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GENETIC GAIN IN RADIATA PINE EXPRESSED AS GROWTH RATE MULTIPLIERS

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EXECUTIVE SUMMARY

This paper describes the methodology used to incorporate genetic gain into five radiata pine growth models. Modified growth models appear to fit the data fairly well and to be the best method of predicting yield of improved seedlots to date. Predictions of modified growth models suggest an average increase in volume over climbing select across New Zealand of 12% for GF14 and 19% for GF22 at age 25 from planting.

The extrapolation of these estimates of percent gain across stands in New Zealand should be done with caution because many untested assumptions were required for their estimation. Predictions of genetic gain for specific sites will improve as genetic gain trials mature and data from trials with spacing treatments becomes available. Further, percent gain is not the best way to measure genetic gain because it changes with rotation age.

ABSTRACT

The methodology used to modify five New Zealand growth models to reflect the differences in genetic quality of radiata pine seedlots is described. Genetic gain is assumed to be expressed through "genetic gain multipliers", that is, a decrease in the time required to achieve a certain height, and, separately, the time required to reach a specific basal area and stocking. Assumptions include no change in carrying capacity, constant density dependant relationships, and genetic gain multipliers constant with stand age, stocking, geographic region, and site quality.

Seedlot ratings from the New Zealand Seed Certification Service (GF ratings) quantify genetic quality, and, as a result of this study, can be used as input to growth models. The growth models and data from seven annual measurements of height, basal area, and stocking in six genetic gain trials aged 12 to 14 years were used to estimate genetic gain multipliers. GF14 seedlots are estimated to grow 1.048 times faster in height than the baseline growth models (assumed to be GF7) and 1.134 times faster in basal area. Based on one measurement of basal area (age 12) and on the additional assumption that the ratio of the height multiplier to the basal area/stocking multiplier is constant, a GF22 seedlot grew 1.078 times faster for height and 1.220 times faster for basal area. Six annual measurements in three trials suggest that a long internode seedlot grew faster than expected for height, but much slower than expected for basal area. A seedlot with 40% of the seed from half-sib matings grew as expected for height, but slower than expected for basal area.

Predictions of modified growth models suggest an average increase across New Zealand in volume at age 25 from planting of 12% for GF14 and 19% for GF22. The extrapolation of these estimates of percent gain across stands in New Zealand should be done with caution because many untested assumptions were required for their estimation. Predictions of genetic gain for specific sites will improve as genetic gain trials mature and data from trials with spacing treatments becomes available. Further, percent gain is not the best way to measure genetic gain because it is calculated relative to a parameter that is always changing through time, that is, the size of the unimproved trees. The modified growth models predict that percent gain reaches a peak at about age 7-10 years, then decreases as stands mature, even though the absolute difference between seedlots of differing genetic quality continues to increase.

CONTENTS

INTRODUCTION

Intensive forest management requires accurate prediction of yield. Accurate planning of wood flows from a forest estate can greatly enhance profitability of a forest enterprise, both for precise regulation of yield and for planning processing facilities. Predictions of stand growth are also used to analyse the economics of silviculture and to determine optimum time of pruning, thinning, and felling specific stands. Growth models are the basic tools used by forest managers to predict stand yield (Goulding 1993).

The growth models for radiata pine (*Pinus radiata*), which are used routinely by most forestry organisations in New Zealand, are based on a state-space model comprising a set of stochastic differential equations (Garcia 1979, Garcia 1983, Garcia 1984). Predictions of the stand parameters of top height, basal area, and stems per hectare depend solely on their values at a previous point in time. The coefficients are simultaneously estimated using maximum likelihood techniques. Seven growth models of this type have been constructed using data from annual assessment of permanent sample plots in seven different growth regions (Goulding 1993).

The New Zealand forest industry has extensively utilised the genetically improved planting stock resulting from intensive tree improvement. Since 1985, improved stock has been used in virtually all of the radiata pine plantings in New Zealand, and an increasing amount (about 10% in 1993) is derived from control crosses among the best parents. With an appreciation of the difference between improved and unimproved stock, New Zealand's forest managers now demand that growth models accurately predict unit-area wood volume of genetically improved stock.

New Zealand's tree breeders have reliably selected the fastest growing parents from progeny trials, where all candidates for selection are grown inter-mixed in "common garden" trials (Carson et. al. 1990). These trials are particularly useful for ranking parents for their growth potential. However, since competition (when expressed as tree stocking) has such a profound effect on final tree size and unit area yield, inter-tree competition is likely to be an important determinant of final tree size. Therefore, accurate measurement of changes in yield in forest stands with genetically improved stock requires comparison of improved and unimproved stock planted, not in mixtures as in progeny trials, but as "pure" stands, or in large-block trials.

The first significant amount of data from large-block trials, called realised genetic gain trials, is now available for radiata pine in New Zealand. The trials contain large blocks of trees from seedlots representing several levels of performance in progeny trials. This paper describes how seven annual measurements of trials up to 12 to 14 years old and planted on six sites have been used to incorporate genetic gain into five of New Zealand's seven regional growth models. Several assumptions, which can be tested as data accumulates, about the nature and expression of genetic gain are required. The growth model modifications represent the best available information on the expected growth of improved radiata pine in New Zealand.

This report 1) proposes a new method for quantifying genetic gain expressed as changes in growth rate, 2) quantifies the increase in growth rate with several levels of genetic improvement of radiata pine in New Zealand using growth data from the large-block genetic gain trials and the New Zealand Growth models, and 3) validates this estimate using trial data not used for estimation.

MATERIALS AND METHODS

Genetic gain trials

Genetic gain trials were planted across New Zealand in the late 1970's in two series. The "1978 genetic gain trials" were planted in 1978 on seven sites, and the "1979 genetic gain trials" were planted on two sites in 1979, and on one site in 1980 (Table 1, Figure 1). Seedlots in these trials were planted in large blocks (ten by ten trees) in a randomised complete block design with six replications. Silviculture at all sites was a direct sawlog regime planted at 1111 stems per ha with thinning to 300 stems per ha in two stages, and pruning in three lifts to 6.2m. In addition, at one site of the 1978 trials (RO2103/2) a pulpwood regime with 711 stems per ha, no thinning, and pruning to 2.2m only was also planted in a randomised complete block design with six replicate blocks of eight by eight tree plots.

Circular permanent sample plots (PSP's) (Skinner 1994) were established in 1986 in a subset of seedlots in five of the "1978 trials" and in all of the "1979 trials". PSP's were established in two seedlots in the "1978 trials" and four seedlots in the "1979 trials" (Table 1). PSP's were measured annually for eight years for mean top height, basal area, diameter, and stocking. In addition to the PSP assessments, diameter was measured on all trees from four seedlots in the "1978 trials" (including the two seedlots with PSP's) in 1983 (age 5) and again in 1990 (age 12) (Table 1).

An initial crop stocking trial (RO972) was planted on one site in 1970 (Figure 1). The trial compared different initial crop stockings leading to the same final crop stocking (James 1979, McClaren and Kimberley 1990). Treatment blocks were 0.2 ha. For one of the silvicultural treatments (1500 stems per ha thinned to 250 stems per ha in three stages at ages five, six, and seven year from planting), there were two seedlots of differing genetic worth with two replicate blocks of each. PSP's were established in 1975 and measured for diameter, height, and stocking annually until 1983, then every two years. Height was measured on a sub-sample of trees, often a different sub-sample at each measurement.

Genetic worth of seedlots in genetic gain trials

The New Zealand Seed Certification Service rates radiata pine seedlots based on their genetic worth, which is largely determined by performance of parents in progeny trials (Vincent 1987). The GF rating, a rating for the Growth and Form breed, reflects a seedlot's genetic worth for growth and form characteristics combined. One class of seed, climbing select seed, that is, seed collected from the best trees before a stand is felled, was planted widely in New Zealand from about 20-25 years ago until the early 1980's. Most of the data used to construct the current set of growth models is probably of climbing select origin. Climbing select seed is used as a bench mark for seed certification and is arbitrarily assigned a rating of GF7. The genetic gain trials often included local sources of climbing select seed (Table 1), which have not been tested in any other trials.

Seedlots that have performed worse than climbing select lots are assigned a lower GF rating, and seedlots made up of seed from parents whose progeny have performed better than climbing select seedlots are assigned progressively higher and higher GF ratings. Seed from the first clonal seed orchards in New Zealand produced the genetically best seed available in New Zealand until the mid 1980's. These orchards, typified by the Gwavas Seed Orchard seed, consisted of 25 parents and are used as another bench mark in the certification system, rated as a GF14. Seed from the very best parents produced in 1993 in control pollinated orchards are rated GF30. Ratings of seedlots in genetic gain trials can be found in Table 1.

Since genetic worth for growth and genetic worth for form are confounded in GF ratings, genetic worth for growth was separated from genetic worth for form traits (where possible) for the seedlots in the genetic gain trials by examining progeny test data. The performance of the parents represented in the seedlots for diameter was compared with the performance of the climbing select and Gwavas seed orchard control seedlots in progeny trials. Parents represented in seedlot FRI 78/2300 performed much like the Gwavas orchard control in progeny tests (Shelbourne *et. al.*, M. Carson, unpublished data) (Table 2), and was, therefore, subsequently treated as a GF14 for estimation of increases in growth rate. Other seedlots performed in progeny trials for tree size as would be expected from their GF rating.

The two seedlots present in the Initial Crop Stocking trial (RO972) were R/67/795, a felling select seedlot (which is similar to climbing select except seed was collected after felling), and WN/68/A1, a very early collection (before the orchard was producing much pollen) of first orchard seed. These seedlots are not represented in any other trials, and would be expected to perform slightly poorer than a GF7 and a GF14, respectively.

New Zealand Growth Models

New Zealand has growth models for seven growth modelling regions (Goulding 1993). Models which predict stand growth were built for each region from PSP survey data, which was collected mostly from climbing select stock (GF7) (P. Wilcox, unpublished data). In five of these regions, changes in site quality (as represented by site index) effected both height and basal area growth in the same way. In these five regions, stand growth is represented by the three functions:

$$
\begin{aligned}
H_{t+1} &= f_1(H_t) \\
B_{t+1} &= f_2(H_t, B_t, N_t) \qquad (1) \\
N_{t+1} &= f_3(H_t, B_t, N_t)
\end{aligned}
$$

where

t = *time t,*

B = *basal area per ha,*

N = *stems per ha, and*

H = *mean top height.*

The functions of f_1, f_2, and f_3 are a multivariate extension of the Bertalanffy-Richards growth model (Garcia 1979, 1983, 1984, 1988a & b, 1989).

Application of genetic gain multipliers to New Zealand Growth Models

Approach and assumptions

Since little is known about growth patterns of improved stands as compared to unimproved stands, assumptions were required in order to use the growth models to estimate increases in growth rate. The assumptions we have adopted are those which simplify incorporation of genetic gain into the structure of the New Zealand growth models. These assumptions appear to be as valid as any others, given the limited knowledge about growth of improved trees in "pure" stands of improved trees.

Growth rate differences reflecting genetic gain were expressed in growth curves as a time-scale compression and quantified as a "time-scale" or "growth rate" multiplier. The assumption is made that improved trees reach the same size in the same way, but reach it more quickly. The only effect of genetic improvement is assumed to be a compression of the time scale. Therefore, we assumed that there will be no increase in carrying capacity with genetic gain and that density dependant relationships are assumed to be the same in improved and unimproved stands. This assumption is "minimal" in so far as in the absence of any evidence to the contrary, only the time taken for a stand to develop is altered. All other growth characteristics of the improved stand remain the same as an improved stand.

The New Zealand growth models were assumed to represent growth of climbing select (GF7) seedlots and thus provide a base line of performance for unimproved seedlots. Since the mechanism of growth is different for height growth than for diameter growth, that is, meristematic growth versus cambium growth, the increase in growth rate in height and the increase in growth rate in basal area with genetic improvement were allowed to be different. Growth rate increases were assumed to be constant over the life of a stand, silvicultural regimes, sites, and regions. These last assumptions are necessary because there is little or no data which would allow the estimation of the differences in changes with stocking, stand age or size, or site type. However, they can be tested as the genetic gain trials used in this analysis age and as genetic gain data from trials with a range of silvicultural treatments becomes available.

Genetic gain multipliers in the prediction equations

The function for height (H) (the first equation in *(1)*) is self-contained and can be examined separately from the functions for basal area (B) and stocking (N). We will therefore present the manner in which a genetic gain multiplier was applied to H, before considering B and N.

The height growth function in the growth model system, is defined as a differential equation:

$$\frac{dH^c}{dt} = a(H^c - b) \qquad (2)$$

where a, b and c are fitted model parameters.

On solving, this gives:

$$H^c = b(1 - e^{at})$$

Under the assumption that genetic gain should operate as a 'time-scale' multiplier, the equation, incorporating the multiplier, m, will be of the following form:

$$H^c = b(1 - e^{amt})$$

where $m=1.0$ implies no genetic improvement,
$m>1.0$ implies an increase in height growth.

To estimate a value for m using field measurements, we first note that:

$$
\begin{aligned}
(H_t^C - b) &= e^{amt} \\
&= e^{am(t-1)} e^{am} \\
&= (H_{t-1}^C - b) e^{am}
\end{aligned}
\qquad (3)
$$

therefore,

$$
m = \frac{1}{a}(ln(H_t^C - b) - ln(H_{t-1}^C - b) \qquad (4)
$$

where

H_t = *height at time t*

$H_{t\text{-}1}$ = *height at previous measurement,*
assumed for simplicity to be one year earlier

This expression provides the basis for estimating m from field measurement pairs of height, as will be explained later.

We will briefly show how the procedure outlined above for height was extended to incorporate basal area and stocking.

The multivariate equivalent of *(2)* is:

$$
\frac{dx^C}{dt} = Ax^C + b
$$

where

$$
x^C = \begin{bmatrix} H^{C_{11}} & 0 & 0 \\ H^{C_{21}} & B^{C_{22}} & N^{C_{23}} \\ H^{C_{31}} & B^{C_{32}} & N^{C_{33}} \end{bmatrix}
$$

$$
A = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}
$$

$$
b = \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix}
$$

The c_{ij}, a_{ij} and b_i being the fitted model parameters.

Following through the development used for height (*H*) above, leads to the multivariate equivalent of *(3)*:

$$\left(x_t^C - b\right) = P^{-1} e^{m \wedge} P\left(x_{t-1}^C - b\right) \qquad (5)$$

where $\wedge$ is a diagonal matrix containing the eigenvalues of *A* and the rows of *P* are the eigenvectors of *A* so that

$$A = P^{-1} \wedge P$$

and *M* is a diagonal matrix containing the genetic gain multipliers, that is,

$$M = \begin{bmatrix} m_1 & 0 & 0 \\ 0 & m_2 & 0 \\ 0 & 0 & m_3 \end{bmatrix}$$

where m_1, is the multiplier for *H* (i.e. *m*, above) and $m_2 = m_3$ is the multiplier for *B* (or equivalently, *N*).

The above expression *(5)*, consists of three simultaneous equations:

$$m_i = \frac{1}{\lambda_i}\left[ln\left(\sum_j P_{ij}\left(x_{jt}^C - b_j\right)\right) - ln\left(\sum_j P_{ij}\left(x_{j(t-1)}^C - b_j\right)\right)\right] \qquad (6)$$

$$\textit{for } i = 1, 2, 3.$$

The equation for $i = 1$ is equivalent to *(4)* since $p_{12} = p_{13} = 0$, $p_{11}=1$ and $\lambda_1 = a$. The equations for $i = 2, 3$ can be used for estimating m_2 and m_3 which are constrained to be equal.

Estimation of Genetic Gain Multipliers

For seedlots rated GF14, inbred GF14, and LI19(GF8).

A significant amount of PSP data was available from seedlots rated GF7, GF14, GF14 (inbred), and LI 19(GF8) (Table 1). To estimate the multiplier for height (*H*) we firstly obtained y_{tgrs}, the value of *(4)* for each measurement pair in each plot, where

t	=	*year of second assessment for each annual measurement pair*
g	=	*seedlot GF rating*
r	=	*replication number*
s	=	*site*

The genetic gain time scale multipliers for a seedlot with genetic worth g_2 (for example, GF14) over a seedlot with a lower genetic worth g_1 (for example, GF7) were calculated as the difference in values of equation *(4)* for the two seedlots. Estimates of the genetic gain time scale multiplier for the mean top height prediction equation were obtained for g_1 = GF7 and for g_2 = GF14, g_2 = GF14 (inbred), and g_2 = LI 19(GF8) (Table 1) as

$$m_{g1/g2} = 1 + \left[\sum_s \left[\sum_t \left[\sum_r \left(Y_{t g_2 r s} - Y_{t g_1 r s} \right) \right] / n_r \right] / n_t \right] / n_s .$$

where n_r, n_t, n_s are the number of reps, measurement pairs and sites respectively. Because errors from annual measurement pairs from the same plots are likely to be correlated, means were obtained for each annual increment within each site and examined for bias. Estimates of multipliers for each site were also inspected.

