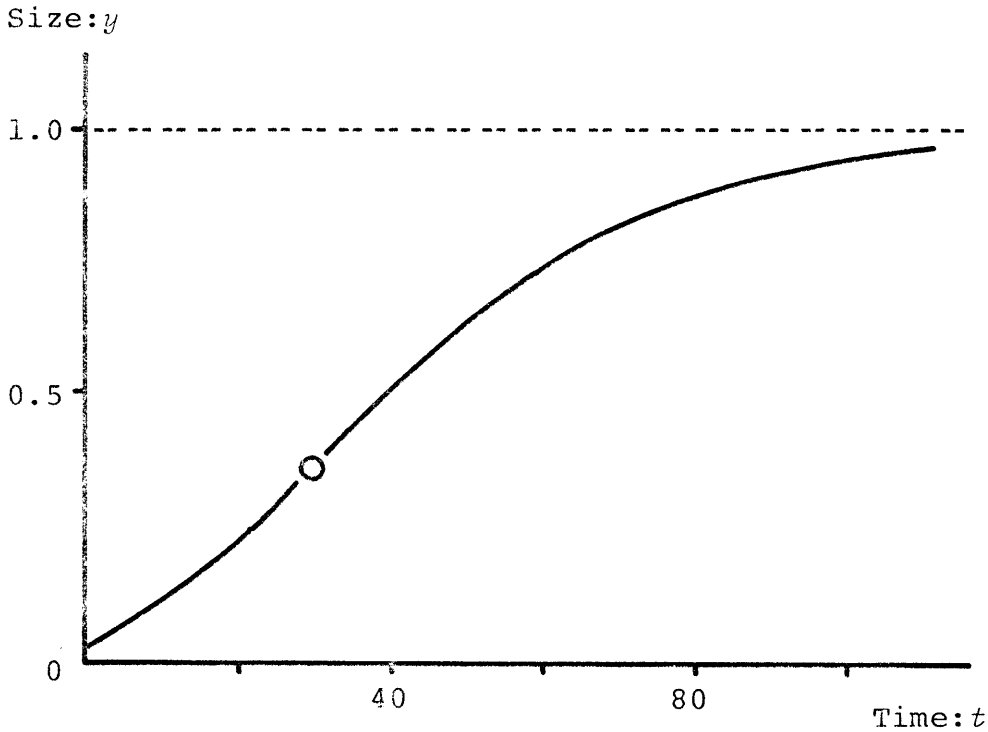


Figure 3. The Gompertz curve.

$y = A exp(-e^{p-qt})$: $A = 1.0$, $p = 1.2$, $q = 0.04$, with the circle denoting the point of inflection and the broken line asymptote.

Table 1. Major characteristics of the Mitscherlich, the logistic and the Gompertz equations

PROPERTY	MITSHERLICH	LOGISTIC	GOMPERTZ
Assumption	Rate of growth proportional to the stretch from the present diameter to the maximum achievable diameter.	Rate of growth proportional to the present diameter and its stretch to the maximum achievable diameter.	Rate of growth proportional to the present diameter and the logarithmic stretch from the present diameter to the maximum achievable diameter.
Differential equation	$\frac{dy}{dt} = k(M - y)$	$\frac{dy}{dt} = ly(C - y)$	$\frac{dy}{dt} = qy(lnA - lny)$
Growth function	$y = M(1 - Le^{-kt})$	$y = \frac{C}{1 + e^{a-bt}}$	$y = Ae^{-e^{p-qt}}$
Nature of parameters	$L = \frac{M - y_0}{M}$, M : asymptotic diameter, k : intrinsic rate of growth, y_0: initial diameter	$a = ln\frac{C - y_0}{y_0}$, $b = Cl$, C : asymptotic diameter, l : intrinsic rate of growth, y_0: initial diameter	$p = ln(ln\frac{A}{y_0})$, A : asymptotic diameter, q : intrinsic rate of growth, y_0: initial diameter
Range of parameters expected from theory	original parameters $M > 0,\ k > 0,\ y_0 \geq 0$ derived parameters $0 < L \leq 1$	original parameters $C > 0,\ l > 0,\ y_0 > 0$ derived parameters $a > 0,\ b > 0$	original parameters $A > 0,\ q > 0,\ y_0 > 0$ derived parameters $p > 0$
Derivatives	$\frac{dy}{dt} = MLke^{-kt}$ $\frac{d^2y}{dt^2} = -MLk^2e^{-kt}$	$\frac{dy}{dt} = \frac{bCe^{a-bt}}{(1 + e^{a-bt})^2}$ $\frac{d^2y}{dt^2} = \frac{b^2Ce^{a-bt}(e^{a-bt} - 1)}{(e^{a-bt} + 1)^3}$	$\frac{dy}{dt} = Aqe^{p-qt}e^{-e^{p-qt}}$ $\frac{d^2y}{dt^2} = Aq^2e^{p-qt}e^{-e^{p-qt}}(e^{p-qt} - 1)$
Asymptotes	$y = M$	$y = 0$ $y = C$	$y = 0$ $y = A$
Inflection	nil	$t = \frac{a}{b}$, $y = \frac{C}{2}$	$t = \frac{p}{q}$, $y = \frac{A}{e} \fallingdotseq \frac{A}{3}$
Maximum growth rate	MLk (when $t = 0$)	$\frac{bC}{4}$ (when $t = \frac{a}{b}$)	$\frac{Aq}{e}$ (when $t = \frac{p}{q}$)
Convexity	convex upward all the way up	convex downward (when $t < \frac{a}{b}$) convex upward (when $t > \frac{a}{b}$)	convex downward (when $t < \frac{p}{q}$) convex upward (when $t > \frac{p}{q}$)
Symmetry	asymmetric	symmetric (with respect to the point of inflection)	asymmetric

curve for human being. Its first theorization as a growth equation was achieved by Wright (1926) in his criticism of Pearl's logistic theory. He reasoned rather inductively that "the average growth power as measured by the percentage rate of increase tends to fall at a more or less uniform percentage rate". This assumption is slightly different from the one given earlier but results in the same growth function. The former was given so as to make a comparison with the assumptions for the other equations easy and distinctive. It should be noted that the above mention by Wright was aimed at the growth of individual organisms but not at the growth of populations.

Accordingly Davidson (1928) applied the Gompertz equation to the growth in body weight of cow. Then Weymouth et al. (loc. cit.) applied it to the linear growth in shell size of the razor clam as well as to the growth of the cockle (Weymouth and Thompson, 1931), reporting a satisfactory agreement with the observations in both cases.

Though there are not many instances of the Gompertz application to the growth of plants, Osumi (1977) mentioned its application to the growth of trees. As with the logistic, considering from its general assumption, it seems that there is no positive reason why shouldn't it be applicable to the growth of plants.

Von Bertalanffy's equation

While all the growth equations discussed above are composed on rather general reasonings, von Bertalanffy's equation is more specific and particular to the subject it is aimed to describe, i.e. the growth of animals. According to von Bertalanffy (1941, 1957, 1968), the growth of animals in weight dw/dt results from the difference between the synthesis $f_1(w)$ and degeneration $f_2(w)$ of body building material, thus

$$\frac{dw}{dt} = f_1(w) - f_2(w) \quad .$$

Thuogh this assumption is very general as such, the synthesis and degeneration functions were determined very specifically as follows. According to Huxley's principle of allometry, both the synthesis and degeneration term in the above equation can be replaced by power functions of the body mass present, thus

$$\frac{dw}{dt} = \eta w^n - \kappa w^m \quad ,$$

where η and κ are the synthesis and degeneration rate constants. Then reasoning from general physiological observations that the degeneration of building materials is proportional to the body mass present, von Bertalanffy replaced the degeneration exponent by unity, i.e., $m = 1$. For the synthesis term, he reasoned that the anabolic processes of an animal is proportional to its energy metabolism, and replaced for the size dependence of animal that of metabolic rate, i.e., $n=\alpha$. Theus the equation finally reduces to

$$\frac{dw}{dt} = \eta w^{\alpha} - \kappa w \quad , \qquad \text{II-12}$$

the solution of which is given by

$$w = [\frac{\eta}{\kappa} - (\frac{\eta}{\kappa} - w_o^{(1-\alpha)})e^{-(1-\alpha)\kappa t}]^{1/(1-\alpha)} \quad . \qquad \text{II-13}$$

This is what is generally known as von Bertalanffy's equation in which depending upon the metabolic type specific to kinds of animals concerned, the exponent α takes on values within the following clearly defined range:

$$2/3 \leq \alpha \leq 1.$$

The case of special interest is when α takes on the smallest limiting value. According to Rubner's surface rule, the methabolic rate in many animals, especially in homeotherms, is proportional not to body weight but to surface, thus

$$\alpha = 2/3.$$

Replacing this in Eqs. II-12 and II-13, we get

$$\frac{dw}{dt} = \eta w^{2/3} - \kappa w \quad . \qquad \text{II-14}$$

and its solution

$$w = [\frac{\eta}{\kappa} - (\frac{\eta}{\kappa} - w_o^{1/3})e^{-\kappa t/3}]^3 \quad . \qquad \text{II-15}$$

Interestingly enough the cubic root of Eq. II-15 is equivalent to the Mitscherlich equation II-4 or II-5. This means, from the dimensional-analysis point of view, that any growth that follows von Bertalanffy's equation with $\alpha = 2/3$ in either mass or volumetric dimension must in linear dimension follow the Mitscherlich, and vice versa. In support of his claim that the growth of trees in stem diameter follows the Mitscherlich equation, Suzuki (1979) reasoned, after von Bertalanffy, for the volumetric growth of trees that the photosynthesis is proportional to the surface area of a tree, whereas the decomposition is proportional to the respiration which further in turn proportional to the volumetric tree biomass present. This premise results in a tree growth which in volume follows von Bertalanffy's equation and thus in linear dimension the Mitscherlich. Obviously this assumption is more specific and particular to the subject of tree growth than the assumption for the Mitscherlich given earlier in this chapter. Thus, this premise, if proved physiologically, would certainly give a firmer ground to the presumption that the diameter growth of trees follow the Mitscherlich.

Other growth equations

Based on physiological laws and a volumenous result of experiments, von Bertalanffy defined the numerical range of his synthesis exponent α as mentioned earlier. Richards (1959) proposed to liberate the parameter α from this restriction and use on an empirical basis the von Bertalanffy's equation for botanical studies as well. In support of his view Osumi (1976, 1977A, 1977B) advocated its use in forestry and applied it to various growth phenomena encountered in this field. Obviously this removal of the parametric restriction adds another degree of freedom to the original equation and improves the agreement with observations so long as the apparent fit is concerned.

Yoshida (1979) reported a more satisfactory fit with this generalized von Bertalanffy's equation than with any of the Mitscherlich, the logistic and the Gompertz for the observed growth of sugi (*Cryptomeria japonica*). However, the libelization of the parameter, which is equivalent to the incorporation of an additional parameter, deprives the original equation of its important trait of theoretical compartibility. In its original equation the parameter α has a definite physiological meaning relevant to the subject of animal growth, and so does the equation itself. In its generalized form, however, it is difficult to find any biologically significant meaning for the newly incorporated parameter. To make the matter worse the new parameter interferes mathematically with the original parameters and deprives of their authentic significance too. Accordingly the equation itself also looses its original significance and deteriorates to a mere empirical equation as Richards had envisaged from the very beginning.

Exactly the same argument may well applies to the generalization of the other theoretical equations. With the generalized Mitscherlich equation by Prodan (loc. cit.):

$$y = M(1-e^{-kt})^{n},$$

we can undoubtedly expect a better fit to the observation than with the original equation II-6. However, it would be difficult to find any significant physical meaning in the newly introduced exponent n. The exponent also affects other parameters in such a way that they also loose their original physical meaning.

The most notorious deterioration of the theoretical quality by introducing physically meaningless parameters is seen in Pearl's (loc. cit.) generalized logistic equation:

$$y = \frac{C}{1+me^{a_1 t^1 + a_2 t^2 + a_3 t^3 + \cdots}}.$$

It is a mathematical rule of thumb that the introduction of additional parameters in an equation adds further flexibility to the equation, which in turn improves the goodness of fit in practical application, but it also dispossesses the original equation and its parameters of their original theoretical meaning. In other words the theoretical equation retrogrades to a mere empirical equation upon meaningless generalization.

Conclusion

According to the directly preceding review and the accompanying discussions, growth equations were classified as in Table 2 by their theoretical quality. The two extremes in this classification are the empirical equations and the theoretical ones. The former is those without any rational reasoning behind them but have been adopted largely due to their graphical resemblance to the observed course of growth. The latter are those constructed on at least some plausible ground and with the parameters clearly defined in terms of the relevant subjects. Between them both fall quasi-theoretical equations, which originally were constructed on

Table 2. A classification of growth equations

	CATEGORY		EXAMPLE
Growth equations	Empirical or Experimental		polynomials
	Quasi-theoretical		RICHARDS's
	Theoretical	General (a priori)	MITSCHERLICH logistic GOMPERTZ
		Particular (a posteriori)	BERTALANFFY's

rational ground but lost theoretical meaning by artificial manipulation made just to improve the quality of fit or something of the kind.

The theoretical equations are further broken down into two sub-categories, the particular equations and the general ones. The terms particular and general refer to the way the differential equations leading to growth equations are built. In particular equations, the differential equations are constructed on some a posteriori principles arrived at by generalizing facts collected and observations made on some particular subject the growth of which is at stake. The best example would be von Bertalanffy's equation which is underlain by the principle of allometry, Rubner's surface rule and other a posteriori physiological knowledge concerning the growth of animal. Usually, in particular equations, not only the subject of growth is clearly envisaged but also the physical dimension in which the growth is to be considered is exactly defined as "the growth of animals in weight" in von Bertalanffy's equation or "the volumetric growth of even-aged stands" in Khilmi's equation mentioned earlier. On the other hand, the general equations are derived from some general a priori assumptions formed by reason alone without any particular reference to any specific subject of growth. The examples of the general equations are the Mitscherlich, the logistic and the Gompertz.

It should be pointed out that the classification made above is not absolute. An equation can be either theoretical or empirical depending upon the user's standpoint, viz., a theoretical equation is degraded to an empirical one when used beyond its rational scope.

All the above discussion has brought us to the point where we can choose the best equation or equations for the growth of trees at least from a priori point of view. It has been already mentioned that the empirical equations are far out of the question mainly because they are not accompanied by any propositions or assumptions which in some way or another explain the mechanism of growth. The similar reasoning helps eliminate the particular theoretical equations. If there were any particular equation for the radial growth of trees reasoned by physiological principles of tree growth, it would be undoubtedly the best of our choice. Unfortunately, however, all the existing particular equations are for something else than the radial growth of trees. Since these particular equations are firmly reasoned by principles obtained by generalizing the facts and observations concerning other particular organisms or their aggregates, it will be readily noticed that the whole logical structures which constitute these equations are crumbled when they are used for the radial growth of trees. Thus at least from logical point of view, the particular equations cannot be used for the present purpose. If they are used for the radial growth of trees, they are no more theoretical but mere empirical equations. The above discussion will give enough ground to discard the particular theoretical equations here.

As a matter of fact, the above argument is the one according to which we have defined the quasi-theoretical equations. Thus they are also disqualified.

Now, the above elimiantion of equations leaves the general theoretical equations, i.e., the Mitscherlich, the logistic and the Gompertz as the prospective equations for describing the radial growth of trees. Since these equations are derived from general a priori assumptions which specifies neither the subject of growth nor the dimension in which the grwoth is to be defined, there is no positive reason why they shouldn't be applicable to the radial growth of trees. However, it is not clear, with the present state of knowledge or from a priori considerations, which one of the Mitscherlich, the logistic and the Gompertz is most suitable for the growth of trees. This will be made clear in the succeeding chapters by applying these equations to the actual growth of trees.

CHAPTER III

APPLICATION OF THE MITSCHERLICH, THE LOGISTIC AND THE GOMPERTZ EQUATIONS TO THE RADIAL STEM GROWTH OF WHITE SPRUCE

Introduction

In view of the discussions made in the preceding chapters, the three most prospective growth equations, i.e. the Mitscherlich, the logistic and the Gompertz equations, were applied to the observed radial growth of white spruce [*Picea glauca* (Moench) Voss], and the problems associated with the application were discussed from theoretical as well as from practical points of view. The criteria adopted here for the comparison of the equations were ease of fitting, goodness of fit and whether or not the equations function as expected from the theory, i.e., theoretical consistency. Before entering the application and the analysis, however, the Mitscherlich, the logistic and the Gompertz equations were compared on an a priori ground in the following.

To begin with, a mention has to be made of the plausibility of the assumption underlying each of these three equations. It seems on an a priori ground that the Mitscherlich assumption is as plausible as the logistic's. Aside from the one given earlier, the assumption for the latter can also be interpreted as follows: the percentage rate of growth is inversely proportional to the proximity of the current diameter to the upper asymptote. Thus the point between the Mitscherlich and the logistic is whether it is the absolute rate of growth or the percentage rate that is proportional to the proximity term. However, even after this interpretation, it seems difficult to judge which assumption, the logistic's or the Mitscherlich's is more plausible. On the other hand, the assumption for the Gompertz looks to be on a more feeble ground than those of the other two, particularly the portion "logarithmically proportional to ...". But why logarithmically? It seems not much appealing to our logic. However, putting the assumption as Wright (loc. cit.) did saves a lot: the percentage rate of change in the percentage rate of growth decreases in a constant manner, i.e.,

$$\frac{d(\frac{dy}{ydt})}{(\frac{dy}{ydt})\,dt} = -q = \text{const.}$$

This interpretation makes the Gompertz assumption as plausible as those of the Mitscherlich's and the logistic's.

As seen from Fig. 1 through 3, the most remarkable difference between the Mitscherlich and the rest is that the former has no inflection, while the latter does. This is one of the consequences arising from the assumptions. Both in the logistic and the Gompertz, the rate of growth is governed by two factors, namely the size-proportional factor and the proximity factor, while it is only the proximity factor that controls the rate of growth in the Mitscherlich. To put it short, the existance of two competing factors in an equation causes inflection. It is generally said that the diameter growth of trees follows a sigmoid having a point of inflection (Bruce and Schumacher, 1950; Husch et al., 1972). Apparently, this general observation seems to be disadvantageous for the Mitscherlich which lacks inflection. It should be noted that the inflection of the logistic and the Gompertz are fixed at certain definite points, i.e., just midway of the entire course of growth in the former and approximately at one-third of the way in the latter. This also looks somewhat unrealistic. From mathematical point of view alone, a point of inflection can be introduced in the Mitscherlich, or it can be made mobile in the logistic and the Gompertz by incorporating a new parameter. Then, however, it would be difficult to find a proper physical meaning for the newly introduced parameter. Moreover, the introduction of a physically meaningless parameters degenerates the whole rational validity of a theoretical equation as mentioned earlier.

The number of the growth-rate controlling factors is also reflected in the asymptote. The Mitscherlich has only one upper asymptote, while both the logistic and the Gompertz curve have two, the upper and the lower ones. It is a logical requirement that the upper asymptotes be positive. However, this is not always the case when the equations are applied to the actual growth of the trees as will be shown in the succeeding analysis.

As for the sign of parameters, the intrinsic rates of growth, k, l and q for the Mitscherlich, the logistic and the Gompertz respectively must be positive in theory.

But this again is not always the case in application as will be shown later.

From operational point of view, the initial diameter or radius y_0 can either be zero or positive in the Mitscherlich, while it must always be positive in the logistic and the Gompertz. If it is equal to zero in the latter two equations, the growth cannot take off forever as will be easily seen in their differential forms. Whether the actual diameter of trees grows from zero or from some infinitesimal but existent amount is a philosophical rather than a biological matter, but from operational point of view, retaining a flexibility in the initial size seems to be more advantageous for the Mitscherlich. A more practical comparison of the three equations will be made in the following in this chapter and the next chapter in association with their application to the observed radial growth of trees.

Materials and methods

The data employed for the present analysis is the growth records of 84 white spruce individuals collected in 1977 from the Northwest Territories, Canada by a joint survey team of Nagoya University, the University of New Brunswick and the University of British Columbia (Sweda, 1979). An increment core was taken at breast height (1.3 m above ground) from each of the 84 white spruce trees randomly chosen in a mixed stand of white spruce and balsam poplar (*Populus balsamifera* L.) growing on the west bank of the Slave River in the vicinity of Fort Smith (Sweda and Yamamoto, 1978). Back in the laboratory, radius of each successive annual ring on every core was measured to a-humdredth of a millimeter with an increment measuring device equipped with a microscope, and the yearly radial growth was restored for all the 84 trees sampled. The age of the trees ranged from 42 to 196 years old with a mean of 101 years and standard deviation 26 years.

Then, the parameters of the Mitscherlich, the logistic and the Gompertz equations were determined for each of the 84 individual trees by fitting the equations to the corresponding observed radial growth. To make a comparison with the empirical equation, two typical empiricals of the form:

$$y = a+bt+ct^2, \qquad \text{III-1}$$

$$y = at+bt^2+ct^3. \qquad \text{III-2}$$

were also applied, and their parameters were determined. These equations were termed temporarily empirical I and II respectively.

For fitting a total of these five growth functions to the observed growth, Deming's (1943) method of least squares was employed. The reason why this particular method was used is twofold. Firstly, since all the five equations employed here are nonlinear, the ordinary method of linear regression was not applicable as such. Secondly. although proper transformation of variables may well reduce the fitting to a matter of simple linear regression, it usually brings about in the result unnecessary bias the magnitude of which varies depending on the type of transformation emplyed (Sweda and Kurokawa, 1979). There consideration called for the method of Deming which is powerful and unbiased for non-linear curve fitting.

Theoretical consistency

The parameters of the Mitscherlich, the logistic, the Gompertz, the empirical equations I and II determined for each of the 84 trees are given in Table 3 through 7 along with their statistics. A few graphical examples of the calculated growth as compared with the corresponding observations are also given for each of the five equations in Fig. 4. through 7. Judging from these graphical comparisons and the others of the kind which could not be given here for short of space, all the equations represent the observed growth reasonably well. However, a closer review of the above tables and figures revealed several discrepancies as in the following.

The parameter M of the Mitscherlich, C of the logistic and A of the Gompertz are all, in theory, supposed to represent the asymptotic radius that a tree will ultimately attain. A comparison among tables 3, 4 and 5 indicates that this theoretical prerequisite is most satisfactorily fulfilled by the Mitscherlich so far as the mean is concerned. According to Sargent (1965) the empirically observed asymptotic diameter for white spruce is some 2 ft., which in terms of radius is 1 ft. or approximately 30 cm. Other authors of dendrology (e.g., Hosie, 1975; Collingwood and Brush, 1978) also give similar figures. The mean

Table 3. Parameters of the Mitscherlich equation as applied to white spruce

Tree No.	k (1/year)	L*	M (cm)
1	0.01183	1.060	27.50
2	0.01925	1.044	21.49
3	0.02103	1.097	20.68
4	-0.01002	1.009	-11.17
5	0.00865	1.027	27.41
6	0.01484	1.065	21.18
7	0.00221	1.007	96.84
8	0.01957	1.125	16.72
9	0.01079	1.080	15.27
10	0.02407	1.059	7.19
11	0.01594	1.080	10.29
12	0.00699	1.098	23.70
13	0.01139	1.097	18.92
14	0.01146	1.003	13.68
15	0.00242	0.994	41.58
16	0.01555	1.060	14.86
17	0.00016	1.000	966.79
18	0.01305	1.084	21.84
19	0.01514	1.005	6.96
20	0.00958	1.033	19.18
21	0.00935	1.102	22.21
22	0.01505	1.071	13.08
23	0.01288	1.051	15.11
24	0.01583	1.014	20.53
25	0.00126	1.003	103.44
26	-0.01521	1.089	-1.21
27	-0.02817	1.030	-0.19
28	0.00490	1.029	30.76
29	-0.00803	0.989	-8.76
30	-0.01486	1.037	-2.71
31	0.01409	1.051	35.00
32	0.02213	1.061	16.49
33	0.01484	1.034	21.74
34	0.00829	1.018	31.36
35	0.00842	1.026	36.48
36	0.02048	1.106	24.83
37	0.00815	1.027	33.14
38	0.01165	1.056	25.89
39	0.01627	1.101	23.26
40	0.01568	1.095	24.65
41	0.00543	1.021	58.85
42	-0.00699	0.990	-16.31
43	0.01166	1.048	26.08
44	0.00916	0.995	21.08
45	0.01946	0.981	83.10
46	-0.02227	1.060	-3.63
47	0.01355	1.039	25.00
48	0.00503	1.011	52.43
49	-0.00481	0.993	-39.84
50	0.01494	1.031	26.79
51	0.01690	1.033	19.13
52	0.02090	1.087	14.38
53	0.00967	1.008	22.23
54	0.02064	1.073	17.34
55	0.00631	1.012	39.31
56	0.01813	1.040	20.54
57	0.01568	1.058	16.32
58	0.00383	1.016	57.36
59	0.02116	1.042	11.66
60	0.00672	1.013	28.15
61	0.00493	1.008	31.78
62	-0.00215	1.004	-58.57
63	0.01179	1.015	17.22
64	0.02287	1.114	16.39
65	-0.00881	1.865	-1.23
66	0.00853	1.034	28.98
67	0.00896	1.009	19.10
68	-0.01310	1.040	-8.04
69	0.00293	1.014	63.59
70	0.01009	1.054	32.13
71	-0.00181	0.978	-62.71
72	0.01725	1.092	22.33
73	0.01053	1.049	25.46
74	0.02008	1.133	20.77
75	0.02898	1.021	85.24
76	0.01615	1.073	26.79
77	0.01515	1.054	14.37
78	-0.00400	0.984	-44.58
79	-0.00069	0.998	-169.22
80	0.01605	1.082	20.75
81	-0.00424	1.017	-18.75
82	0.00951	1.054	30.52
83	0.01147	1.049	35.85
84	0.01848	1.076	21.67
Mean	0.00883	1.052	29.47
Standard Dev.	0.01078	0.097	108.88
Coef. of Var.	1.22	0.09	3.69

* dimensionless

Table 4. Parameters of the logistic equation as applied to white spruce

Tree No.	a*	b (1/year)	C (cm)
1	2.984	0.08885	15.16
2	2.210	0.07816	16.02
3	2.551	0.08305	16.38
4	2.783	0.05121	16.84
5	2.528	0.07348	12.69
6	2.173	0.08655	13.42
7	2.600	0.06201	15.76
8	3.008	0.09119	12.76
9	2.607	0.05021	11.05
10	1.828	0.05808	6.67
11	2.327	0.05172	8.74
12	1.839	0.03570	14.55
13	2.841	0.05550	14.22
14	2.600	0.05276	14.30
15	2.108	0.02819	13.89
16	2.444	0.06866	10.93
17	2.380	0.03680	19.43
18	2.735	0.05817	16.74
19	1.906	0.04977	5.69
20	2.269	0.04920	12.39
21	2.834	0.04609	15.96
22	2.130	0.04821	10.96
23	2.255	0.05103	11.48
24	1.815	0.04773	17.10
25	2.502	0.03614	16.51
26	3.187	0.03765	7.26
27	4.662	0.03297	45.13
28	2.781	0.04247	15.05
29	2.887	0.04399	12.08
30	3.263	0.03587	16.33
31	2.508	0.08004	21.72
32	2.337	0.08952	12.55
33	2.207	0.06774	14.98
34	2.418	0.07131	14.17
35	2.497	0.07139	16.73
36	2.732	0.08824	19.12
37	2.616	0.06828	15.90
38	2.762	0.07721	15.09
39	2.968	0.08549	16.38
40	2.903	0.08222	17.22
41	2.681	0.06651	20.70
42	2.801	0.06071	12.13
43	2.492	0.06488	16.50
44	2.056	0.05991	11.17
45	1.698	0.06798	6.29
46	2.888	0.07404	11.34
47	2.448	0.08228	14.73
48	2.446	0.06230	17.45
49	2.841	0.12116	8.93
50	2.386	0.08136	17.12
51	2.215	0.07506	13.54
52	2.576	0.08916	10.93
53	2.264	0.06860	11.53
54	2.448	0.08386	13.37
55	2.309	0.05320	17.62
56	2.206	0.07183	15.60
57	2.354	0.06496	12.30
58	2.716	0.05765	17.10
59	1.991	0.06709	9.68
60	2.248	0.04954	13.84
61	2.252	0.04239	12.51
62	2.403	0.04239	15.81
63	2.051	0.05273	11.77
64	2.631	0.08455	13.71
65	4.616	0.01145	139.52
66	2.562	0.06292	15.09
67	2.184	0.05921	10.19
68	3.145	0.03608	36.99
69	2.863	0.06033	14.78
70	2.683	0.06467	18.92
71	3.516	0.05921	15.47
72	2.619	0.07328	17.19
73	2.595	0.06392	15.03
74	2.986	0.08777	16.38
75	3.231	0.06378	19.93
76	2.580	0.07090	19.02
77	2.375	0.07015	10.08
78	2.969	0.05403	20.47
79	2.744	0.04998	12.31
80	2.525	0.07043	15.30
81	2.315	0.04306	10.41
82	2.843	0.06921	16.83
83	2.574	0.06499	22.80
84	2.378	0.07257	15.61
Mean	2.580	0.06268	16.40
Standard Dev.	0.478	0.01786	14.64
Coef. of Var.	0.19	0.28	0.89

* dimensionless

Table 5. Parameters of the Gompertz equation as applied to white spruce

Tree No.	p*	q (1/year)	A (cm)
1	1.455	0.05240	16.38
2	1.078	0.04967	17.01
3	1.290	0.05391	17.07
4	1.286	0.02117	26.35
5	1.216	0.04272	14.12
6	1.335	0.05257	14.39
7	1.231	0.03368	18.46
8	1.562	0.05884	13.24
9	1.315	0.03194	11.64
10	0.921	0.04167	6.80
11	1.133	0.03489	9.03
12	0.854	0.02155	16.13
13	1.432	0.03513	14.84
14	1.214	0.02793	16.96
15	0.989	0.01572	16.19
16	1.206	0.04338	11.55
17	1.115	0.01917	23.73
18	1.360	0.03667	14.49
19	0.909	0.03284	5.97
20	1.106	0.03043	13.38
21	1.456	0.02947	16.71
22	1.080	0.03279	11.36
23	1.109	0.03286	12.11
24	0.880	0.03240	17.85
25	1.171	0.01925	19.59
26	1.490	0.01156	19.08
27	—	—	—
28	1.307	0.02410	16.58
29	1.327	0.01896	17.87
30	1.512	0.01124	41.58
31	1.231	0.04899	23.42
32	1.155	0.05737	13.22
33	1.068	0.04226	16.10
34	1.155	0.04121	15.89
35	1.206	0.04178	18.60
36	1.382	0.05641	19.97
37	1.236	0.03907	17.65
38	1.353	0.04634	16.28
39	1.513	0.05388	17.17
40	1.468	0.05154	18.11
41	1.278	0.03752	23.35
42	1.290	0.02797	16.49
43	1.219	0.03791	17.76
44	0.968	0.03624	12.50
45	1.811	0.04513	6.69
46	1.354	0.02585	23.03
47	1.292	0.04977	16.01
48	1.162	0.03498	20.03
49	1.304	0.05969	11.17
50	—	—	—
51	1.107	0.04687	14.50
52	1.285	0.05669	11.47
53	1.069	0.03995	12.84
54	1.164	0.04165	14.03
55	1.096	0.03067	19.87
56	1.069	0.04573	16.51
57	1.164	0.04165	12.95
58	1.293	0.03220	19.41
59	0.979	0.04499	10.10
60	1.079	0.02933	15.41
61	1.074	0.02745	14.24
62	1.118	0.02052	20.04
63	0.988	0.03315	12.69
64	1.355	0.05581	14.14
65	—	—	—
66	1.231	0.03690	16.61
67	1.041	0.03505	11.33
68	—	—	—
69	1.359	0.03226	16.82
70	1.315	0.03900	20.42
71	1.655	0.02421	18.18
72	1.324	0.04691	17.93
73	1.269	0.03871	16.25
74	1.548	0.04691	17.93
75	1.573	0.03617	22.12
76	1.282	0.04829	20.12
77	1.174	0.04419	10.73
78	1.369	0.02638	25.91
79	1.275	0.02561	14.97
80	1.269	0.04505	16.11
81	1.090	0.02021	14.25
82	1.394	0.04133	18.18
83	1.252	0.03955	24.49
84	1.194	0.04717	16.36
Mean	1.240	0.03753	16.52
Standard Dev.	0.180	0.01154	4.99
Coef. of Var.	0.15	0.31	0.30