A similar procedure was adopted for estimating the multiplier for basal area (*B*) an stocking (*N*), firstly obtaining y_{2tgrs} and y_{3tgrs}, the values of the second and third equations in *(6)* for each measurement of seedlot g_2 against seedlot g_1. The genetic gain multiplier was estimated as:

$$m_{g1/g2} = 1 + \left[\sum_s \left[\sum_t \left[\sum_r \sum_{i=2,3} \left(Y_{t g_2 r s} - Y_{t g_1 r s} \right) w_{isr} \right] / n_r \right] / n_t \right] / n_s .$$

In this expression, the values from the second and third equation in *(6)* are combined using the weighting w_{isr}, based on the estimated variance of (y_{itg_2rs}- y_{itg_1rs}) within a site and assessment year.

<u>For seedlots rated GF2 and GF22</u>

Only very limited data was available for seedlots rated GF2 and GF22 (Table 1). A genetic gain time scale multiplier was estimated graphically assuming the ratio of the height multiplier to the basal area/stocking multiplier to be the same as for the GF14 multipliers estimated as described above. Values for the multipliers for both height and stocking were obtained which best fitted the 12 year assessment of the GF2 and GF22 seedlots, which was available only for basal area and diameter and only on three sites.

Validation of genetic gain multipliers

Genetic gain multipliers were validated in two ways: by comparing the data to the model predictions for the trials from which the genetic gain multipliers were estimated, and by comparing data from a site not used for multiplier estimation. The program GROPAK was used to calculate model predictions using site indices and silvicultural regimes listed in Appendix 1. Site indices were projected from existing data. Plots of both predicted and measured mean top height, basal area per ha, quadratic mean diameter, and volume per ha were produced for all sites used to estimate the multiplier using the growth models listed in Table 1, and for the initial crop stocking trial (RO972) using PPM88.

Data from the two genetic gain trial sites not used for multiplier estimation, AK1058 and WN377, were plotted in order to see if genetic gain was also occurring on these sites.

Model predictions to age 50 were obtained for all genetic gain trials and the initial crop stocking trial, both with and without the genetic gain multipliers. Since genetic gain has been traditionally expressed as a gain in percent of the mean, percent gain was calculated and plotted for each site at ages 1-50 for mean top height, basal area per ha, diameter, and volume per ha. For example, percent mean top height at a specific age was calculated as follows.

$$P_{H g_1/g_2} = \frac{\left[H_{g_2} - H_{g_1}\right]}{H_{g_1}}$$

where

$P_{H g1/g2}$ = *percent gain in mean top height of seedlot* g_2 *over seedlot* g_1,
H_{g_2} = *predicted mean top height of seedlot* g_2, *and*
H_{g_1} = *predicted mean top height of seedlot* g_1.

Percent gain in basal area per ha, diameter, and volume per ha were calculated similarly.

RESULTS

Estimation of genetic gain growth rate multipliers

GF14 multipliers

Genetic gain multipliers representing the improvement from using GF14 over GF7 were greater than 1.0 for both basal area and height (Table 3), although the height multiplier was not significantly so. The multiplier for basal area and stocking equations was three times as large as for mean top height. Average multipliers for mean top height were not greater than 1.0 for all measurement intervals (Figure 2 and Appendix 2), but there did not appear to be a consistent trend with age. The multiplier for the basal area and stocking equations was consistently greater on some sites than others, with no consistent trend with age (Figure 3 and Appendix 2). The two obvious outliers in Figure 3 were the result of mortality in the one genetic gain site which remained unthinned (RO2103/2).

Model predictions appeared to fit the data very well for some sites and reasonably well for others (Appendices 3 and 4). The difference between the predictions for the GF7 and GF14 seedlots was in most cases very close to the actual measured difference. Fit was reasonable for mean top height, basal area per ha, volume per ha, but best for quadratic mean diameter.

The prediction of genetic gain was close to the actual difference for the site (RO972) which did not contribute to the overall multiplier estimate (Appendix 5). The model appeared to over predict growth at the older ages, but the predicted difference between the improved and unimproved was very close to the actual difference. Genetic gain on the two sites with growth models for which multiplier estimates could not be calculated (AK1058 and WN377) was evident (Appendix 6). Gain on the Hawke's Bay site (WN377) appeared especially high.

GF2 and GF22 multipliers

Estimates of the GF2 height and basal area/stocking multipliers were lower than 1.0 (the GF7 multiplier) (Table 3). Estimates of the GF22 multipliers were both higher than the GF14 multiplier. The predictions made using the GF2 and GF22 multipliers appeared to fit the data reasonably well (Appendix 4). There was very little data to fit, however, and the magnitude of these multipliers depends heavily on the assumption of the same ratio of gain for height as for diameter, which has not been tested. There appears to be a strong relationship of the GF2, GF7, GF14, and GF22 multipliers and GF rating (Figure 4).

Other seedlots

The mean top height multiplier estimated for the long-internode seedlot (LI19(GF8) was greater than for the GF14 seedlot, but the basal area/stocking multiplier estimate was substantially lower (Table 3, Appendix 7). The height multiplier estimated for the inbred GF14 seedlot was about the same as that estimated for GF14 non-inbred seedlots, but the basal area/stocking multiplier was lower than for GF7 (Table 3, Appendix 8).

Genetic gain at rotation age

Predictions of genetic gain using growth model multipliers showed the absolute difference between seedlots increasing until age 25 and in most cases until age 50 (Appendix 9). The predicted percentage gain varied with stand variable, GF rating, rotation age, site, and with the base line seedlot used as the denominator in the percentage calculation. Average percent gain in height was the lowest of the stand variables (5.5% for GF22 at age 25), and percent gain in volume was the highest (18.8% for GF22 at age 25). Percent gain increased with GF rating and decreased from a 25 year to a 30 year rotation age. Use of a seedlot with a lower GF as a baseline rating increased the percent gain substantially. Predicted percentage gain was different on different sites, but predicted gain in volume for GF22 was greater on all sites than predicted gain for GF14 on any site.

The average percent gains in volume calculated at a rotation age of 25 years were about 12 percent for a GF14 and about 19 percent for GF22.

The level of percent gain was highly variable to age 50 (Appendix 10). The usual pattern for percent gain for all four stand variables was a peak at about 8-10 years, then a steady decline, but not disappearance, at age 50. Percent gain varied within the range of conceivable rotation ages, that is, from age 15 to 40 years (Figure 5). Differences in percent gain with age were greater when the genetic difference between the seedlots was greater, that is, greater for the comparison of GF7 and GF22 than for the comparison of GF7 and GF14.

DISCUSSION

The magnitude of genetic gain in New Zealand radiata pine

Increased growth can be expected from using improved radiata pine in New Zealand. If the seven genetic gain trial sites are assumed to be representative of all forest sites in New Zealand, the assumptions used to estimate the multipliers are true, and the growth models yield accurate predictions, volume per ha at age 25 can be expected to be increased over climbing select stands (GF7) by an average of about 12 percent for GF14 seedlots and about 19 percent for GF22 seedlots. Higher GF ratings will probably yield even greater increases in volume.

Although gain from genetic improvement of forest trees has been traditionally expressed as a percent of the mean, this measure should be used with caution. The percent gain will change throughout the life of a stand, even though the difference between the improved and unimproved will probably steadily increase. Percent gain is influenced heavily by the size of the tree (the denominator of percent gain), and thus also indirectly by silvicultural history and site conditions. Further, the percent gains in the different stand parameters, that is, mean top height, basal area per ha, average diameter, and volume per ha for a stand are not the same. A more accurate method of quantifying the increase in growth resulting from genetic selection is desirable in order to take into account different patterns of regional growth, silvicultural regimes, site qualities, and harvesting ages.

The nature of genetic gain in New Zealand

Estimation of the growth rate multipliers using the methods described allows changes in the rate of height growth with genetic selection to be different than changes in the rate of basal area growth. Genetic selection in New Zealand radiata pine appears to have increased basal area growth more than height growth. The change in the rate of increase of basal area for the growth and form breed was about three times the change in rate of increase in mean top height. This indicates that benefits from using genetically improved stock from the growth and form breed will be greater than what would be predicted from increasing in site index alone. Additional growth in basal area must be taken into account in order to make accurate prediction of volume per ha.

In contrast, the rate of height growth for the long-internode breed appeared to be increased more than would be expected for it's seed certification rating of GF8, but basal area growth was much slower than expected. If the limited amount of data used to obtain these estimates is representative, an increased capacity for height growth and a substantially decreased capacity for basal area growth may be characteristic of the long-internode habit. In addition, inbreeding appeared to reduce basal area growth but not to effect height growth. Clearly, inbreeding should be avoided in production crosses.

Genetic gain "growth rate" multipliers

The expression of genetic gain as a change in growth rate is intuitively appealing. Growth models are used to quantify the effects of silviculture, region, and site quality, and represent the best understanding of how these influence final stand volume. Modification of growth models to reflect genetic improvement as a change in the rate of growth yields predictions of genetic gain which take tree size, and all the important factors which influence it, into account.

Assumptions are required for implementation of the concept of genetic gain as an increase in growth rate. The validity of these assumptions can be directly tested using the models and the genetic gain trial data which will become available as these trials age and as large-block trials with spacing treatments yield information. For example, the hypothesis that age, site quality, spacing, and other conditions affecting tree growth do not alter the magnitude of the multiplier can be tested as soon as future trial data is available.

The growth rate multipliers were estimated under the assumption that the asymptote of the growth curves did not increase with genetic selection. Many tree breeders believe that this will not be the case, but that genetic selection for faster growth will result in an increased carrying capacity of the site. This assumption did not appear to have a large effect on the volume predicted at a rotation age of 25-30 years, especially with a direct sawlog regime, because this age was well before the asymptote was reached. If longer rotation ages or tighter stockings were considered, this assumption might have a very important effect on the volume at harvest age.

The concept of genetic gain expressed as a change in the time taken to obtain a change in a stand parameter can be implemented in other growth models. It is a simple concept which can be added to many types of growth models without re-estimating parameters from raw data. Use of the concept of a multiplier also allows prediction for circumstances, that is, regions, site qualities, and silvicultural regimes for which no data is available. Predictions of this type, that is, outside the range of data from which a model was built, must always be used with caution. However, these predictions may be more accurate than applying a fixed percent gain to stands which have different site qualities and silvicultural histories. In any case, trials should be designed and planted to test model predictions, as well as, assumptions required for implementation.

Implementation of growth rate multipliers in New Zealand

The genetic gain multipliers for GF2 to GF22 have been implemented in five of the seven regional growth models used in New Zealand. Straight line extrapolations have been made between the estimated genetic gain multipliers for ratings between GF2, GF7, GF14, and GF22. GF rating can be specified in the models used to estimate the multipliers, that is, PPM88 (the Pumice Plateau), Nelson region (Golden Downs), and Southland. In addition, GF rating can be specified for the Auckland Clays and the Canterbury region, even though no genetic gain data is yet available from these regions.

By using the modified growth models with genetic gain multipliers, growth differences related to site quality, silvicultural regime, and regional variation in growth patterns are taken into account. However, predictions at rotation age, especially for silvicultural regimes not represented by the genetic gain trial data used to estimate the multiplier, are highly dependant on the assumptions required for multiplier estimation. The predictions are the best that can be made until data illustrating genetic gain on additional sites and with different regimes is available. As this data accumulates, growth model predictions can be made more accurate and dependable.

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Table 1. Seedlots used to estimate genetic gain growth rate multipliers.

Site	Planting	Unimproved seedlot		Improved seedlot				
	Year	GF2[1]	climbing select (assumed GF7)	GF14	≈GF22[1]	LI19(GF8)	inbred GF14[2]	regional growth model
<u>1978 genetic gain trial:</u>								
RO2103/1	1978	Kaingaroa Bulk	Kaingaroa R/76/01	Gwavas SO WN/76/3	850-55 x 850-96	-	-	PPM88
RO2103/2	1978	"	"	"	"	-	-	"
NN530/2	1978	"	Golden Downs NN/C/75/2	"	"	-	-	Golden Downs
AK1058	1978	"	Kaingaroa R/76/01	"	"	-	-	-
WN377	1978	"	Ngaumu WN/C/75/15	"	"	-	-	-
<u>1979 genetic gain trial:</u>								
RO2103/3	1979	-	Kaingaroa R/76/01	FRI 78/2300[3]	-	FRI 78/2301	FRI 78/2299	PPM88
NN530/1	1979	-	"	"	-	"	"	Golden Downs
SD682	1980	-	Rankleburn[4] SD/C/76/2	"	-	"	"	Southland

1. PSP's not established in these seedlots
2. Forty percent of seed were crosses between half-sibs.
3. Rated approximately GF18, but performs like GF14 for growth.
4. Seedlot not part of trial. PSP's established in surrounding stand.

Table 2. Growth performance of "268" series seedlot (FRI 78/2300) in 1968 "268" series progeny test (Kaingaroa, Cpt 1350).[1]

Seedlot	GF	Mean diameter (age 10)
Top 16 parents	GF19	262.88
FRI 78/2300[2]	≈GF18	250.54
R68/A1	GF13	248.75

1. M. Carson, unpublished data
2. Seedlot FRI 78/2300 performing like a GF14 for growth

Table 3. Genetic gain multipliers for growth and form seedlots (GF2, GF7, GF14 and GF22), a long internode seedlot (LI 19(GF8)), and a growth and form seedlot (GF14) which is highly inbred.

Breed and seed certification rating	growth rate multiplier	
	mean top height	basal area/stocking
Growth and Form Breed:		
GF2	0.960	0.890
GF7	1.000	1.000
GF14[1]	1.048	1.134
GF22	1.078	1.220
Long Internode Breed:		
LI 19(GF8)	1.069	0.892
Inbred Growth and Form Breed:		
GF14	1.052	0.976

1. Or growth rate equivalent to GF14.

Table 4. Average percent gain (seven sites) of GF14 and GF22 seedlots over a GF7.

GF rating	rotation age	site	average percent gain: mean top height	basal area (per ha)	diameter (quadratic mean)	volume (per ha)
Base line seedlot = GF7						
GF14	25	RO2103/1	3.2	7.7	4.1	11.1
		RO2103/2	3.2	6.9	4.8	10.3
		NN530/2	3.7	9.0	6.1	12.8
		RO2103/3	3.3	7.9	4.1	11.2
		NN530/1	3.7	11.5	7.3	15.0
		SD682	3.4	6.3	3.9	10.0
		RO972	3.1	7.7	4.2	10.9
		Mean	**3.4**	**8.1**	**4.9**	**11.6**
GF14	30	RO2103/1	2.6	6.8	4.1	9.7
		RO2103/2	2.9	6.0	5.0	8.8
		NN530/2	3.1	8.2	5.9	11.2
		RO2103/3	2.9	6.9	4.0	10.0
		NN530/1	3.0	9.7	7.3	12.8
		SD682	3.3	6.7	4.6	9.8
		RO972	2.6	6.8	3.7	9.5
		Mean	**2.9**	**7.3**	**4.9**	**10.2**
GF22	25	RO2103/1	5.2	12.2	6.6	17.9
		RO2103/2	5.2	10.9	7.7	16.5
		NN530/2	6.0	14.6	9.7	21.0
		RO2103/3	5.3	12.5	6.6	18.1
		NN530/1	6.0	18.2	11.8	24.6
		SD682	5.7	10.4	6.5	16.4
		RO972	5.0	12.2	6.4	17.6
		Mean	**5.5**	**13.0**	**7.9**	**18.8**
GF22	30	RO2103/1	4.4	10.9	6.4	15.6
		RO2103/2	4.4	9.5	7.7	14.0
		NN530/2	4.8	13.3	9.7	18.1
		RO2103/3	4.7	10.9	6.4	15.9
		NN530/1	4.5	15.4	11.6	20.4
		SD682	5.0	10.9	7.4	16.1
		RO972	4.3	10.8	6.0	15.2
		Mean	**4.6**	**11.6**	**7.9**	**16.5**

See page 24 for "Base line seedlot = GF2"

GF rating	rotation age	site	average percent gain mean top height	basal area (per ha)	diameter (quadratic mean)	volume (per ha)
Base line seedlot = GF2						
GF22	25	RO2103/1	8.4	20.6	10.8	30.0
		RO2103/2	8.4	18.5	12.5	27.6
		NN530/2	9.8	24.5	15.4	35.4
		RO2103/3	8.3	20.9	11.0	30.6
		NN530/1	9.4	31.5	19.5	42.6
		SD682	9.5	16.5	10.2	26.5
		RO972	8.1	20.5	10.4	29.7
		Mean	**8.9**	**21.9**	**12.8**	**31.8**
GF22	30	RO2103/1	7.2	18.5	10.2	26.4
		RO2103/2	7.0	16.1	12.4	23.8
		NN530/2	7.6	22.1	15.9	30.7
		RO2103/3	7.3	18.5	10.4	26.8
		NN530/1	7.5	26.7	19.1	35.5
		SD682	8.0	17.4	11.4	26.1
		RO972	6.8	18.0	9.9	25.6
		Mean	**7.3**	**19.6**	**12.8**	**27.8**

Figure 1. Location of genetic gain trials used to estimate genetic gain growth rate multipliers.

Location of Genetic Gain Trials

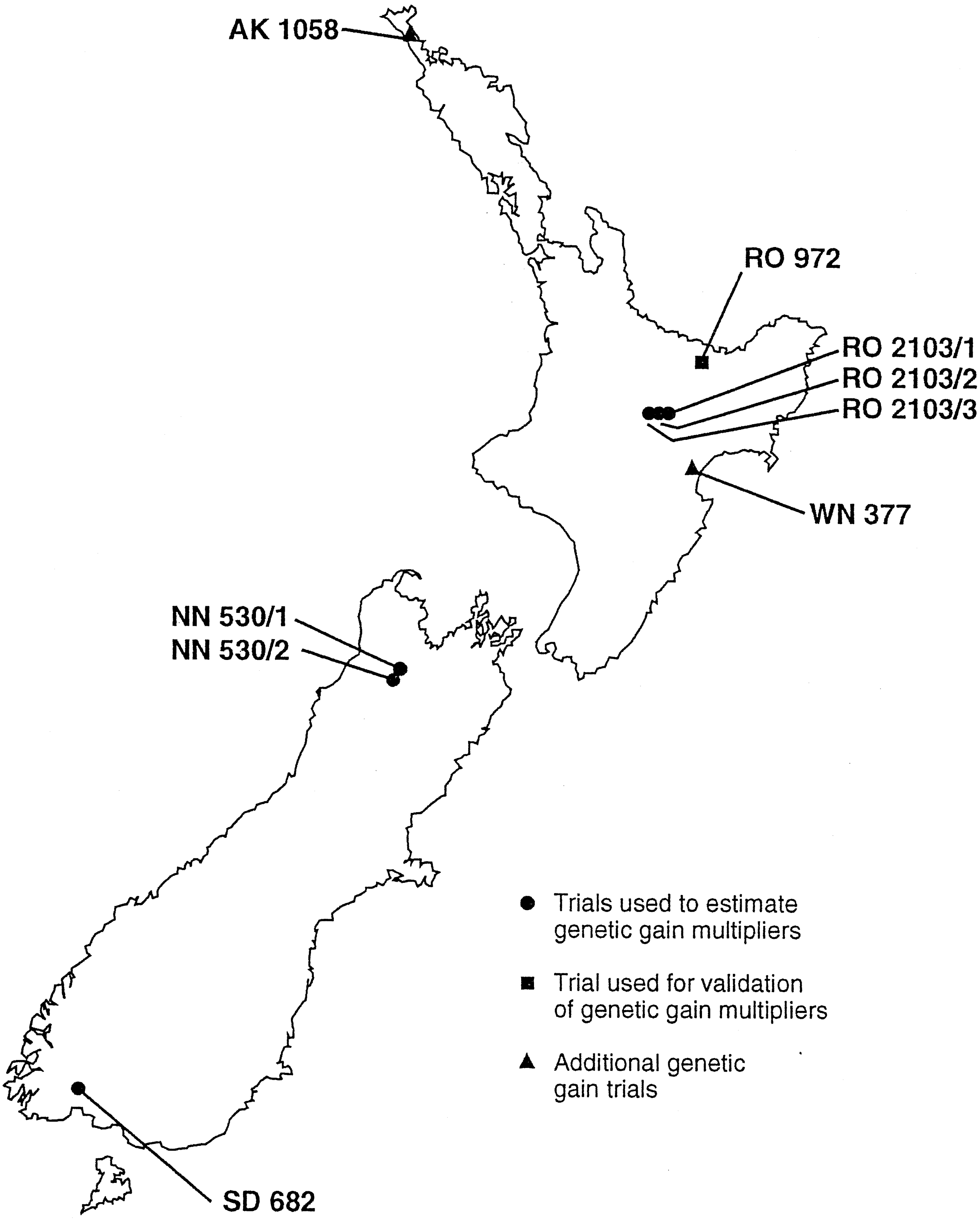


Figure 2. GF14 genetic gain multipliers for height growth by site and year.

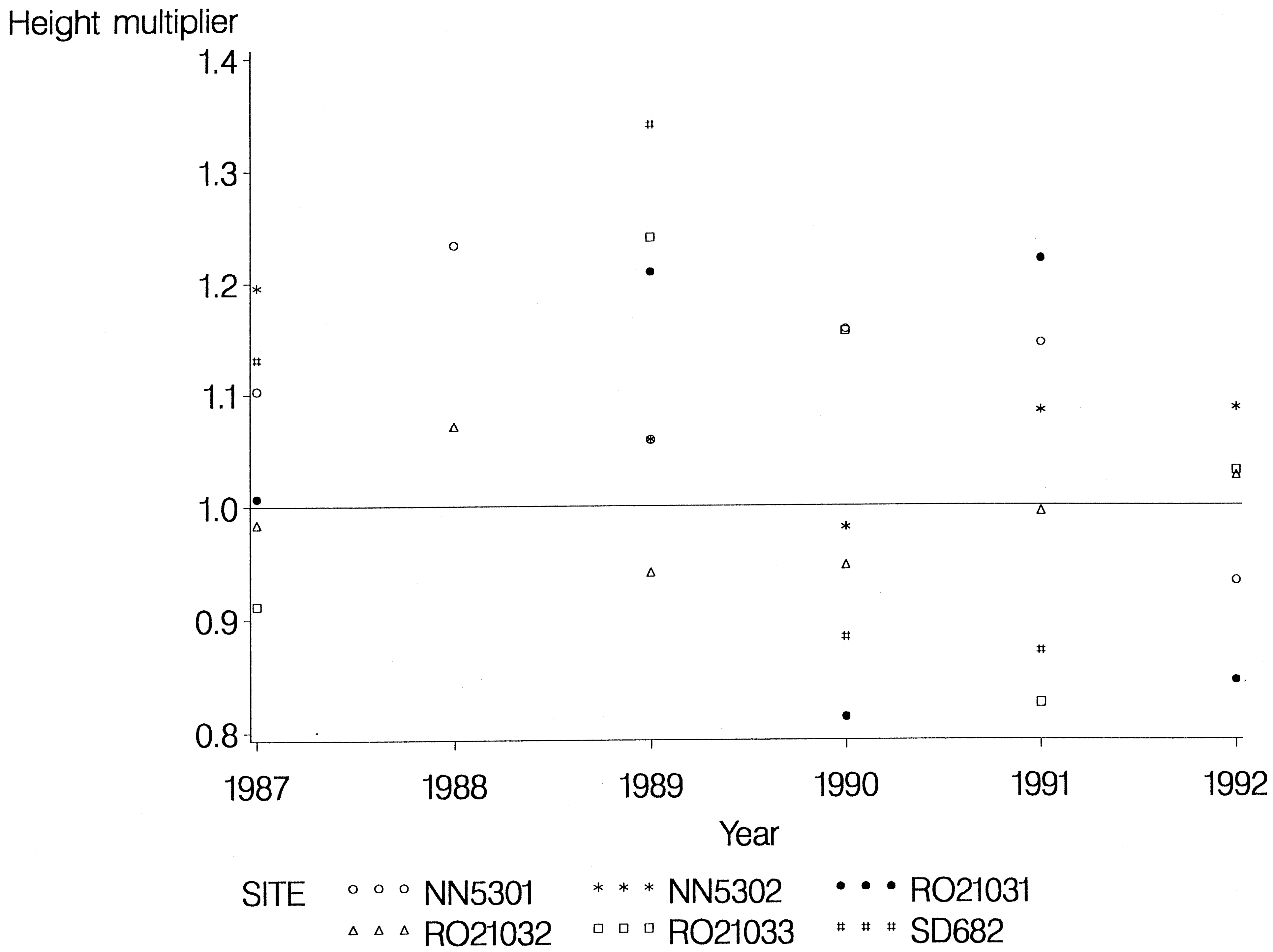

Height multiplier
1.4
1.3
1.2
1.1
1.0
0.9
0.8
1987
1988
1989
1990
1991
1992
Year
SITE
NN5301
NN5302
RO21031
RO21032
RO21033
SD682

Figure 3. GF14 genetic gain multipliers for basal area growth by site and year.

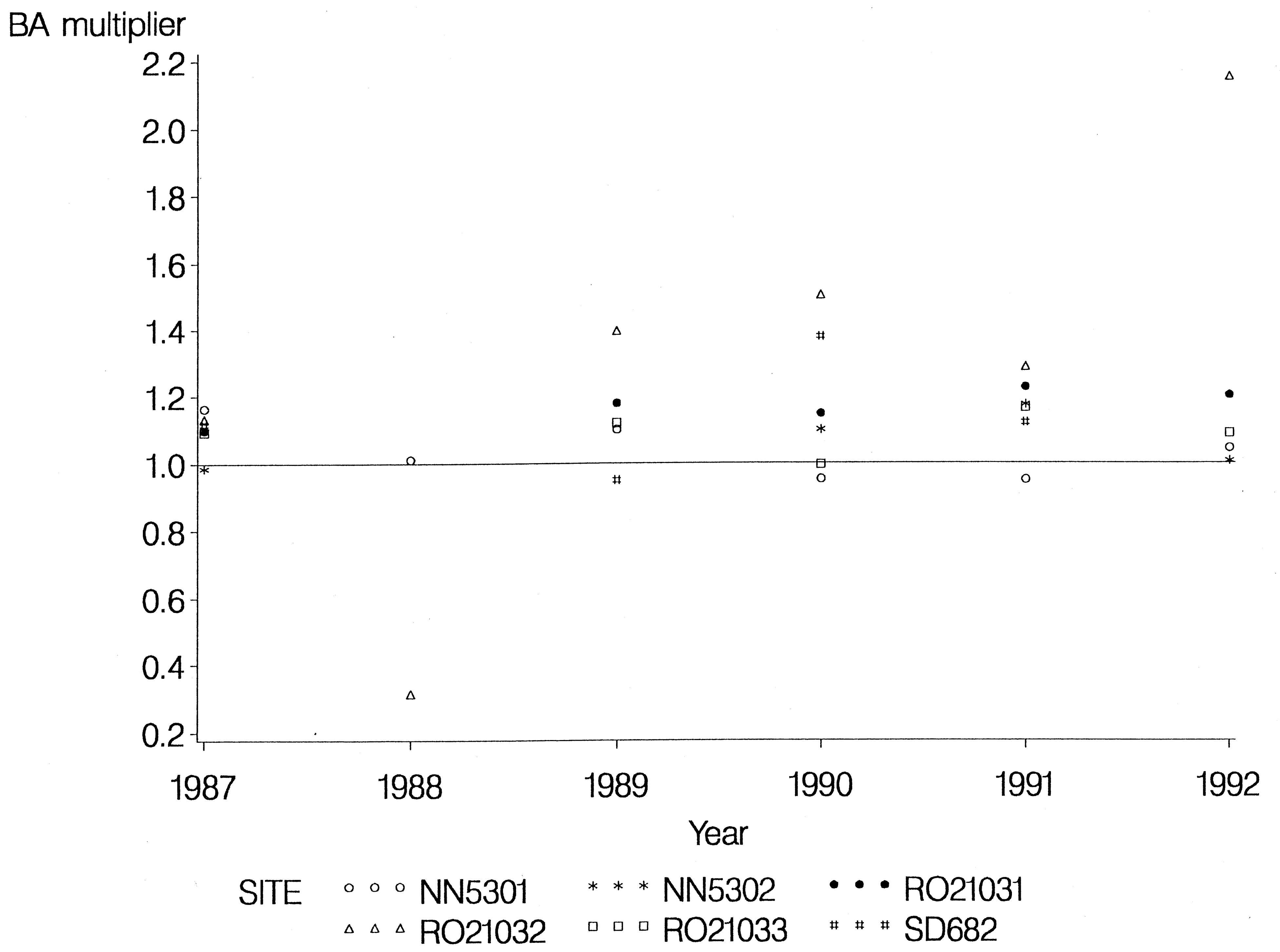

BA multiplier
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
1987
1988
1989
1990
1991
1992
Year
SITE
NN5301
NN5302
RO21031
RO21032
RO21033
SD682

Figure 4. Relationship of genetic gain multipliers to GF rating.