* dimensionless

Table 6. Parameters of the empirical equation I as applied to white spruce

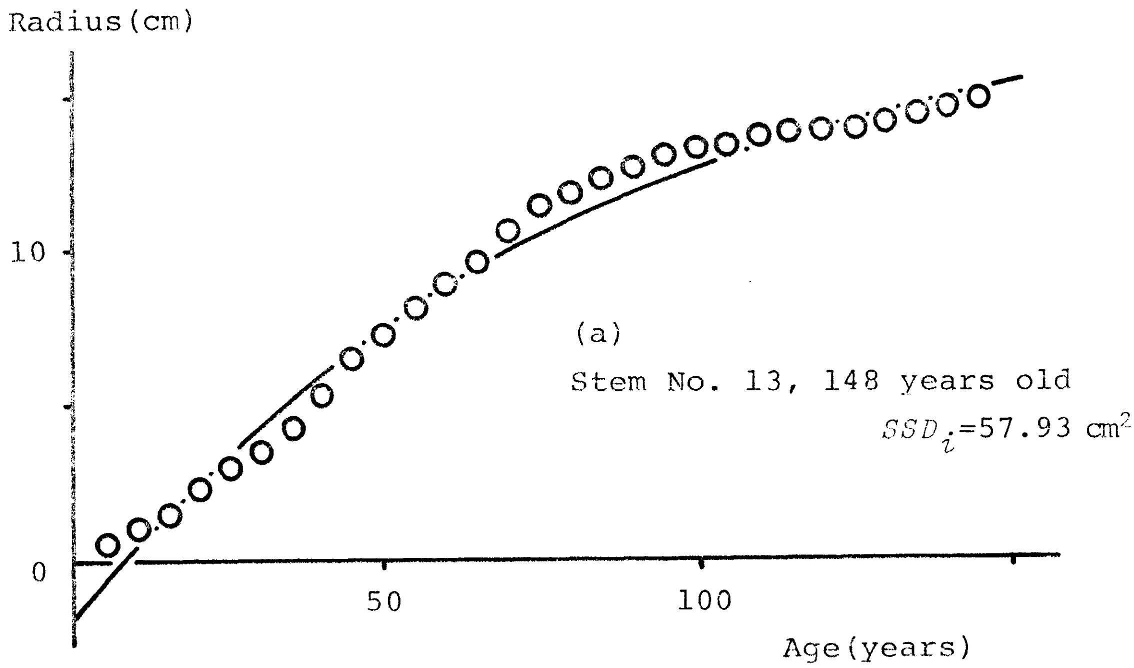
Tree No.	*a* (cm)	*b* (cm/year)	*c** (µm/year^2)	Tree No.	*a* (cm)	*b* (cm/year)	*c** (µm/year^2)
1	-1.695	0.3363	-14.53	43	-1.104	0.2962	-11.27
2	-0.551	0.3710	-19.85	44	0.162	0.1836	-6.08
3	-1.500	0.3947	-21.24	45	0.345	0.1330	-6.98
4	0.299	0.0940	8.16	46	0.305	0.0675	17.31
5	-0.694	0.2365	-7179	47	-0.859	0.3304	-15.14
6	-1.264	0.3103	-14.83	48	-0.566	0.3633	-5.53
7	-0.664	0.2151	-22.09	49	-0.264	0.1783	-5.52
8	-1.900	0.3210	-17.14	50	-0.747	0.3874	-19.20
9	-1.035	0.1567	-4.84	51	-0.404	0.2967	-14.86
10	0.403	0.1074	-4.44	52	-1.006	0.2808	-16.02
11	-0.379	0.1350	-4.90	53	-0.148	0.2096	-7.56
12	0.687	0.1151	-3.57	54	-0.981	0.3302	-18.58
13	-1.608	0.2186	-7.32	55	-0.419	0.2441	-5.93
14	-0.348	0.1576	-0.91	56	-0.522	0.3372	-17.19
15	0.273	0.0982	-0.97	57	-0.705	0.2356	-10.35
16	-0.712	0.2158	-9.61	58	-0.965	0.2232	-3.81
17	0.035	0.1511	-0.12	59	-0.054	0.2015	-10.25
18	-1.658	0.2735	-9.98	60	-0.290	0.1836	-4.51
19	1.148	0.0884	-3.49	61	-0.189	0.1533	-2.91
20	-0.435	0.1713	-5.07	62	0.247	0.1261	1.51
21	-21007	0.2022	-5.41	63	-0.068	0.1864	-6.62
22	-0.303	0.1612	-5.62	64	-1.266	0.3257	-17.29
23	-0.549	0.1776	-0.40	65	-1.062	0.0143	1.92
24	0.403	0.2617	-10.18	66	-0.959	0.2475	-7.81
25	-0.356	0.1310	-0.78	67	-0.097	0.1639	-5.21
26	0.199	0.0107	3.47	68	0.641	0.0749	14.61
27	0.723	-0.0219	10.04	69	-0.924	0.1901	-2.66
28	-0.958	0.1457	-3.05	70	-1.669	0.3258	-11.39
29	-0.041	0.0635	4.20	71	-1.297	0.1079	1.29
30	0.161	0.0308	6.13	72	-1.663	0.3588	-16.58
31	-1.610	0.4830	-22.40	73	-1.195	0.2603	-9.21
32	-0.724	0.3333	-20.31	74	-2.487	0.4061	-21.53
33	-0.509	0.3001	-13.40	75	-1.881	0.2556	-3.65
34	-0.517	0.2578	-8.27	76	-1.691	0.4151	-19.79
35	-0.907	0.3059	-9.80	77	-0.587	0.2023	-9.95
36	2.217	0.4810	-26.38	78	-0.629	0.1691	4.61
37	-0.930	0.2746	-8.92	79	-0.390	0.1167	0.45
38	-1.427	0.3050	-12.41	80	-1.683	0.3364	-16.96
39	-2.223	0.7748	-18.38	81	0.304	0.0816	1.81
40	-2.195	0.3847	-18.14	82	-1.665	0.2974	-10.32
41	-1.263	0.3248	-7.56	83	-1.685	0.4082	-15.69
42	-1.318	0.1079	5.27	84	-1.105	0.3338	-16.15
			Mean		-0.678	0.2346	-7.81
			Standard Dev.		0.838	0.1267	8.78
			Coef. of Var.		-1.24	0.54	-1.12

* micro-meter/year^2

Table 7. Parameters of the empirical equation II as applied to white spruce

Tree No.	*a* (cm/year)	*b** (μm/year^2)	*c*** (nm/year^3)	Tree No.	*a* (cm/year)	*b** (μm/year^2)	*c*** (nm/year^3)
1	0.1153	5.035	-518.8	43	0.1983	1.050	-136.9
2	0.3393	-1.518	-17.5	44	0.2061	-1.293	56.6
3	0.2759	0.387	-154.8	45	0.2042	-3.403	266.3
4	0.1242	0.228	50.8	46	0.1202	-0.553	280.1
5	0.1604	1.324	-165.1	47	0.2377	1.099	-212.6
6	0.1763	2.095	-271.0	48	0.2072	0.882	105.2
7	0.1469	1.568	-133.9	49	0.9555	6.290	-927.1
8	0.1411	2.461	-271.7	50	0.2795	-1.504	-294.0
9	0.0995	0.333	-33.5				
10	0.1499	-1.222	36.7	51	0.2664	-0.852	-39.7
				52	0.1835	0.828	-174.0
11	0.1244	-0.424	-0.5	53	0.1816	0.196	-83.3
12	0.2036	-1.321	49.2	54	0.2312	0.647	-179.3
13	0.1113	0.921	-70.8	55	0.2115	0.090	-41.8
14	0.1044	1.360	-102.2	56	0.2868	-0.494	-84.4
15	0.1223	-0.507	18.4	57	0.1794	0.109	-66.3
16	0.1558	0.311	-76.6	58	0.1163	2.209	-169.5
17	0.1563	-0.132	7.0	59	0.2189	-1.683	52.6
18	0.1063	0.634	-41.2	60	0.1735	-0.398	3.1
19	0.0952	-0.456	5.0				
20	0.1606	-0.509	6.3	61	0.1572	-0.623	30.6
				62	0.1474	-0.315	29.2
21	0.1063	0.634	-41.2	63	0.1952	-1.077	32.2
22	0.1601	-0.702	10.0	64	0.2398	-0.153	-85.1
23	0.1417	-0.037	-28.9	65	0.0797	-0.642	28.3
24	0.4165	-2.226	68.9	66	0.1488	1.615	-160.6
25	0.1040	0.389	-22.2	67	0.1639	-0.647	14.8
26	0.0275	-0.016	22.3	68	0.1427	0.115	99.0
27	0.0599	-1.033	137.2	69	0.0741	2.686	-199.1
28	0.0661	1.198	-66.1	70	0.1670	0.244	-223.1
29	0.0603	0.489	-4.2				
30	0.0623	-0.311	68.0	71	-0.0052	2.153	-96.3
				72	0.2309	0.871	-143.0
31	0.3104	2.476	-367.4	73	0.1460	1.100	-167.2
32	0.2587	-0.019	-156.9	74	0.1767	2.967	-319.1
33	0.2614	-0.545	-51.1	75	0.0346	4.860	-326.7
34	0.1963	0.974	-147.8	76	0.2593	1.661	-241.7
35	0.2119	1.540	-193.9	77	0.1635	-0.181	-39.4
36	0.2762	2.175	-322.2	78	0.0780	2.931	-117.5
37	0.1382	3.091	-306.7	79	0.0674	1.278	-81.2
38	0.1444	2.985	-306.7	80	0.2097	0.642	-118.4
39	0.1610	3.311	-340.6				
40	0.1738	3.312	-322.2	81	0.1371	-1.686	162.7
				82	0.1194	3.250	-280.6
41	0.1676	3.615	-330.2	83	0.2279	2.716	-276.4
42	0.0865	1.249	-64.7	84	0.2680	-0.473	-59.4
			Mean		0.1744	0.710	-102.8
			Standard Dev.		0.1113	1.702	173.0
			Coef. of Var.		0.64	2.40	-1.68

* micro-meter/year^2
** nano-meter/year^3



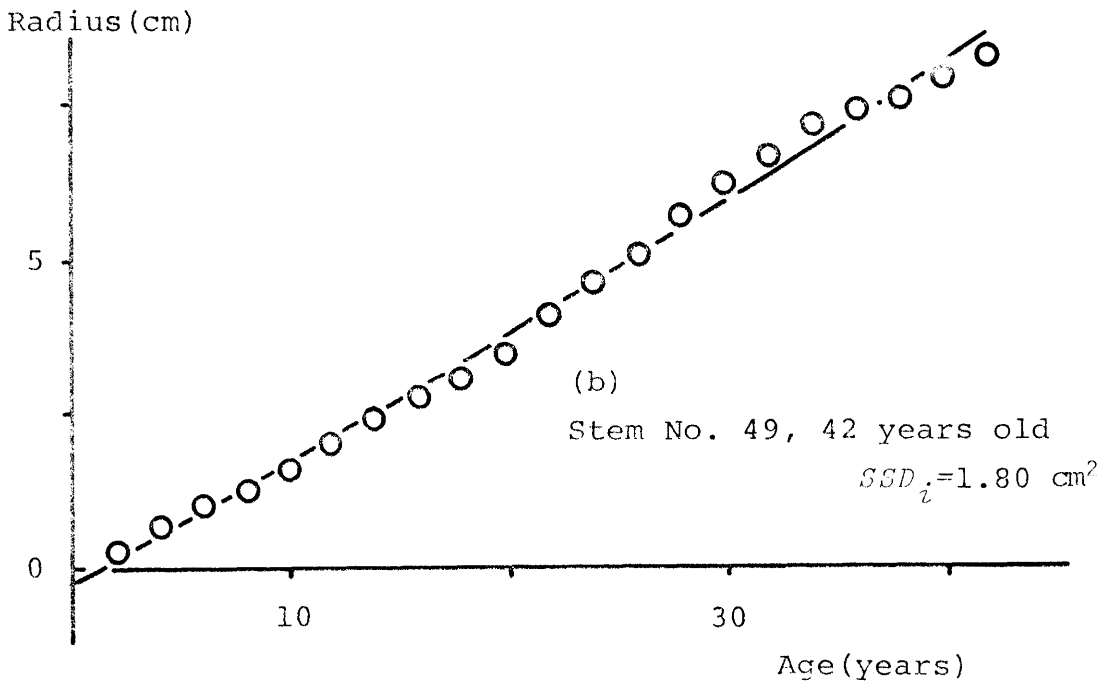
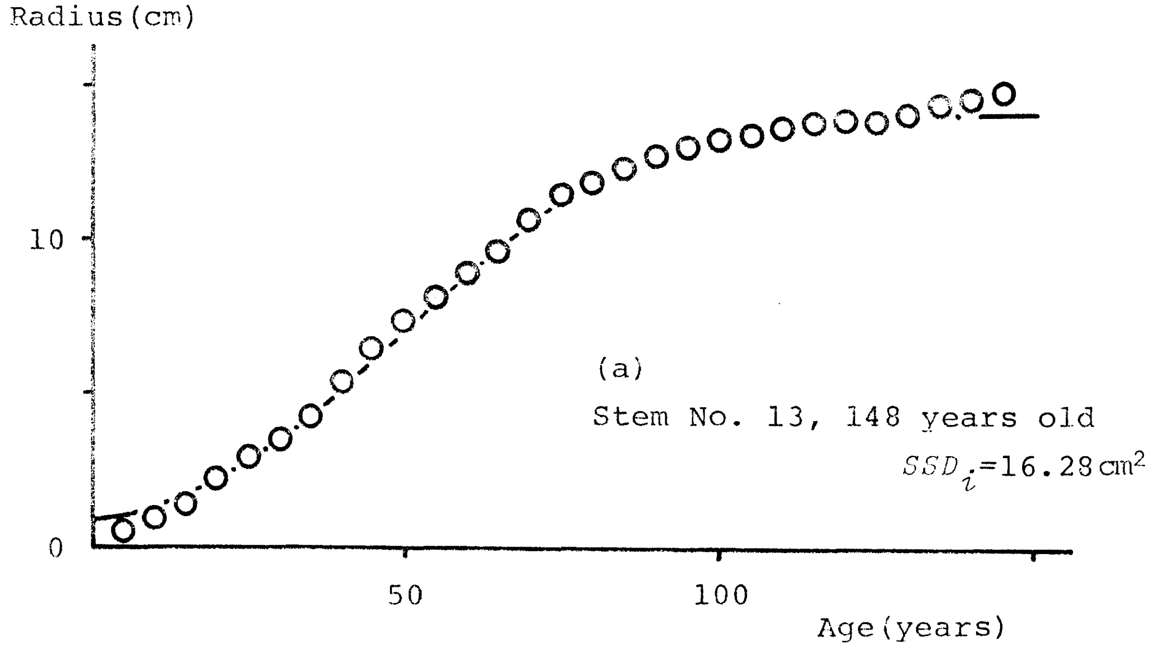


Figure 4. The Mitscherlich curve as compared with the observed radial stem growth of white spruce.



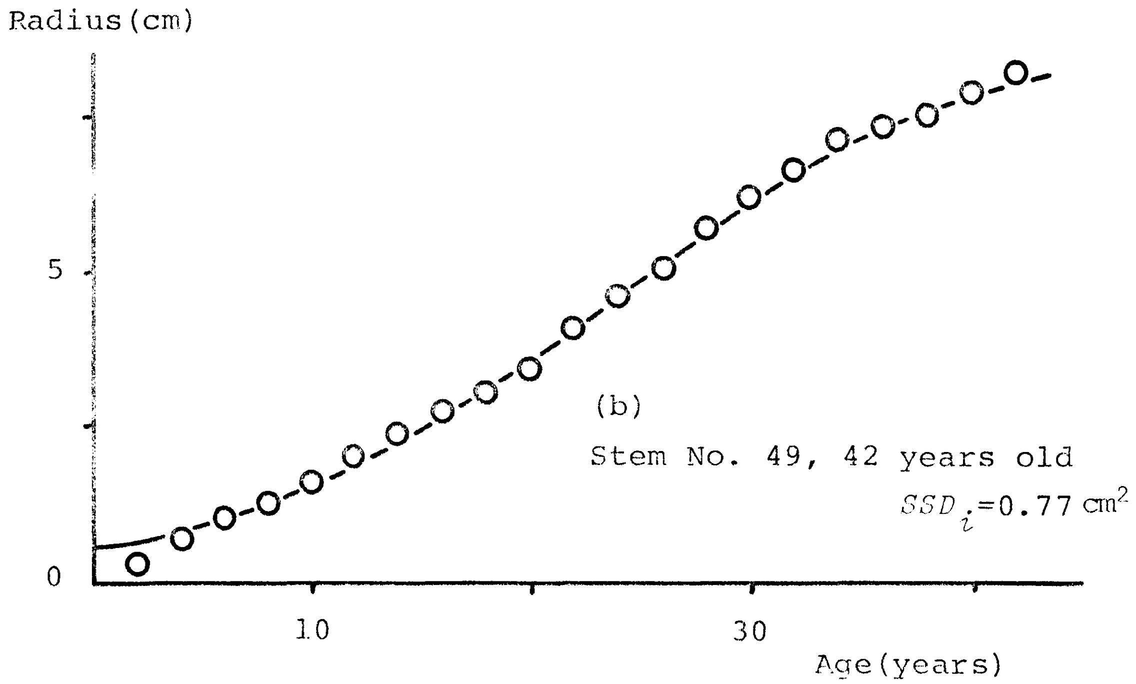


Figure 5. The logistic curve as compared with the observed radial stem growth of white spruce.

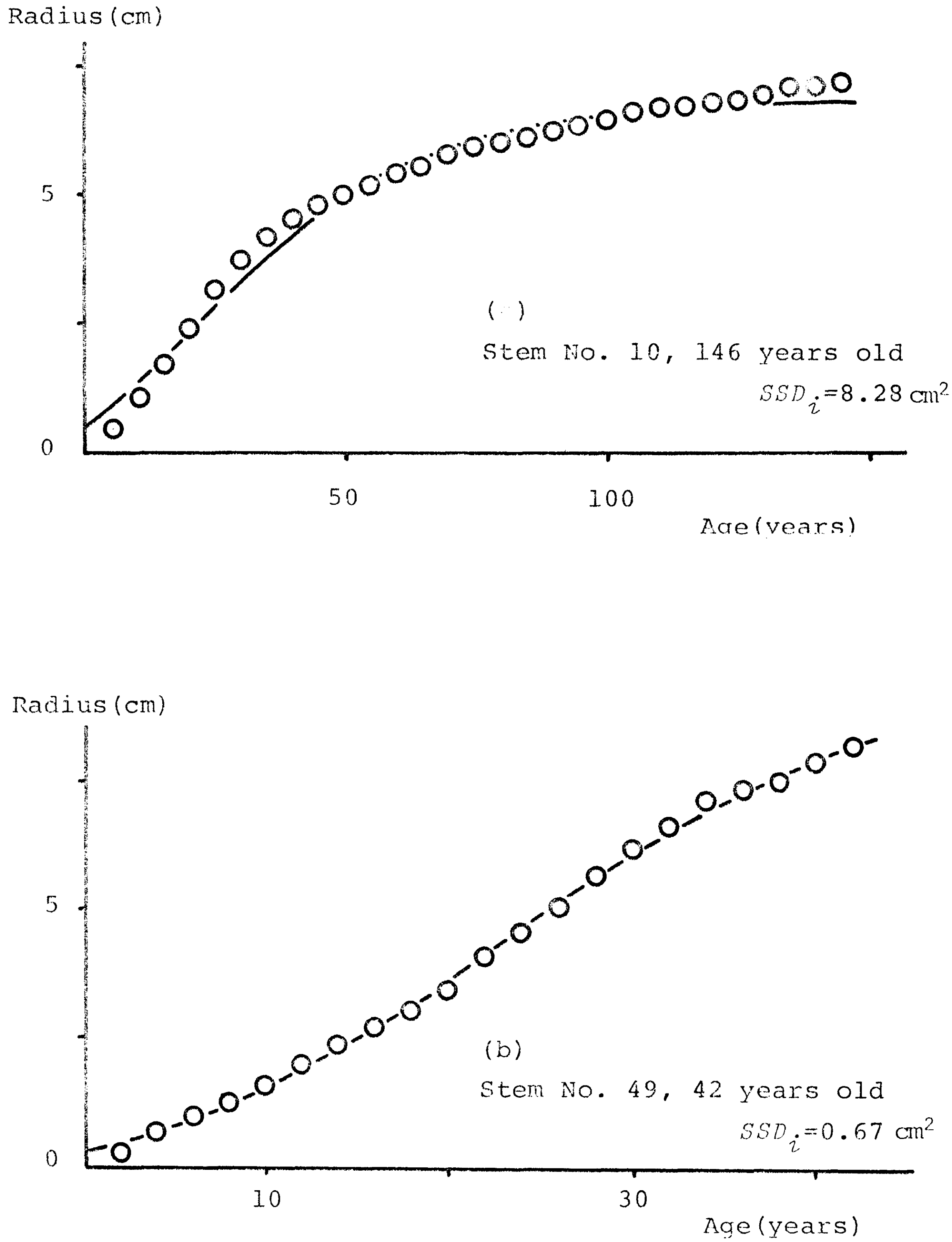
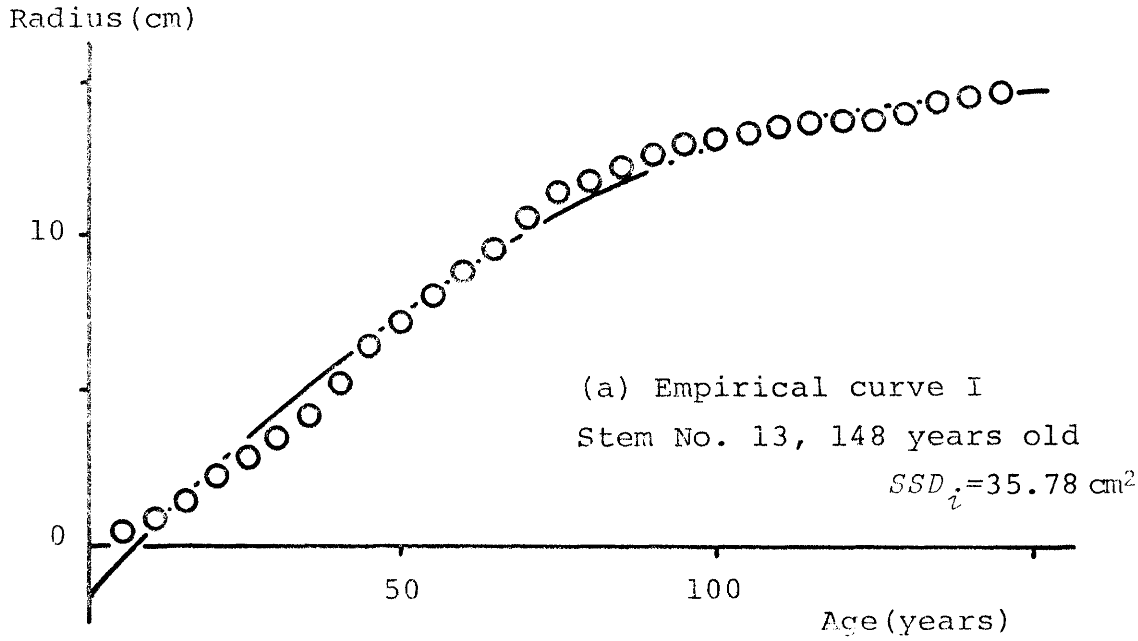
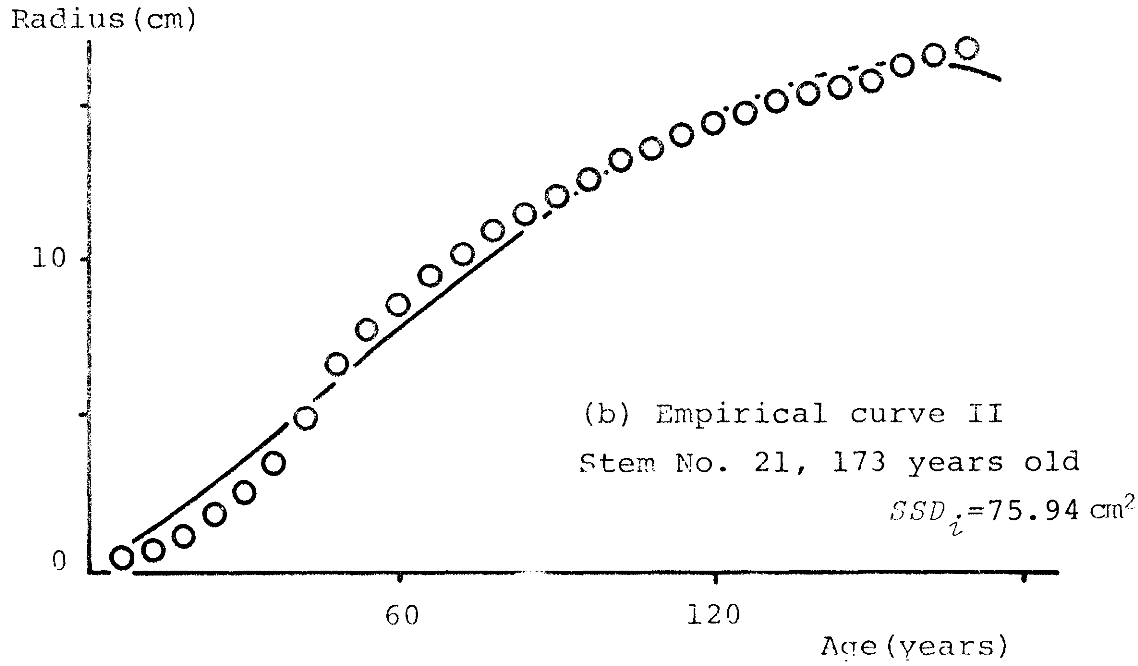


Figure 6. The Gompertz curve as compared with the observed radial stem growth of white spruce.


Radius (cm)
10
0
50
100
Age (years)
(a) Empirical curve I
Stem No. 13, 148 years old
SSD$_i$=35.78 cm^2


Radius (cm)
10
0
60
120
Age (years)
(b) Empirical curve II
Stem No. 21, 173 years old
SSD$_i$=75.94 cm^2

asymptotic radius of 29.47 cm for the Mitscherlich almost exactly matches this figure, while the means of 16.40 cm and 16.52 cm for the logistic and the Gompertz asymptotes respectively seem unrealistically small. This indicates that the asymptotes of the logistic and the Gompertz didn't function as satisfactorily as expected from the theory. Not only the means but also the individual asymptotic radii of the logistic and the Gompertz failed to comply with their respective theoretical prerequisites. It sometimes happened that the individual asymptotic radius was even smaller than the corresponding observed final radius in both cases as shown by Figs. 5(a) and 6(a). This result casts a skepticism on the growth forecasting capability of the logistic and the Gompertz equations.

The logistic and the Gompertz revealed another discrepancy of similar nature in their parameters a and p which are closely related to the initial radius y_o as shown in Table 1. The mean 2.58 cm of the parameter a's of the logistic is equivalent to y_o=$C/14$, which is too much for the initial radius. This resulted in a considerable overestimation in the early stage of growth as typically seen in Fig. 5(b). This consistent deviation in the early stage of growth was often compensated by the deviation in the opposite direction in a later stage as seen in the same figure. This tendency of constant deviation revealed in the present analysis also undermines the theoretical credibility of the logistic equation. Though not as conspicuous as in the logistic, the Gompertz too showed a similar discrepancy. The mean 1,240 of the parameter p's is equivalent to $y_o = A/30$, which, though better than the logistic, is still too large especially for a shade species as white spruce. This resulted in a more or less consistent overestimation in the initial stage of growth as seen in Fig. 6(a).

Although the parameters of the Mitscherlich equation revealed the most satisfactory consistency with their theoretical prerequisites on an average basis, an examination of Table 3 revealed the following discrepancies.

The most striking evidence found in Table 3 of the Mitscherlich equation would be sporadic negative values of the asymptote M and the rate constant k, both of which are supposed to be positive according to the theory. It will be readily noticed that the negative M's are always associated with negative k's. Although this fact may look strange and undoubtedly impairs the theoretical quality of the Mitscherlich equation, it doesn't affect the credibility of the equation as far as the agreement between the observed and calculated growth is concerned as shown in Fig. 4(b). As seen from the same figure, this concurrent occurrence of negative parameters took place whenever the general shape of the observed radial growth followed a course convex downward. This never happened in the logistic and the Gompertz. In these two equations, the calculated parameters observed the sign expected from the theory.

Another discrepancy found in the Mitscherlich was sporadic occurrence of unrealistically large values of the parameter M. A close examination of Table 3 shows that they are associated with extremely small values of the rate parameter k in a compensating manner, which nevertheless again results in a reasonable agreement between the observed and calculated growth. However, since M is supposedly the radius ultimately attained in a long run, its extremely large values are damaging to the theoretical credibility of the Mitscherrich equation. That individual values of M are rather fickle and not much reliable as the ultimate radius is seen in its relatively large standard deviation and coefficient of variation given at the bottom of Table 3. On the other hand the upper asymptotes C and A of the logistic and the Gompertz respectively are much less variable as seen in Tables 4 and 5. In accordance with the large variation in M, the rate constant k is also more variable than the corresponding parameters b and q of the logistic and the Gompertz.

Table 3 shows that the parameter L is greater than unity for most of the cases. This means that the calculated initial diameters are negative, which in turn indicates the equation underestimates the reality in the very early stage of growth, but it is not to such an extent as the logistic and the Gompertz overestimate. My experience shows that putting the initial radius equal to zero, i.e. L=1, do not deteriorate fit much. This suggests that the two-parametered form

$$y=M(1-e^{-kt})$$

may be a more proper expression for the Mitscherlich equation than the three-parametered one employed here. Since increased number of parameters progressively improves the quality of fit for any equation, this indication of being enough with only two parameters is a great advantage for the Mitscherlich as a theoretical growth equation.

Judging from Figs. 4 through 6 and those that couldn't be given here, it seemed that whether or not an equation has an inflection doesn't really matter in application. In other words, being devoid of it didn't seem to have worked to the disadvantage of the Mitscherlich as would have been foreseen. In Fig. 4 it seems as if the observed growth is weaving its way about the Mitscherlich which represents a hypothetical mean course of growth. On the other hand, having an inflection didn't seem to have any beneficial effect especially for the logistic. This may, most probably, be due to the fact that irregularities in actual growth process make it difficult to identify a definite point of inflection in the observed growth. However, the generally better agreement of the Gompertz with the observation than that of the logistic indicates that the inflection in the actual growth, if any, appears in earlier stage of growth than it does in the logistic.

Since the empiricals have no theoretical reference base to be judged upon, there is not much to be said of their parametric values. But it was found that the parameters were more variable than in the logistic and the Gompertz but less so than in the Mitscherlich. A comparison between the observed and calculated radial growth for the empirical equations is given in Fig. 7. Althoug the fit itself is satisfactory, the calculated radius sometimes decreases after a certain age even within the time range of fitting as seen in Fig. 7(b). There is no doubt that these empirical equations take on illogical and unrealistic values once beyond the range of fitting. This is one of the major reasons why the empirical equation is rated inferior to the theoretical in general.

Goodness of fit

Although the goodness of fit alone cannot constitute any absolute basis (Feller, 1940), there is no doubt that it is one of the important criteria for choosing the best growth equation, if any, for the radial growth of trees. Thus, the goodness of fit of each equation was calculated for every tree and compared with each other. The goodness of fit of any equation to the i^{th} tree was evaluated by the sum of squared deviations (SSD) of the calculated yearly radii from the corresponding observed radii, i.e.

$$SSD_i = \sum_{j=1}^{n} (Y_{ij} - y_{ij})^2, \qquad \text{III-3}$$

where SSD_i : goodness of fit for the i^{th} tree,

Y_{ij} : observed radius at age j,

y_{ij} : calcualted radius at age j,

n : total age of the i^{th} tree.

Thus the smaller is the SSD_i value, the better is the fit.

Since all the equations employed here have the same number of parameters, i.e. the same degree of mathematical freedom, this measure of the quality of fit provides with a fair basis of comparison among the equations.