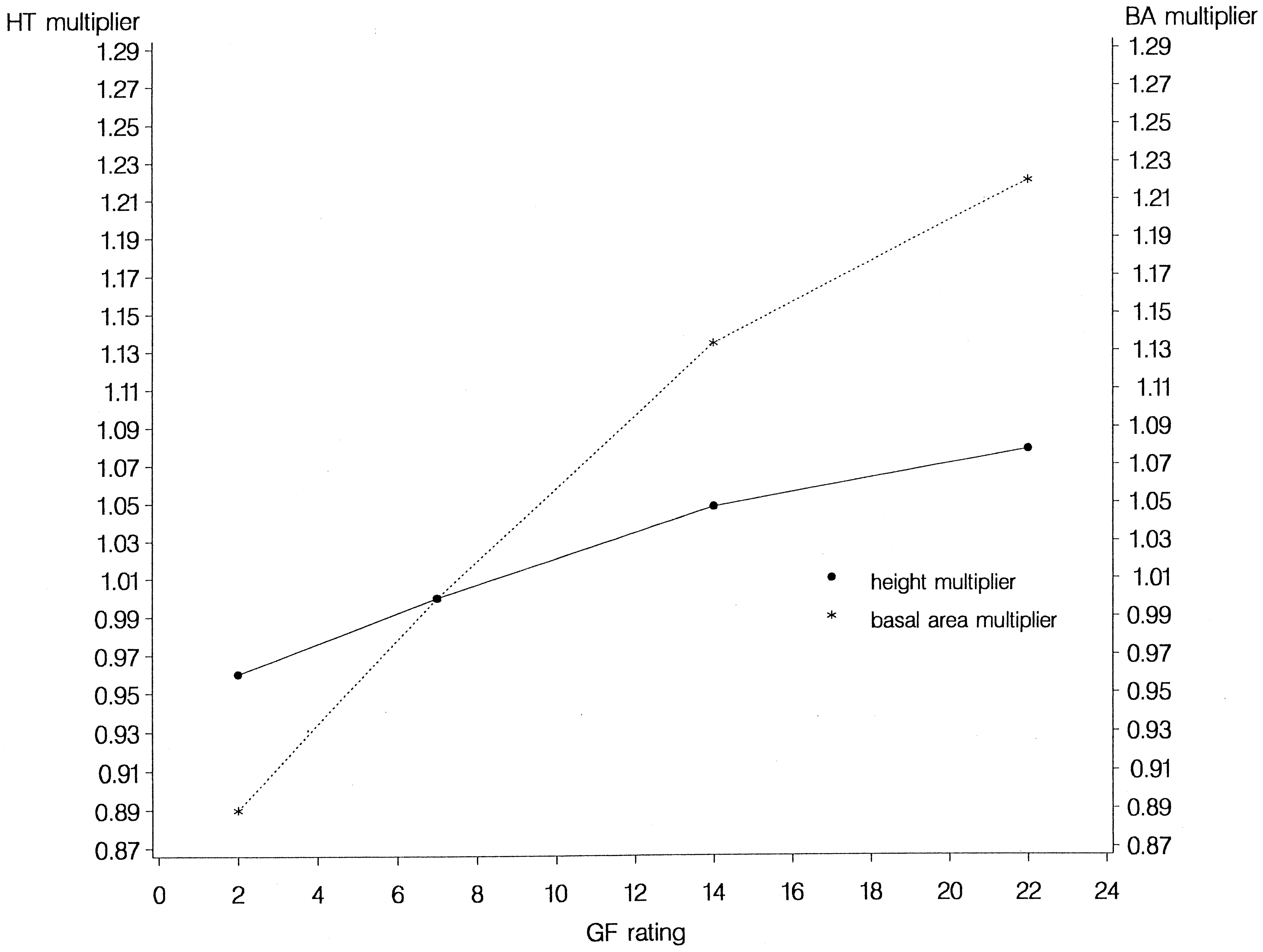
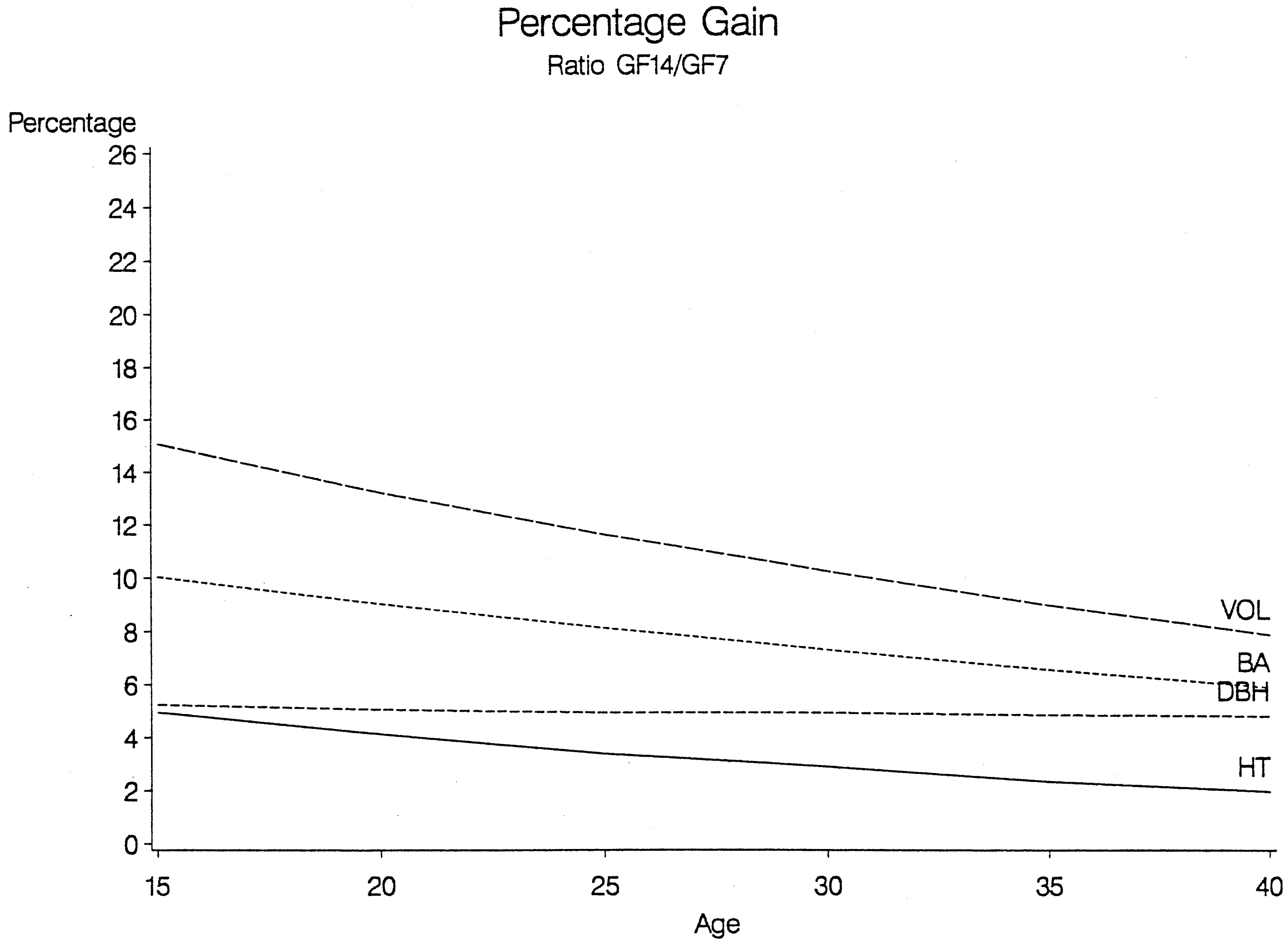
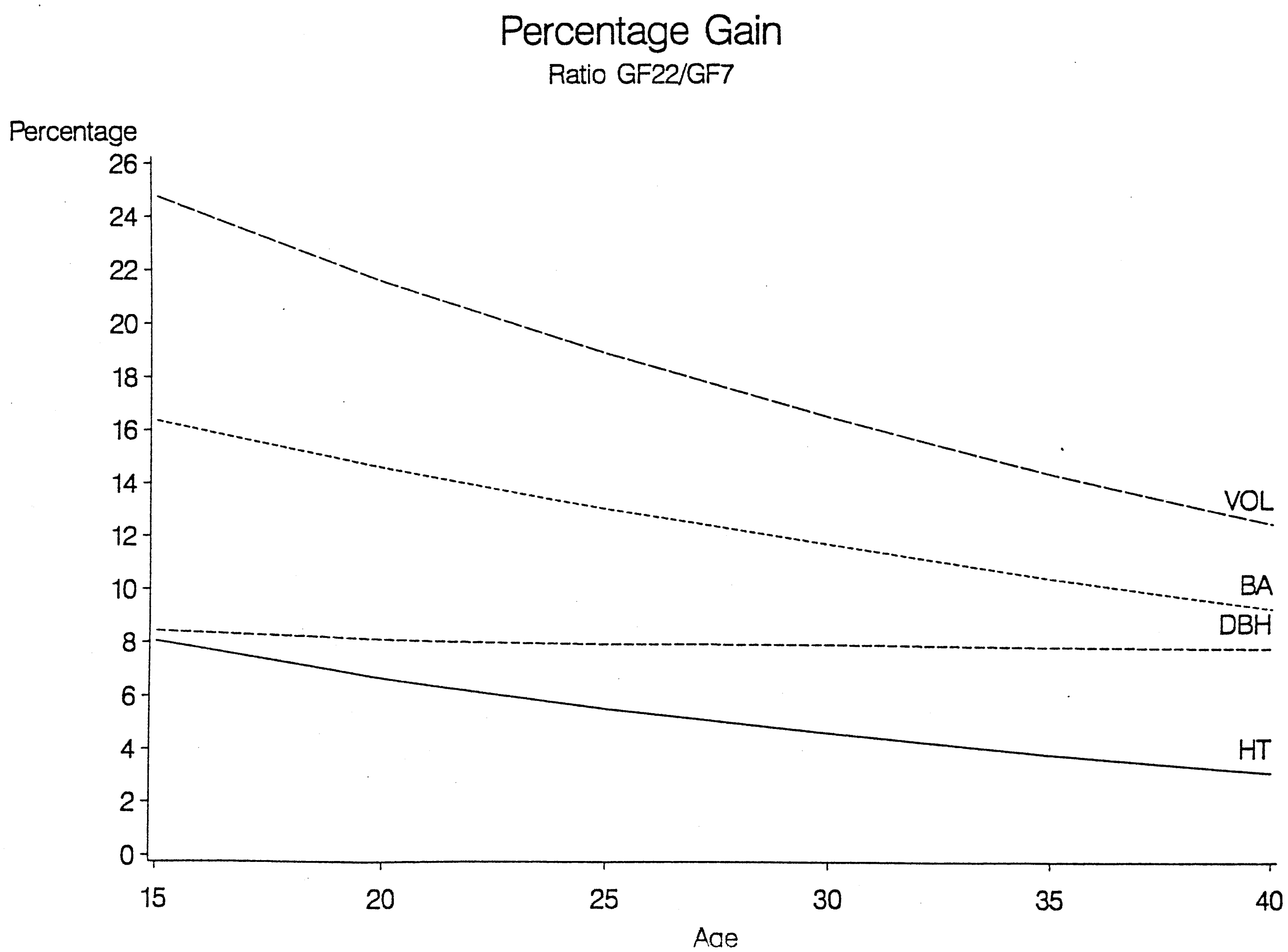

HT multiplier
BA multiplier
1.29
1.27
1.25
1.23
1.21
1.19
1.17
1.15
1.13
1.11
1.09
1.07
1.05
1.03
1.01
0.99
0.97
0.95
0.93
0.91
0.89
0.87
0
2
4
6
8
10
12
14
16
18
20
22
24
GF rating
height multiplier
basal area multiplier

Figure 5. Percent gain in mean top height, basal area, diameter at breast height, and volume per ha over climbing select (GF7) predicted for ages 15 to 40 years for both GF14 and GF22.


Percentage Gain
Ratio GF14/GF7
Percentage
26
24
22
20
18
16
14
12
10
8
6
4
2
0
15
20
25
30
35
40
Age
VOL
BA
DBH
HT


Percentage Gain
Ratio GF22/GF7
Percentage
26
24
22
20
18
16
14
12
10
8
6
4
2
0
15
20
25
30
35
40
Age
VOL
BA
DBH
HT

Appendix 1. Site indices and silvicultural regimes for genetic gain trials.

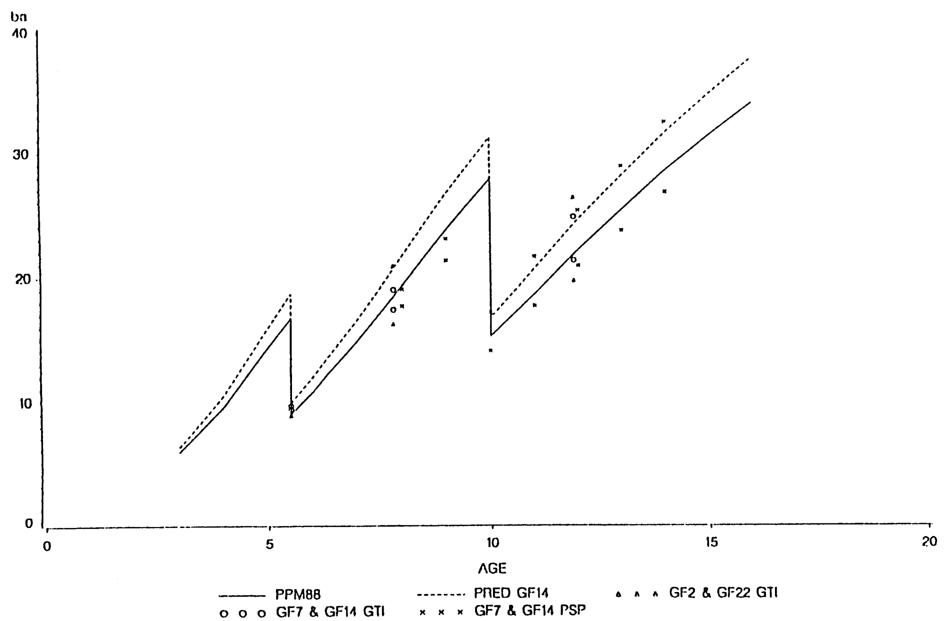
Trial	Site index	Regime used
RO 2103/1	34.18	Initial stocking 1111 s/ha. Prune to 2.2m at age 5. Thin to 600 s/ha at age 5.5. Prune to 4.2m at age 6. Prune to 6m at age 10. Thin to 300 s/ha at age 10.
RO 2103/2	34.12	Initial stocking 711 s/ha. Prune to 2.2m at age 5.
RO 2103/3	33.44	Initial stocking 1111 s/ha. prune to 2.2m at age 4.9. Thin to 600 s/ha at age 5.8. Prune to 4.2m at age 6.6. Thin to 300 s/ha at age 8.9.
RO 972	35.36	Initial stocking 1500 s/ha. Prune to 2m at age 5. Thin to 750 s/ha at age 5. Prune to 4m at age 6. Thin to 500 s/ha. Prune to 6m at age 7. Thin to 250 s/ha at age 7.
NN 530/1	29.42	Initial stocking 1111 s/ha. Thin to 600 s/ha at age 6. Thin to 300 s/ha at age 9.
NN 503/2	28.98	Initial stocking 884 s/ha. Thin to 600 s/ha at age 8. Thin to 300 s/ha at age 10.
WN 377	33.67	Initial stocking 1021 s/ha. Thin to 600 s/ha at age 5. Thin to 300 s/ha at age 8.
SD 682	28.67	Initial stocking 600 s/ha. Thin to 300 s/ha at age 8.

Appendix 2. GF14 genetic gain growth rate multipliers for each site and year.

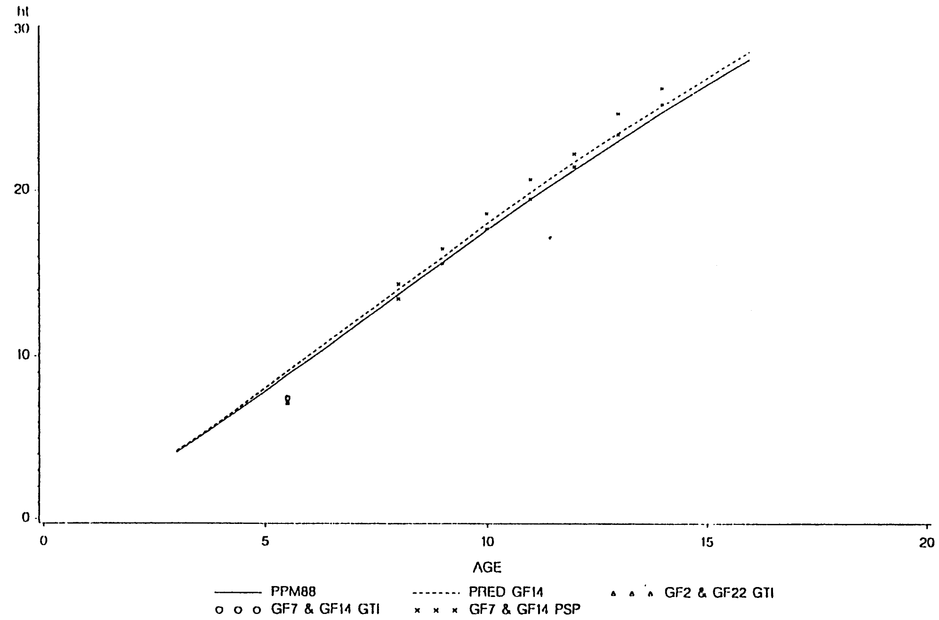
		1978 genetic gain trials				1979 genetic gain trials					
Year	Mean	Age	RO2103/1	RO2103/2	NN530/2	Age	RO2103/3	Age	NN530/1	Age	SD682
Growth rate multiplier for mean top height:											
1987	1.040	9	1.007	0.984	1.196	8	0.912	8	1.103	7	-
1988	1.145	10	-	1.171	-	9	-	9	1.234	8	1.131
1989	1.102	11	1.209	0.9942	1.059	10	1.240	10	1.059	9	-
1990	1.066	12	0.813	0.948	0.981	11	1.156	11	1.158	10	1.341
1991	1.026	13	1.220	0.995	1.085	12	0.825	12	1.145	11	0.884
1992	1.009	14	0.845	1.027	1.087	13	1.031	13	0.934	12	0.871
Mean	1.048		1.019	0.994	1.082		1.033		1.105		1.057
Growth rate multiplier for basal area / stocking:											
1987	1.094	9	1.098	1.131	0.986	8	1.093	8	1.163	7	-
1988	0.814	10	-	0.314	-	9	-	9	1.012	8	1.116
1989	0.958	11	1.178	1.395	-	10	1.119	10	1.100	9	-
1990	1.108	12	1.146	1.503	1.099	11	0.996	11	0.952	10	0.950
1991	1.196	13	1.225	1.287	1.173	12	1.164	12	0.950	11	1.378
1992	1.268	14	1.201	2.149	1.006	13	1.088	13	1.144	12	1.120
Mean	1.134		1.169	1.297	1.066		1.092		1.037		1.141

Appendix 3. Predicted and actual growth using site specific estimates of genetic gain growth rate multipliers.

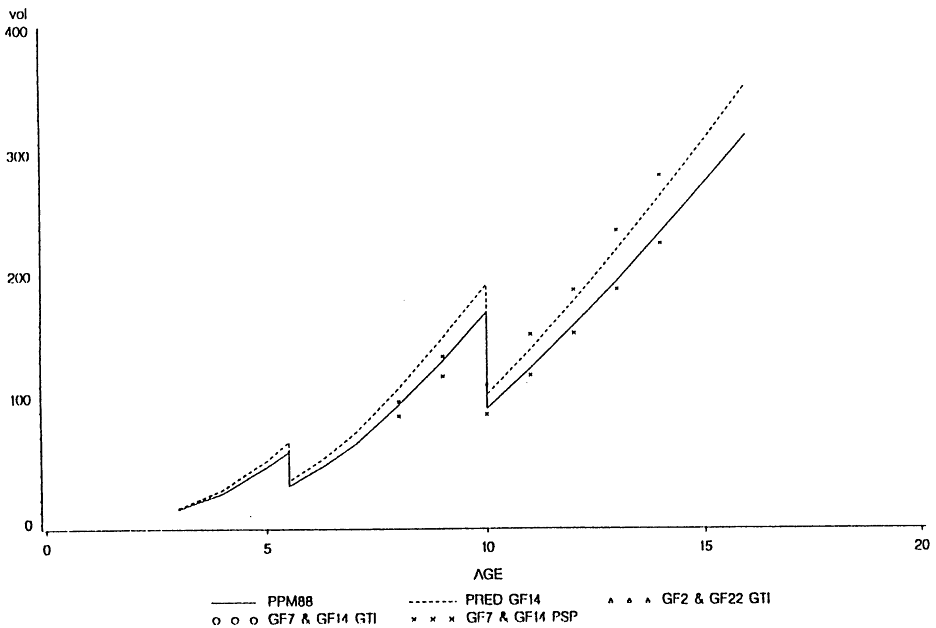
RO21031 : basal area
Individual Modifiers (Thu Apr 15 10:05:08 1993)



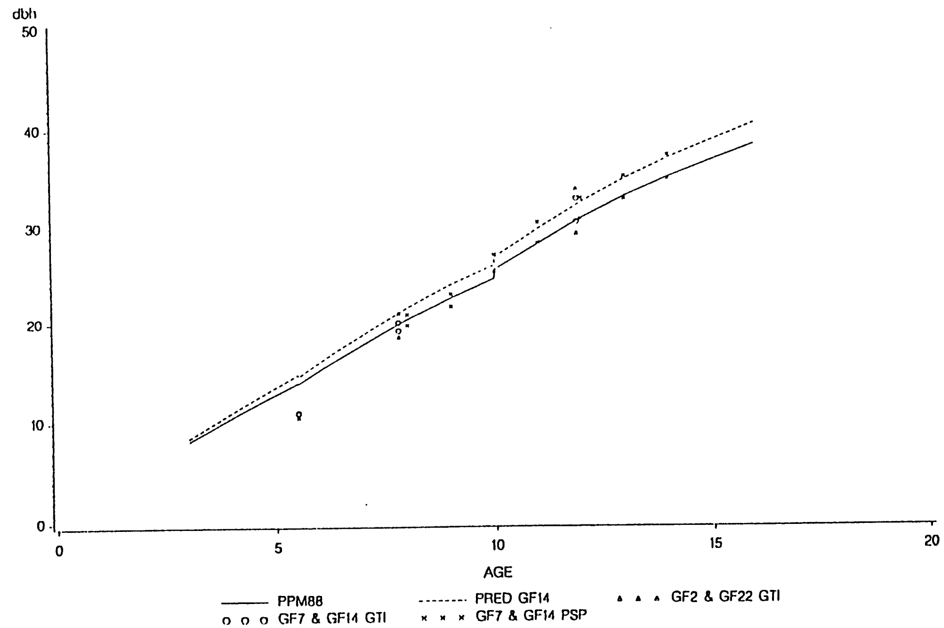
RO21031 : mean top height
Individual Modifiers (Wed Apr 14 08:39:56 1993)



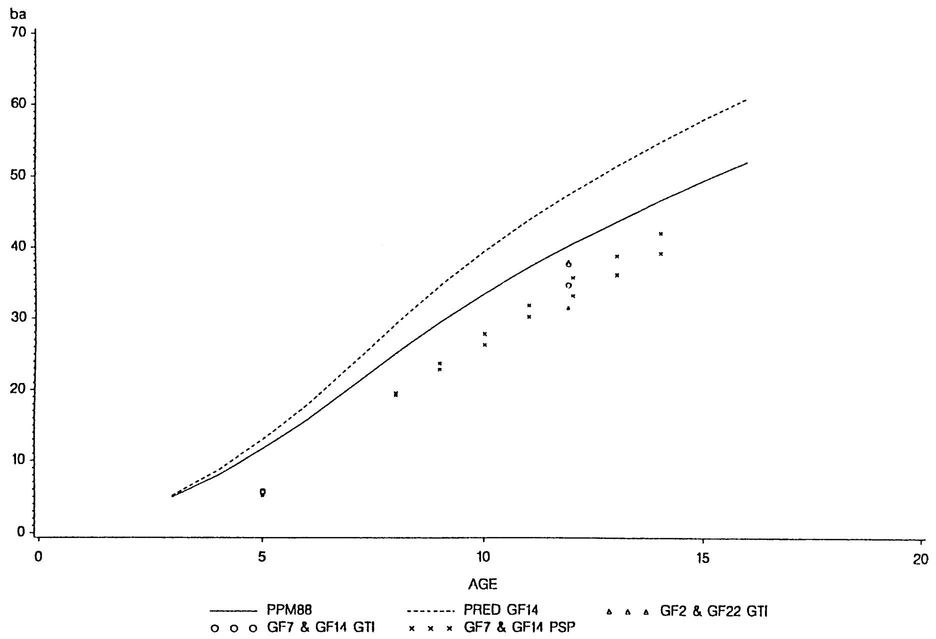
RO21031 : volume
Individual Modifiers (Wed Apr 14 08:39:58 1993)



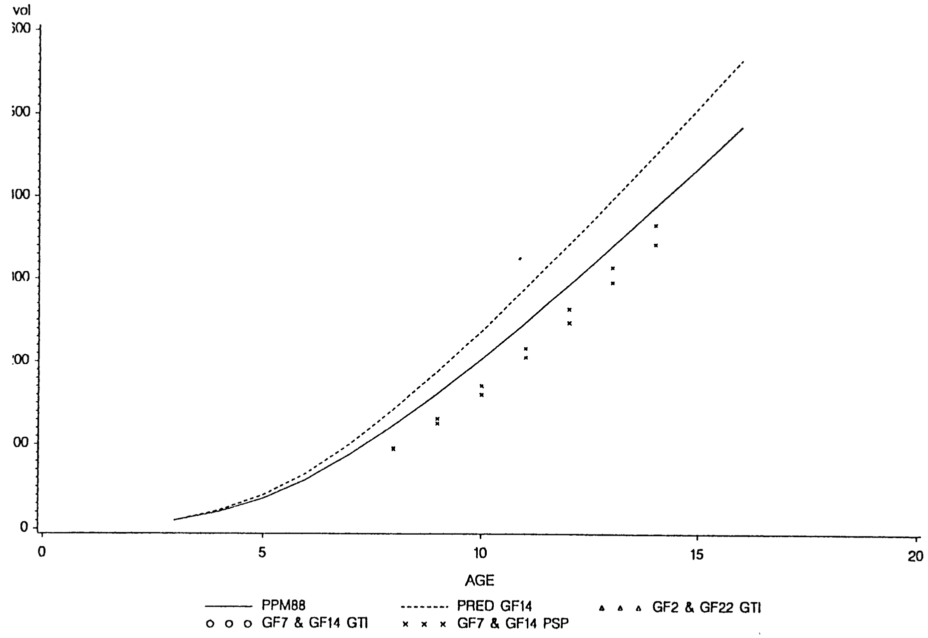
RO21031 : quadratic mean dbh
Individual Modifiers (Wed Apr 14 08:39:59 1993)



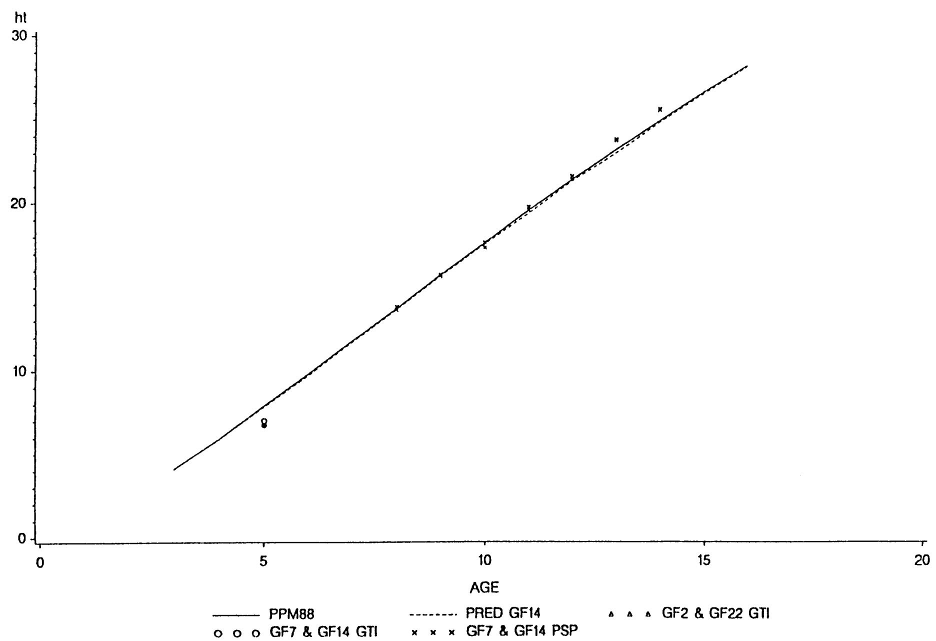
RO21032 : basal area
Individual Modifiers (Wed Apr 14 08:44:32 1993)



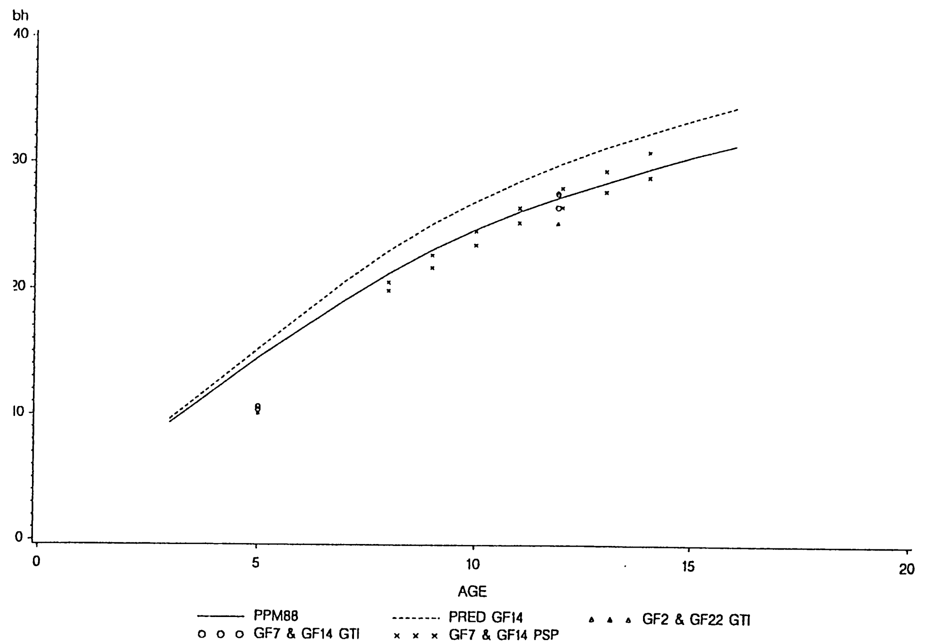
RO21032 : volume
Individual Modifiers (Wed Apr 14 08:44:34 1993)

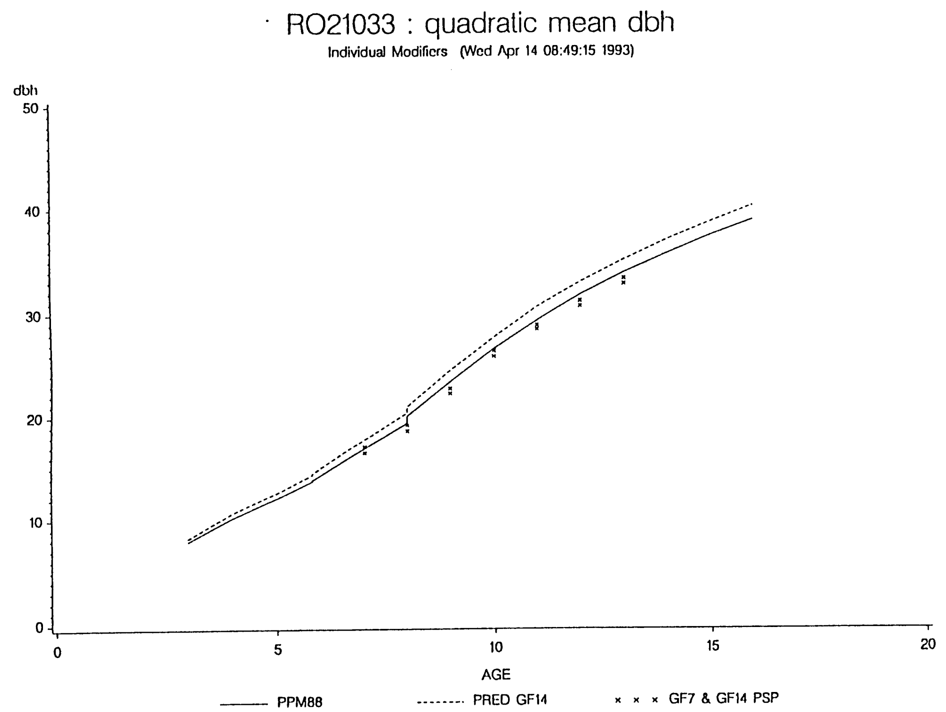


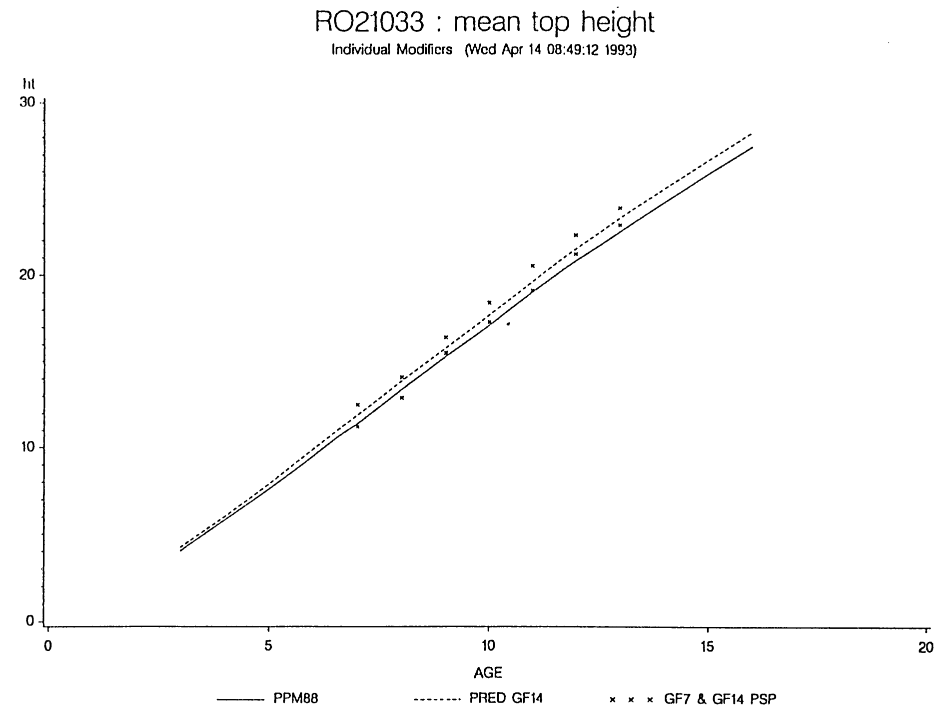
RO21032 : mean top height
Individual Modifiers (Wed Apr 14 08:44:33 1993)