The results are given in Fig. 8 and Table 8. The former shows the distribution of *SSD* for each of the five equations compared, while the latter gives the statistics. Judging from the mean of SSD_i, the Gompertz yielded the least value, i.e. the best fit on an average basis, while the logistic revealed the worst fit of all. Between them both, ranked the empirical II, the empirical I and the Mitscherlich in degrading order. The Gompertz is characterized by small mean and standard deviation. The Mitscherlich has a smaller mean but greater standard deviation than the logistic, which can also be seen graphically in Fig. 8. It is interesting that the both empirical equations achieved better fit than the logistic and the Mitscherlich.

For a more detailed comparison, a paired bilateral t-test of significance on goodness of fit was conducted between all the conceivable pairs of the five equations. The test between any two competing equations (e.g., the Mitscherlich vs. the logistic) was executed as follows:

1. Difference in goodness of fit for the i^{th} tree,

$$di=xi-yi,$$

where xi and yi are the *SSD* values of two competing equations for the i^{th} tree.

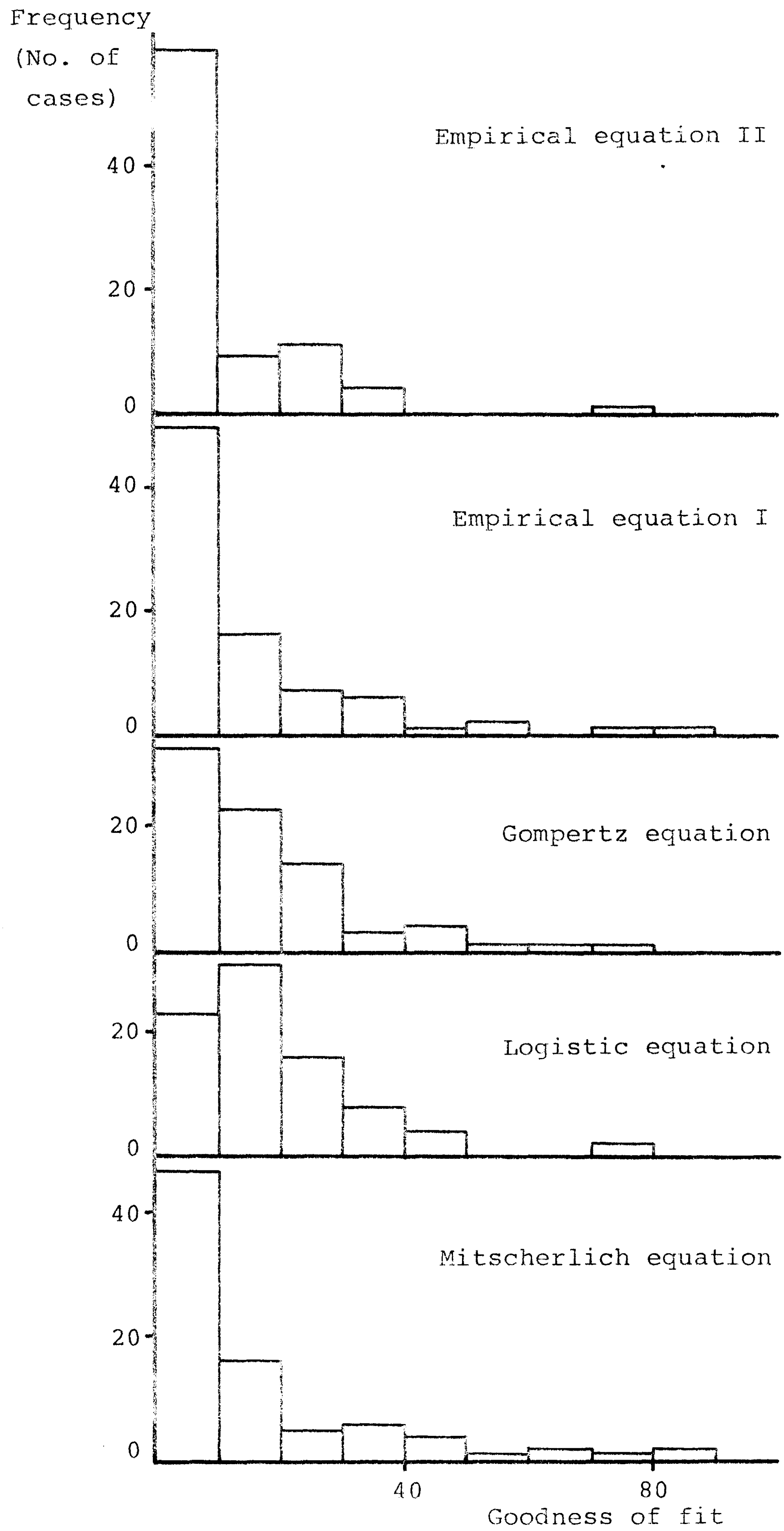


Figure 8. Distribution of the goodness of fit, *SSD*.

Table 8. Statistics on goodness of fit

	MIT.	LOG.	GOMP.	EMP.I	EMP.II
No. of Samples	84	84	80	84	84
Mean	16.34	19.18	8.28	13.50	10.28
Standard Dev.	20.07	13.48	7.38	15.72	11.77

2. Mean and standard deviation of the difference in goodness of fit,

$$\overline{di} = \frac{1}{n} \sum_{i=1}^{n} di,$$

$$Sdi = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (di-\overline{di})^2} \quad ,$$

where n is the number of trees used in comparison.

3. Calculated t-value,

$$t_o = \frac{\overline{di}}{Sdi/\sqrt{n}} .$$

4. This calculated t-value was checked against the tabulated one to test a null hypothesis $\overline{di} = 0$ against the altenative $di \neq 0$.

The results of test is tabulated in Table 9. Among the theoretical equations, it was found that there was no significant difference in goodness of fit between the Mitscherlich and the logistic, while the Gompertz revealed a significantly better fit than these two. The two empiricals showed significantly better fit than the Mitscherlich and the logistic but significantly poorer fit than the Gompertz.

Ease of fitting.

A mention has to be made on the technical difficulties associated with the curve fitting as this will

Table 9. t-test of significance on goodness of fit among the five competing equations

	MIT.	LOG.	GOMP.	EMP.I	EMP.II
MITSCHERLICH		1.017	3.488	3.538	3.862
LOGISTIC	n.s.		10.158	2.668	6.242
GOMPERZ	**	**		2.850	1.703
EMPIRICAL I	**	**	**		2.386
EMPIRICAL II	**	**	n.s.	*	

** highly significant, i.e. significant at the 99% level of confidence.

* significant, i.e. significant at the 95% level of confidence.

n.s. non-significant difference.

certainly cast an important problem in practical application of these equations. As mentioned earlier Deming's method of least squares is one of the best way for fitting complex nonlinear functions. It is an iterative method in which initial estimates of the parameters have to be given prior to the least squares calculation, which in turn gives a new set of calculated parameters. These new parameters are fed in again as the secondary estimates for the second round of calculation, and the process is repeated on and on until the parametric values converge, i.e. the newly calculated parameters become identical with those input as the directly preceding estimates. The difficulty encountered in this entire process of fitting is twofold, i.e. the one associated with giving the initial estimates and the other with iteration time.

According to the present analysis, ease of fitting was rated as follows:

easy ⟵——————————————————⟶ difficult

empiricals > Mitscherlich > logistic > Gompertz

With the empiricals, even what had seemed very far-off initial estimates converged easily in a few iteration times. With the Gompertz on the other hand, even meticulously chosen initial estimates sometimes took more than a score of iteration times before converging, and in a few cases never converged. The Mitscherlich and the logistic came between these two extremes, but in general the former was easier than the latter.

Conclusion

It is a rather stunning finding in the present analysis that all of the three theoretical equations did not work as expected from the theories, though the way and extent those discrepancies appeared differ from one equation to another. In spite of its sporadic extreme parametric values, the indication of being enough with only two parameters would make the Mitscherlich the most prospective of all at least from theoretical point of view. The liability to overestimate in early stage of growth and the accompanying opposite liability in the late stage of growth was shared by the logistic and the Gompertz, but it was more pronounced in the former. This would make the Gompertz more favourable than the logistic as a theoretical growth equation.

The best agreemtnt with the observed growth was achieved by the Gompertz, followed by the Mitscherlich with the logistic closing up the rear. The easiest to fit was the Mitscherlich, followed by the logistic and then by the Gompertz. Though this dependence of rank upon the criterion makes it difficult to draw a clear-cut overall conclusion, the Mitscherlich would be the most promising of all as a theoretical growth equation for the breast-height stem radial growth of trees.

CHAPTER IV

APPLICATION OF THE MITSCHERLICH, THE LOGISTIC AND THE GOMPERTZ EQUATIONS TO THE RADIAL STEM GROWTH OF JACK PINE

Introduction

In the preceding chapter, the Mitscherlich, the logistic and the Gompertz equations were applied to the growth of white spruce, one of the representative shade-tolerant species. In this chapter these equations were applied to the observed radial growth of jack pine *(Pinus banksiana* Lamb.*)* a representative of shade-intolerant pioneer species, and the characteristics of each equation was analyzed.

Although the methods of analysis employed in this chapter is almost similar to those in the preceding chapter, several minor improvements were made according to the experience learned and the recommendation made in the preceding chapter. First of all, the number of growth data to be used for the analysis was increased significantly, i.e. from approximately 85 trees to 350, to enhance the statistical credibility of the analysis. Secondly, the Mitscherlich equation was used in its two-parametered form instead of the three-parametered one, while the other equations were left unchanged. In accordance with the above alteration, the goodness of fit was evaluated by a slightly modified formula which enables us a comparison among growth equations of different degrees of parametric freedom. Lastly, ease of fitting was analyzed in a more objective and statistically reliable manner.

Materials and methods

The growth data employed for the analysis is individual growth records of 349 jack pine trees collected in 1977 from the Northwest Territories, Canada by the joint servey team mentioned in the preceding chapter. A 0.882-ha square sample plot was established in an even-aged, single-species jack pine stand regenerated after fire in the vicinity of Forth Smith. Though an increment core was taken at breast height from all the live trees present in the plot, the removal of illegible cores resulting from inner decay ended up with a total of 349 cores on which the annual rings could be traced back to the very center of the stem. The measurement of annual rings was made in exactly the same manner as for the white spruce described in the preceding chapter, i.e. with the increment measuring device equipped with a microscope to the precision of 0.01 millimeter. The age of the trees counted at breast height ranged from 94 to 136 years with a mean of 126.7 years and standard deviation of 6.03 years. For a more detailed account of the data collection and measurement as well as the raw growth data, see Sweda and Umemura (1979).

As in the preceding chapter, a total of five growth equations, i.e. the Mitscherlich, the logistic and the Gompertz plus the empiricals I and II for reference, was applied by the same Deming's method of least squares to each of the 349 jack pine growth records, and their parameters were determined. Considering one of the results obtained in the preceding chapter that only two parameters would suffice for the Mitscherlich, the two parametered form was employed here instead of the three parametered one. The rest of the equations were adoped unchanged. Just to avoid confusion, the five growth equations used in this chapter are renumbered and listed below:

Mitscherlich	$y=M(1-e^{-kt})$	IV-1
Logistic	$y=\dfrac{C}{1+e^{a-bt}}$	IV-2
Gompertz	$y=Ae^{-e^{p-qt}}$	IV-3
Empirical I	$y=a+bt+ct^2$	IV-4
Empirical II	$y=at+bt^2+ct^3$	IV-5

To obtain some quantitative measure of ease of fitting, the least-squares calculation was conducted in the following rather mechanical but systematic manner. First of all, the parameters of each growth equation were calculated for the first twenty individual trees, i.e. from stem No. 1 to No. 20 inclusively, and the mean of these twenty figures was obtained for each paramter. Then, with these means as the common initial estimates, the least-squares fitting was executed for all the 349 trees. In determining a set of parameters of any equation for any individual tree, the least-squares calculation was repeated until two successive estimates for every parameter involved became identical within the prescribed precision of 1/1000, i.e. until the inequality

$$|(A_i - A_{i+1})/A_{i+1}| \leq 0.001,$$

where A_i : the i^{th} estimate of any parameter,

is reached. Not to prolong the calculation, however, an iteration allowance of 10 times-per-tree was also set up. In other words, the least-squares calculation was terminated as a "failure in fitting" when the estimate of any parameter would not converge within the above prescribed precision after ten repetition times. Then the number of the failures was tallied for each equation as a measure of ease of fitting. For those trees which succeeded in fitting, the iteration times were tallied as another measure of ease of fitting.

Theoretical consistency

The parameters of the above five equations determined for each of the 349 trees were so volumeneous that they are given in Appendix I through V and only the final statistics are given in Table 10. A few graphical examples of the calculated growth as compared with the corresponding observed one are also given for each equation in Figs. 9 through 13. Generally speaking it seemed that all the five worked better with jack pine than with white spruce in every criterion.

Table 10. Statistics on the parameters of the five growth equations

Statistics**	Mitscherlich k (1/year)	Mitscherlich M (cm)	Logistic a*	Logistic b (1/year)	Logistic C (cm)	Gompertz p*	Gompertz q (1/year)	Gompertz A (cm)
	$\times 10^{-2}$			$\times 10^{-2}$		$\times 10^{-1}$	$\times 10^{-2}$	
Mean	2.03	10.75	1.62	4.89	9.18	7.61	3.48	9.57
Var.	0.49	14.90	0.05	1.37	3.51	1.41	0.89	4.41
S.D.	0.70	3.86	0.22	1.17	1.87	1.19	0.95	2.10
C.V.(%)	34.6	35.9	13.7	23.9	20.4	15.6	27.1	21.9

Statistics**	Empirical I a (cm)	Empirical I b (cm/year)	Empirical I c (cm/year^2)	Empirical II a (cm/year)	Empirical II b (cm/year^2)	Empirical II c (cm/year^3)	Final radius (cm)
	$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$	$\times 10^{-1}$	$\times 10^{-3}$	$\times 10^{-6}$	
Mean	7.75	1.31	-5.11	2.00	-1.84	6.96	9.51
Var.	16.41	0.10	4.03	0.21	0.56	10.07	3.50
S.D.	4.05	0.32	2.01	0.46	0.75	3.17	1.87
C.V.(%)	52.3	24.2	39.4	23.1	40.7	45.6	19.7

* dimensionless

** The statistical measures, Var., S.D. and C.V. stand for variance, standard deviation and coefficient of variation respectively.

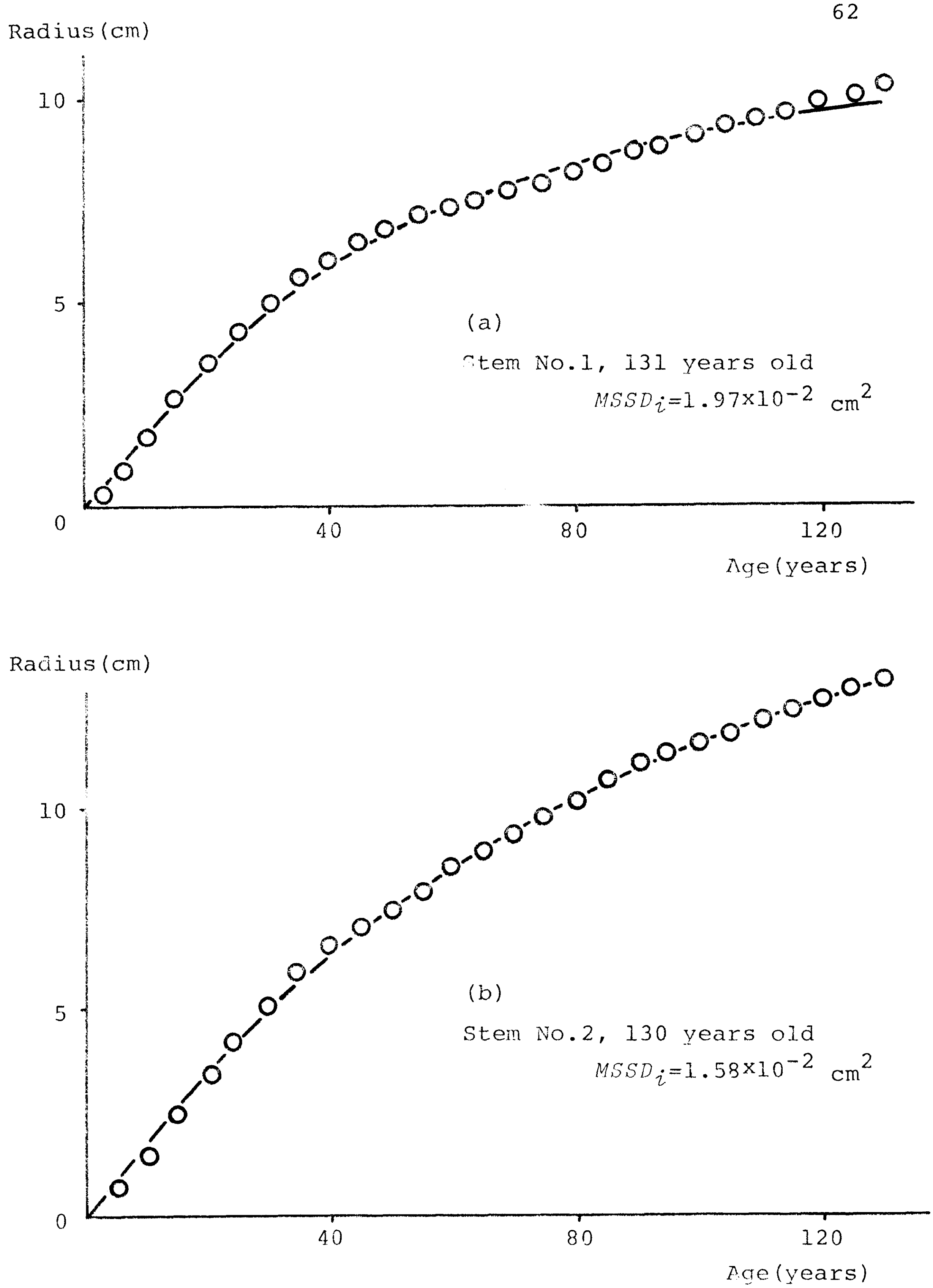
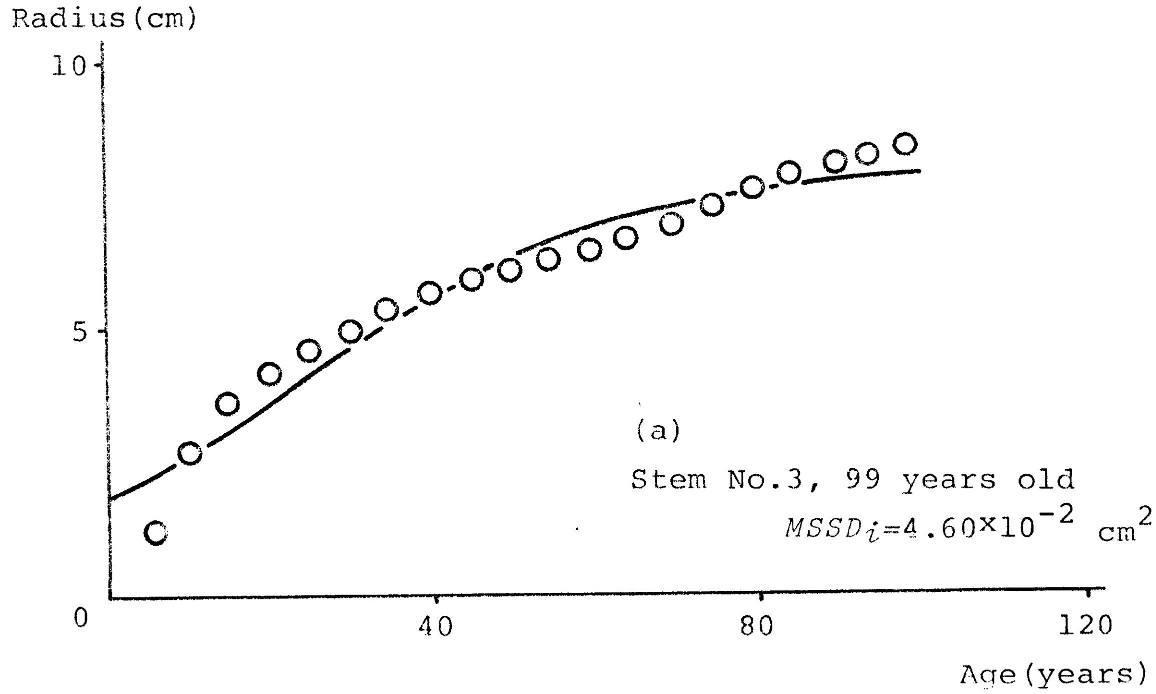


Figure 9. The Mitscherlich curve as compared with the observed radial stem growth of jack pine.



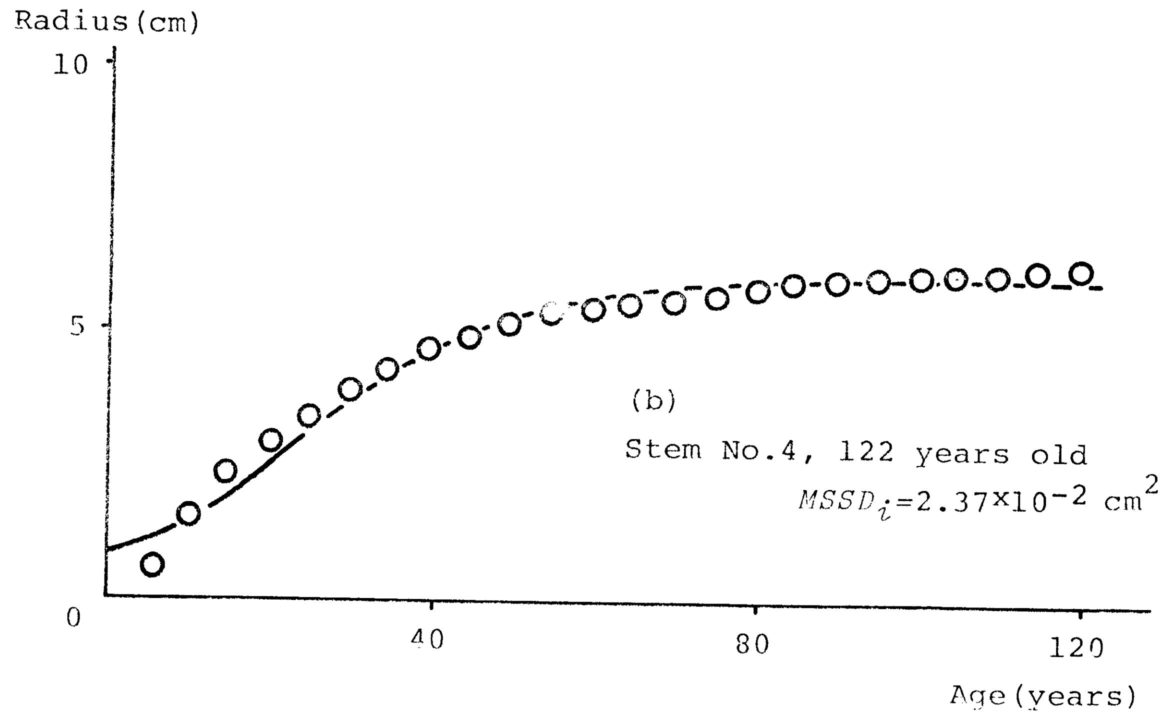
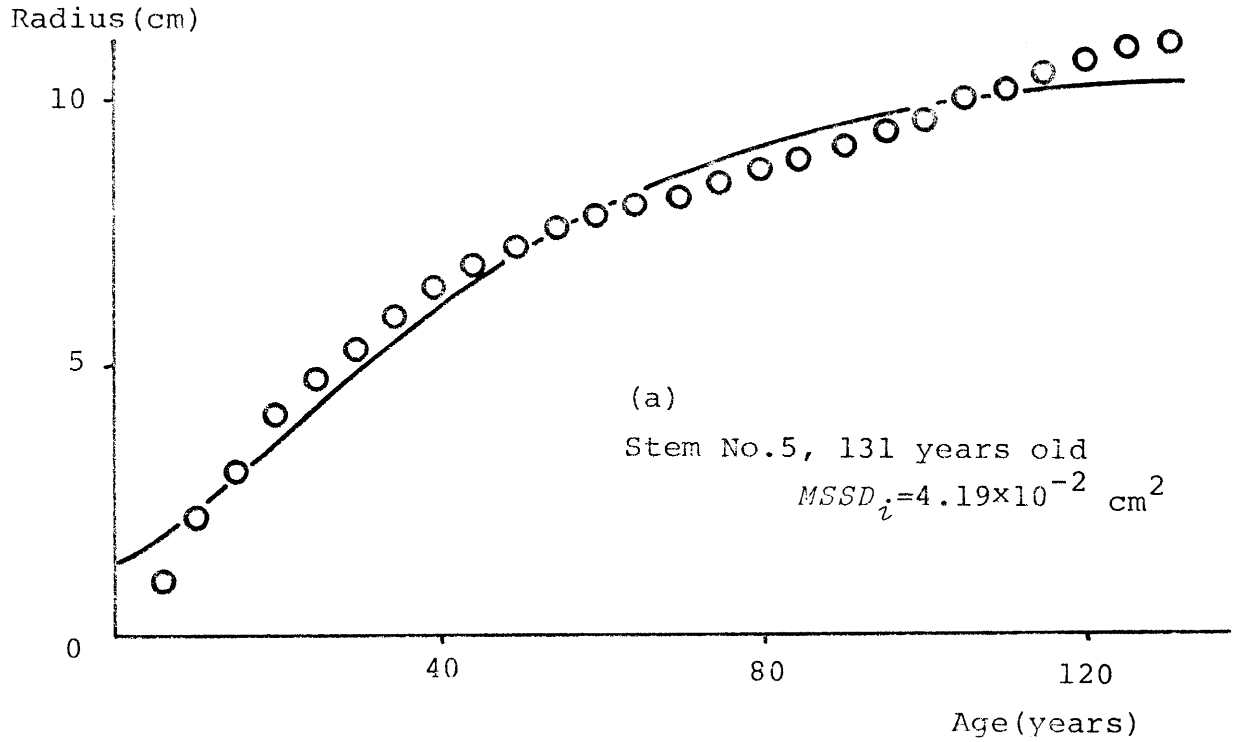


Figure 10. The logistic curve as compared with the observed radial stem growth of jack pine.



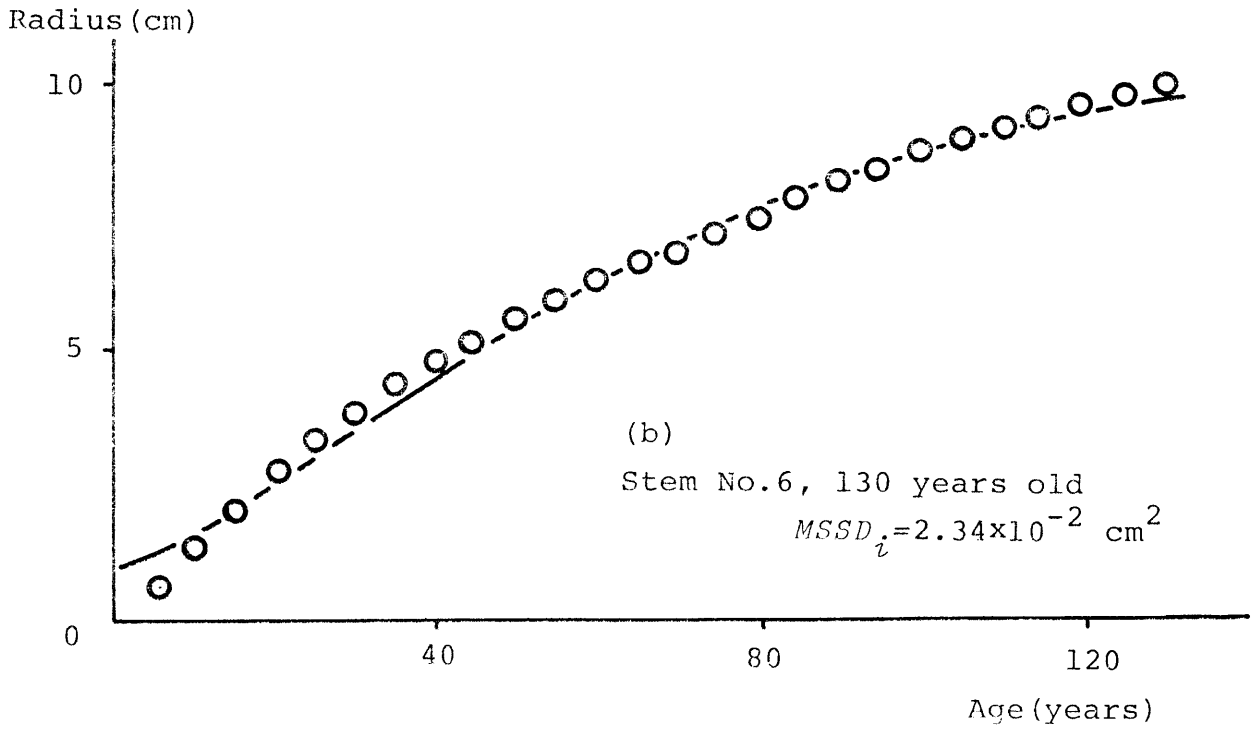
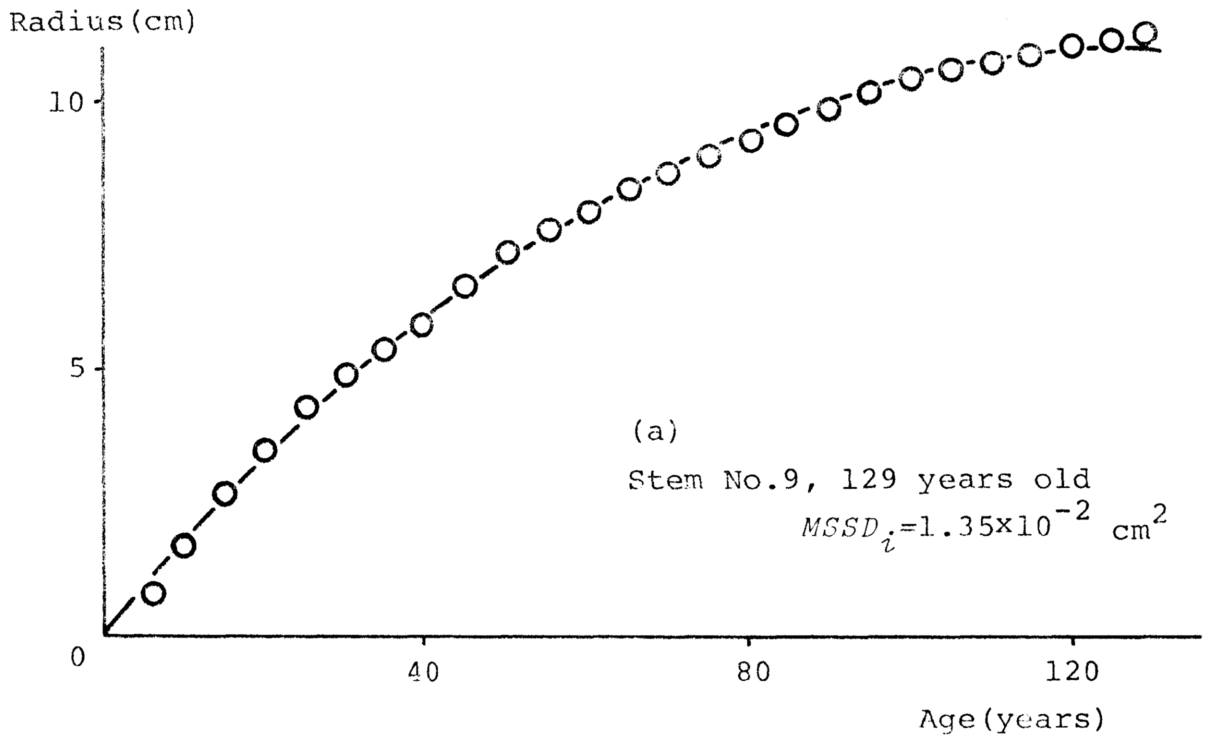


Figure 11. The Gompertz curve as compared with the observed radial stem growth of jack pine.