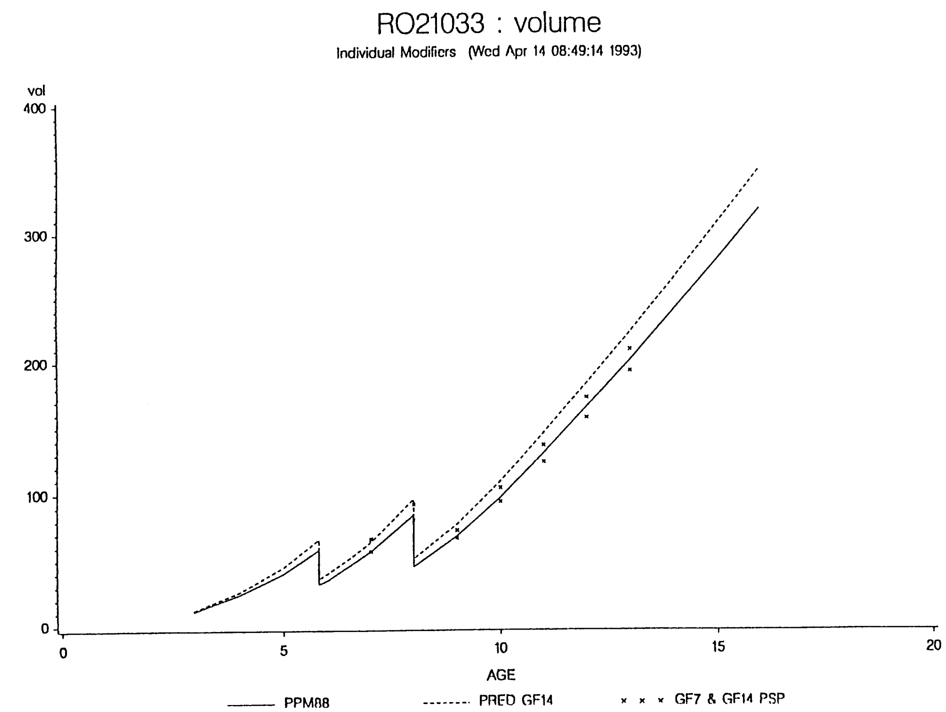


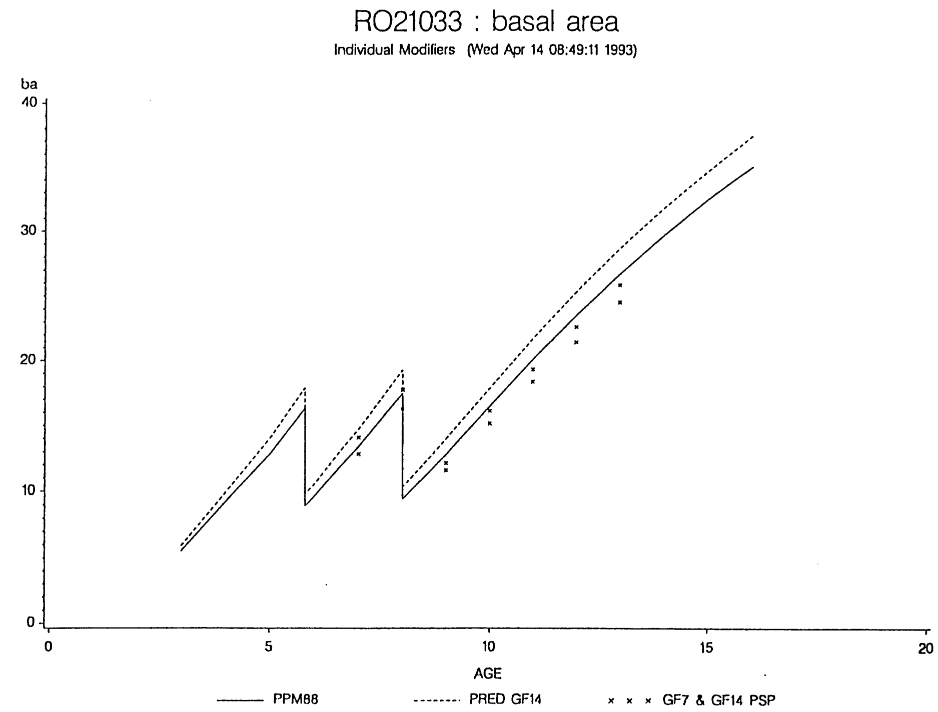
RO21032 : quadratic mean dbh
Individual Modifiers (Wed Apr 14 08:44:36 1993)



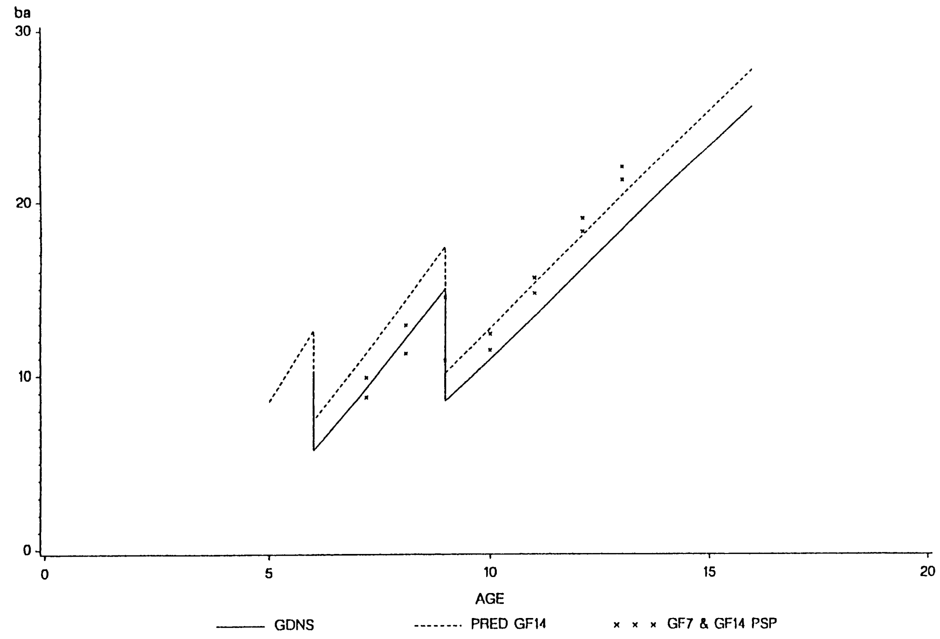

RO21033 : quadratic mean dbh
Individual Modifiers (Wed Apr 14 08:49:15 1993)
dbh
AGE
PPM88
PRED GF14
GF7 & GF14 PSP


RO21033 : mean top height
Individual Modifiers (Wed Apr 14 08:49:12 1993)
ht
AGE
PPM88
PRED GF14
GF7 & GF14 PSP

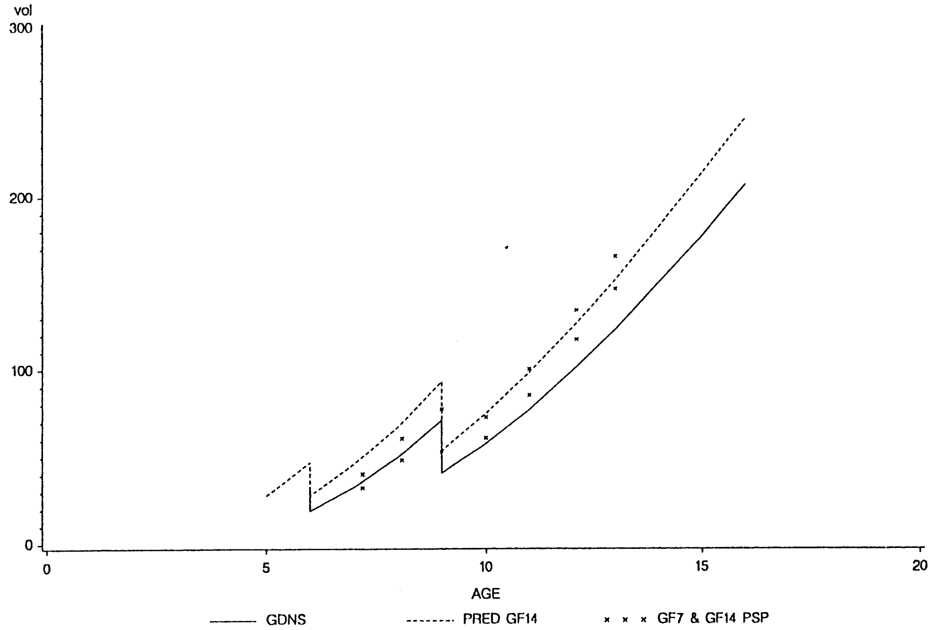

RO21033 : volume
Individual Modifiers (Wed Apr 14 08:49:14 1993)
vol
AGE
PPM88
PRED GF14
GF7 & GF14 PSP


RO21033 : basal area
Individual Modifiers (Wed Apr 14 08:49:11 1993)
ba
AGE
PPM88
PRED GF14
GF7 & GF14 PSP

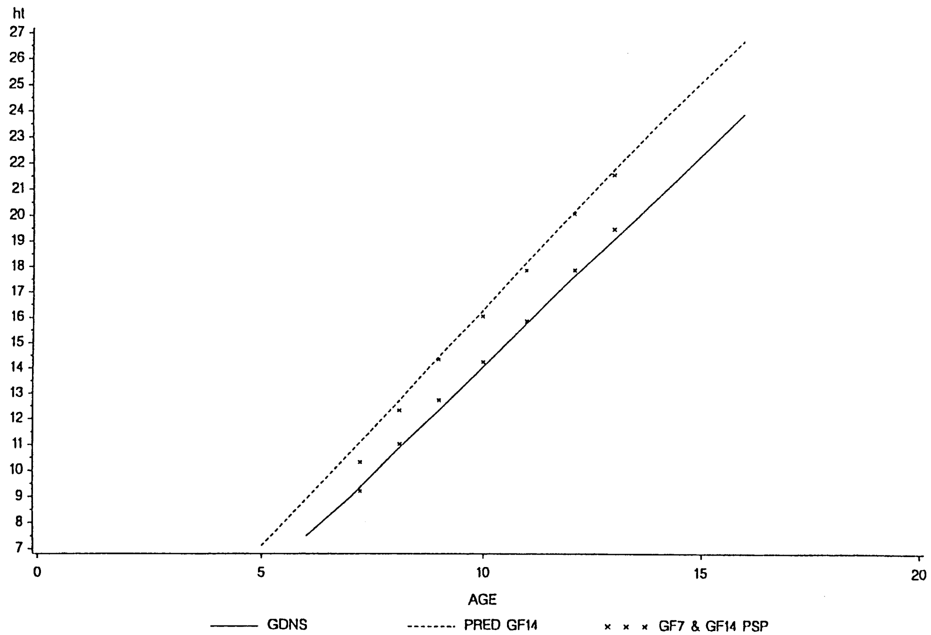
NN5301 : basal area
Individual Modifiers (Wed Apr 14 09:01:44 1993)



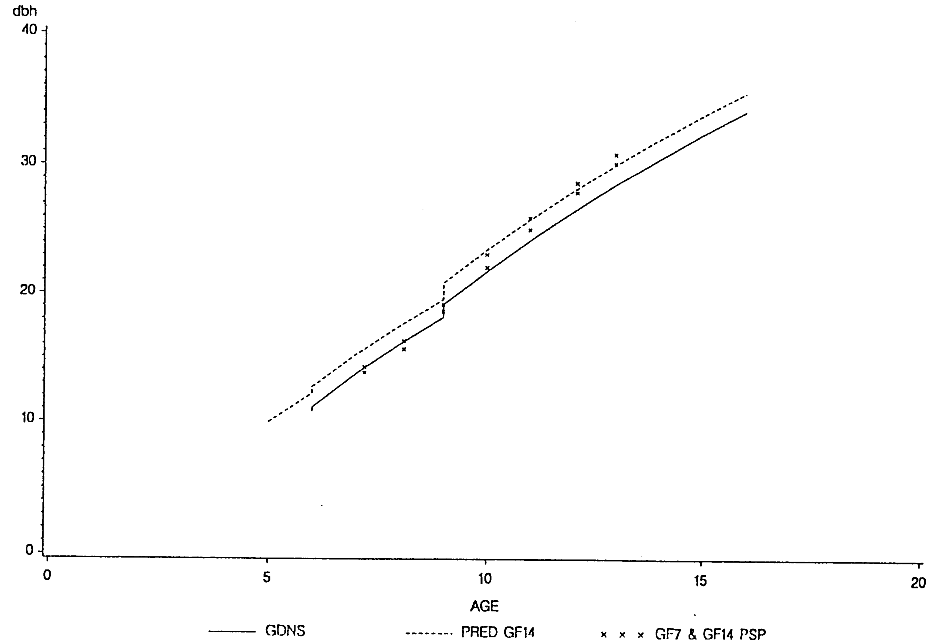
NN5301 : volume
Individual Modifiers (Wed Apr 14 09:01:47 1993)



NN5301 : mean top height
Individual Modifiers (Wed Apr 14 09:01:46 1993)

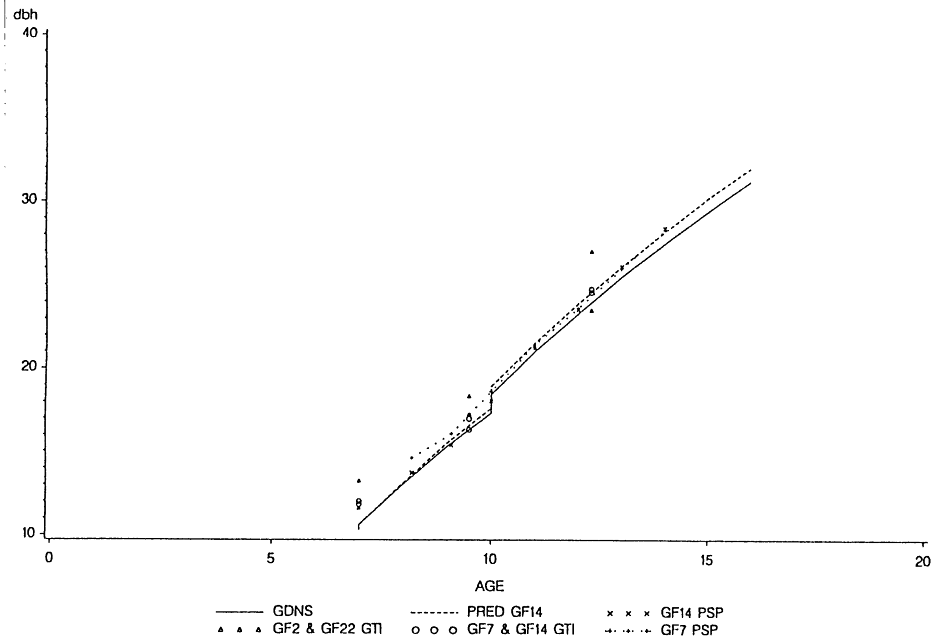


NN5301 : quadratic mean dbh
Individual Modifiers (Wed Apr 14 09:01:49 1993)

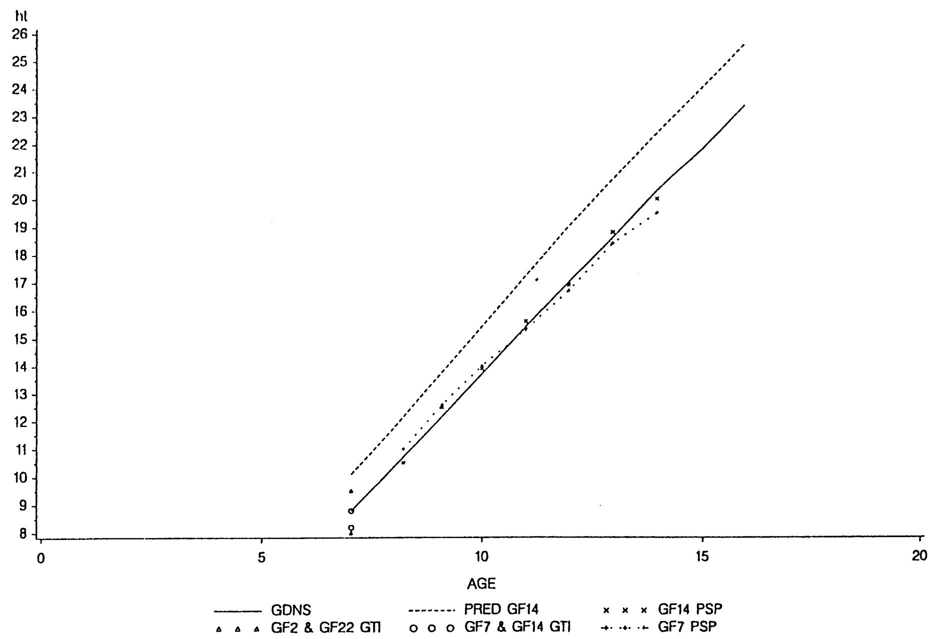


NN5302 : quadratic mean dbh

Individual Modifiers (Wed Apr 14 09:05:45 1993)