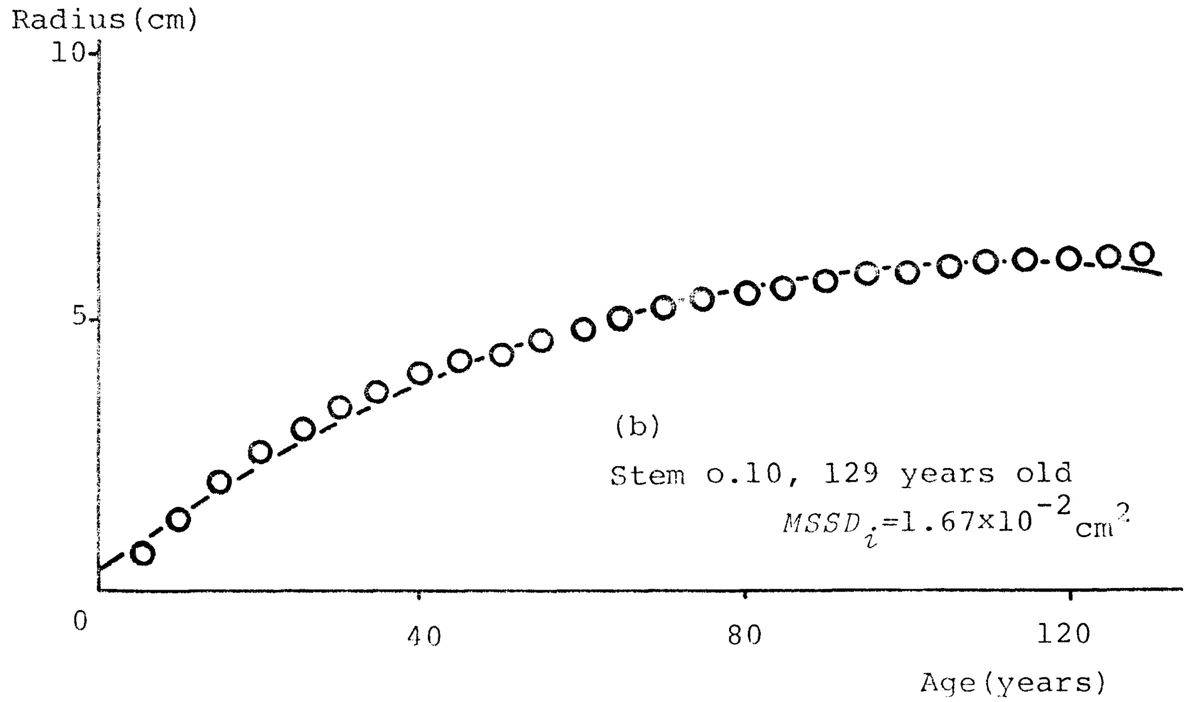
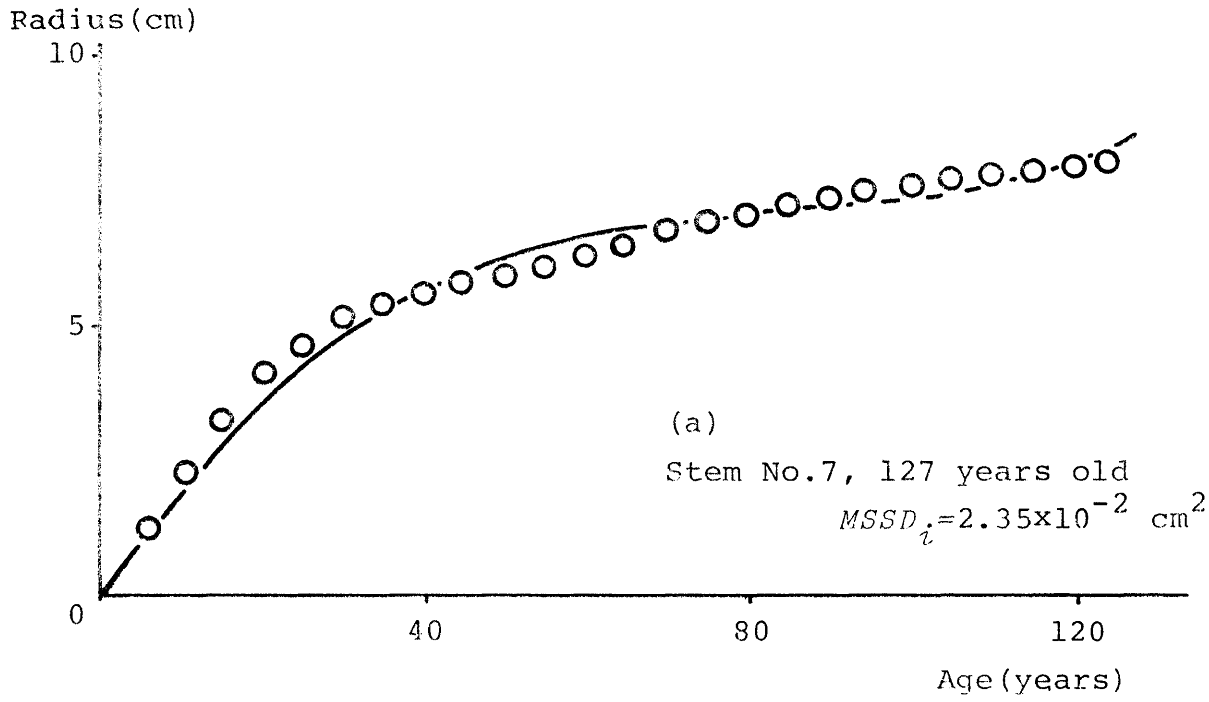


Figure 12. The empirical growth curve I as compared with the observed radial stem growth of jack pine.



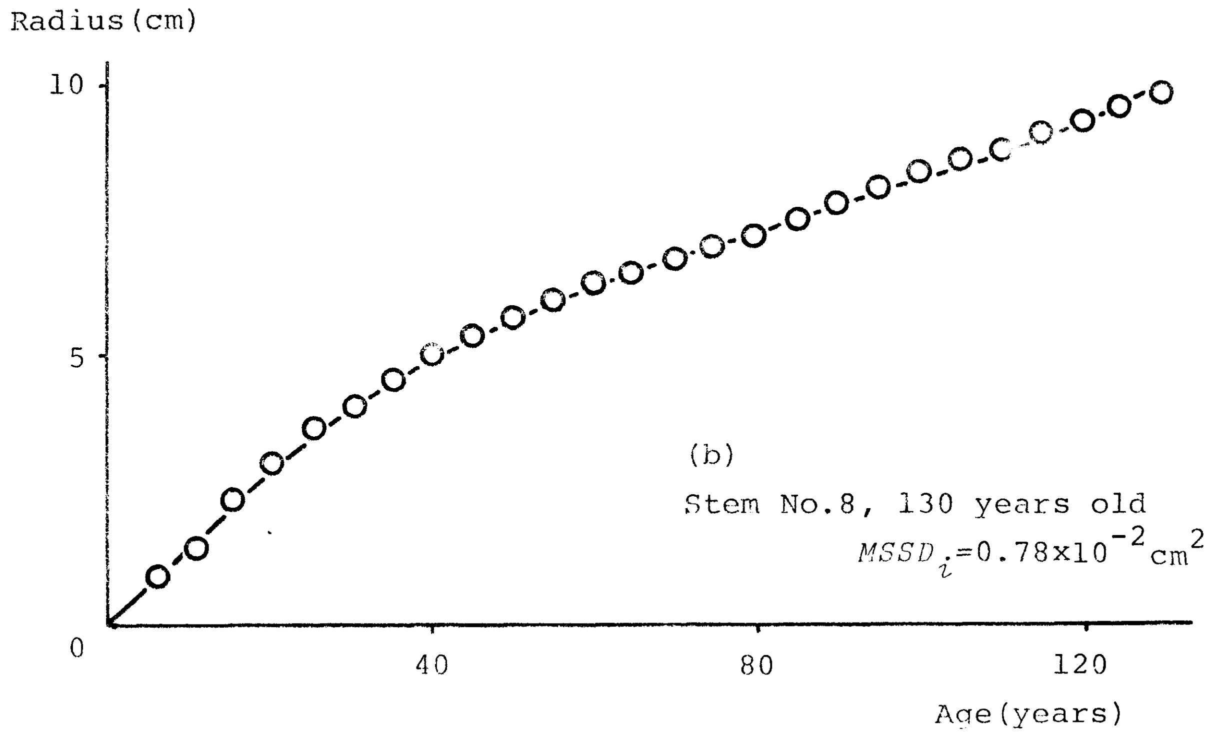


Figure 13. The empirical growth curve II as compared with the observed radial stem growth of jack pine.

From Fig. 9, it seems that the Mitscherlich fits jack pine better than it does white spruce. Though they were spared here, the other graphical comparisons between the calcualted Mitscherlich curve and the observations revealed a similar trend. One of the major reasons for this is most probably attributable to the adoption of the two-parametered form. As has been discussed earlier, this characteristic of being enough with fewer parameters suggests, to its great theoretical advantage, that the Mitscherlich has a powerful potential capability of being a growth curve by itself with little aid of parameters. Another reason for the improved agreement is considered to be attributable to the specific characteristic of jack pine. Being a representative shade-intolerant pioneer species, jack pine shoots rapidly in early stage of growth, gradually leveling off through the maturity toward the senescence. This growth pattern might well have helped the Mitscherlich fit jack pine better.

Figs. 10 and 11 confirm the inflexibility of the logistic and the Gompertz suspected in the preceding chapter. Here again, both of the curves overestimate the actual growth in the early stage and underestimate in the old age. This rather definite tendency of constant deviation undoubtedly impairs the theoretical credibility of the logistic and the Gompertz at least for the breast-height radial growth of trees.

Table 10, which gives the statistics on the parameters of the five equations compared, reveals the same characteristics as those pointed out in the preceding chapter. Considering the fact that jack pine individuals of age nearly 130 years old are at their senescence and do not have much room to grow, the Mitscherlich's mean asymptotic radius of 10.75 cm, as compared with the mean final radius of 9.51, seems to be a reasonable figure. The logistic's 9.18 cm, which is even smaller than the mean final radius, seems inappropriate as an asymptote. The same is true for the Gompertz's 9.57 cm which is barely greater than the mean final radius. However, the relatively large standard deviation or the coefficient of variation of the Mitscherlich's asymptote indicates that individual asymptotes may not be very reliable for forecasting future growth. In spite of this fact, a thorough check through the individual parameters of the Mitscherlich in Appendix I reveals no peculiarly extreme values, i.e., neither negative nor extremely large values as found in the preceding chapter. Though it is not clear whether this is attributable to the adoption of the two-parametered form, the specific growth pattern of jack pine, or both, there is no doube it works to the advantage of the Mitscherlich. The fact that the means of parameters a's and p's of the logistic and the Gompertz are equal to 1.62 (dimensionless) and 0.761 (do.) is synonymus with their calculated initial radius being 1.52 and 1.13 cm respectively. Obviously they are too much for the initial redius as are also seen in Figs. 10 and 11.

Goodness of fit

As in the preceding chapter, the goodness of fit of each equation was calculated for every tree. Unfortunately, however, since the number of parameters involved is not the same for all the equations compared, the previous measure of goodness of fit is no more applicable. Thus to ensure a fair comparison, a new measure which also account for the number of parameters is introduced. It is of the form:

$$MSSD_i = \frac{1}{n-f}\sum_{j=1}^{n} (Y_{ij}-y_{ij})^2,$$

where

$MSSD_i$: goodness of fit for the i^{th} tree, (mean squared sum of deviations)

Y_{ij} : observed radius at age j,

y_{ij} : calcualted radius at age j,

n : total age of the i^{th} tree,

f : number of parameters involved in an equation concerned.

As in the previous case, the smaller is the $MSSD_i$ for an equation, the better is the fit. The results of the $MSSD_i$ calculation is given in Table 11, in which only the statictics are given rather than listing volumenous $MSSD_i$ values calculated for every equation and every tree.

Table 11. Statistics on goodness of fit

$MSSD_i$	Mitscherlich	Logistic	Gompertz	Empirical I	Empirical II
Mean	2.00	3.88	2.97	2.78	1.50
Maximum	6.14	7.27	6.18	6.34	7.08
Minimum	0.46	1.30	0.83	0.77	0.52
Variance	0.73	0.96	0.76	1.09	0.45
Standard deviation	0.86	0.98	0.87	1.04	0.67
Coefficient of variation	43.0	25.3	29.3	37.4	44.7
No. of successful fitting	348	345	347	349	349

Note : The figures are given in hundredths (i.e., to be multiplied by 10^{-2} to get the exact values) except for the coefficient of variation and the No. of successful fitting.

Table 11 shows that among the theoreticals, the Mitscherlich fitted the observation best, followed by the Gompertz and then by the logistic. The most remarkable difference from the white spruce case is the reverse of rank between the Mitscherlich and the Gompertz in favour of the former. This result may most probably be attributable to the adoption of the two-parametered Mitscherlich as well as to the specific growth pattern of jack pine mentioned earlier. It is interesting to note that the empirical II scored best of all and the empirical I did better than the logistic and the Gompertz.

For a more statistically regorous comparison in goodness of fit, a paired bilateral *t*-test of significance was also conducted between the four neighbouring pairs of competing equations in exactly the same manner as had been done in the preceding chapter. The test results are given in Table 12, which shows that there was a highly significant difference in goodness of fit between the every neighbouring ranks.

Ease of fitting

The ease of fitting as measured in terms of the failure count and statistics on the iteration times are given in Table 13. In comparison with white spruce, jack pine was easier to fit for all the equations. This may largely be due to the rather simple growth pattern of jack pine mentioned earlier. By far the easiest to fit was the empiricals in which all the 349 trees were successful in

Table 12. The t-test of significance on goodness of fit

	Empirical II	Mitscherlich	Empirical I	Gompertz	Logistic
Ranking in goodness of fit	1	2	3	4	5
Statistics on goodness of fit					
Mean difference, $\bar{d_i}$		0.50	0.77	0.21	0.90
S.D. of the difference, s_{d_i}		0.66	0.94	0.74	0.41
No. of comparisons, n		348	348	347	345
Calculated value, t_o		14.06**	15.31**	5.24**	42.32**

** Highly significant difference detected, i.e., significantly different at the 99% level of confidence for which the critical value of t is equal to 2.58.

Table 13. Statistics on ease of fitting

	Mitscherlich	Logistic	Gompertz	Empirical I	Empirical II
Failure count	1	4	2	0	0
Success count	348	345	347	349	349
Iteration time*					
Mean	3.52	5.12	4.53	2.00	2.00
Var.	0.48	1.56	1.01	0.0	0.0
S.D.	0.96	1.25	1.00	0.0	0.0
C.V.(%)	19.6	24.4	22.2	0.0	0.0

* The row sub-headings Var., S.D., and C.V. stand for variance, standard deviation and coefficient of variation respectively of the iteration time for the successful cases.

only and exactly two iteration times each. Among the theoreticals, the Mitscherlich scored best both in number of successes and iteration times. Different from the white spruce case, the Gompertz turned out to be easier to fit than the logistic.

Conclusion

Generally speaking, all the theoreticals worked better with jack pine than they had done with white spruce. This may largely be due to the rather simple growth pattern of jack pine. Of the three theoretical equations, the most remarkable improvement was achieved by the Mitscherlich, which ranked first in all the criteria, i.e. the theoretical consistency, goodness of fit, and ease of fitting. As for the theoretical consistency, both the logistic and the Gompertz still maintained their proneness to constant deviation which had been found in the preceding chapter. This would undoubtedly impair their credibility as the theoretical growth equations. The Gompertz scored better than the logistic both in goodness of fit and ease of fit.

To facilitate the overall rating, the three theoretical equations were ranked by each category of criterion in Table 14, in which the equation scoring the first place was given figure 1 and so on. Thus, the smaller is the figure, the better is the equation. As seen from the botton of the table, the Mitscherlich ranked first in the overall rating, followed by the Gompertz, then by the logistic.

It should be noted that the above method of comparison may be objective, but it is just one of other

Table 14. Overall ranking of the Mitscherlich, the logistic and the Gompertz equations

		Mitscherlich	Logistic	Gompertz
White spruce	Theoretical consistency	1	3	2
	Goodness of fit	2	3	1
	Ease of fitting	1	2	3
	Sub-total	4	8	6
Jack pine	Theoretical consistency	1	3	2
	Goodness of fit	1	3	2
	Ease of fitting	1	3	2
	Sub-total	3	9	6
Ground Total		7	17	12

The figures in the main body of the table indicate the ranking by each category of criterion.

thousands of objective methods of comparison. However, the subjective judgement, which has been accumulated throughout the entire course of the annual ring measurement, curve fitting and analysis, also endorses the ranking given above. Thus, with the present state of our knowledge, it can be concluded that the Mitscherlich is the most powerful and prospective growth equation for the breast-height radial growth of trees, followed by the Gompertz, then by the logistic.

CHAPTER V

A THEORETICAL STEM TAPER CURVE

Introduction

The subject of stem taper curve is not only interesting, but it also constitutes one of the important bases of mensuration and forest biometrics. However, most of the works conducted to date on this subject were either experimental or empirical. This chapter deals with the construction of a theoretical stem taper curve as one of further applications of the theoretical growth equation for trees. That is, based on the theory of tree growth discussed in the preceding chapters, a theoretical equation expressing stem taper curve was derived. In contrast with the empirical or experimental ones currently used, the proposed equation gives an account of what generates the stem form, and its parameters convey biological meaning pertinent to the growth of trees. The equation was also applied to 50 jack pine stems to get numerical values of parameters involved. Further more it was compared with some of the representative empirical stem taper curves in terms of goodness of fit to actual data.

Literature review

Since stem taper curves constitute an important basis for evaluating the trunk volume of trees which is the ultimate objective of forestry, many authors have presented numerous stem taper curves. According to Prodan (1965), Höjer presented as early as 1903 a stem tatper curve of the form:

$$d = DC\log\frac{c+l}{c},$$

where

d: stem diameter at l meters below the tip,

D: diameter at ground,

C, c: constants.

Prodan also mentioned a modification of this equation by Tor Jonson.

One of the most often used formulas may be Behre's of the form:

$$y = \frac{x}{a+bx},$$

where

x: relative position on the stem as expressed in terms of the percentage of the stem length above the breast height,

y: relative diameter at relative height x as expressed in the percentage of the normal diameter, i.e. breast height diameter,

a, b: constants.

Hada (1958) applied this formula to sugi (*Cryptomeria joponica*, D. Don.) and obtained a reasonable agreement with his observed data. A similar work also was conducted by Ueno and Hasegawa (1970). Prodan modified Behre's formula to get

$$y=\frac{x^2}{a+bx+cx^2},$$

where the variables remain the same as in Behr's formula. In this equation only the power of the denominator increased by one as did the number of constants accordingly.

Osumi (1959) proposed the following third parial sum of a power series as a relative stem taper curve:

$$y=ax+bx^2+cx^3,$$

where

x: relative position on the stem expressed in a ratio relative to total stem length,

y: relative stem radius at position x expressed in a ratio relative to the stem radius at 9/10 of total stem length from the tip,

a, b, c: constants.

He applied this equation to *C. japonica* and obtained a satisfactory agreement with his observations. Osumi's equation can be sophisticated by increasing the sum up to the higher powers of the series as suggested by Fries and Matérn (1965) or by Kajihara (1973).

By far the most popular stem generatrix may be Kunze's formula of the form:

$$y=ax^m,$$

where

y: stem radius at height x,

a: constant,

m: form exponent,

which generates stem taper curves of various convexity for various integral values of parameter m.

It should be noted that all the stem curves quoted above have their apexes at the origin of the coordinates in which stem diameter (radius) and height (position on the stem) are represented by the ordinate and abscissa respectively.

This brief review of stem taper curves implies that to date much effort has been made to find mathematical expressions which resemble the actual stem taper curves as well as to fit those mathematical expressions to observations to get a numerical account of the parameters involved. However, it seems that even an equal amount of effort or attention has not been paid to derive stem taper curves underlain by theoretical reasonings. All the mathematical expressions given above are simply experimental equations, and they are not accompanied by any rational or theoretical reasoning relevant to the subject. These equations may fit well to the observed data as many authors have proven. They may be useful in practice as concise expressions to save a great deal of numerical data. But they have no biological meaning, nor do they explain why the stem of a tree is shaped as it really is.

Derivation

It has been revealed in the preceding chapters that the growth of individual trees in stem radius (diameter) is most successfully represented by the Mitscherlich equation. Since the growth in diameter is of linear dimension, it would be readily apprehended that the growth of trees in height, which is also of linear dimension, follows the Mitscherlich equation as well. This expectation is supported by Meyer (1940) in general terms as well as by Nagumo and Sato (1965) experimentally. Thus, we assume here that the growth of individual trees both in height and diameter follows the Mitscherlich equation, i.e.

$$\text{height} \quad x(t)=H(1-e^{-kt}), \qquad \text{V-1}$$

$$\text{diameter} \quad y(t)=D(1-e^{-lt}), \qquad \text{V-2}$$

where

$x(t)$, $y(t)$: height and diameter respectively at age t,

H, D: upper asymptotes,

k, l: intrinsic rates of growth,

e: base of natural logarithm.

One of the assertions that Eq. V - 1 implies is that an individual tree has its own specific asymptote H and intrinsic rate k for its height growth. The same argument applies to diameter growth insofar as the height of observation is fixed, for example, at breast height. It has been shown in the preceding chapters that these parameters vary from one individual tree to another. However, it is yet unknown whether or not the upper asymptote D and intrinsic rate l for diameter growth vary with height even within an individual tree. Thus in this work it is assumed that both the upper asymptotic diameter and the intrinsic rate of growth are consistent for a given tree regardless of the height at which the diameter growth is considered. For example, the diameter growths at stump height and breast height are supposed to have the same asymptote and intrinsic rate of growth. This assumption makes the derivation that follows much more simple than might otherwise be assumed.

Suppose a tree which has attained a height h by age t as shown in Fig. 14 and consider its stem diameter at any arbitrary height $x \leq h$. Then according to Eq. V - 1 the relationship between height h and age t is given by

$$h = H(1 - e^{-kt}). \qquad \text{V - 3}$$

Also according to Eq. VI-1, the relationship between height x and the time τ taken to bring the tree up to this height is given by

$$x = H(1 - e^{-k\tau}). \qquad \text{V - 4}$$

On the other hand, the diameter growth at height x took place only when the tree had reached the height x, which left the tree a growth period of lengh $t-\tau$ till it reached present height h. This delay in the start of diameter growth increases toward the apex and causes the tapering form of the stem. Thus according to Eq. V - 2 the stem diameter at height x at age t is given by

$$y = D[1 - e^{-l(t-\tau)}]. \qquad \text{V - 5}$$

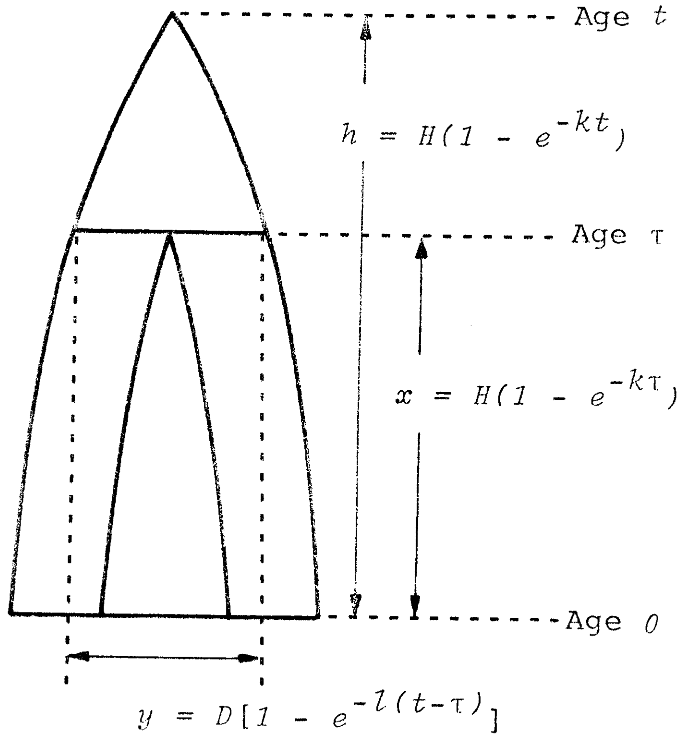


Figure 14. Schematic growth of an individual tree in height and diameter.

In words, the stem diameter at height x of a tree which has attained height h by age t is a function of time t and τ. It is now possible to rewrite tnis equaiton in terms of height h and x. Solving Eqs. V - 3 and V - 4 for time t and τ respectively and substituting the resultant equations in VI-5 to eliminate the time parameters, we get

$$y(h,\ x) = D\left[1-\left(\frac{H-h}{H-x}\right)^{l/k}\right], \qquad \text{V - 6}$$

where

$y(h,\ x)$: stem diameter at height x of a tree of total height h,

$D,\ H$: asymptotes for diameter and height growths,

$l,\ k$: intrinsic rates of growth for diameter and height.

Equation V - 6 gives stem diameter y at any given height x, i.e. a stem taper curve.

<u>Characteristics</u>

From the view point of theoretical reasoning, Eq. VI-6 may be the most appropriate expression with each of its five parameters carrying a specific biological meaning relevant to the subject. However, the following rearrangement will make the proposed stem taper curve easier to handle for all practical purposes. Since both the numerator l and the denominator k in the exponent of Eq. V - 6 are constants the quotient l/k can be replaced by another constant, i.e.

$$m=\frac{l}{k}, \qquad \text{V - 7}$$

which reduces the apparent number of parameters to four yielding

$$y(h,\ x)=D\left[1-\left(\frac{H-h}{H-x}\right)^{m}\right]. \qquad \text{V - 8}$$

The general shape of the proposed stem taper curve V - 6 or V - 8 is shown in Figs. 15 and 16. It should be noted that contrary to the aforementioned experimental equations, this stem curve has its base attached to the ordinate representing diameter or radius and the tip at the far end of the abscissa representing tree height. Since the derivative of stem diameter y with respect to height x is negative, i.e.

$$\frac{dy}{dx}=-mD\frac{(H-h)^{m}}{(H-x)^{m+1}}<0$$

y is monotonously decreasing function of x, which can be observed intuitively from Fig. 15. Since the second order derivative is negative, i.e.

$$\frac{d^2y}{dx^2}=-m(m+1)D\frac{(H-h)^{m}}{(H-x)^{m+2}}<0$$

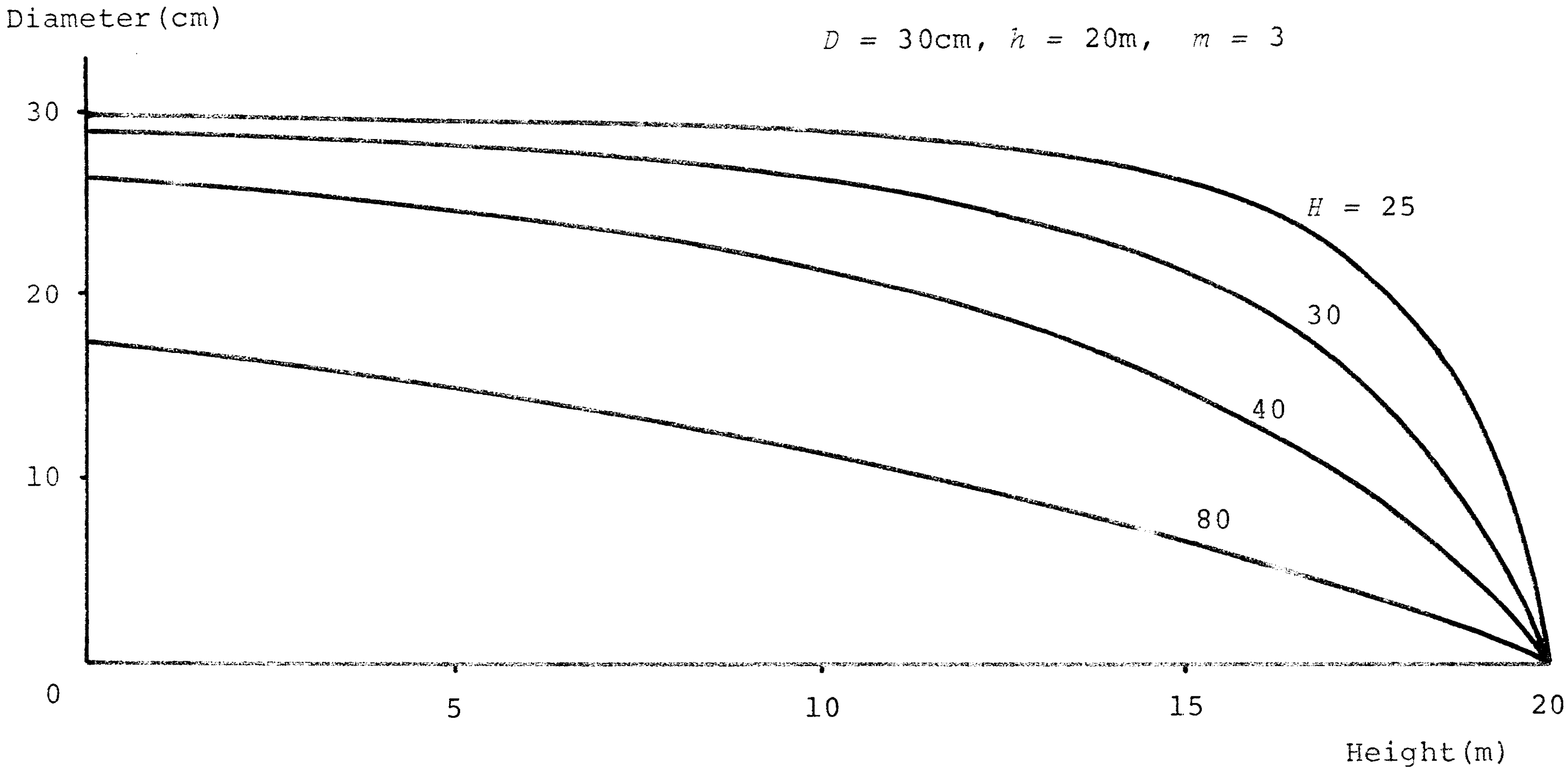


Figure 15. Proposed stem taper curves for various values of parameter H while other parameters fixed.

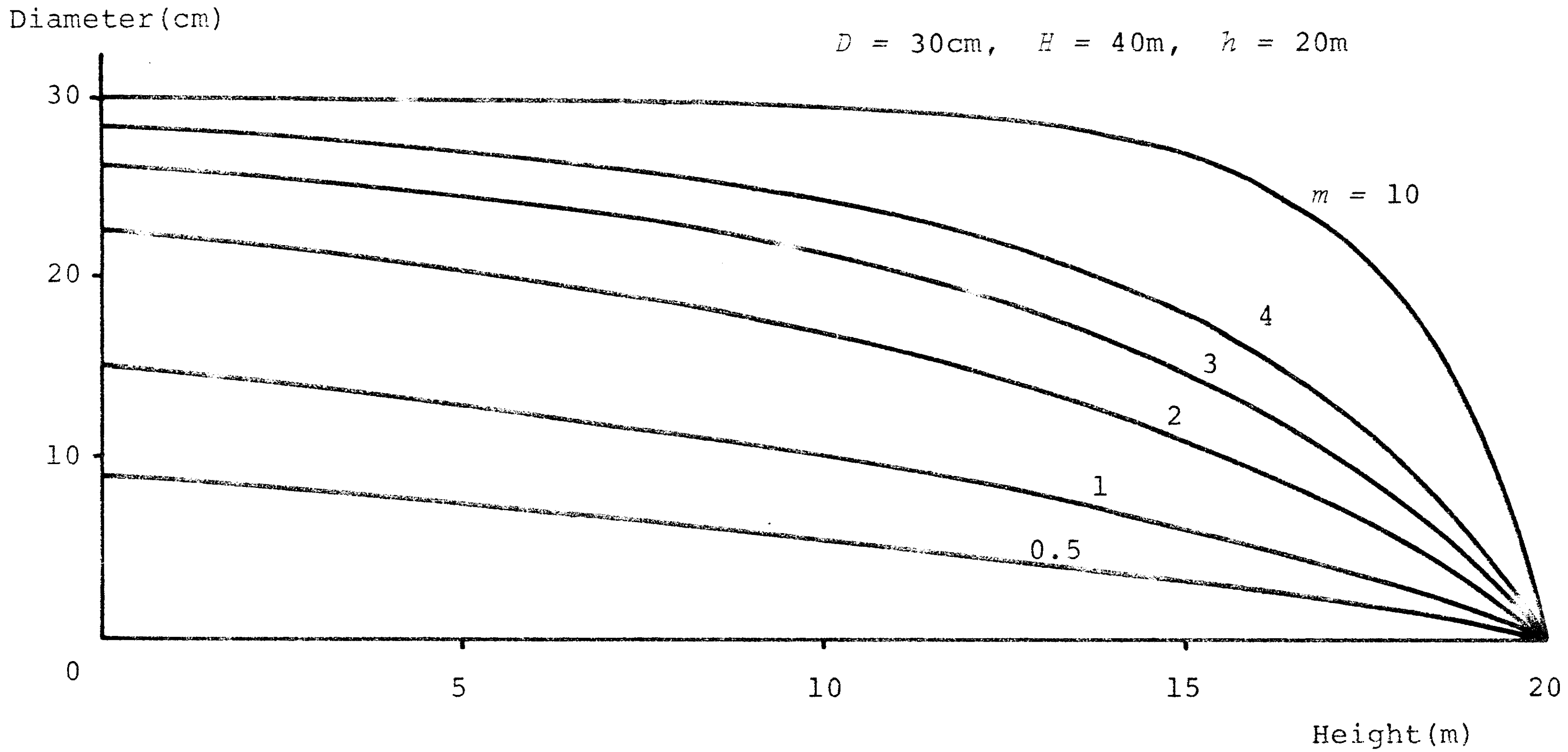


Figure 16. Proposed stem taper curves for various values of form exponent m while other parameters fexed.

the stem curve is always convex upward. As seen from Figs. 15 and 16 the proposed equation failed to express butt swell properly, which may be the most apparent imperfection of the model.