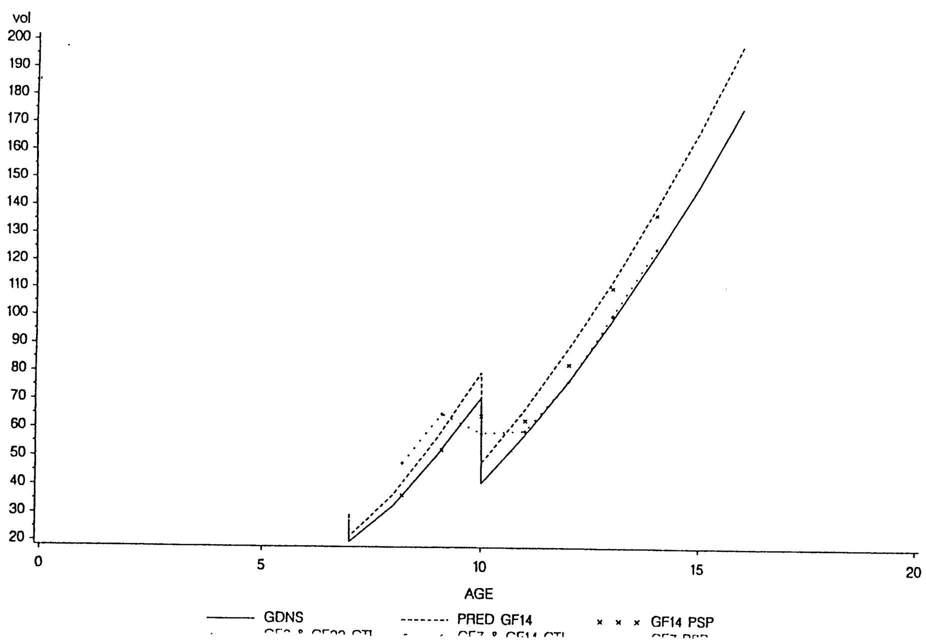


Individual Modifiers (Wed Apr 14 09:05:42 1993)



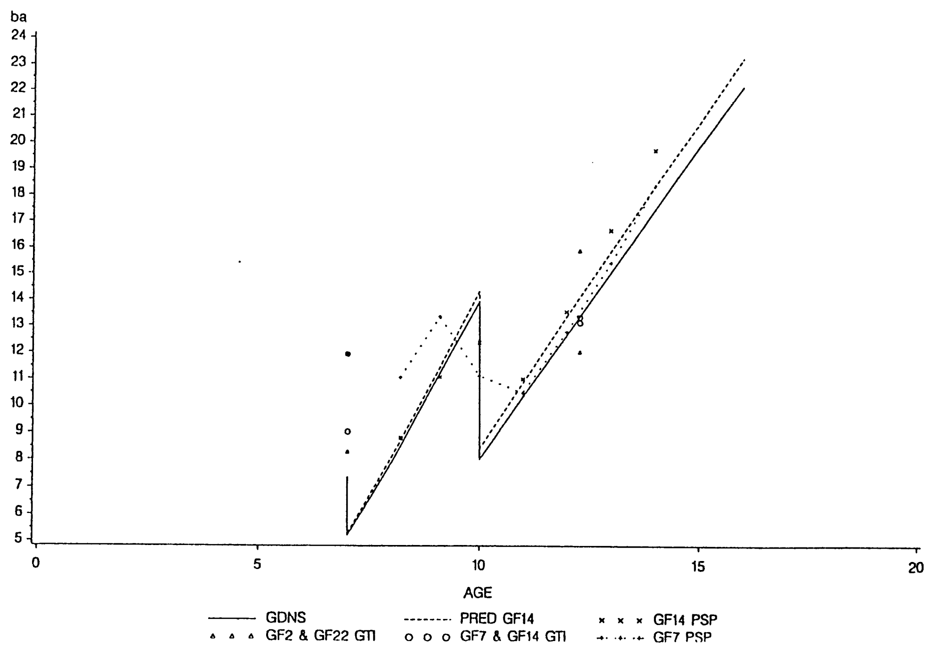
NN5302 : volume

Individual Modifiers (Wed Apr 14 09:05:43 1993)

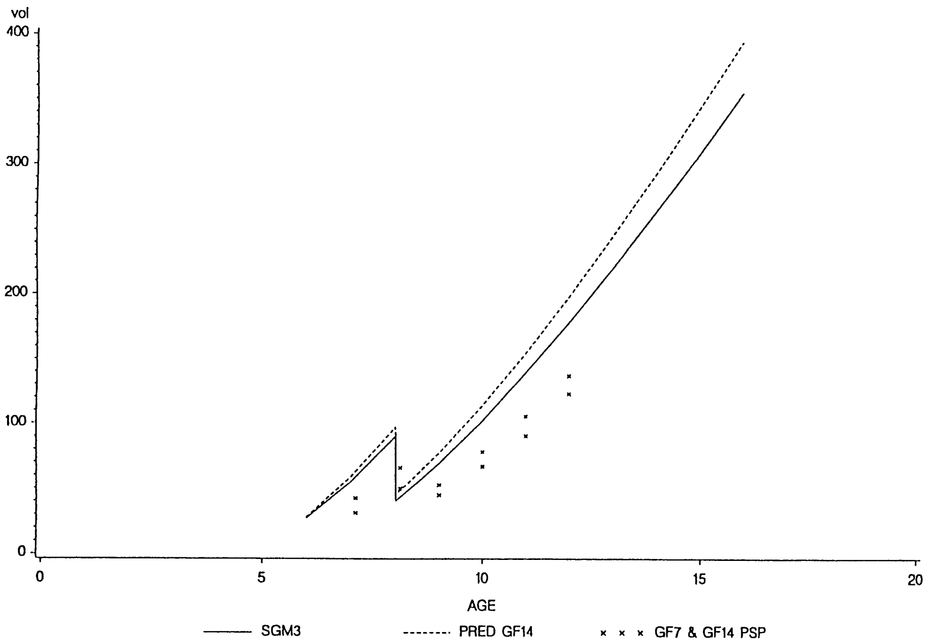


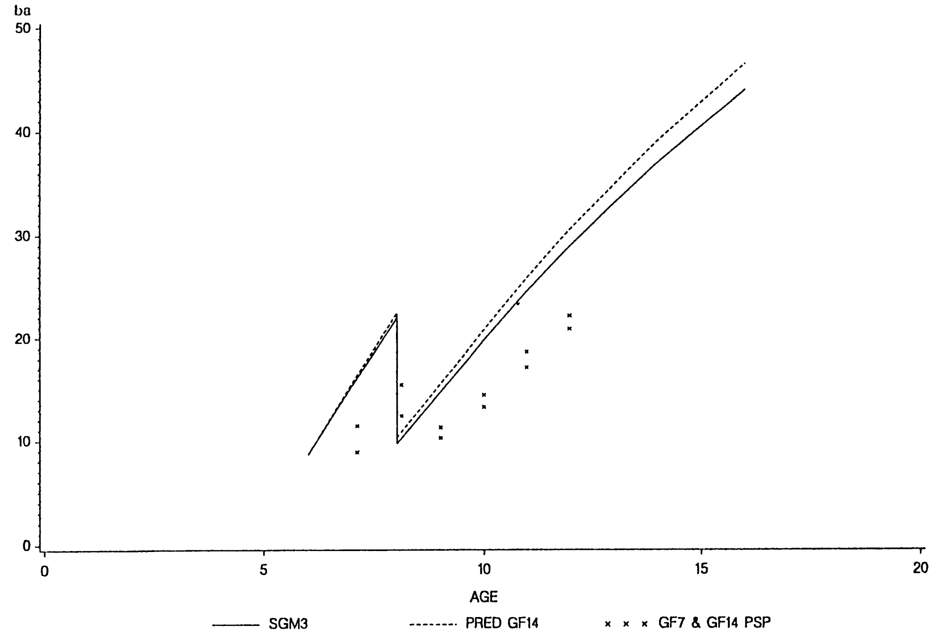
NN5302 : basal area

Individual Modifiers (Wed Apr 14 09:05:41 1993)



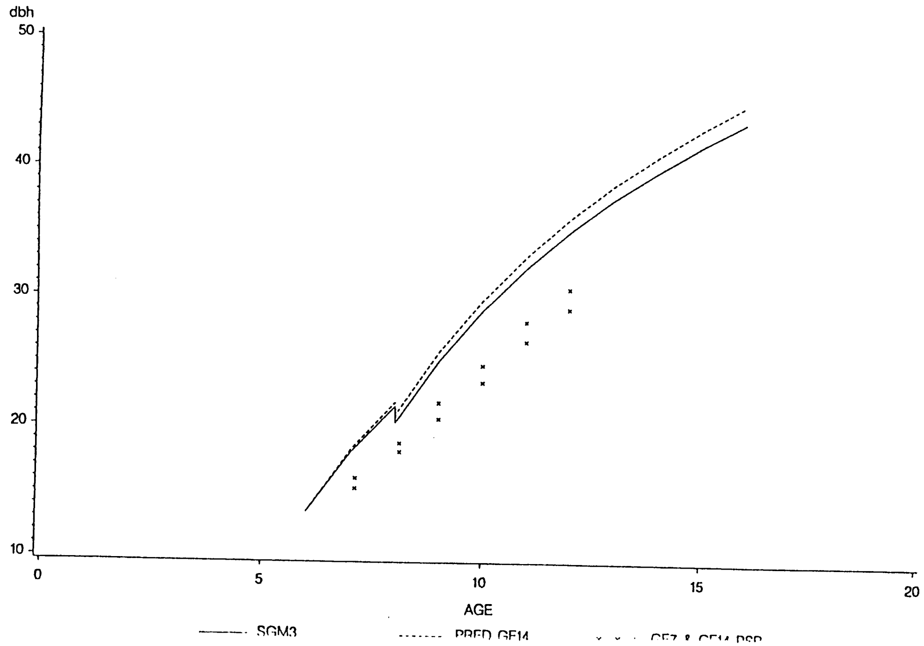
Individual Modifiers (Wed Apr 14 09:10:57 1993)





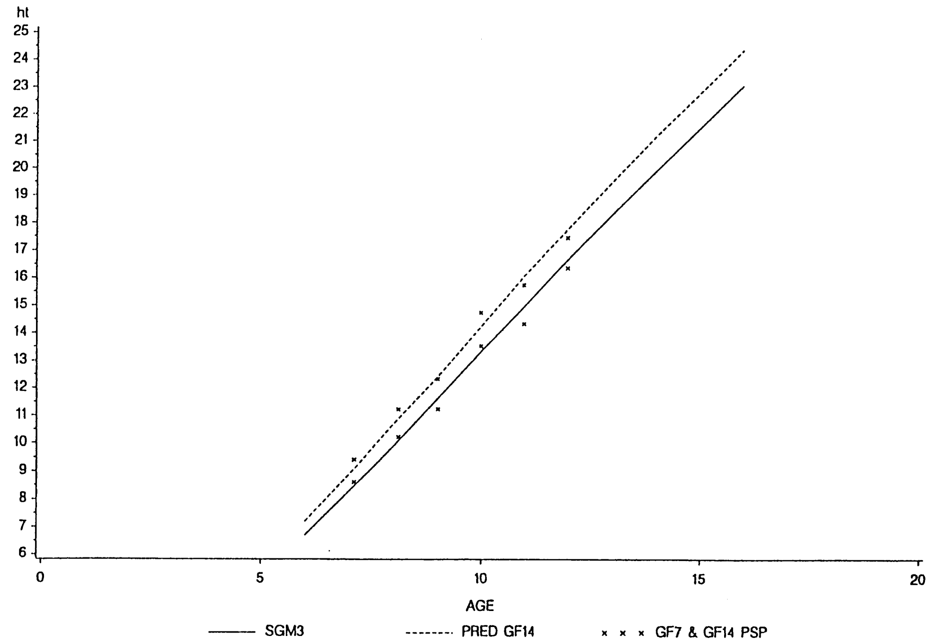
SD682 : quadratic mean dbh

Individual Modifiers (Wed Apr 14 09:10:58 1993)



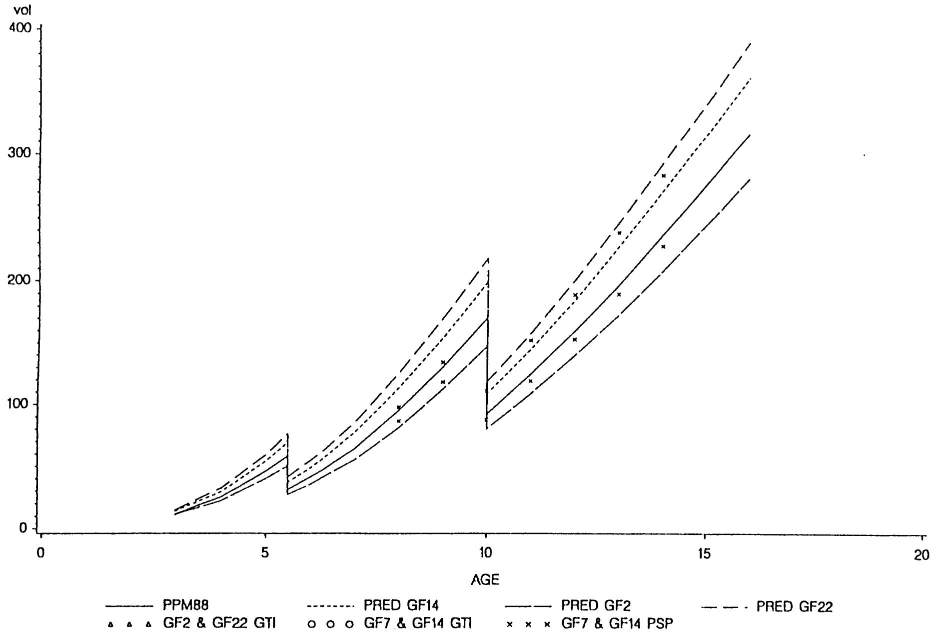
SD682 : mean top height

Individual Modifiers (Wed Apr 14 09:10:55 1993)

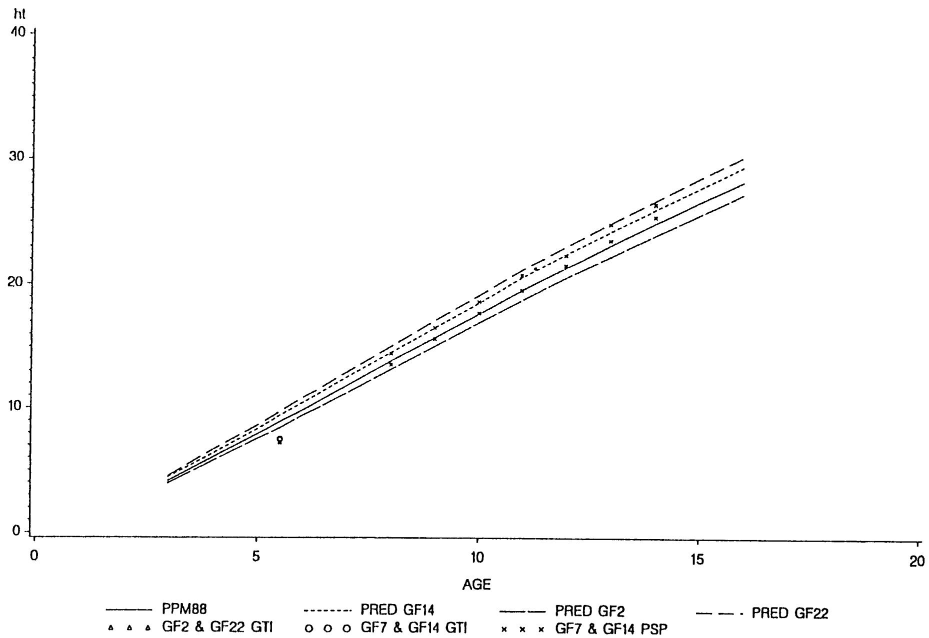


Appendix 4. Predicted and actual growth using overall estimate of genetic gain growth rate multipliers on sites used for multiplier estimation.