Figure 15 shows the effect of parameter H upon stem form. It will be readily seen that the decrease in H results in the increase in overall thickness as well as in the fullness of the stem. Figure 16 indicates a similar effect of parameter m. The difference is that it works inversely, i.e., it is an increase in m that corresponds to the increase in both fullness and overall thickness. It is obvious from Eqs. V - 6 and V - 8 that parameters h and D work in a less sophisticated manner. The former just represents overall height, while the latter is simply a multiplying factor, and its increase causes proportional stem thickening all along the stem.

These four parameters can be determined from observed data. Parameter h can be replaced directly by the observed actual height. The remaining three, D, H and m can be determined by the method of least-squares fitting as will be mentioned in more detail in the succeeding section.

Application

The proposed stem taper curve was fitted to the actual stem curves of 50 jack pine trees ranging from 29 to 139 years of age (annual ring counts at stump height, i.e., 20 cm above ground) to determine the numerical values of the parameters appearing in the proposed equation.

The data presented in this work had been collected from even-aged jack pine stands in Norther Canada by the joint survey team mentioned earlier. First, sample trees were chosen randomly in numerous even-aged jack pine stands of various ages, then felled for direct measurement of height and diameter. The height measurement was made directly on the stem with a tape to the nearest tenths of a meter. For each stem, diameter was measured with a tree caliper at nine successive points along the stem to the nearest tenths of a centimeter and denoted by symbols $d_{0.1}$, $d_{0.2}$, ... , $d_{0.9}$ from the tip downward to the base. The points of measurement were placed along the stem at equal intervals of one tenth of the total height. Thus as shown in Fig. 17 a total of ten measurements, one for height and the remaining nine for diameter, comprise a set for expressing the actual stem taper curve. A total of 50 such sets were used for the present analysis. It is worth mentioning that jack pine has a rather straight and upright stem in contrast to its rather crooked Japnese domestic counterparts, as akamatsu and kuromatsu (*P. densiflora* Sieb. *et* Zucc., *P. Thunbergii* Parl. respectively).

To determine the parameters the proposed theoretical stem taper curve V-8 was fitted to these 50 sets of stem measurements as follows. Of the four parameters of Eq. V-8, the total height h was replaced directly by the observations. the remaining three were determined by Deming's method of least-squares, in which errors were assumed only in diameter measurement and not in the height measurements. The results

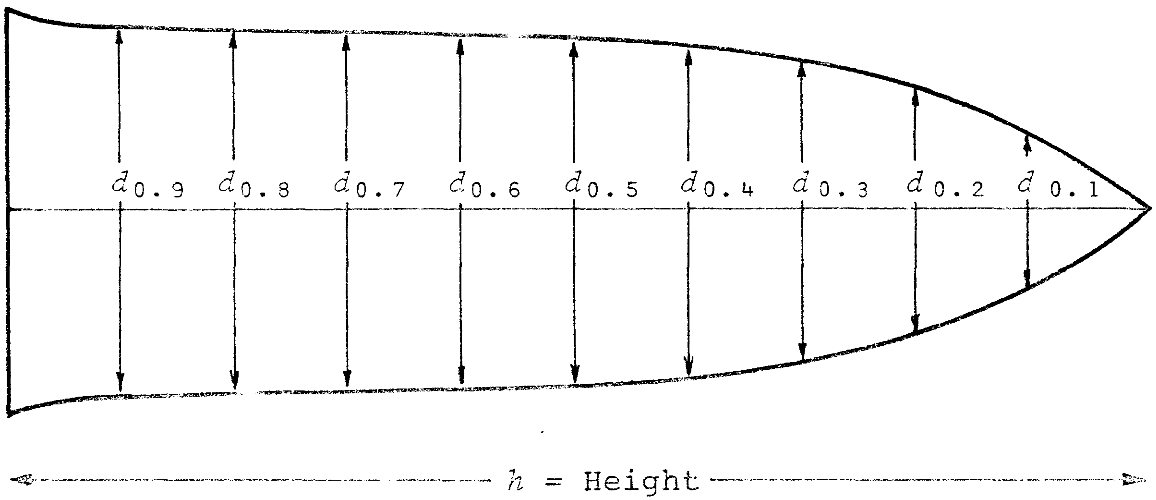


Figure 17. Stem diameters and height measured, and their abbreviations.

of the fitting are shown in Table 15, in which numerical values of parameters determined are given for each tree along with such characteristics as tree age, total height, and diameter at breast height (dbh).

According to the theory, the asymptotic diameters *D* and heights *H* are those that these jack pine trees are supposed to attain ultimately in the long run. As seen in Table 15 the calculated asymptotic heights seem of themselves to be reasonable and realistic figures as asymptote. Moreover, they are always greater than the corresponding present heights. Exactly the same is true for the diameter. These facts indicates that the asymptotes *D* and *H* are primarily functioning as expected from the theory.

However, a close examination of Table 15 reveals a minor discrepancy as in the following. According to our field observations, jack pine trees over about 130 years old are close to their senescence and do not seem to have much room left for both height and diameter growths. This expectation seems to be satisfactory for the diameter since the mean dbh for the individuals over 130 years old is 19.39 cm against the overall mean asymptote of 21.73 cm. On the other hand, the mean height of 17.83 m for the same individuals seems to be a little too short of the overall mean asymptote 26.72 m. Although there is a little possibility that this discrepancy between the calculated asymptotic height and the observed near-asymptotic height has resulted from some imperfection in the assumption which underlies the present

Table 15. Parameters of the proposed stem taper curve

Stem No.	Stem characteristics[1] Age[3] (years)	D.B.H. (cm)	Height (m)	Parameters[2] D (cm)	H (m)	$m=l/k$
1	90	15.0	14.8	19.58	23.56	1.46
2	88	14.5	15.8	56.91	17.82	0.14
3	104	14.7	16.9	60.69	19.49	0.14
4	105	14.8	14.7	25.47	19.33	0.62
5	108	15.7	16.3	24.74	22.86	0.82
6	104	18.3	18.0	24.39	35.64	1.80
7	104	12.4	14.0	13.48	45.62	6.48
8	105	12.6	13.1	24.95	29.72	1.28
9	56	7.2	9.7	13.16	26.16	1.98
10	57	9.3	10.9	15.02	19.23	1.35
11	73	9.9	12.0	21.49	16.76	0.52
12	125	18.1	15.5	28.51	28.79	1.31
13	92	13.6	13.0	17.80	29.89	2.62
14	92	17.2	14.7	20.58	30.65	2.40
15	32	3.4	6.3	4.84	12.06	1.98
16	36	10.4	12.3	41.67	16.45	0.22
17	37	12.4	12.8	19.10	32.16	2.25
18	33	7.0	11.0	24.14	14.10	0.24
19	38	11.9	13.0	15.23	30.50	2.78
20	89	10.6	12.7	12.03	39.29	5.46
21	86	7.8	14.3	15.67	29.13	1.04
22	88	17.5	16.8	19.74	38.05	3.40
23	88	17.8	16.8	25.41	23.78	0.93
24	90	17.0	16.2	22.46	31.83	1.96
25	89	17.4	18.5	28.60	26.25	0.80
26	84	13.8	13.1	18.61	47.60	4.42
27	82	11.2	11.6	20.46	42.30	2.92
28	86	16.1	15.8	22.67	31.42	1.78
29	107	13.0	14.2	21.79	18.75	0.64
30	31	5.8	8.3	8.50	21.48	2.75
31	29	3.1	5.8	6.30	8.99	0.72
32	130	12.1	12.1	17.93	19.57	1.24
33	104	16.0	17.2	19.23	24.49	1.26
34	102	14.0	14.9	17.26	64.06	5.43
35	133	20.1	18.2	29.62	26.74	0.91
36	47	5.5	7.5	8.83	15.71	1.65
37	51	8.9	11.0	13.84	27.23	2.22
38	51	10.6	11.5	15.52	19.90	1.37
39	46	5.7	7.8	8.74	12.21	1.11
40	56	6.8	8.3	10.23	15.18	1.60
41	52	8.2	9.4	9.60	29.63	5.63
42	107	20.4	19.7	32.57	35.28	1.23
43	104	19.5	15.4	26.69	32.80	2.00
44	126	22.3	17.2	40.95	25.70	0.69
45	134	21.2	18.3	37.97	24.56	0.62
46	139	16.8	17.0	34.06	26.80	0.69
47	104	21.0	20.0	31.52	58.62	2.72
48	36	4.6	5.3	9.79	7.97	0.74
49	33	5.0	6.2	8.22	14.06	1.96
50	108	12.0	14.4	19.80	25.70	1.20
Mean	81.8	12.80	13.41	21.73	26.72	1.83
S.D.[4]	32.1	5.11	3.79	11.59	11.44	1.47

1) Observed.
2) Calculated, D, H and $m=l/k$ are as in equations V - 6 and V - 8 in the text.
3) Annual ring count at stump height, i.e. 20 cm above ground.
4) Standard deviation.

stem taper curve, it most probably is simply a consequence of random fluctuation which sometimes results in what is seemingly a rather extreme value, especially in such a small sample as the present one.

Another problem with the present model may be that the asymptotic height and diameter are rather variable even among the individual trees of a species growing under rather similar conditions. To indicate the magnitude of the variation, the asymptotic diameter D and height H were plotted against age in Figs. 18 and 19 respectively for all the stems examined. The following two features are obvious from these figures. One is that both of the asymptotes have a large variance, which is also numerically clear from Table 15. The other is that both the asymptotic height and diameter reveal a tendency to increase with age. Interestingly enough these two features, especially the former, of the proposed stem taper curve are also shared by the Mitscherlich equation itself as applied to radial growth directly. According to the direct application of the Mitscherlich equation in the preceding chapters, the asymptotic radius M showed a coefficient of variation of as much as nearly 370 percent for white spruce (Table 3), and about 36 percent for jack pine (Table 10). In view of these figures, it will be readily noticed that the rather drastic variation in the asymptotic diameter of the proposed stem taper curve is a direct inheritance from the Mitscherlich equation. Although the direct application of the Mitscherlich equation to the height growth of

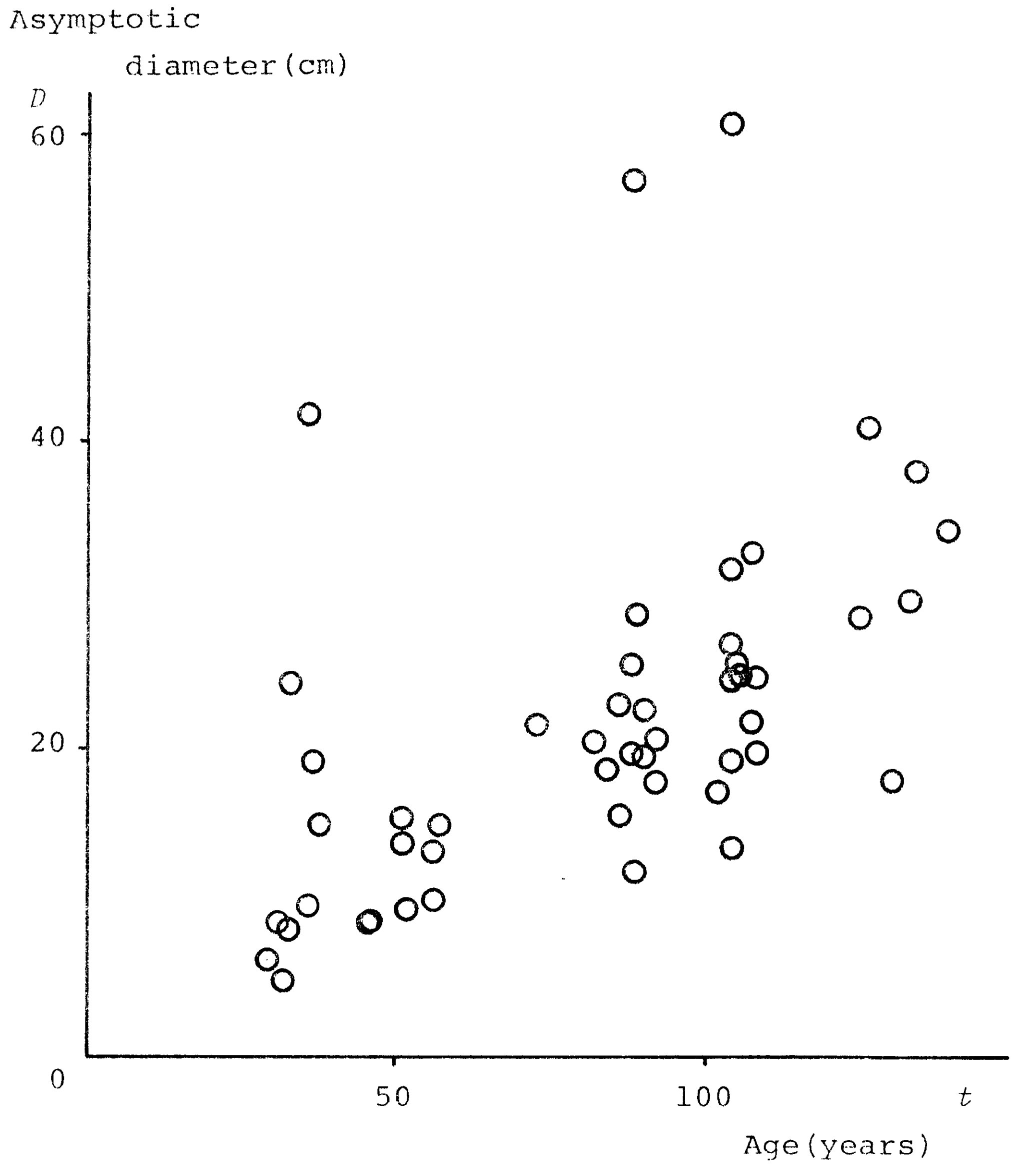


Figure 18. Variation of the estimated asymptotic Diameter D.

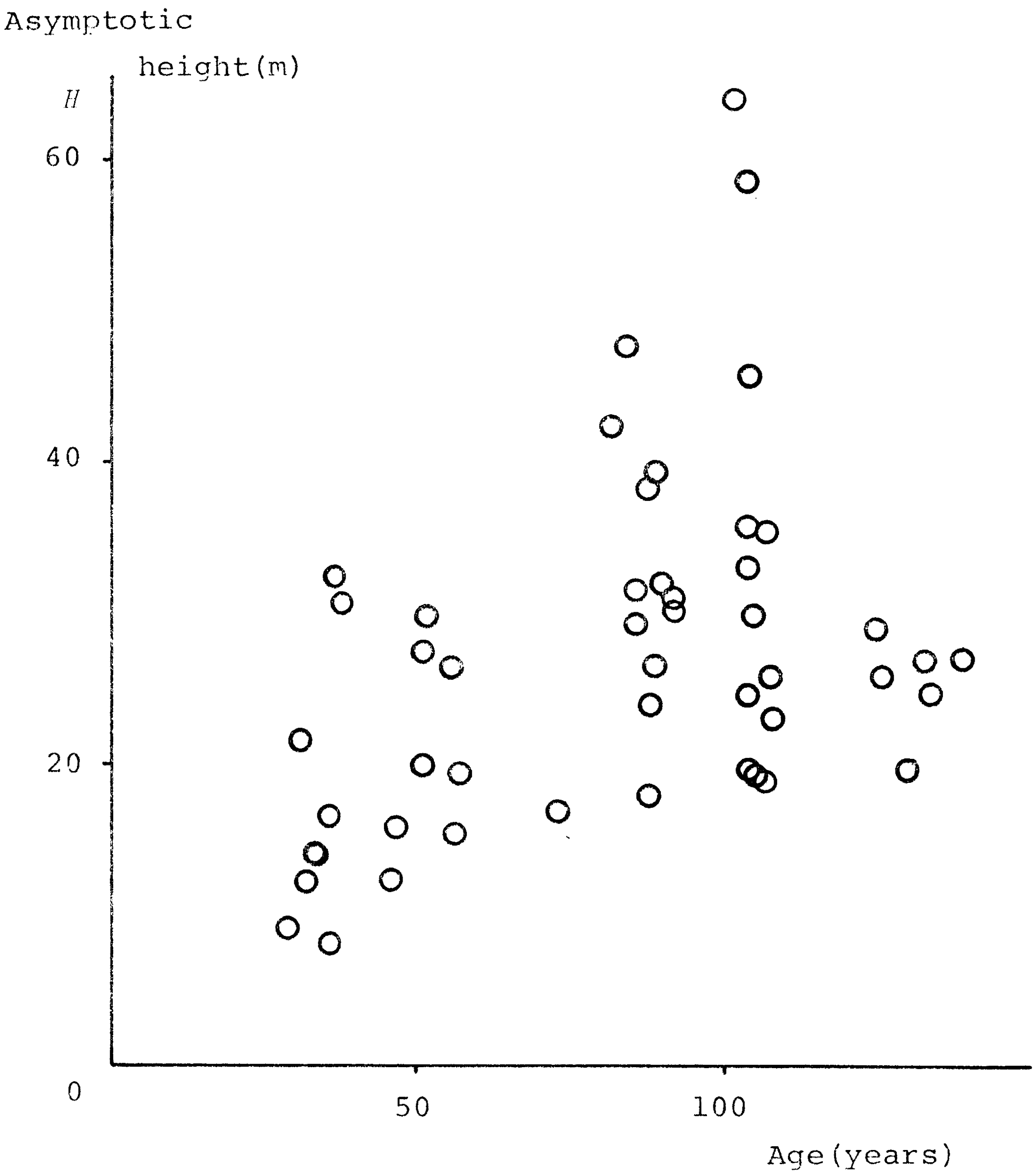


Figure 19. Variation of the estimated asymptotic height H.

trees are scarce, and thus we are short of hard evidence, it is almost certain that the same agrument may well hold for the asymptotic height H of the stem taper curve.

It was also shown in the preceding chapters that in spite of the drastic variation of the asymptotic parameter, the Mitscherlich curve exhibits remarkable fit to observations due to the counteraction of the rate parameter which works in a compensating manner. This compensation mechanism is also seen in Table 15, in which large values of asymptotic diameter D are almost always associated with small m's, i.e., small l's. The same compensation is observed between the asymptotic height H and its corresponding intrinsic rate of growth k. It is very much likely that this compensation mechanism is also an inheritance from the Mitscherlich equation which constitutes the important basis of this stem taper curve.

In the light of the large variance in the parameters, our sample of size 50 would not have been enough to get exact estimates of the parameters precisely matching the theory. However, with the present state of knowledge it is difficult to determine whether the deviation of the estimated parameters is simply a result of random fluctuation or it results from more serious cause related in some way or another to the basic assumption of the present theory. Further case studies with large samples as well as with different tree species than jack pine are necessary. Even more important would be the investigation to check the validity of the present assumption by some other means than the one employed in the present work.

Considering the large variations of the estimated parameters, and slight deviations of their means from what is expected from the theory, the following statements can be made for sure. The estimates of the parameters obtained by fitting the proposed stem taper curve are rather tentative as are the parameters of the Mitscherlich equation. No single example nor small sample is enough to draw any biologically relevant conclusions of the numerically estimated parameters of the proposed stem tatper curve.

Comparison with other stem taper curves

A theory or reasoning is one of the most important factors for adopting a mathematical expression to let it stand for an observed phenomenon, because it not only gives a concise description of a complex outcome but it also helps us to get into the mechanism which brings forth the apparently complex outcome. Another important factor, but over emphasized much too often, is the goodness of fit to the observations. However, a mathematical expression with a nice theory but with poor agreement with reality is simply a dead letter. Thus the proposed stem taper curve V - 8 was compared with representative existing stem taper curves in terms of goodness of fit to observed data.

The same data as employed in the preceding section was used for this analysis, i.e., observed stem taper curves of 50 jack pine trees, each consisting of one height and nine diameter measurements.

Two representative classes of stem taper curves which are now in practical use were chosen for the comparison, the power series and Kunze's formula mentioned in the review of literature. However, they were changed so that the base of the stem corresponded with the ordinate and the tip came to the far end of the abscissa as is the proposed stem taper curve V - 6 or V - 8.

The first class consists of eight partial sums, from the first up to the eighth, of a power series, i.e.,

$$y=a(h-x),$$

$$y=a(h-x)+b(h-x)^2, \qquad \text{V - 9}$$

$$\cdots$$

$$y=a(h-x)+b(h-x)^2+c(h-x)^3+\ldots+g(h-x)^8,$$

where

y: stem diameter at height x,

h: total stem height as in Eq. V - 6 or V - 8,

$a,b,\ldots,g$: parameters.

Of these eight equations generated from the same power series, the third and fourth partial sums are the most popular in practice.

The second class is Kunze's formula changed as follows:

$$y=\alpha(h-x)^r, \qquad \text{V - 10}$$

where

y: stem diameter at height x,

h: total stem height as in the preceding case,

α, r: parameters.

As is widely acknowledged, this equation yields various stem curves as form exponent r varies. The revolution about the x axis generates a cylinder, paraboloid, cone, and neiloid for r=0, 1/2, 2/2 and 3/2 respectively. Usually the equation is applied to only a portion rather than to the entire stem with the form exponent r fixed at the most suitable of the numerical values given above. In this analysis, however, Eq. V - 10 was applied to the entire stem with the form exponent r left free as a parameter to be determined by the least-squares fitting.

It should be noted that notwithstanding their extensive usage in practice and research, these two classes of equations are just empirical or experimental ones and are not accompanied by any theoretical derivation or reasoning relevant and pertinent to the subject.

A total of nine of these empirical equations were fitted to the observations exactly in the same manner as had been done with the proposed theoretical equation. More particular to the point, the total height h in Eqs. V - 9 and V - 10 was replaced by the observed values, then the rest of the parameters, i.e., $a, b, \ldots, g$ in Eq. V - 9 and α, r in Eq. V - 10 were determined by Deming's method of least-squares. As in the preceding section errors assumed only in diameter.

Once the numerical values of the parameters had been determined, stem curves were calculated according to each of the ten equations for each stem. Examples of actual and calculated stem curves are shown in Table 16 and Fig. 20.

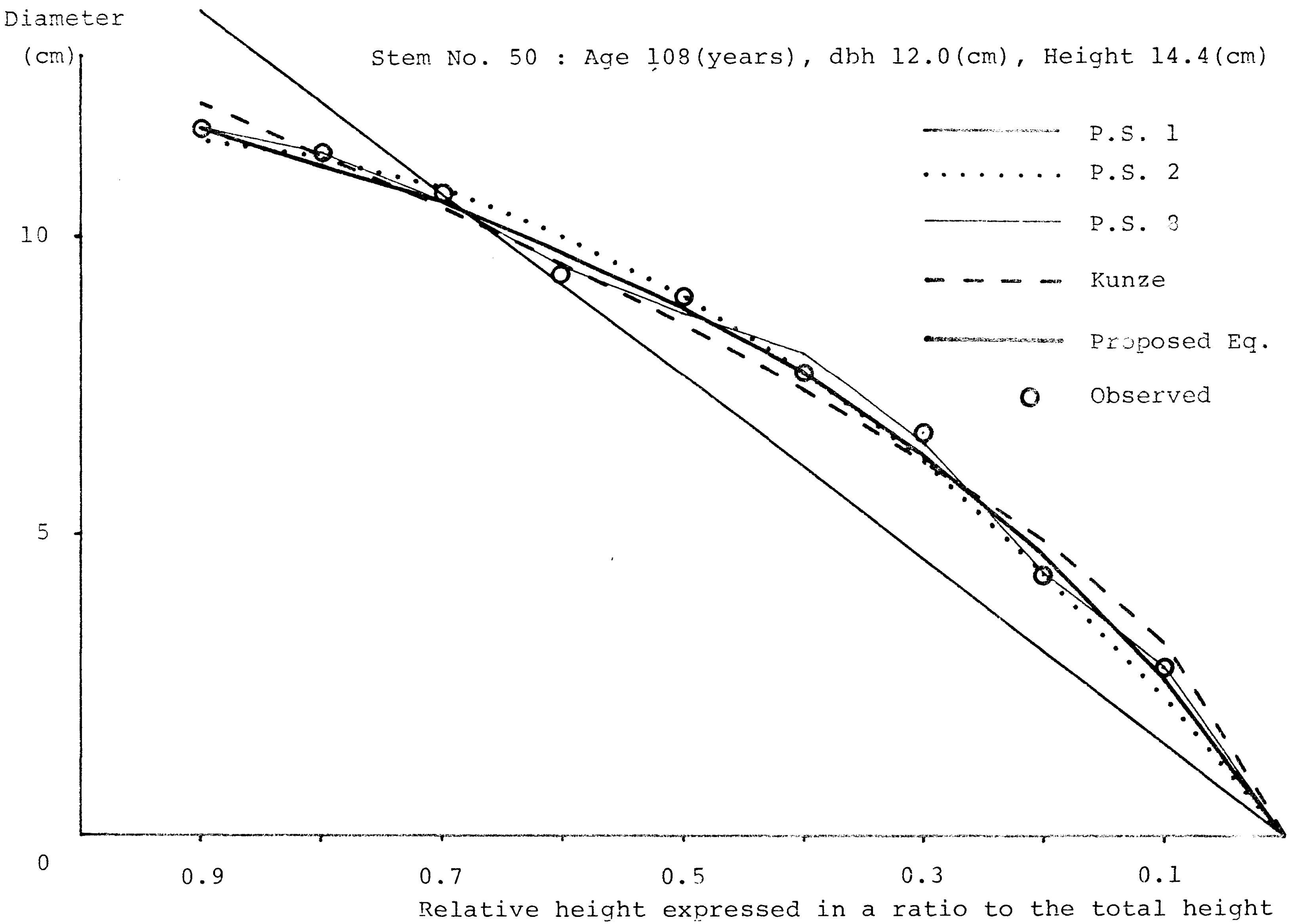


Figure 20. Observed and calculated stem taper curves.

Table 16. Observed and calculated stem taper curves (Stem No. 50)

Age 108 (years), D.B.H. 12.0 cm, Height 14.4 m

Equations	Stem Diameter (cm)								
	$D_{0.1}$	$D_{0.2}$	$D_{0.3}$	$D_{0.4}$	$D_{0.5}$	$D_{0.6}$	$D_{0.7}$	$D_{0.8}$	$D_{0.9}$
(Observed)	2.8	4.3	6.7	7.7	9.0	9.3	10.7	11.4	11.8
P.S. 1 2)	1.53	3.06	4.58	6.11	7.64	9.17	10.69	12.22	13.75
P.S. 2	2.31	4.36	6.16	7.70	8.98	10.01	10.79	11.31	11.57
P.S. 3	2.58	4.68	6.38	7.75	8.85	9.75	10.52	11.21	11.91
P.S. 4	2.64	4.72	6.37	7.71	8.81	9.75	10.56	11.27	11.87
P.S. 5	2.52	4.73	6.47	7.75	8.76	9.65	10.55	11.39	11.82
P.S. 6	2.66	4.60	6.39	7.86	8.86	9.57	10.42	11.53	11.78
P.S. 7	2.78	4.39	6.49	7.99	8.72	9.47	10.63	11.42	11.80
P.S. 8	2.78	4.38	6.51	7.99	8.71	9.49	10.62	11.42	11.80
Kunze	3.18	4.87	6.24	7.44	8.53	9.54	10.48	11.38	12.23
Proposed Eq.	2.65	4.71	6.36	7.70	8.82	9.76	10.57	11.26	11.86

Legend
1) Abbreviated as in Fig. 17
2) Row headings "P.S. n" stand for the n^{th} partial sum of the power series, Eq. V - 9

Goodness of fit for each equation was evaluated by the mean deviation of the form

$$s=\frac{\sqrt{\sum_{t=1}^{n} (X_i-x_i)^2}}{n-f}, \qquad \text{V - 11}$$

where X_i: observed diameter at the i^{th} section, i=1, 2, ..., 9,

x_i: calculated diameter at the i^{th} section,

n: 9, i.e., number of sections,

f: degree of freedom of the equations concerned, i.e., number of parameters involved.

It is a methematical rule of thumb that apparent goodness of fit improves as the number of parameters involved in an equation increases, and the calculated curve exactly coincides with the observations when the number of parameters matches the number of observations. The subtraction term f in the denominator of Eq. V - 11 counterbalances this bias and provides a fair basis for a comparison of the mathematical expressions with different numbers of parameters. For every equation used the goodness of fit was calculated for each of the 50 stems. Then such statistics as the mean, variance, standard deviation, and range of the goodness of fit were calculated for each equation and given in Table 17.

Judging from the mean in Table 17 the proposed equation reveals the third best fit to the observations, exceeded only by the third and fourth parital sums of the power series, and followed by the fifth partial sum, then the sixth. The lower and the higher power series, as well as Kunze's formula, show obviously

Table 17. Statistics on goodness of fit

	P.S. 1[1]	P.S. 2	P.S. 3	P.S. 4	P.S. 5	P.S. 6	P.S. 7	P.S. 8	Kunze	Proposed Eq.
Mean	0.595	0.193	0.123	0.135	0.146	0.160	0.180	0.219	0.188	0.136
Standard deviation	0.067	0.010	0.004	0.006	0.006	0.008	0.018	0.046	0.007	0.005
Variance	0.259	0.099	0.064	0.074	0.078	0.091	0.132	0.214	0.085	0.072

Legend 1) Abbreviated as in Table 16.

poorer degrees of fit. The variance, or standard deviation, serves as the measure of consistency of the fit, i.e., the smaller variance indicates a consistently similar degree of fit to different stems, while greater variance is more fickle. Again in this measure the proposed equation, along with the third and fourth partial sums, reveals superiority over the others. But the order is reversed with the proposed equation scoring better than the fourth parital sum.

To determine the exact and statistically significant order in goodness of fit among the competing equations, a paired bilateral t-test of significance was conducted and is shown in Table 18. In this table the section below the diagonal gives the calculated t-values, while the section above gives the evaluation. Rearrangement of Table 18 results in the overall ranking in goodness of fit as given in Table 19. The proposed stem taper curve shows a remarkably good fit to the observations, exceeded only by the third partial sum of the power series.

Conclusion

The most remarkable characteristics of the proposed stem taper curve V - 6 is that it has a theoretical background. As a result, each of the five parameters appearing in Eq. V - 6 carries a pertinent biological meaning associated with tree growth which no doubt is the most significant agent to shape up trees in the forms we actually see. It was revealed by the analysis in the section on application that these parameters, especially the asymptotes take

Table 18. The *t*-test of significance on the goodness of fit among the ten stem taper curves

	P.S. 1	P.S. 2	P.S. 3	P.S. 4	P.S. 5	P.S. 6	P.S. 7	P.S. 8	Kunze	Proposed Eq.
P.S. 1 [1]		**	**	**	**	**	**	**	**	** [2]
P.S. 2	16.91		**	**	**	**	n.s.	n.s.	n.s.	**
P.S. 3	15.11	7.73		**	**	**	**	**	**	**
P.S. 4	15.09	6.48	-4.25		**	**	**	**	**	n.s.
P.S. 5	15.15	5.49	-4.77	-2.76		*	*	*	**	n.s.
P.S. 6	15.06	3.27	-4.68	-3.53	-2.24		*	*	**	**
P.S. 7	14.02	0.83	-3.74	-3.12	-2.48	-2.03		n.s.	n.s.	**
P.S. 8	10.07	-0.94	-3.48	-3.06	-2.67	-2.28	-1.64		n.s.	**
	15.32	0.94	-10.72	-8.20	-5.76	-3.06	-0.48	1.16		**
Proposed Eq.	15.45	7.67	-4.90	-0.35	1.87	2.87	2.88	3.06	12.01	

Legend 1) Abbreviated as in Table 16.

2) ** ; highly significant, i.e. significant at the 1% level

* ; significant, i.e. significant at the 5% level

n.s. ; non-significant.

Table 19. Overall rating on goodness of fit

		P.S. 4				P.S. 7		
						Kunze		
P.S. 3	>	Proposed Eq.	>	P.S. 6	>	P.S. 2	>	P.S. 1
		P.S. 5				P.S. 8		

Legend 1) Equation identities abbreviated as in Table 16.
2) >; significant difference detected in favour of the equation on the open side of the inequality.

on reasonable numerical values as expected from the theory. However, since the variations of the estimated parameters are relatively large, it is dangerous to make any biological inference of the numerical values obtained from small samples. The comparison with existing empirical stem taper curves showed a significantly better degrees of fit to the actual observations than most of the others.

In spite of these virtues the proposed equation has three drawbacks at its present stage of development. One of them is that it does not account for the butt swell of the stem. This could be overcome by introducing other theoretical growth functions than the one used here.

The second one is that the asymptotic height turned out to be somewhat different from the expected value. This may just be a result of random variation, or it may be due to more serious reason related to the assumption of the theory. To make a clear-cut conclusion on this subject, further investigation has to be conducted at the following two fronts. One of them is concerned with the statistical credibility of the numerical results obtained in the present analysis. This could be improved by further accumulation of case studies with larger samples as well as with different species than jack pine. The other front consists of splitting the assumption underlying the present theory into two to check the validity of each independently. The part of the assumption concerning the Mitscherlich growths of stem height and diameter can be checked through the direct application of the equation to actual growth processes. The other part of the assumption that the asymptote D and the intrinsicsic rate of growth l for the diameter do not vary with height can be checked by stem analysis and subsequent application of the Mitscherlich equation to the diameter growth at various height of the stem. However, considering the large variation in Mitscherlich's coefficients, considerably large and uniform sample is inevitable for a statistically significant conclusion.

The last one is the difficulty associated with fitting. Since the proposed equation is not linear with respect to the parameters to be determined, the ordinary method of least-squares is not applicable. Thus Deming's method had to be employed, but it is more complex than the ordinary method. Differing from the ordinary method, Deming's method requires initial estimates for the parameters to be determined. This is also rather difficult with the proposed stem taper curve. Further research is necessary to overcome these difficulties and make the proposed stem taper curve applicable to practical forest inventory work.

CHAPTER VI

A THEORETICAL HEIGHT-DIAMETER CURVE

Introduction

This chapter is devoted to another application of the theoretical growth equation to what is seemingly unrelated to but is actually deep-rooted in the growth of trees, i.e. the height-diameter curve. The relationship between tree height and diameter has been one of the important topics of mensuration largely due to its practical usefulness. Once this relationship is established for a forest stand the time-consuming and still inaccurate height measurement in the field can be replaced by an easy estimation from diameter which is relatively easy and fast to determine.

Somewhat subjective but the simplest and most commonly applied method of estimating tree height from diameter is the free-hand fitting of a height-diameter curve to a set of observations. A more objective method is the least-square fitting of mathematical equations which relate stem diameter to height in some way or another, and for this purpose numerous mathematical expressions have been presented to date. Most of them give height as one of the following functions of diameter, i.e. either parabolic or logarithmic or exponential. For example

$H=a+bD+cD^2$, (Trorey, 1932)

$H=a+b(1-e^{-cD})$, (Meyer, 1940)

$H=a+b\log D$, (Myers, 1966)

where H: height,

D: diameter,

a,b,c: constants.

In addition to those there are literally countless modifications or applications (Nishizawa, 1972) so that now it seems almost impossible to decide which one to choose for a specific mensurational purpose. As a matter of fact all those height-diameter curves are convex upward and show a reasonable degree of fit to observations. No wonder why, since the goodness of fit has long been the only criterion for adopting new mathematical expressions popping up everywhere.

Now it seems to be the time for us to emphasize another important but often unduly ignored criterion, i.e. theoretical reasoning or logical derivation which lead us to certain mathematical expressions. As a matter of fact all the above-mentioned height-diameter curves are simply empirical or experimental equations with no theoretical reasoning behind them. The only height-diameter curves that carry any theoretical reasoning may be Ogawa's (1965) and its sophistication by Ogino et al. (1967). Based on the assumption that height and diameter satisfy the following modified allometric relationship;

$$\frac{1}{H}\frac{dH}{dt} = h\frac{1}{D}\frac{dD}{dt}\left(\frac{H_{max}-H}{H_{max}}\right)$$

where H: height,

D: diameter,

H_{max}: maximum height corresponding to D=infinity,

t: time, and

h: allometric coefficient,

Ogawa derived a height-diameter curve of the form;

$$\frac{1}{H} = \frac{1}{AD^h} + \frac{1}{H_{max}}$$

where
$$\frac{1}{A} = \frac{\left(H_{max} - H_0\right) D_0^h}{H_{max} H_0}$$

H_0; minimun height corresponding to the minimun diameter D_0.

Ogino's modification consists of incorpo ating another asymptotic factor;

$$\frac{D_{max} - D}{D_{max}} \quad ,$$

where D_{max}: maximum diameter,

in Ogawa's differential equation given above. This results in a differential equation of the form;

$$\frac{1}{H}\frac{dH}{dt} = h \frac{1}{D}\frac{dD}{dt} \frac{\left(\frac{H_{max} - H}{H_{max}}\right)}{\left(\frac{D_{max} - D}{D_{max}}\right)}$$

which upon integration produces a curve of the form;

$$\frac{1}{H} = \frac{1}{A'} \left(\frac{D_{max} - D}{D_{max}}\right)^h + \frac{1}{H_{max}}$$

where

$$\frac{1}{A'} = \frac{H_{max}-H_0}{H_{max}H_0}\left(\frac{D_0}{D_{max}-D_0}\right)^h$$

As is often the case with any theoretical work entirely different line of reasoning may well be possible. The height-diameter relationship and its theoretical reasoning given in the following sections is one of them. Beseides the underlying assumption and mathematical derivation, a discussion is also made on the applicability of the proposed equations as well as on the mensurational significance of the coefficients appearing in the equations.

Height-diameter relationship for all-aged stand

As has been shown in the preceding chapter, the growth of individual trees both in height and diameter is most properly expressed by the Mitscherlich equation, i.e.,

height $y=H(1-e^{-kt})$, VI-1

diameter $x=D(1-e^{-ht})$, VI-2

where t: time,

y: height at time t,

x: diameter at time t,

H: upper asymptote for height,

D: upper asymptote for diameter,

k: intrinsic rate of height growth,

h: intrinsic rate of diameter growth,

e: base of natural logarithm.

This fact means that both the height and diameter growths are governed by the following differential equations;

$$\text{height} \qquad \frac{dy}{dt} = k(H-y), \qquad \text{VI - 3}$$

$$\text{diameter} \qquad \frac{dx}{dt} = h(D-x). \qquad \text{VI - 4}$$

In other words Eqs. VI - 1 and VI - 2 are the solutions of Eqs. VI - 3 and VI - 4 respectively.

It is now possible to derive a height-diameter relationship from these equations. Dividing Eq. VI - 3 by VI - 4 to eliminate the time parameter, we get

$$\frac{dy}{dx} = \frac{k(H-y)}{h(D-x)} \qquad \text{VI - 5}$$

For the boundary condidion we assume that

$$y=y_0 \qquad \text{at} \qquad x=x_0, \qquad \text{VI - 6}$$

which in terms of tree growth means that the initial height and diameter are equal to y_0 and x_0 respectively at the very beginning of individual tree growth. Separation of variables and subsequent integration with Eq. VI - 5 result in

$$\frac{1}{k} \int_{y_0}^{y} \frac{1}{H-y}\, dy = \frac{1}{h} \int_{x_0}^{x} \frac{1}{D-x}\, dx$$

the solution of which is given by

$$y = H\left[1 - \frac{H-y_0}{H} \left(\frac{D-x}{D-x_0}\right)^{k/h}\right] \qquad \text{VI - 8}$$

This is the general soluiton for Eq. VI - 5; general, since no specific mention has been made as to how or at which portion of the stem the height and diameter are to be measured.

If it is the total height and the stem diameter at ground level that is under consideration, then

$$y_0 = 0 \quad \text{and} \quad x_0 = 0 \qquad \text{VI - 8}$$

in solution VI - 7. Thus

$$y = H\left[1 - \left(\frac{D-x}{D}\right)^{k/h}\right] \qquad \text{VI - 9}$$

where y: total height,

x: diameter at ground,

results. This is the relationship between the total height and diameter at ground.

In the ordinary practice of forestry, however, it is the relationship between total height and diameter at breast height (dbh) that is most commonly employed and therefore sought after. To obtain this relationship we put

$$y_0 = H_b \quad \text{and} \quad x_0 = 0 \qquad \text{VI - 10}$$

where H_b: breast height,

i.e., the growth in dbh is initiated just when the tree reaches breast height. Substituting VI - 10 in VI - 7 we get

$$y = H\left[1 - L\left(\frac{D-x}{D}\right)^{k/h}\right] \qquad \text{VI - 11}$$

where $L = \frac{H - H_b}{H}$,

y: total height,

x: dbh.

It is worth mentioning that the same result can be obtained directly from Eqs. VI - 1 and VI - 2 throught arithmetical manipulations. Or more precisely by solving VI - 2 for time parameter t and substituting in VI - 1, the height-diameter curves VI - 7, VI - 9, or VI - 11 result with an appropriate choice of boundary conditions.

According to the reasoning given so far, Eqs. VI - 7, VI - 9 and VI - 11 represent the relationship between the height and diameter of an individual tree. However, the following assumption or approximation makes these equations also applicable to all-aged stands as their height-diameter curves. Assume an all-aged stand in a steady state, where trees of every developmental stage, or generation exist and every generation is in a process of being replaced by the directly succeeding one, i.e. schematically

seed supply and germinaiton ... die off

. . . → seedling → young → mature → senescent . . . →

For this kind of stand, we can assume such a mean height growth curve of form VI - 3 and a mean diameter growth curve of form VI - 4 that represent the growth of trees in every generation on an average basis. It is the process already experienced by the dying trees as well as the course yet to be followed by the seedlings coexisting in the stand. Then as a logical consequence, equation VI - 7, VI - 9 and VI - 11 represent the height-daimeter relationship of all-aged stands.

Height-diameter relationship for even-aged stands

Tree growth as a function of time is meant by the Mitscherlich equations VI - 1 and VI - 2. However, the Mitscherlich equation was originally proposed to express plants' response to fertilization, which usually referred to as the law of diminishing return (Mitscherlich, 1919)

An application of this original reasoning for the Mitscherlich equation leads us to individual trees' response in height and diameter growths to their environmental conditions.

The Mitscherlich equation originally proposed was of the form:

$$y = A(1-e^{-c_1x_1})(1-e^{-c_2x_2})(1-e^{-c_3x_3})\ldots,$$

where y: yield,

$x_1, x_2, \ldots$: amount of factors affecting plant growth,

$c_1, c_2, \ldots$: intrinsic response coefficients for individual growth factors,

A: maximum yield attainable when every growth factor is available in good surplus, and

e: base of natural logarithm.

In this equation the effect of each growth factor is considered separately and then multiplicatively. However, for the height and diameter growths we consider a single site factor which represents the combined effect of all the conceivable growth factors such as nutrients, moisture, sunlight etc. Then we get another set of the Mitscherlich equations which in appearance are exactly the same as Eqs. VI - 1 and VI - 2 but are different in meaning, i.e.

height $\qquad y = H'(1-e^{-k'f})$, $\qquad$ VI - 12

diameter $\qquad x = D'(1-e^{-h'f})$, $\qquad$ VI - 13

where y: height,

x: diameter,

H', D': maximum height and diameter attained during a given time interval by an individual tree when it is grown under the most favourable conditions,

k', h': intrinsic response coefficients for height and diameter,

f: site index, i.e. a combined effect of numerous growth factors, accumulated for a fixed time interval.

It should be noted that here the growth is considered in alimental domain, while it was in time domain in Eqs. VI - 1 and VI - 2. Parks (1973) argued that growth of animal must be considered in food-consumption domain rather than in time domain since the former is more closely related to the growth than the latter. The same argument may well apply to plant growth. It sounds reasonable that the plant growth corresponds more closely with the amount of nutrients taken up and the amount of material photosynthesized during a given time period than with the length of the time period itself. It suffices to mention an often-quoted observation that spruce seedlings suffering under canopy for decades show a rapid and vigorous growth once they are exposed to full sunlight as canopy species fall out.

For the derivation of the height-diamter relationship, the same logic as to the preceding case applies. Thus rewriting Eqs. VI - 12 and VI - 13 in differential form

$$\frac{dy}{df} = k'(H'-y), \qquad \text{VI - 14}$$

$$\frac{dx}{df} = h'(D'-x), \qquad \text{VI - 15}$$

and by dividing VI - 14 by VI - 15 we get

$$\frac{dy}{dx} = \frac{k'(H'-y)}{h'(D'-x)}$$

the general solution of which is given by

$$y = H'\left[1 - \frac{H'-y_0}{H'}\left(\frac{D'-x}{D'-x_0}\right)^{k'/h'}\right] \qquad \text{VI - 17}$$

where y_0 is the initial height corresponding to the initial diameter x_0. From this equation, the relationship between the total height and diameter at ground is given by

$$y = H'\left[1 - \left(\frac{D'-x}{D'}\right)^{k'/h'}\right] \qquad \text{VI - 18}$$

where y: total height,

x: diameter at ground.

The relationship between the total height and dbh is given by

$$y = H'\left[1 - L'\left(\frac{D'-x}{D'}\right)^{k'/h'}\right], \qquad \text{VI - 19}$$

where $L' = \frac{H'-H_b}{H'}$,

H_b: breast height,

y : total height,

x : dbh.

Obviously, Eqs. VI - 17, VI - 18 and VI - 19 represent the height-diameter relationship of an individual tree. However, the similar logic as in the preceding section makes these equations applicable as the height-diameter curves for even-aged stands as follows. Assume that the growth up to a certain definite age of an even-aged stand in which the growth of every constituent tree is governed by Eq. VI - 12 in height and by VI - 13 in diameter. Here, apart form the original meaning, these equations signify the mean growth responses in height and diameter respectively for the stand in question. It is unlikely that all the trees are governed by exactly the same equations, but this assumption may hold nearly true on an average basis.

Though all the trees grow under nearly similar conditions, some enjoy more favourable conditions than the others depending on the difference in individual site factor and the competition with the surrounding trees. This difference results in the difference in f values of Eqs. VI - 12 and VI - 13 received by individual trees. For a given f value, there exist a definite and unique height determined by VI - 12 and a definite and unique diameter determined by VI - 13, which are interrelated with each other by Eqs. VI - 17, VI - 18 or VI - 19. This relationship holds true for any tree in the stand regardless of the growing conditions it has been subjected to and thus regardless of f values it has experienced. Thus Eqs. VI - 17, VI - 18 and VI - 19 represent the height-diameter relationship for even-aged stands.

In terms of the stand growth, the parameters H' and D' represent the maximum height and diameter to be attained in a specific time period by a few dominant individuals which have been exposed to the most favourable conditions. The other individuals suffered under less favourable conditions for the same period of time take on the values smaller than those, depending on the severity of individual conditions.

Discussion

As has been noticed already the proposed height-diameter curves VI - 7, VI - 9, VI - 11 for all-aged stands and VI - 17, VI - 18, VI - 19 for even-aged stands do not differ in appearance at all but they do in what they mean. In the former set of equations, the variation in height and diameter are supposed to be attributable to the variation in age among the individual trees which constitute an all-aged stand. Thus the asymptotic height H and diameter D are supposed to be reached by the oldest individuals in the stand, while younger individuals are of the height somewhere between zero and the asymptote H with the diameter between zero and the asymptote D depending upon their respective ages.

Although in reality difference both in height and diameter may well exist even among the individuals of the same age class as well, it is assumed negligible when compared with the difference among the age classes.

In the latter set of equations, however, the variation in height and diameter are supposed to be attributable to the difference in productivity of site on which each tree grows. Since the asymptotic height H' and diamter D' are the maxima attained by the best growing individuals of an even-aged stand by the time the stand reaches a certain age, they increase with the stand age. In other words they are functions of time yet unknown. On the contrary the asymptotes H and D for all-aged stands are independent of time.

The above argument concerning the applicability of the proposed equations and the corresponding difference in the significance of the coefficients holds both for Ogawa's and Ogino's height-diameter curves. Since both of the equations were derived by eliminating time parameter, they are good only for all-aged stands. Accordingly Ogawa (1965) applied his equation to several types of forests, all of which were at their climax stages of succession and thus were all-aged presumably.

Though Ogawa's and Ogino's original equations are thus limited to all-aged stands they can be easily modified so that they would also apply to even-aged stands as in the present work, i.e. just rewriting the original equations in terms of site factor f instead of time t. It should be noted then the meaning of the coefficients undergoes respective change.

A graphical representation of total-height vs. diameter-at-ground VI - 18 for even-aged stands is shown in Fig. 21 for a hypothetical case of H'=20 m, D'=40 cm and k'/h'=1.2, 2,0, 3.0. Also an example of total height vs. dbh VI - 19 for even-aged stands is shown in Fig. 22 for another hypothetical case of H'=20 m, H_b'=1.2 m, D'=40 cm and k'/h'=1.2, 2.0, 3.0. It will be readily seen that the proposed height-diameter curves are convex upward in agreement with general observations as well as with the most of the empirical equations. It can be also noticed that the convexity increases as k'/h' ratio increases.

In forestry management and planning, tree height at a certain age, say 50 years, is often used as in index of site's productivity, i.e. site index. This common practice is based on a silvicultural rule of thumb that tree height responds more quickly and sensitively to site's productivity than does diameter. This in terms of the Mitscherlich equations VI - 12 and VI - 13 means that intrinsic response coefficient k' for height growth is greater than coefficient h' for diameter growth. Thus the ratio k'/h' in equations VI - 18 and VI - 19 is usually greater than unity. This results in the upward convexity of the proposed height-diameter curves. The proposed equations produce curves convex downward if we put k'/h' ratio smaller than unity. However, this is not likely the case in reality.

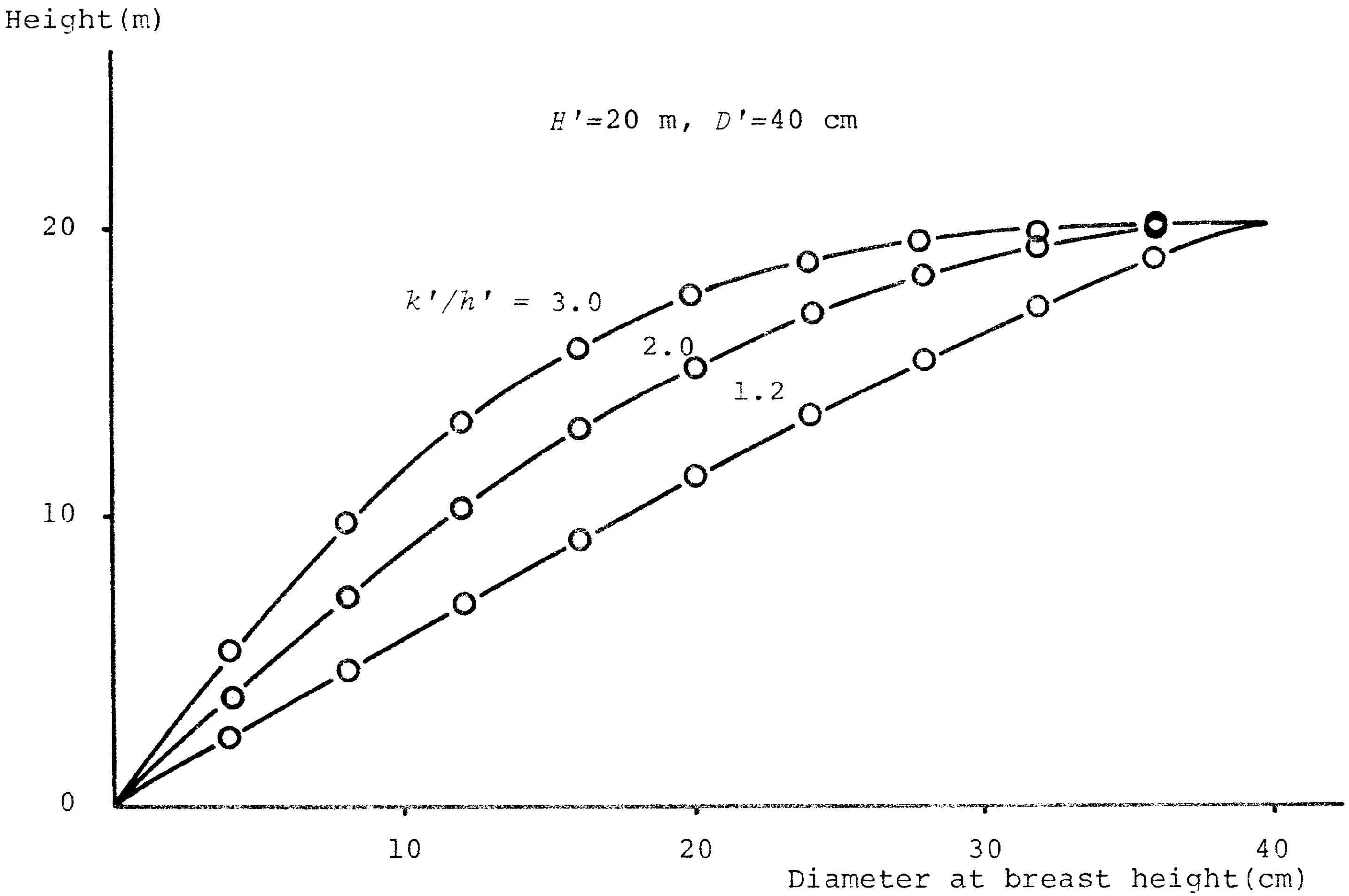


Figure 21. Total height against diameter at ground as expressed by the proposed equation VI - 18 for various values of k'/h' ratio with the other parameters fixed.

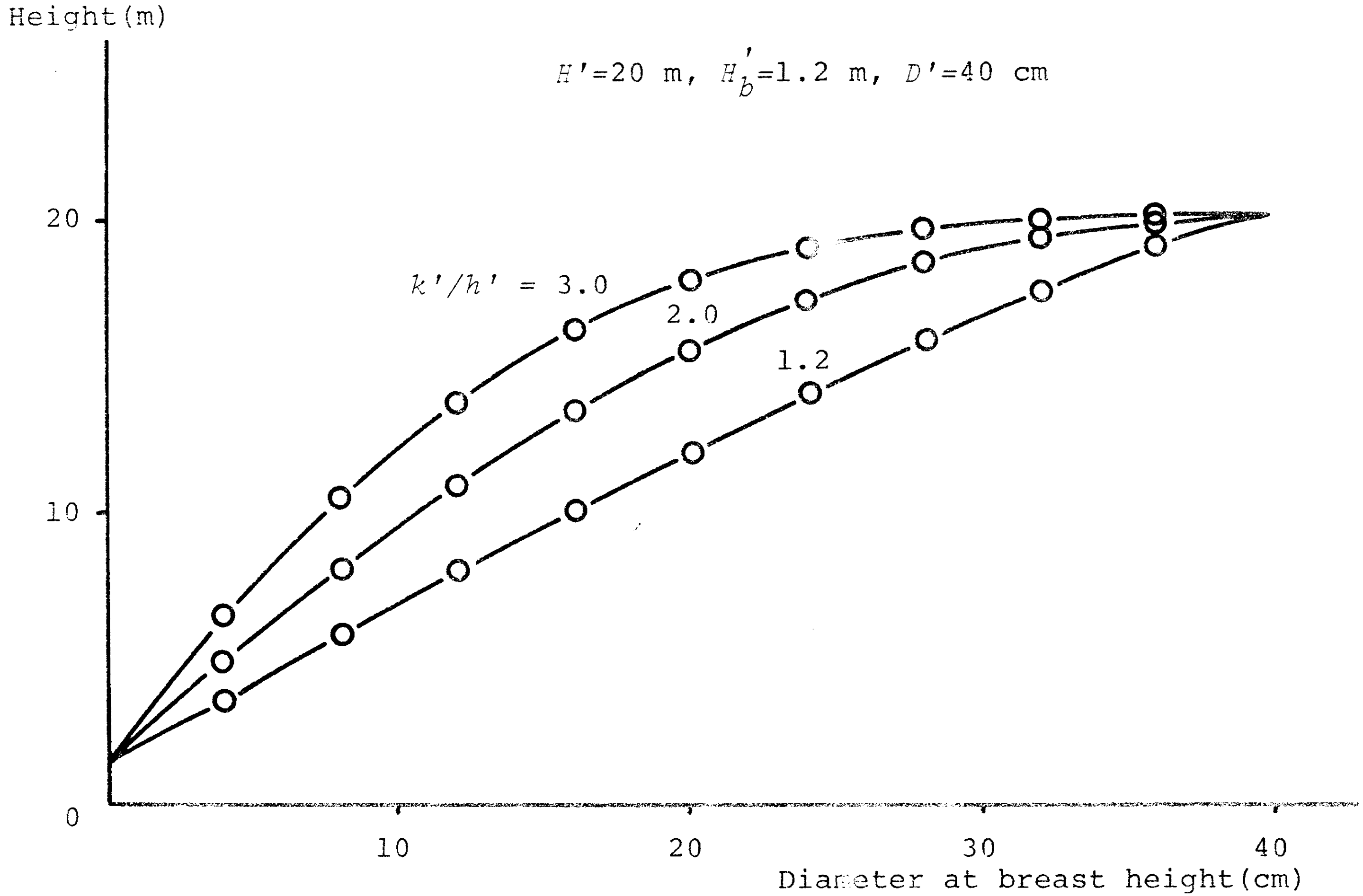


Figure 22. Total height against diameter at breast height as expressed by the proposed equation VI - 19 for various values of k'/h' ratio with the other parameters fixed.

The same argument on the shape of the curve applies to the height-diameter relationship VI-7, VI-9 and VI-11 for all-aged stands. The quicker response of the height growth to site's productivity than that of diameter is just another manifestation of the fact that the height growth has a greater intrinsic rate than the diameter growth, i.e.,

$$k > h.$$

Thus the ratio k/h is greater than unity, which eventually ends up with upward convexity of the height-diameter curves VI-7, VI-9 and VI-11. It is interesting to note that k/h ratio is nearly equal to unity for open growing individual trees (Kobayashi, 1978). Although his sample is small, being of size three, this fact suggests a close relationship between stands' stem density and the k/h ratio.

An example

Just to indicate how the proposed height-diameter curve represents the observed height-diameter relationship, an example is given in Figure 23. The data used for this example was collected in March 1977 from an even-aged hinoki (*Chamaecyparis obtusa* Endlicher) stand of estimated age 80 years old. The stand is located on a mountain slope of north-east aspect facing the Nagura River in Inabu, Aichi Prefecture, Japan and is the property of Furuhashi Foundation. For the application of Eq. VI-18 which represents the relationship between the diameter at ground and total height for even-aged stands, Deming's method of least-squares was

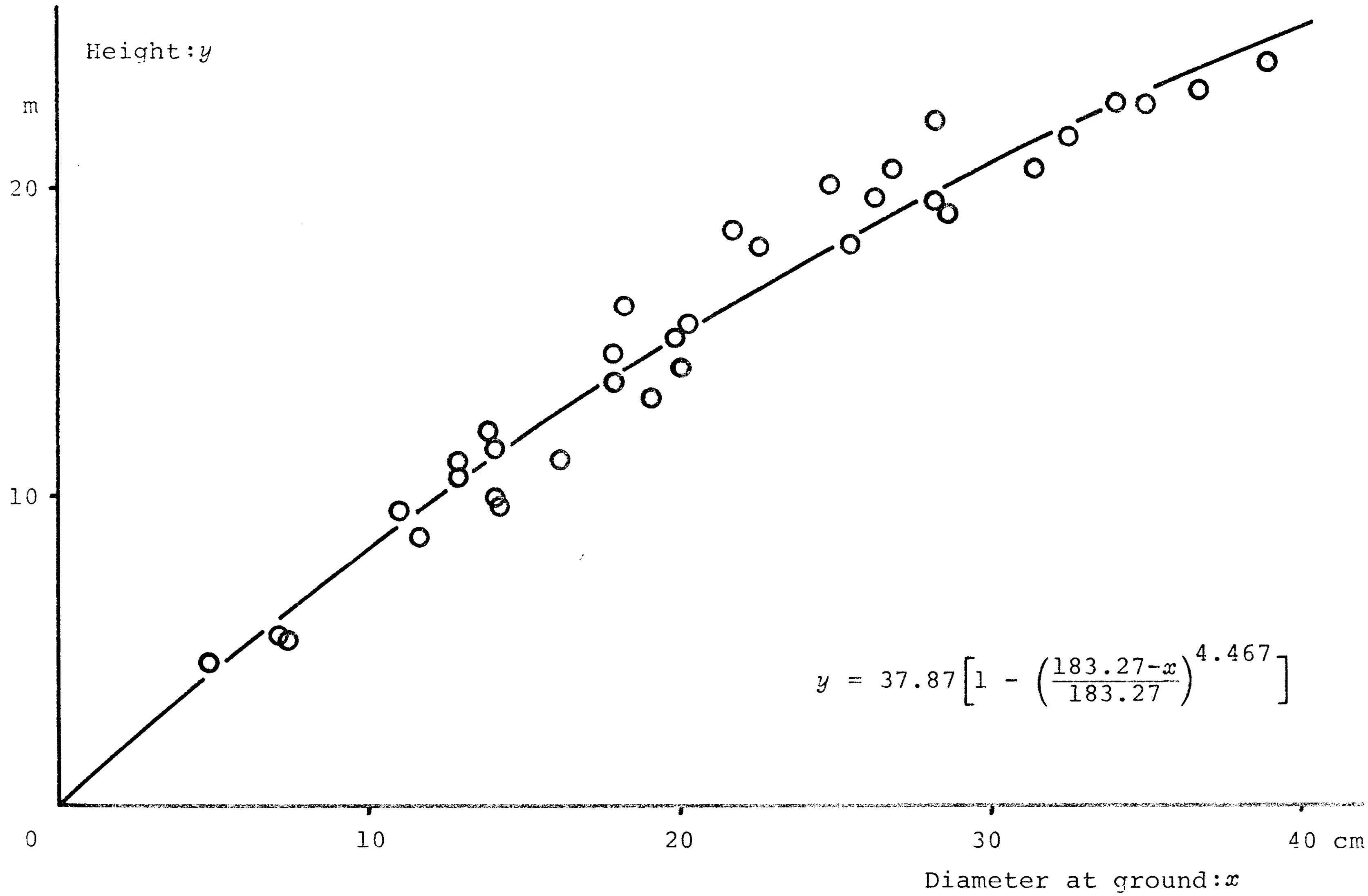


Figure 23. An example of the proposed curve fitted to observed height-diameter relationship

adopted. It seems that the result is quite satisfactory as far as the agreement with the observation is concerned. However, some of the parameters deviate to a certain extent from what are expected from the theory. It would also be worth mentioning that fitting the proposed equation to the observed height-diameter relationship is rather difficult. Thus further research has to be conducted to solve these practical problems.

Conclusion

In this chapter the emphasis was placed on the derivation of a set of height-diameter curves as well as on the theoretical reasoning underlying the derivation. Also, a discussion was made on the applicability of the relultant equations rather from theoretical point of view than from practical one. For the proposed equations to be functional in practice, further research has to be continued on their practical characteristics and feasibility. Among them are: i) technical research associated with fitting the proposed equations to observations, ii) an investigation in the goodness of fit to observed data, especially in comparison with the other existing height-diameter curves either empirical or theoretical, iii) the determination of numerical range of parameters, particularly k/h ratio, and their relationship with different types of forest stands.

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* In Japanese with English summary

** Only in Japanese

The titles in parenthesis are tentative translation from the original Japanese titles by the author of this paper.

APPENDIX I

PARAMETERS OF THE MITSCHERLICH EQUATION AS APPLIED TO THE RADIAL STEM GROWTH OF JACK PINE

Stem No.	M (cm)	k (1/year) $\times 10^{-2}$	Stem No.	M (cm)	k (1/year) $\times 10^{-2}$
1	10.66	2.016	41	13.93	1.508
2	16.39	1.244	42	14.81	2.008
3	8.11	3.123	43	16.64	1.182
4	6.52	3.063	44	11.10	1.946
5	11.42	2.013	45	11.25	1.996
6	12.52	1.188	46	12.87	1.490
7	7.92	3.177	47	10.19	1.942
8	11.39	1.385	48	9.93	1.302
9	13.17	1.562	49	12.57	1.440
10	6.64	2.307	50	9.86	2.425
11	11.43	1.587	51	11.49	1.390
12	8.51	2.283	52	13.29	1.492
13	7.480	1.829	53	12.75	1.134
14	9.67	2.032	54	10.99	2.255
15	10.53	1.516	55	13.14	1.541
16	8.71	2.256	56	8.98	2.624
17	10.54	1.999	57	16.79	1.601
18	8.09	2.392	58	11.35	2.079
19	14.83	1.421	59	10.57	1.820
20	12.37	1.680	60	11.57	2.550
21	12.46	1.313	61	10.69	0.863
22	9.55	2.571	62	14.73	0.733
23	11.45	2.286	63	5.17	2.487
24	15.85	0.835	64	14.13	1.374
25	12.90	1.508	65	9.15	2.910
26	13.64	1.377	66	11.16	1.969
27	7.05	3.316	67	10.37	1.209
28	30.21	0.368	68	11.86	1.624
29	23.18	0.817	69	14.40	1.211
30	13.57	1.285	70	8.05	2.239
31	16.90	0.956	71	13.56	2.301
32	7.06	1.435	72	20.55	0.704
33	12.33	1.301	73	8.44	2.050
34	8.70	2.341	74	9.46	2.369
35	7.27	3.047	75	10.77	2.433
36	8.79	3.444	76	11.55	2.716
37	9.88	2.007	77	4.77	5.061
38	9.63	2.483	78	7.52	2.265
39	10.39	2.082	79	14.53	1.433
40	14.37	1.468	80	4.37	2.925

Stem No.	M (cm)	k (1/year)	Stem No.	M (cm)	k (1/year)
		$\times 10^{-2}$			$\times 10^{-2}$
81	6.68	2.483	121		
82	7.14	2.560	122	12.41	1.349
83	10.03	3.129	123	8.12	1.976
84	12.04	2.283	124	12.10	1.438
85	7.17	2.442	125	9.74	2.594
86	15.11	1.326	126	8.54	2.220
87	11.14	1.486	127	8.31	1.926
88	11.11	2.070	128	9.92	1.516
89	9.36	1.825	129	9.41	2.254
90	9.84	2.340	130	9.72	1.488
91	19.44	1.063	131	8.10	3.302
92	10.55	1.958	132	18.74	0.972
93	13.50	1.930	133	11.37	1.565
94	15.79	0.600	134	10.57	1.683
95	11.37	2.010	135	9.39	2.447
96	10.34	2.242	136	14.33	1.300
97	7.42	3.173	137	7.25	3.233
98	8.15	3.024	138	8.46	1.838
99	16.08	1.228	139	10.15	2.008
100	7.69	2.356	140	9.15	1.724
101	8.29	2.488	141	6.54	2.234
102	8.62	1.871	142	8.66	2.167
103	7.17	3.016	143	6.48	2.855
104	10.17	0.962	144	8.94	2.208
105	8.27	2.275	145	12.56	1.893
106	8.52	1.525	146	13.79	1.874
107	7.02	2.312	147	34.15	0.409
108	7.62	1.541	148	18.02	1.080
109	9.62	1.643	149	12.31	1.579
110	11.83	1.177	150	8.26	3.205
111	3.35	3.708	151	9.23	2.014
112	11.13	0.983	152	11.05	1.599
113	9.60	1.614	153	46.21	0.201
114	8.24	2.595	154	9.93	2.253
115	11.78	2.767	155	10.44	2.258
116	8.08	3.660	156	8.12	2.521
117	10.57	1.332	157	9.23	1.927
118	23.08	0.414	158	10.83	1.710
119	10.51	1.803	159	11.03	1.295
120	9.65	1.823	160	7.00	2.561

Stem No.	M (cm)	k (1/year)	Stem No.	M (cm)	k (1/year)
		$\times 10^{-2}$			$\times 10^{-2}$
161	7.48	2.186	201	11.56	1.665
162	7.34	2.256	202	10.13	2.274
163	6.86	3.099	203	7.83	2.946
164	10.02	1.812	204	15.65	1.039
165	9.63	1.192	205	13.22	1.961
166	10.14	1.035	206	6.95	3.135
167	9.83	1.339	207	13.06	1.581
168	6.47	2.378	208	14.84	2.147
169	11.41	1.641	209	6.69	3.523
170	6.05	3.118	210	9.12	1.937
171	10.00	1.518	211	8.78	3.866
172	7.55	2.200	212	8.89	2.483
173	11.04	1.167	213	11.58	1.388
174	10.63	1.560	214	7.73	2.376
175	8.29	3.008	215	12.19	2.403
176	11.40	3.049	216	9.66	2.544
177	9.80	2.530	217	10.49	1.431
178	11.12	1.647	218	9.85	3.125
179	9.49	2.834	219	11.47	2.156
180	7.58	1.588	220	9.39	1.254
181	8.42	1.869	221	7.73	2.427
182	9.42	2.247	222	9.22	2.714
183	7.35	2.465	223	8.41	2.797
184	8.54	1.822	224	11.37	1.597
185	10.54	1.515	225	6.89	2.944
186	8.31	2.870	226	9.76	2.371
187	10.90	1.627	227	13.33	1.298
188	8.90	1.085	228	8.09	2.759
189	13.39	1.332	229	10.15	1.948
190	6.51	2.056	230	10.73	1.506
191	6.55	2.473	231	12.08	1.178
192	7.61	3.385	232	7.51	2.281
193	11.79	1.209	233	11.97	2.030
194	10.36	1.680	234	9.79	1.649
195	19.25	0.412	235	8.98	1.694
196	11.15	3.254	236	14.37	1.442
197	6.36	1.673	237	9.17	3.204
198	9.86	1.619	238	9.62	2.153
199	9.65	2.954	239	17.70	0.940
200	7.50	3.586	240	13.60	1.171

Stem No.	M (cm)	k (1/year) $\times 10^{-2}$	Stem No.	M (cm)	k (1/year) $\times 10^{-2}$
241	10.06	2.443	281	11.27	2.050
242	9.82	2.189	282	11.07	1.768
243	8.42	2.719	283	6.84	2.691
244	8.46	2.564	284	7.73	1.762
245	8.71	2.041	285	9.65	2.874
246	9.48	2.071	286	9.38	2.122
247	9.66	2.095	287	8.20	2.571
248	9.17	1.440	288	9.84	3.368
249	11.41	1.898	289	11.33	2.026
250	9.43	2.496	290	11.40	1.855
251	14.62	0.929	291	10.82	2.336
252	8.78	2.741	292	10.68	2.319
253	13.28	1.143	293	7.74	2.783
254	7.22	3.533	294	8.77	2.718
255	8.94	2.202	295	10.74	2.235
256	11.45	1.607	296	8.99	2.103
257	10.74	1.658	297	12.01	1.586
258	7.72	3.073	298	7.95	2.408
259	12.77	1.658	299	8.20	2.063
260	7.60	2.129	300	9.86	2.451
261	10.83	2.351	301	12.63	2.276
262	10.78	2.717	302	6.25	3.286
263	9.91	1.503	303	8.52	2.816
264	11.13	2.210	304	8.83	2.476
265	11.93	1.568	305	12.40	1.792
266	9.93	3.170	306	10.40	2.083
267	11.54	1.455	307	7.95	2.399
268	8.60	2.081	308	8.48	1.702
269	8.89	2.244	309	9.41	1.836
270	13.05	1.496	310	12.28	2.049
271	9.93	1.213	311	6.16	3.431
272	7.20	2.046	312	10.34	2.247
273	8.37	1.993	313	10.21	2.186
274	12.00	1.647	314	15.38	1.028
275	11.04	1.530	315	13.65	1.772
276	12.57	1.364	316	11.39	1.602
277	8.35	2.084	317	14.44	1.599
278	7.02	3.089	318	11.40	1.948
279	10.74	1.837	319	10.50	3.004
280	10.96	1.642	320	9.53	2.448

Stem *No.*	*M* (cm)	*k* (1/year)
		$\times 10^{-2}$
321	8.89	2.503
322	7.88	2.327
323	12.21	2.206
324	7.25	2.261
325	10.27	3.195
326	9.29	1.626
327	10.24	1.909
328	8.10	2.416
329	9.86	2.499
330	9.21	3.146
331	8.32	2.029
332	13.83	1.265
333	23.04	0.494
334	12.87	2.244
335	13.00	2.112
336	14.36	0.901
337	11.02	2.242
338	15.98	0.856
339	20.26	0.706
340	12.15	1.532
341	10.09	2.386
342	10.33	2.371
343	10.87	2.120
344	12.97	2.644
345	9.65	1.451
346	10.17	1.814
347	15.57	1.448
348	15.35	1.300
349	15.96	1.396
Mean	10.75	2.026
Var.	14.90	0.493
S.D.	3.86	0.702
Max.	46.21	5.061
Min.	3.35	0.368
n	348	348
C.V. (%)	35.9	34.6

APPENDIX II

PARAMETERS OF THE LOGISTIC EQUATION AS APPLIED TO THE RADIAL STEM GROWTH OF JACK PINE

Stem No.	a^*	b (1/year) $\times 10^{-2}$	C (cm)	Stem No.	a^*	b (1/year) $\times 10^{-2}$	C (cm)
1	1.641	5.070	9.55	41	1.638	4.064	11.92
2	1.914	4.488	12.73	42	1.756	5.412	13.17
3	1.209	5.181	7.91	43	1.758	3.869	13.09
4	1.798	7.682	6.09	44	1.789	5.509	9.71
5	1.512	4.581	10.41	45	1.502	4.455	10.85
6	1.811	4.033	9.79	46	1.897	9.965	10.47
7	1.266	5.570	7.67	47	1.914	5.844	8.88
8	1.649	3.861	9.58	48	2.018	5.049	7.64
9	1.845	4.866	11.00	49	1.665	4.035	10.60
10	1.640	5.526	6.09	50	1.975	7.135	8.88
11	1.907	5.093	9.55	51	1.820	4.487	9.31
12	1.619	5.408	7.81	52	1.685	4.453	11.00
13	1.570	4.378	6.72	53	2.050	4.786	9.30
14	1.459	4.388	8.90	54	1.533	5.085	10.12
15	1.640	4.056	9.05	55	1.668	4.128	11.25
16	1.467	4.826	8.10	56	1.599	6.028	8.35
17	1.513	4.474	9.65	57	1.705	4.469	14.36
18	1.577	5.458	7.48	58	1.607	5.031	10.28
19	1.708	4.227	12.53	59	1.846	5.382	9.13
20	1.873	5.103	10.54	60	1.367	4.992	10.95
21	1.862	4.530	9.83	61	1.833	3.499	7.43
22	1.494	5.486	8.96	62	1.948	3.994	8.53
23	1.641	5.598	10.42	63	1.286	4.408	5.00
24	1.879	3.494	10.94	64	1.825	4.872	10.78
25	1.477	3.346	11.74	65	1.290	5.243	8.79
26	1.587	3.541	11.80	66	1.627	5.160	9.67
27	1.219	5.524	6.89	67	1.731	3.935	8.09
28	2.176	3.514	12.02	68	1.802	5.332	9.68
29	2.122	4.245	14.85	69	1.924	5.005	10.21
30	1.619	3.489	11.48	70	1.672	5.863	7.08
31	2.036	4.352	11.60	71	1.679	5.978	12.04
32	1.571	3.683	6.09	72	2.005	4.246	11.23
33	1.609	3.524	10.41	73	1.658	5.183	7.57
34	1.499	5.130	8.07	74	1.516	5.202	8.79
35	1.623	6.918	6.82	75	1.478	5.250	10.01
36	1.720	8.186	8.33	76	1.396	5.369	10.96
37	1.580	4.736	8.96	77	–	–	–
38	1.440	5.101	9.05	78	1.134	3.168	7.74
39	1.349	3.992	9.82	79	1.684	4.069	12.22
40	1.690	4.154	12.13	80	1.088	4.289	4.35

*Dimensionless

Stem *No.*	a^*	b (1/year)	C (cm)	Stem No.	a^*	b (1/year)	C (cm)
		$\times 10^{-2}$				$\times 10^{-2}$	
81	1.121	3.630	6.70	121	–	–	–
82	1.403	5.065	6.77	122	1.813	4.436	9.94
83	1.887	8.312	9.36	123	1.533	4.571	7.36
84	1.530	5.107	11.12	124	1.716	4.242	10.06
85	1.326	4.585	6.82	125	1.534	5.753	9.08
86	1.898	4.825	11.62	126	1.183	3.486	8.50
87	1.618	3.949	9.55	127	1.659	4.975	7.37
88	1.730	5.518	9.88	128	1.662	4.145	8.48
89	1.563	4.410	8.36	129	1.526	5.081	8.65
90	1.403	4.712	9.25	130	1.494	3.371	8.77
91	1.772	3.680	14.84	131	0.926	3.956	8.33
92	1.721	5.219	9.34	132	1.828	3.659	13.72
93	1.799	5.503	11.76	133	1.598	4.620	9.88
94	1.925	2.266	12.20	134	1.321	2.901	10.49
95	1.949	6.132	9.92	135	1.158	3.790	9.29
96	1.316	4.130	9.88	136	1.741	4.033	11.62
97	1.623	7.183	7.01	137	1.500	6.791	6.90
98	–	–	–	138	1.641	4.055	7.45
99	1.773	3.985	12.85	139	1.643	5.032	9.11
100	1.633	5.648	7.04	140	1.392	3.471	8.55
101	1.518	5.502	7.70	141	1.358	4.354	6.17
102	1.488	4.222	7.82	142	1.534	4.860	7.99
103	1.652	7.003	6.71	143	1.559	6.146	6.14
104	2.398	5.193	6.87	144	1.458	4.702	8.30
105	1.326	4.297	7.85	145	1.505	4.301	11.42
106	1.451	3.463	7.77	146	1.446	4.025	12.66
107	1.428	4.765	6.57	147	2.367	4.268	13.55
108	1.521	3.652	6.77	148	1.859	3.986	13.52
109	1.611	4.366	8.35	149	1.428	3.220	11.54
110	1.753	3.820	9.35	150	1.404	6.232	7.93
111	1.279	6.546	3.24	151	1.577	4.804	8.34
112	3.547	1.787	8.28	152	1.831	4.963	9.24
113	1.364	2.952	9.36	153	2.257	3.501	11.06
114	1.301	4.782	7.87	154	1.546	5.148	9.12
115	1.261	4.842	11.39	155	1.721	5.839	9.43
116	1.586	8.069	7.72	156	1.478	5.419	7.57
117	1.679	3.880	8.74	157	1.881	5.722	8.03
118	2.069	3.226	10.47	158	1.448	3.652	9.96
119	1.414	3.756	9.72	159	1.777	4.133	8.88
120	1.416	3.796	8.91	160	1.707	6.329	6.43

*Dimensionless

Stem No.	a^*	b (1/year) $\times 10^{-2}$	C (cm)	Stem No.	a^*	b (1/year) $\times 10^{-2}$	C (cm)
161	1.231	3.635	7.33	201	1.601	4.284	10.08
162	1.219	4.868	7.11	202	1.682	5.767	9.20
163	1.293	5.622	6.61	203	1.493	6.141	7.52
164	1.638	4.634	8.94	204	2.126	4.759	11.02
165	1.794	3.641	8.11	205	1.721	5.164	11.77
166	1.693	3.208	8.08	206	1.269	5.522	6.73
167	1.482	2.758	9.48	207	1.610	4.084	11.36
168	1.397	4.732	6.10	208	1.357	4.160	14.01
169	1.557	4.007	10.09	209	1.070	5.134	6.64
170	1.819	7.902	5.67	210	1.417	3.983	8.49
171	1.714	4.315	8.48	211	1.540	8.285	8.41
172	2.100	6.970	6.69	212	1.461	5.340	8.28
173	1.631	3.327	9.10	213	1.649	3.865	9.75
174	1.553	3.812	9.38	214	1.534	5.366	7.13
175	1.222	5.099	8.05	215	1.522	5.323	11.28
176	1.716	7.346	10.69	216	1.587	5.835	8.96
177	1.442	5.196	9.23	217	1.801	4.539	8.56
178	1.579	4.142	9.75	218	2.077	9.302	9.12
179	1.274	5.023	9.17	219	1.600	5.220	10.38
180	1.730	4.528	6.45	220	1.494	2.713	7.83
181	1.700	4.969	7.42	221	1.685	5.962	7.10
182	1.412	4.590	8.81	222	1.540	5.959	8.65
183	1.725	6.144	6.75	223	1.689	6.706	7.83
184	1.429	3.854	7.87	224	1.744	4.620	9.64
185	1.528	3.619	9.34	225	1.686	6.878	6.57
186	1.554	6.273	7.83	226	1.393	4.714	9.20
187	1.641	4.315	9.44	227	1.637	3.613	11.17
188	1.663	3.266	7.16	228	1.619	6.316	7.57
189	1.557	3.350	11.63	229	1.422	4.049	9.41
190	1.492	4.550	5.98	230	1.606	3.923	9.27
191	1.692	6.126	6.01	231	1.720	3.710	9.63
192	1.657	7.797	7.20	232	1.827	6.306	6.73
193	1.666	3.556	9.64	233	1.479	4.492	10.96
194	1.594	4.279	9.06	234	1.760	4.751	8.37
195	–	–	–	235	1.552	4.090	7.98
196	1.842	8.290	10.49	236	1.576	3.718	12.39
197	1.344	3.016	6.20	237	1.576	7.050	8.66
198	1.451	3.475	9.05	238	1.393	4.357	8.99
199	1.205	4.981	9.37	239	1.875	3.825	12.49
200	1.283	6.310	7.30	240	1.577	4.259	12.01

*Dimensionless

Stem No.	a*	b (1/year)	C (cm)	Stem No.	a*	b (1/year)	C (cm)
		$\times 10^{-2}$				$\times 10^{-2}$	
241	2.032	7.208	9.09	281	1.444	4.216	10.46
242	1.566	5.105	8.96	282	1.596	4.362	9.85
243	1.606	6.233	7.86	283	1.310	5.001	6.62
244	1.628	5.941	7.89	284	1.348	3.320	7.38
245	1.384	4.078	8.15	285	1.384	5.730	9.23
246	1.850	6.007	8.30	286	1.419	4.391	8.71
247	1.418	4.347	8.98	287	1.270	4.560	7.90
248	1.751	4.431	7.52	288	1.550	7.229	9.46
249	1.377	3.760	10.70	289	1.304	3.658	10.90
250	1.435	5.209	8.88	290	1.738	5.164	9.92
251	1.708	2.941	11.54	291	1.358	4.512	10.24
252	1.437	5.627	8.29	292	1.637	5.660	9.19
253	1.867	4.158	10.09	293	1.334	5.315	7.36
254	1.648	7.875	6.90	294	1.382	5.262	8.36
255	1.613	5.309	8.13	295	1.725	5.749	9.71
256	1.944	6.073	8.69	296	1.394	4.221	8.42
257	1.717	4.809	9.01	297	1.653	4.223	10.41
258	1.713	7.336	7.26	298	1.565	5.417	7.38
259	1.596	4.150	11.26	299	1.385	4.106	7.69
260	1.275	3.763	7.33	300	1.627	5.781	9.10
261	1.710	5.914	9.88	301	1.776	6.067	11.40
262	1.321	5.044	10.31	302	1.531	7.079	5.95
263	1.704	4.269	8.39	303	1.352	5.481	8.09
264	1.550	5.066	10.19	304	1.503	5.423	8.22
265	1.866	5.078	9.79	305	1.861	5.418	10.62
266	1.465	6.459	9.47	306	1.576	4.959	9.44
267	1.542	3.528	10.18	307	1.637	5.736	7.32
268	1.550	4.822	7.83	308	1.363	3.206	8.13
269	1.540	5.098	8.16	309	1.582	4.536	8.36
270	1.639	4.025	11.18	310	1.573	4.851	11.14
271	1.665	3.582	8.10	311	1.285	6.120	5.97
272	1.724	5.518	6.33	312	1.592	5.301	9.46
273	1.533	4.606	7.60	313	1.426	4.528	9.51
274	2.277	6.504	9.76	314	1.800	3.668	11.58
275	1.797	4.641	9.23	315	1.761	5.323	11.36
276	1.613	3.671	10.67	316	1.499	3.698	10.23
277	1.462	4.265	7.78	317	1.653	4.287	12.46
278	1.616	7.100	6.55	318	1.617	4.808	10.22
279	1.726	5.018	9.39	319	1.913	8.148	9.81
280	1.588	3.988	9.67	320	1.444	5.094	8.93

*Dimensionless

Stem No.	a*	b (1/year)	C (cm)
		$\times 10^{-2}$	
321	1.307	4.582	8.60
322	1.455	4.911	7.34
323	1.721	5.712	10.98
324	1.518	5.011	6.70
325	1.888	8.504	9.59
326	2.005	5.596	7.66
327	1.627	4.799	9.12
328	1.849	6.470	7.37
329	1.521	5.703	8.99
330	1.973	8.539	8.57
331	1.503	4.69[illegible]	7.59
332	2.030	4.884	10.65
333	2.036	3.308	11.70
334	1.811	6.190	11.49
335	1.873	6.123	11.47
336	1.770	3.180	10.75
337	1.755	5.854	9.96
338	1.962	4.112	11.16
339	1.892	3.185	13.28
340	1.826	4.803	10.04
341	1.513	5.223	9.38
342	1.526	5.271	9.58
343	1.654	5.320	9.79
344	1.785	6.887	11.90
345	1.574	3.727	8.34
346	1.653	4.692	8.98
347	1.801	4.531	12.80
348	1.715	3.927	12.55
349	1.876	4.703	12.81
Mean	1.616	4.889	9.18
Var.	0.0493	1.369	3.51
S.D.	0.222	1.170	1.87
Max.	2.398	9.302	14.84
Min.	0.926	2.266	4.35
n	345	345	345
C.V.(%)	13.7	23.9	20.4

*Dimensionless

APPENDIX III

PARAMETERS OF THE GOMPERTZ EQUATION AS APPLIED TO THE RADIAL STEM GROWTH OF JACK PINE

Stem No.	p*	q (1/year)	A (cm)	Stem No.	p*	q (1/year)	A (cm)
	$\times 10^{-1}$	$\times 10^{-2}$			$\times 10^{-1}$	$\times 10^{-2}$	
1	8.008	3.619	9.82	41	7.821	2.798	12.46
2	9.317	2.993	13.36	42	8.718	3.857	13.50
3	5.377	3.840	8.12	43	8.350	2.533	13.95
4	8.971	5.542	6.18	44	8.934	3.905	9.97
5	7.224	3.287	10.72	45	7.053	3.167	11.20
6	8.616	2.637	10.39	46	9.279	3.365	10.91
7	5.955	4.288	7.78	47	9.738	4.017	9.13
8	7.782	2.593	10.11	48	9.872	3.329	8.01
9	8.930	3.300	11.45	49	7.876	2.720	11.15
10	8.022	4.001	6.22	50	10.143	5.083	9.05
11	9.340	3.472	9.90	51	8.858	3.051	9.73
12	7.800	3.873	8.00	52	7.996	2.996	11.58
13	7.137	2.958	7.02	53	9.953	3.098	9.84
14	6.809	3.125	9.20	54	7.432	3.672	10.38
15	7.834	2.802	9.44	55	7.968	2.898	11.74
16	7.039	3.542	8.29	56	7.712	4.349	8.53
17	6.974	3.130	9.99	57	8.183	3.076	14.94
18	7.664	3.982	7.64	58	7.720	3.574	10.57
19	8.190	2.895	13.08	59	9.195	3.784	9.39
20	9.120	3.501	10.91	60	6.652	3.806	11.14
21	8.938	2.981	10.37	61	8.495	1.906	8.89
22	7.092	3.993	9.15	62	9.041	2.218	10.00
23	8.150	4.077	10.65	63	5.643	3.075	5.23
24	8.833	2.149	12.00	64	8.576	3.101	11.58
25	6.664	2.203	12.54	65	5.736	3.778	9.07
26	7.210	2.284	12.66	66	7.622	3.501	10.13
27	5.472	4.203	6.99	67	7.990	2.410	8.92
28	10.191	1.957	13.94	68	8.678	3.589	10.14
29	10.149	2.637	16.00	69	8.916	3.039	11.17
30	7.434	2.246	12.34	70	8.025	4.095	7.32
31	9.629	2.701	12.51	71	8.253	4.270	12.37
32	7.259	2.437	6.48	72	9.305	2.370	13.05
33	7.468	2.302	11.14	73	8.139	3.717	7.77
34	7.167	3.724	8.27	74	7.276	3.792	8.99
35	7.908	5.048	6.94	75	7.089	3.838	10.25
36	8.582	5.959	8.44	76	6.556	3.965	11.19
37	7.452	3.340	9.24	77	6.416	7.152	4.70
38	6.848	3.766	9.24	78	4.782	2.305	8.01
39	6.271	2.933	10.09	79	7.932	2.722	12.87
40	8.100	2.848	12.67	80	4.546	3.225	4.45

*Dimensionless

Stem No.	p*	q (1/year)	A (cm)	Stem No.	p*	q (1/year)	A (cm)
	$\times 10^{-1}$	$\times 10^{-2}$			$\times 10^{-1}$	$\times 10^{-2}$	
81	4.842	2.732	6.87	121	–	–	–
82	6.575	3.725	6.92	122	8.647	2.924	10.49
83	9.522	5.940	9.49	123	7.134	3.189	7.63
84	7.442	3.751	11.37	124	8.216	2.872	10.55
85	6.202	3.423	6.97	125	7.357	4.188	9.28
86	9.042	3.122	12.33	126	5.072	2.482	8.87
87	7.711	2.718	9.99	127	8.066	3.519	7.60
88	8.668	3.978	10.12	128	7.755	2.768	8.93
89	7.347	3.067	8.69	129	7.346	3.684	2.87
90	6.608	3.462	9.48	130	6.965	2.335	9.19
91	8.206	2.277	16.19	131	3.778	3.187	8.42
92	8.290	3.635	9.63	132	8.665	2.325	14.81
93	8.741	3.799	12.15	133	7.674	2.822	10.27
94	9.096	1.111	16.10	134	5.729	1.853	11.36
95	9.728	4.265	10.18	135	5.093	2.837	9.54
96	5.902	2.994	10.18	136	8.202	2.756	11.94
97	8.071	5.309	7.11	137	7.263	5.030	7.00
98	7.626	4.987	7.78	138	7.913	3.337	7.71
99	8.283	2.557	13.76	139	7.922	3.557	9.38
100	7.995	4.089	7.20	140	6.270	2.370	9.02
101	7.412	4.053	7.86	141	6.238	3.154	6.35
102	6.874	2.931	8.15	142	7.100	3.417	8.23
103	8.148	5.126	6.82	143	7.453	4.494	6.24
104	11.753	3.301	7.23	144	6.906	3.418	8.52
105	6.077	3.132	8.08	145	7.129	3.064	11.80
106	6.469	2.260	8.32	146	6.738	2.856	13.13
107	6.686	3.462	6.74	147	11.335	2.512	15.01
108	7.000	2.461	7.15	148	8.729	2.519	14.55
109	7.617	3.006	8.70	149	6.471	2.186	12.20
110	8.226	2.461	10.01	150	6.699	4.684	8.05
111	5.826	4.919	3.30	151	7.569	3.429	8.58
112	8.380	2.216	9.02	152	8.966	3.404	9.59
113	6.077	1.989	9.95	153	11.041	1.784	13.67
114	6.105	3.600	8.03	154	7.404	3.703	9.36
115	5.733	3.634	11.61	155	8.446	4.146	9.66
116	7.673	5.868	7.82	156	7.017	3.928	7.75
117	7.847	2.542	9.30	156	9.293	3.976	8.26
118	9.593	1.721	12.58	158	6.580	2.483	10.50
119	6.379	2.571	10.21	159	8.404	2.713	9.40
120	6.653	2.741	9.22	160	8.394	4.558	6.56

*Dimensionless

Stem No.	p*	q (1/year)	A (cm)	Stem No.	p*	q (1/year)	A (cm)
	$\times 10^{-1}$	$\times 10^{-2}$			$\times 10^{-1}$	$\times 10^{-2}$	
161	5.458	2.647	7.57	201	7.642	2.875	10.50
162	5.542	3.669	7.26	202	8.393	4.139	9.41
163	5.994	4.227	6.73	203	7.146	4.527	7.65
164	7.876	3.256	9.24	204	10.329	3.056	11.67
165	8.486	2.337	8.72	205	8.373	3.641	12.11
166	7.782	1.962	8.93	206	5.960	4.237	6.82
167	6.665	1.712	10.48	207	7.550	2.781	11.90
168	6.437	3.432	6.27	208	6.208	3.003	14.45
169	7.347	2.785	10.52	209	4.610	4.001	6.73
170	9.236	5.745	5.74	210	6.502	2.822	8.80
171	8.002	2.868	8.92	211	7.423	6.051	8.53
172	10.675	4.862	6.82	212	7.023	3.915	8.47
173	7.530	2.103	9.91	213	7.832	2.621	10.25
174	7.189	2.587	9.26	214	7.418	3.830	7.30
175	5.489	3.842	8.20	215	7.308	3.877	11.54
176	8.477	5.307	10.86	216	7.718	4.241	9.15
177	6.893	3.850	9.41	217	8.796	3.103	8.93
178	7.397	2.832	10.21	218	10.399	6.395	9.27
179	5.925	3.823	9.32	219	7.742	3.728	10.67
180	8.308	3.104	6.72	220	6.708	1.613	8.88
181	8.150	3.445	7.68	221	8.350	4.325	7.24
182	6.635	3.351	9.05	222	7.502	4.385	8.81
183	8.543	4.437	6.88	223	8.235	4.834	7.98
184	6.521	2.678	8.22	224	8.408	3.167	10.04
185	7.067	2.451	9.85	225	8.239	4.986	6.68
186	7.536	4.603	7.97	226	6.552	3.475	9.42
187	7.741	2.941	9.87	227	7.516	2.320	12.01
188	7.614	1.987	7.95	228	7.881	4.592	7.71
189	7.124	2.166	12.52	229	6.537	2.865	9.76
190	6.944	3.216	6.18	230	7.467	2.631	9.78
191	8.358	4.419	6.13	231	8.178	2.448	10.24
192	8.171	5.685	7.30	232	9.052	4.435	6.89
193	7.710	2.272	10.40	233	6.952	3.199	11.32
194	7.545	2.953	9.45	234	8.450	3.244	8.71
195	—	—	—	235	7.305	2.845	8.31
196	9.209	5.929	10.64	236	7.247	2.441	13.21
197	5.991	2.062	6.55	237	7.740	5.212	8.79
198	6.591	2.357	9.56	238	6.394	3.114	9.29
199	5.568	3.822	9.53	239	8.843	2.378	13.60
200	5.917	4.797	7.39	240	7.475	2.966	12.49

*Dimensionless

Stem No.	p^*	q (1/year)	A (cm)	Stem No.	p^*	q (1/year)	A (cm)
	$\times 10^{-1}$	$\times 10^{-2}$			$\times 10^{-1}$	$\times 10^{-2}$	
241	10.176	5.028	9.27	281	6.956	3.199	10.70
242	7.572	3.686	9.19	282	7.575	3.055	10.20
243	7.732	4.489	8.02	283	6.000	3.683	6.79
244	8.071	4.367	8.02	284	5.997	2.278	7.77
245	6.556	3.019	8.36	285	6.722	4.383	9.35
246	9.157	4.195	8.54	286	6.617	3.159	9.00
247	6.615	3.132	9.26	287	5.808	3.418	8.04
248	8.533	3.030	7.86	288	7.515	5.328	9.60
249	6.232	2.683	11.10	289	5.812	2.598	11.32
250	6.911	3.853	9.08	290	8.485	3.600	10.25
251	7.845	1.724	13.12	291	6.402	3.362	10.47
252	6.859	4.154	8.45	292	8.120	4.121	9.39
253	8.901	2.698	10.73	293	6.293	3.972	7.51
254	8.098	5.781	6.98	294	6.539	3.941	8.51
255	7.839	3.810	8.34	295	8.535	4.126	9.93
256	9.357	3.970	9.18	296	6.355	3.002	8.71
257	8.161	3.246	9.45	297	8.044	2.983	10.77
258	8.486	5.326	7.37	298	7.583	3.960	7.53
259	7.566	2.890	11.70	299	6.333	2.931	7.96
260	5.571	2.663	7.62	300	8.037	4.231	9.28
261	8.449	4.254	10.09	301	8.762	4.290	11.67
262	6.203	3.797	10.50	302	7.406	5.191	6.04
263	8.130	2.908	8.77	303	6.233	3.992	8.29
264	7.452	3.656	10.46	304	7.379	4.026	8.38
265	9.049	3.425	10.22	305	9.291	3.799	10.93
266	7.118	4.844	9.61	306	7.625	3.569	9.69
267	7.105	2.366	10.78	307	8.093	4.184	7.46
268	7.364	3.432	8.07	308	6.156	2.229	8.53
269	7.350	3.663	8.38	309	7.523	3.171	8.67
270	7.640	2.692	11.78	310	7.634	3.502	11.44
271	7.714	2.286	8.75	311	5.930	4.624	6.06
272	8.178	3.780	6.56	312	7.701	3.812	9.69
273	7.214	3.249	7.86	313	6.765	3.322	9.75
274	11.527	4.372	10.06	314	8.550	2.362	12.43
275	8.692	3.169	9.60	315	8.479	3.619	11.87
276	7.444	2.398	11.40	316	6.881	2.510	10.77
277	6.953	3.262	7.92	317	8.000	3.007	12.92
278	7.868	5.159	6.67	318	7.621	3.342	10.58
279	7.973	3.231	9.83	319	9.615	5.768	9.97
280	7.709	2.852	9.94	320	6.792	3.704	9.14

*Dimensionless

Stem No.	p^*	q (1/year)	A (cm)
	$\times 10^{-1}$	$\times 10^{-2}$	
321	5.991	3.391	8.81
322	6.901	3.583	7.53
323	8.573	4.124	11.23
324	7.286	3.645	6.86
325	9.397	5.995	9.74
326	10.125	3.877	7.90
327	7.690	3.361	9.37
328	9.137	4.586	7.52
329	7.066	3.891	9.42
330	10.071	6.154	2.69
331	7.120	3.351	7.83
332	9.971	3.245	11.14
333	9.446	1.816	13.75
334	9.041	4.397	11.76
335	9.431	4.336	11.75
336	8.275	1.971	11.80
337	8.668	4.175	10.19
338	9.402	2.616	11.97
339	8.855	1.895	14.88
340	9.007	3.332	12.41
341	7.259	3.808	9.59
342	7.354	3.840	9.80
343	8.151	3.829	10.04
344	8.810	4.879	12.14
345	7.211	2.440	8.89
346	7.983	3.301	9.28
347	8.668	3.054	13.40
348	8.084	2.589	13.31
349	8.995	3.114	13.45
Mean	7.611	3.484	9.57
Var.	1.414	0.893	4.41
S.D.	1.189	0.945	2.10
Max.	11.753	7.152	16.19
Min.	3.778	1.111	4.45
n	347	347	3[illegible]7
C.V.(%)	15.6	27.1	21.9

* Dimensionless

APPENDIX IV

PARAMETERS OF THE EMPIRICAL GROWTH EQUATION I AS APPLIED TO THE RADIAL STEM GROWTH OF JACK PINE

Stem No.	*a* (cm)	*b* (cm/year)	*c* (cm/year^2)	Stem No.	*a* (cm)	*b* (cm/year)	*c* (cm/year^2)
	$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-1}$		$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$
1	7.175	1.465	–5.954	41	7.292	1.560	–5.378
2	1.024	1.798	–6.293	42	6.722	2.150	–9.064
3	1.334	1.287	–6.287	43	5.813	1.579	–4.761
4	5.564	1.213	–6.349	44	4.452	1.590	–6.649
5	1.039	1.469	–5.663	45	10.533	1.540	–6.060
6	3.375	1.233	–2.906	46	1.137	1.641	–6.436
7	14.005	1.194	–5.518	47	2.274	1.529	–6.605
8	6.245	1.175	–3.732	48	0.008	1.160	–4.275
9	2.735	1.688	–6.604	49	6.476	1.358	–4.554
10	4.593	1.026	–4.612	50	3.883	1.667	–7.801
11	1.215	1.518	–6.059	51	2.067	1.336	–4.847
12	6.603	1.277	–5.621	52	5.994	1.563	–5.772
13	5.960	0.943	–3.682	53	0.661	1.349	–4.703
14	3.636	1.238	–4.818	54	10.002	1.573	–6.700
15	5.259	1.191	–4.136	55	6.261	1.528	–5.464
16	9.290	1.180	–4.766	56	9.177	1.417	–6.558
17	9.180	1.401	–5.692	57	6.790	2.072	–7.842
18	6.733	1.242	–5.582	58	8.446	1.585	–6.583
19	5.619	1.715	–6.121	59	2.190	1.574	–6.365
20	1.662	1.718	–7.118	60	16.030	1.575	–6.420
21	2.834	1.364	–4.737	61	5.334	0.663	–0.833
22	11.270	1.418	–6.272	62	4.244	0.874	–1.402
23	8.708	1.700	–7.353	63	7.403	0.710	–2.969
24	3.558	1.131	–2.679	64	3.983	1.616	–6.008
25	12.534	1.250	–3.645	65	12.830	1.474	–7.469
26	10.009	1.322	–3.984	66	6.331	1.621	–7.299
27	13.207	1.090	–5.234	67	5.061	0.953	–2.675
28	1.316	1.055	–1.388	68	2.896	1.640	–7.076
29	–2.187	1.870	–5.447	69	3.540	1.492	–5.205
30	9.061	1.253	–3.580	70	3.964	1.331	–6.625
31	0.615	1.500	–4.611	71	7.255	2.227	–10.799
32	5.377	0.700	–2.128	72	4.350	1.229	–2.237
33	8.220	1.141	–3.209	73	5.235	1.208	–5.088
34	9.101	1.135	–5.228	74	9.417	1.375	–5.928
35	7.115	1.333	–7.064	75	12.120	1.541	–6.585
36	12.532	1.527	–7.720	76	15.895	1.708	–7.616
37	7.044	1.367	–5.689	77	13.661	0.767	–4.105
38	10.463	1.433	–6.373	78	13.933	0.805	–2.586
39	12.564	1.257	–4.599	79	6.840	1.592	–5.446
40	5.843	1.632	–5.726	80	8.860	0.581	–2.456

Stem No.	a (cm)	b (cm/year)	c (cm/year²)	Stem No.	a (cm)	b (cm/year)	c (cm/year²)
	$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$		$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$
81	12.575	0.771	–2.725	121	13.234	–0.103	5.387
82	8.600	1.063	–4.759	122	3.796	1.360	–4.721
83	10.620	1.760	–8.760	123	7.164	1.054	–4.167
84	10.921	1.729	–7.327	124	4.969	1.350	–4.682
85	9.737	0.964	–3.933	125	10.973	1.474	–6.598
86	2.532	1.746	–6.367	126	14.639	0.956	–3.260
87	6.355	1.206	–3.998	127	4.962	1.130	–4.575
88	5.353	1.640	–7.033	128	5.507	1.120	–3.939
89	7.058	1.174	–4.490	129	8.845	1.381	–5.575
90	11.587	1.348	–5.559	130	8.069	0.958	–2.807
91	3.116	1.606	–4.215	131	20.390	0.996	–3.929
92	5.274	1.509	–6.415	132	4.886	1.523	–4.029
93	5.490	1.951	–8.343	133	6.392	1.293	–4.479
94	9.389	0.598	0.161	134	15.212	0.952	–2.400
95	2.139	1.785	–8.023	135	16.917	1.096	–3.895
96	13.422	1.335	–5.303	136	5.237	1.477	–4.783
97	9.423	1.266	–6.277	137	10.713	1.201	–5.915
98	11.828	1.262	–5.810	138	5.006	1.110	–4.386
99	6.385	1.581	–4.951	139	6.937	1.400	–5.745
100	5.782	1.129	–5.367	140	10.600	0.948	–2.947
101	9.130	1.205	–5.178	141	8.447	0.832	–3.221
102	8.272	1.039	–3.830	142	7.863	1.221	–5.200
103	6.673	1.309	–6.859	143	7.294	1.074	–5.205
104	–4.338	1.062	–3.794	144	9.370	1.210	–4.930
105	11.254	1.047	–4.042	145	11.357	1.537	–5.683
106	9.220	0.843	–2.535	146	13.631	1.629	–5.835
107	7.929	0.871	–4.060	147	–4.364	1.518	–3.233
108	6.334	0.790	–2.501	148	4.456	1.644	–4.933
109	6.217	1.153	–4.269	149	12.896	1.200	–3.435
110	4.827	1.102	–3.280	150	13.461	1.305	–6.220
111	5.765	0.607	–3.387	151	6.649	1.267	–5.201
112	4.286	0.871	–2.165	152	2.560	1.426	–5.582
113	12.324	0.876	–2.256	153	3.569	0.810	–0.840
114	12.343	1.118	–4.601	154	9.119	1.471	–6.019
115	18.996	1.667	–7.260	155	6.997	1.585	–6.995
116	15.057	1.312	–6.460	156	9.812	1.174	–5.091
117	5.538	1.062	–3.341	157	2.150	1.388	–6.071
118	4.314	0.803	–6.641	158	10.650	1.182	–3.913
119	11.674	1.163	–3.928	159	3.694	1.151	–3.816
120	9.836	1.088	–3.672	160	4.450	1.206	–5.955

Stem No.	a (cm)	b (cm/year)	c (cm/year²)	Stem No.	a (cm)	b (cm/year)	c (cm/year²)
	$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$		$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$
161	11.674	0.851	−2.925	201	7.684	1.354	−4.821
162	12.794	1.021	−4.392	202	7.311	1.512	−6.544
163	12.654	0.986	−4.373	203	10.223	1.286	−6.175
164	6.436	1.285	−4.913	204	−2.411	1.590	−5.441
165	3.311	0.807	−2.479	205	6.245	1.894	−7.980
166	6.008	0.767	−1.739	206	1.242	1.025	−4.649
167	11.285	0.777	−1.541	207	8.056	1.497	−5.304
168	7.588	0.916	−3.945	208	18.505	1.848	−7.017
169	8.230	1.299	−4.521	209	14.585	0.999	−4.766
170	5.834	1.086	−5.490	210	10.001	1.071	−3.852
171	4.456	1.177	−4.341	211	17.986	1.417	−7.051
172	0.463	1.296	−6.107	212	11.075	1.249	−5.250
173	7.603	0.908	−2.219	213	5.853	1.203	−3.862
174	8.091	1.150	−3.848	214	7.806	1.118	−4.798
175	15.160	1.185	−5.279	215	10.715	1.879	−8.594
176	12.807	1.358	−9.690	216	9.393	1.499	−6.821
177	11.434	1.440	−6.313	217	2.417	1.286	−4.453
178	8.056	1.276	−4.494	218	10.779	1.693	−8.245
179	15.348	1.360	−5.960	219	9.340	1.613	−6.736
180	2.906	0.935	−3.532	220	9.915	0.604	−1.048
181	4.598	1.139	−4.613	221	5.751	1.218	−5.532
182	10.653	1.264	−5.123	222	10.998	1.410	−6.347
183	5.098	1.191	−5.522	223	8.573	1.381	−6.561
184	0.900	0.973	−3.391	224	4.278	1.407	−5.319
185	8.394	1.087	−3.429	225	7.117	1.211	−6.028
186	9.744	1.354	−6.472	226	11.935	1.330	−5.465
187	6.383	1.295	−4.734	227	8.678	1.252	−3.666
188	6.128	0.679	−1.516	228	8.297	1.327	−6.320
189	10.899	1.206	−3.253	229	10.463	1.242	−4.651
190	6.271	0.854	−3.407	230	7.040	1.160	−3.890
191	5.095	1.041	−4.777	231	4.910	1.114	−3.221
192	10.471	1.336	−6.850	232	3.910	1.187	−5.377
193	7.002	1.050	−2.900	233	11.595	1.541	−6.003
194	7.048	1.225	−4.432	234	3.787	1.249	−4.849
195	12.705	0.368	−1.443	235	6.449	1.059	−3.821
196	12.699	1.990	−1.008	236	11.012	1.435	−4.414
197	8.394	0.594	−1.577	237	10.798	1.644	−8.579
198	9.708	1.018	−3.178	238	11.507	1.225	−4.764
199	18.642	1.283	−5.290	239	4.454	1.407	−3.696
200	14.473	1.216	−6.093	240	9.393	1.634	−5.994

Stem No.	a (cm)	b (cm/year)	c (cm/year^2)	Stem No.	a (cm)	b (cm/year)	c (cm/year^2)
	$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$		$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$
241	3.010	1.783	−8.721	281	10.308	1.495	−6.003
242	8.156	1.394	−5.877	282	6.821	1.401	−5.391
243	9.035	1.351	−6.354	283	10.393	0.983	−4.354
244	7.854	1.313	−5.874	284	9.788	0.790	−2.424
245	9.495	1.072	−3.968	285	13.567	1.515	−7.093
246	2.963	1.490	−6.797	286	9.928	1.231	−4.913
247	10.538	1.237	−4.841	287	12.457	1.103	−4.524
248	3.284	1.031	−3.570	288	14.057	1.744	−9.023
249	12.990	1.302	−4.491	289	15.188	1.299	−4.535
250	12.176	1.314	−5.446	290	5.752	1.538	−6.187
251	9.363	0.953	−1.646	291	13.366	1.449	−5.856
252	1.241	1.277	−5.576	292	7.760	1.521	−6.696
253	2.394	1.307	−4.208	293	13.017	1.046	−4.309
254	10.880	1.266	−6.508	294	11.625	1.319	−5.954
255	7.071	1.286	−5.456	295	5.731	1.681	−7.588
256	0.377	1.657	−7.783	296	10.053	1.154	−4.537
257	4.257	1.394	−5.642	297	5.732	1.415	−5.050
258	8.672	1.336	−6.649	298	6.480	1.212	−5.674
259	7.835	1.519	−5.516	299	9.227	1.028	−3.938
260	11.019	0.885	−3.270	300	7.879	1.549	−7.046
261	7.341	1.690	−7.606	301	8.031	1.935	−8.539
262	15.836	1.544	−6.704	302	11.174	0.941	−4.305
263	4.097	1.152	−4.148	303	14.514	1.168	−4.898
264	8.326	1.196	−6.803	304	9.871	1.270	−5.401
265	2.095	1.561	−6.305	305	2.424	1.767	−7.391
266	14.800	1.606	−7.739	306	7.840	1.456	−6.057
267	8.902	1.157	−3.560	307	6.468	1.263	−5.396
268	6.933	1.191	−4.955	308	10.286	0.839	−2.414
269	7.997	1.273	−5.435	309	7.276	1.165	−4.357
270	7.527	1.444	−4.983	310	9.412	1.669	−6.732
271	5.950	0.882	−2.416	311	12.317	0.928	−4.355
276	3.609	1.093	−5.006	312	8.803	1.490	−6.338
273	7.052	1.106	−4.423	313	10.886	1.355	−5.411
274	−3.683	1.816	−7.917	314	4.550	1.301	−3.549
275	2.564	1.379	−5.296	315	4.110	1.940	−8.533
276	8.419	1.230	−3.735	316	9.958	1.219	−3.997
277	8.192	1.094	−4.332	317	6.695	1.736	−6.363
278	7.055	1.299	−6.899	318	7.868	1.549	−6.361
279	5.036	1.465	−5.983	319	10.174	1.838	−9.024
280	6.435	1.310	−4.807	320	11.528	1.346	−5.718

Stem No.	a (cm)	b (cm/year)	c (cm/year^2)
	$\times 10^{-1}$	$\times 10^{-1}$	$\times 10^{-4}$
321	12.647	1.229	−5.127
322	8.560	1.104	−4.638
323	6.019	1.912	−8.652
324	6.923	1.022	−4.282
325	11.828	1.294	−2.952
326	−0.719	1.317	−5.505
327	6.685	1.368	−5.489
328	3.290	1.401	−6.812
329	10.603	1.482	−6.642
330	6.043	1.830	−9.962
331	7.620	1.112	−4.476
332	−1.199	1.610	−5.915
333	4.551	0.967	−1.177
334	5.764	2.065	−8.500
335	3.980	2.045	−9.179
336	5.639	1.020	−2.235
337	5.688	1.736	−7.257
338	0.346	1.393	−4.130
339	4.984	1.203	−2.280
340	1.579	1.556	−6.081
341	9.979	1.479	−6.428
342	10.655	1.483	−6.313
343	7.206	1.566	−6.620
344	10.679	2.145	−10.167
345	7.576	0.966	−2.388
346	5.737	1.328	−5.199
347	4.023	1.840	−6.758
348	6.667	1.552	−4.941
349	2.826	1.285	−7.014
Mean	7.749	1.310	−5.107
Var.	16.411	0.100	4.028
S.D.	4.051	0.317	2.007
Max.	20.390	2.150	5.387
Min.	−4.364	−0.103	−10.799
n	349	349	349
C.V.(%)	52.3	24.2	39.4

APPENDIX V

PARAMETERS OF THE EMPIRICAL GROWTH EQUATION II AS APPLIED TO THE RADIAL STEM GROWTH OF JACK PINE

Stem No.	a (cm/year)	b (cm/year^2)	c (cm/year^3)	Stem No.	a (cm/year)	b (cm/year^2)	c (cm/year^3)
	$\times10^{-1}$	$\times10^{-3}$	$\times10^{-6}$		$\times10^{-1}$	$\times10^{-3}$	$\times10^{-6}$
1	2.199	−2.040	7.450	41	2.271	−1.933	7.240
2	2.014	−1.120	2.707	42	2.884	−2.364	7.480
3	2.655	−3.866	21.020	43	2.174	−1.669	6.277
4	1.805	−1.875	6.838	44	2.185	−1.923	6.729
5	2.433	−2.410	9.373	45	2.386	−2.149	7.680
6	1.534	−0.962	2.904	46	1.856	−1.139	2.794
7	2.327	−2.653	10.688	47	1.909	−1.492	4.492
8	1.736	−1.452	5.452	48	1.281	−0.742	1.832
9	1.966	−1.213	2.886	49	1.944	−1.578	5.758
10	1.439	−1.251	4.045	50	2.260	−2.060	6.875
11	1.717	−1.038	2.332	51	1.628	−1.116	3.442
12	1.845	−1.628	5.381	52	2.199	−1.962	8.021
13	1.295	−0.921	2.523	53	1.372	−0.571	0.674
14	2.027	−1.945	7.402	54	2.462	−2.370	8.741
15	1.721	−1.458	5.411	55	2.105	−1.653	5.653
16	2.018	−2.055	7.935	56	2.255	−2.284	8.473
17	2.006	−1.584	4.841	57	2.687	−1.969	6.114
18	1.842	−1.708	5.919	58	2.341	−2.093	7.297
19	2.265	−1.687	5.544	59	1.872	−1.414	4.221
20	1.879	−1.025	1.610	60	3.049	−3.453	14.270
21	1.668	−1.091	3.269	61	1.166	−1.209	6.999
22	2.369	−2.396	8.900	62	1.246	−0.949	4.933
23	2.612	−2.553	9.468	63	1.406	−1.864	9.809
24	1.448	−0.872	3.087	64	2.027	−1.557	6.038
25	2.184	−2.035	8.314	65	2.685	−3.463	17.215
26	1.968	−1.463	5.025	66	2.247	−2.171	9.133
27	2.101	−2.372	9.377	67	−1.445	−1.362	6.658
28	1.150	−0.305	0.804	68	2.031	−1.668	6.119
29	1.721	−0.295	1.184	69	1.661	−0.731	0.712
30	1.898	−1.478	5.441	70	1.789	−1.768	7.114
31	1.486	−0.387	−0.516	71	3.146	−3.259	13.444
32	1.139	−1.030	4.160	72	1.555	−0.874	3.784
33	1.876	−1.738	7.346	73	1.718	−1.521	5.285
34	2.041	−2.055	7.828	74	2.193	−2.130	7.772
35	2.007	−2.103	2.816	75	2.662	−2.844	11.393
36	2.697	−3.048	1.181	76	3.039	−3.264	12.806
37	1.898	−1.521	4.729	77	1.904	−2.606	11.650
38	2.324	−2.338	8.840	78	1.887	−2.240	10.029
39	2.333	−2.488	10.019	79	2.169	−1.627	5.514
40	2.228	−1.758	6.195	80	1.218	−1.372	5.584

Stem No.	a (cm/year)	b (cm/year²)	c (cm/year³)
	$\times 10^{-1}$	$\times 10^{-3}$	$\times 10^{-6}$
81	1.793	−2.163	9.553
82	1.739	−1.720	6.312
83	2.909	−3.212	12.383
84	2.745	−2.688	10.006
85	1.814	−2.025	8.469
86	1.975	−1.162	2.965
87	1.859	−1.695	6.726
88	2.297	−2.073	7.318
89	1.752	−1.526	5.483
90	2.322	−2.374	9.198
91	2.198	−1.402	4.627
92	1.996	−1.589	4.936
93	2.551	−2.074	6.672
94	1.423	−1.572	8.253
95	2.142	−1.599	4.400
96	2.308	−2.249	8.488
97	2.140	−2.332	8.886
98	2.386	−2.793	11.584
99	2.000	−1.198	3.366
100	1.746	−1.635	5.765
101	2.073	−2.199	8.634
102	1.699	−1.596	6.106
103	1.982	−2.104	7.976
104	0.714	−2.465	−3.060
105	1.986	−2.157	8.904
106	1.468	−1.326	5.218
107	1.614	−1.593	5.998
108	1.308	−1.211	4.861
109	1.689	−1.442	5.192
110	1.470	−0.987	3.258
111	1.138	−1.494	6.941
112	1.233	−0.892	3.417
113	1.901	−2.138	9.707
114	2.235	−2.645	11.497
115	3.092	−3.263	12.506
116	2.638	−3.175	12.985
117	1.522	−1.195	4.397
118	1.044	−0.430	1.611
119	2.078	−2.073	8.521
120	2.041	−2.242	9.785
121	0.621	−0.541	4.768
122	1.739	−1.229	3.956
123	1.619	−1.447	5.170
124	1.853	−1.472	5.272
125	2.466	−2.571	9.860
126	2.043	−2.261	9.568
127	1.631	−1.451	5.185
128	1.517	−1.009	3.382
129	2.160	−2.179	8.422
130	1.758	−1.857	8.201
131	2.577	−3.272	14.475
132	2.052	−1.472	5.629
133	1.987	−1.860	7.489
134	2.155	−2.433	10.996
135	2.525	−3.087	13.827
136	2.015	−1.546	5.546
137	2.158	−2.453	9.746
138	1.608	−1.431	5.236
139	2.020	−1.745	5.913
140	1.797	−1.869	8.027
141	1.532	−1.618	6.531
142	1.763	−1.446	4.458
143	1.655	−1.581	5.305
144	1.986	−1.926	7.179
145	2.500	−2.328	8.643
146	2.804	−2.785	1.112
147	1.177	−0.297	−3.103
148	1.969	−1.066	2.815
149	2.319	−2.476	10.991
150	2.402	−2.464	10.152
151	1.873	−1.697	6.122
152	1.771	−1.297	4.012
153	0.884	2.326	−0.640
154	2.239	−2.181	8.140
155	2.307	−2.142	7.550
156	2.057	−2.214	8.843
157	1.681	−1.235	3.413
158	2.060	−2.085	9.020
159	1.468	−0.977	3.021
160	1.660	−1.540	5.212

Stem No.	a (cm/year)	b (cm/year^2)	c (cm/year^3)
	$\times 10^{-1}$	$\times 10^{-3}$	$\times 10^{-6}$
161	1.828	−2.128	9.389
162	2.105	−2.536	11.100
163	2.050	−2.432	10.152
164	1.876	−1.601	5.529
165	1.228	−0.870	3.183
166	1.202	−0.930	3.671
167	1.697	−1.882	8.901
168	1.496	−1.452	5.357
169	2.008	−1.273	6.631
170	1.695	−1.771	6.431
171	1.446	−0.863	1.983
172	1.517	−1.151	3.050
173	1.529	−1.373	5.821
174	1.736	−1.403	4.919
175	2.362	−2.671	10.781
176	3.190	−3.402	12.769
177	2.402	−2.426	9.077
178	1.959	−1.734	6.548
179	2.559	−2.757	10.694
180	1.198	−0.859	2.593
181	1.552	−1.246	3.894
182	2.164	−2.201	8.599
183	1.687	−1.522	4.998
184	1.669	−1.594	6.229
185	1.776	−1.616	6.404
186	2.188	−2.220	8.031
187	1.828	−1.469	5.060
188	1.120	−0.925	3.789
189	2.065	−1.894	7.873
190	1.344	−1.226	4.403
191	1.561	−1.518	5.469
192	2.321	−2.648	10.471
193	1.585	−1.251	4.760
194	1.862	−1.676	6.403
195	1.264	−1.408	7.566
196	3.225	−3.432	12.572
197	1.308	−1.500	6.848
198	1.792	−1.244	7.216
199	2.838	−3.406	14.436
200	2.367	−2.759	11.077
201	2.108	−1.966	7.707
202	2.282	−2.167	7.723
203	2.140	−2.221	8.198
204	1.472	−0.386	−0.637
205	2.476	−1.912	5.666
206	2.023	−2.291	9.147
207	2.137	−1.703	5.893
208	3.325	−3.386	13.246
209	2.104	−2.512	10.477
210	1.846	−1.758	6.763
211	2.974	−3.669	15.265
212	2.312	−2.622	10.999
213	1.803	−1.575	6.200
214	1.853	−1.914	7.454
215	2.841	−2.775	10.329
216	2.360	−2.347	8.609
217	1.578	−1.206	4.155
218	2.860	−3.159	12.129
219	2.529	−2.482	9.460
220	1.297	−1.303	5.823
221	1.788	−1.670	5.269
222	2.402	−2.514	9.512
223	2.216	−2.298	8.560
224	1.842	−1.397	4.515
225	1.866	−1.875	6.626
226	2.317	−2.358	9.020
227	1.858	−1.408	5.033
228	2.069	−2.055	7.327
229	2.049	−1.930	7.357
230	1.704	−1.369	4.865
231	1.643	−1.384	5.551
232	1.666	−1.540	5.377
233	2.552	−2.533	9.967
234	1.571	−1.085	3.022
235	1.599	−1.394	5.149
236	2.285	−1.986	7.758
237	2.678	−2.987	11.778
238	2.146	−2.169	8.524
239	1.792	−1.104	3.806
240	2.468	−2.193	8.192

Stem No.	a (cm/year)	b (cm/year²)	c (cm/year³)	Stem No.	a (cm/year)	b (cm/year²)	c (cm/year³)
	$\times 10^{-1}$	$\times 10^{-3}$	$\times 10^{-6}$		$\times 10^{-1}$	$\times 10^{-3}$	$\times 10^{-6}$
241	2.214	−1.809	5.114	281	2.293	−2.042	7.164
242	2.168	−2.100	7.868	282	1.957	−1.556	5.059
243	2.163	−2.202	8.127	283	1.872	−2.143	9.091
244	2.013	−1.871	6.270	284	1.537	−1.580	6.622
245	1.948	−2.094	8.785	285	2.667	−2.887	11.174
246	1.875	−1.524	4.736	286	2.017	−1.936	7.299
247	2.113	−2.124	8.399	287	2.151	−2.426	10.106
248	1.469	−1.289	5.019	288	3.038	−3.502	14.091
249	2.408	−2.531	10.618	289	2.487	−2.624	10.937
250	2.439	−2.702	11.031	290	2.176	−1.917	6.857
251	1.647	−1.398	6.098	291	2.603	−2.768	11.163
252	2.368	−2.616	10.435	292	2.315	−2.259	8.359
253	1.510	−0.798	1.879	293	2.229	−2.700	11.645
254	2.228	−2.487	9.435	294	2.251	−2.309	8.634
255	1.917	−1.856	6.735	295	2.275	−1.952	6.289
256	1.787	−1.198	3.248	296	1.922	−1.857	7.115
257	1.795	−1.411	4.866	297	2.015	−1.668	5.863
258	2.155	−2.266	8.348	298	1.785	−1.592	5.242
259	2.193	−1.807	6.297	299	1.749	−1.717	6.705
260	1.667	−1.679	6.408	300	2.296	−2.159	7.516
261	2.440	−2.244	7.701	301	2.813	−2.615	9.160
262	2.905	−3.270	13.456	302	1.905	−2.211	8.826
263	1.519	−1.115	3.585	303	2.474	−3.012	13.086
264	2.451	−2.343	8.653	304	2.201	−2.329	9.119
265	1.791	−1.116	2.689	305	2.168	−1.629	4.872
266	2.866	−3.145	12.098	306	2.193	−2.042	7.458
267	1.845	−1.596	6.099	307	1.843	−1.755	6.219
268	1.771	−1.585	5.574	308	1.746	−1.981	8.990
269	1.987	−1.919	7.128	309	1.851	−1.761	6.796
270	2.008	−1.510	5.044	310	2.580	−2.439	9.034
271	1.375	−1.158	4.649	311	1.979	−2.446	10.454
272	1.383	−1.064	3.058	312	2.316	−2.229	8.176
273	1.690	−1.537	5.589	313	2.301	−2.327	9.090
274	1.796	−0.960	1.398	314	1.774	−1.290	4.832
275	1.636	−1.042	2.691	315	2.439	−2.047	7.504
276	1.861	−1.504	5.637	316	1.990	−1.804	7.060
277	1.792	−1.741	6.629	317	2.427	−2.016	7.219
278	2.024	−2.291	9.369	318	2.145	−1.705	5.311
279	1.944	−1.536	4.881	319	2.925	−3.082	11.380
280	1.872	−1.554	5.539	320	2.324	−2.403	9.279

Stem No.	a (cm/year)	b (cm/year^2)	c (cm/year^3)
	$\times 10^{-1}$	$\times 10^{-3}$	$\times 10^{-6}$
321	2.261	−2.441	9.874
322	1.840	−1.857	7.124
323	2.580	−2.250	7.469
324	1.627	−1.562	5.705
325	3.004	−3.318	12.748
326	1.446	−0.929	2.292
327	1.884	−1.743	6.183
328	1.757	−1.415	3.943
329	2.378	−2.363	8.765
330	2.563	−2.600	9.055
331	1.809	−1.816	7.216
332	1.656	−0.777	1.192
333	1.237	−0.541	1.925
334	2.797	−2.529	8.705
335	2.654	−2.256	7.342
336	1.553	−1.238	5.105
337	2.326	−1.964	6.168
338	1.563	−0.798	2.136
339	1.678	−1.138	4.617
340	1.871	−1.339	4.136
341	2.350	−2.291	8.395
342	2.434	−2.427	9.068
343	2.299	−2.111	7.515
344	3.279	−3.325	12.289
345	1.521	−1.280	4.834
346	1.865	−1.551	5.252
347	2.260	−1.522	4.464
348	2.134	−1.595	5.607
349	2.144	−1.207	2.650
Mean	2.001	−1.844	6.964
Var.	0.213	0.564	10.074
S.D.	0.462	0.751	3.174
Max.	3.325	−0.571	21.020
Min.	0.621	−3.669	−3.103
n	349	349	349
C.V.(%)	23.1	40.7	45.6

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