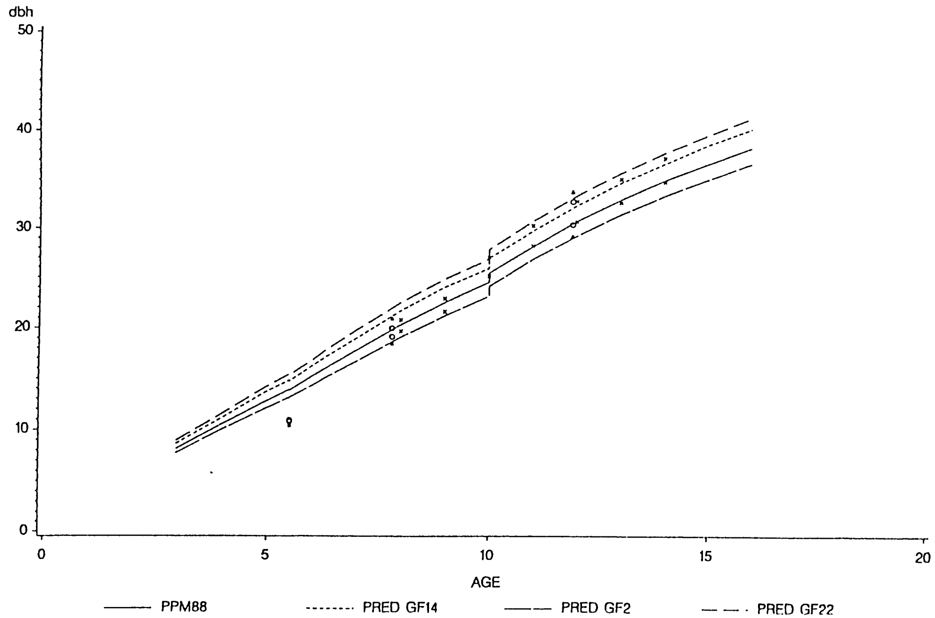
RO21031 : volume
Common Modifiers (Thu Apr 08 11:53:18 1993)



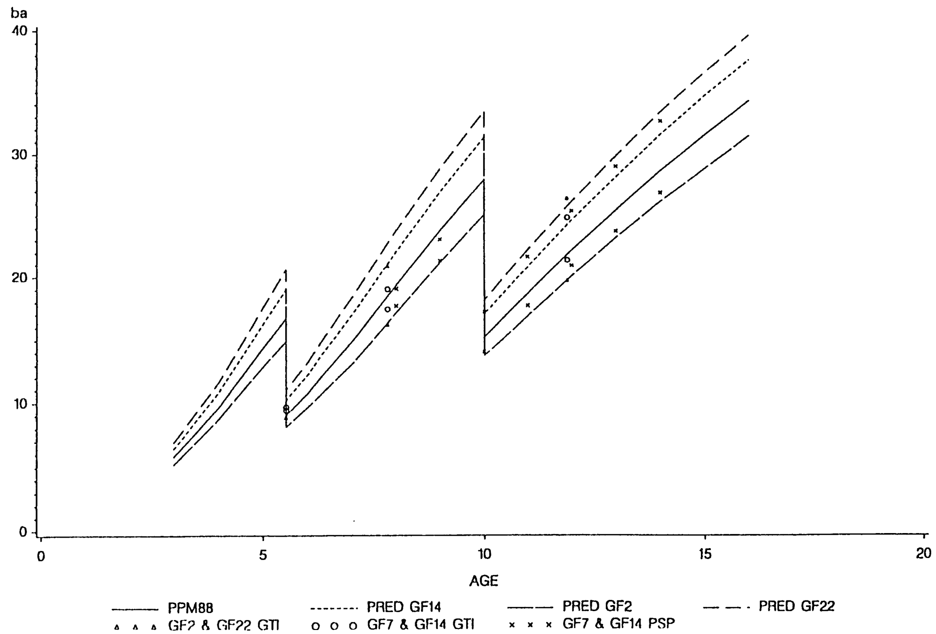
RO21031 : mean top height
Common Modifiers (Thu Apr 08 11:53:17 1993)

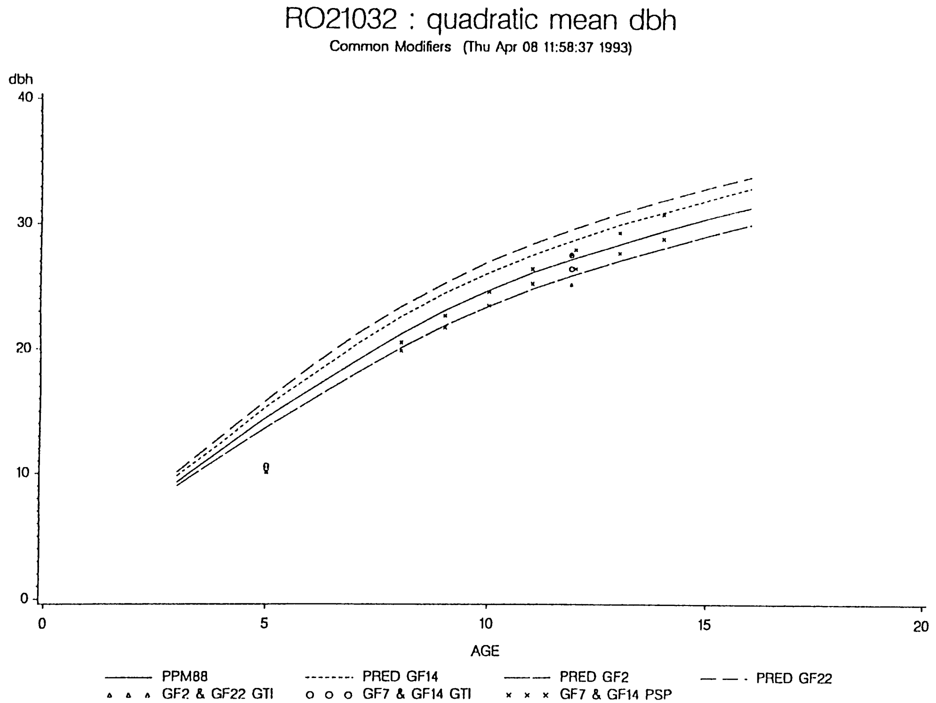


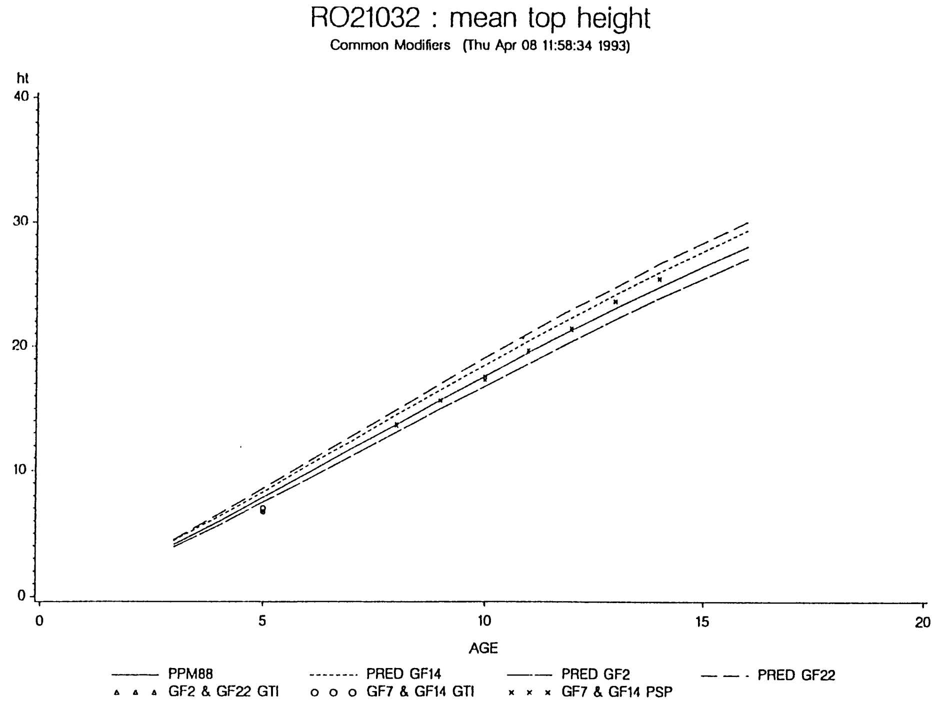
RO21031 : quadratic mean dbh
Common Modifiers (Thu Apr 08 11:53:20 1993)

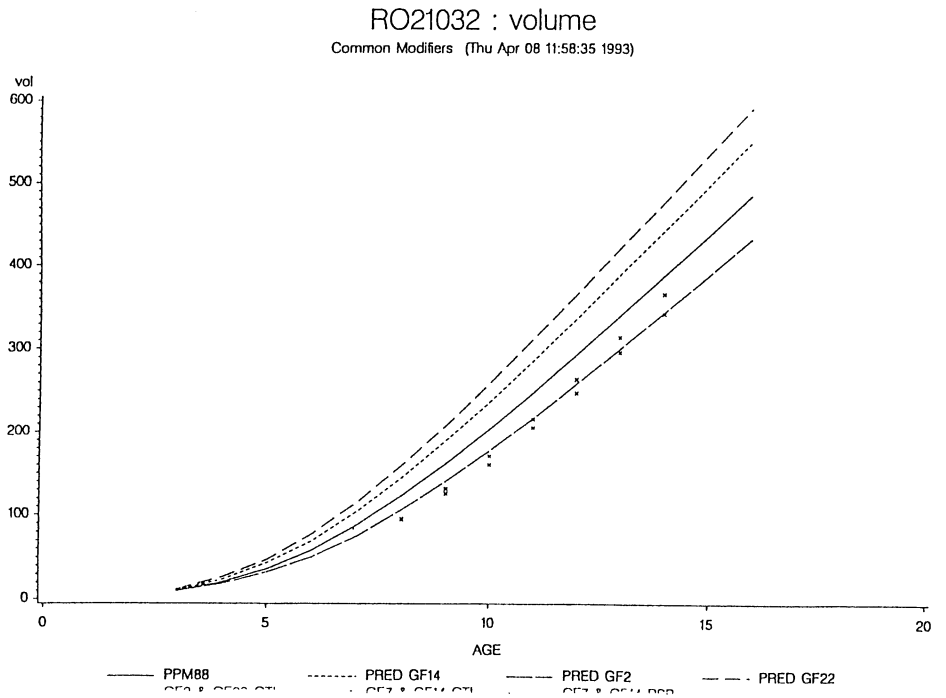


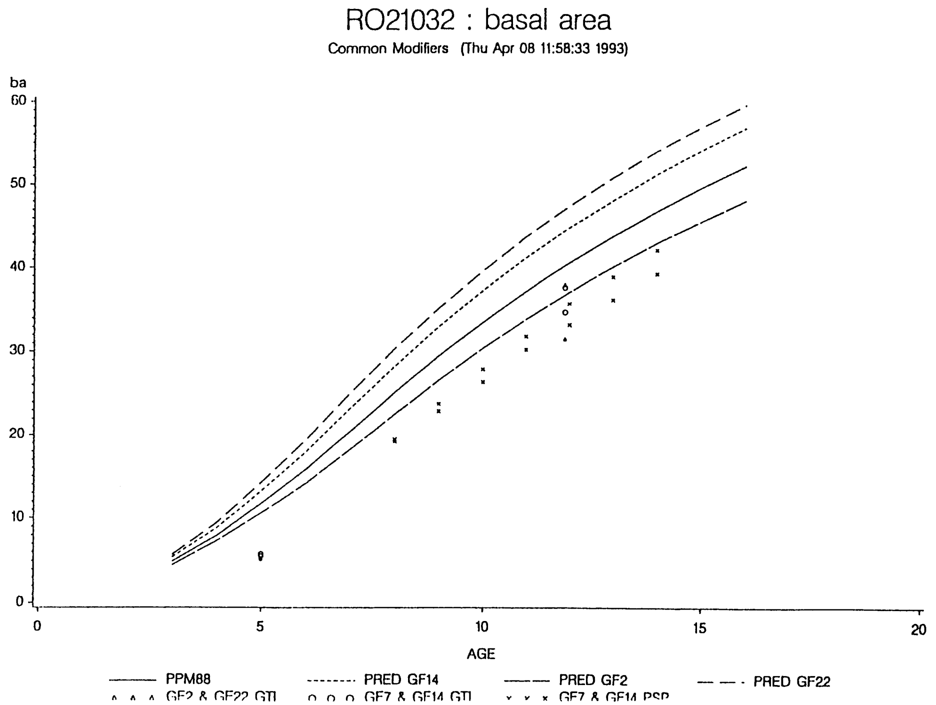
RO21031 : basal area
Common Modifiers (Thu Apr 08 11:53:15 1993)




RO21032 : quadratic mean dbh
Common Modifiers (Thu Apr 08 11:58:37 1993)
dbh
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF2 & GF22 GTI
GF7 & GF14 GTI
GF7 & GF14 PSP

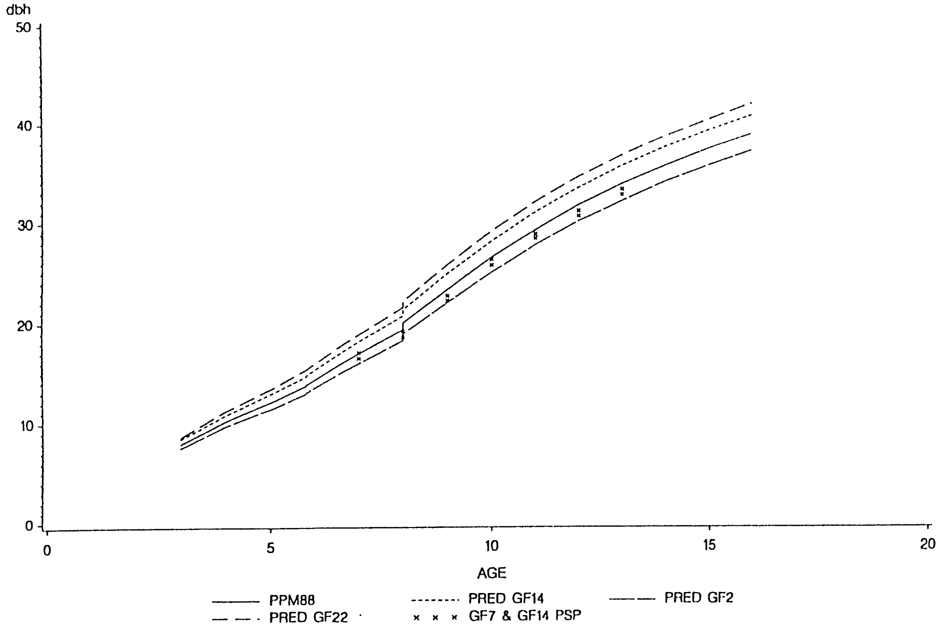

RO21032 : mean top height
Common Modifiers (Thu Apr 08 11:58:34 1993)
ht
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF2 & GF22 GTI
GF7 & GF14 GTI
GF7 & GF14 PSP


RO21032 : volume
Common Modifiers (Thu Apr 08 11:58:35 1993)
vol
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22


RO21032 : basal area
Common Modifiers (Thu Apr 08 11:58:33 1993)
ba
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22

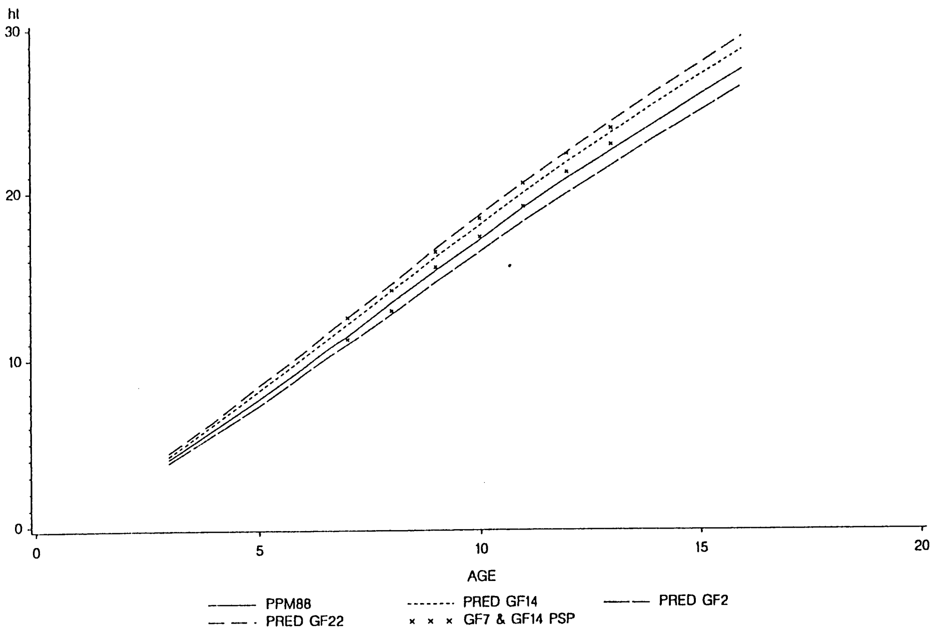
RO21033 : quadratic mean dbh

Common Modifiers (Thu Apr 08 12:03:58 1993)



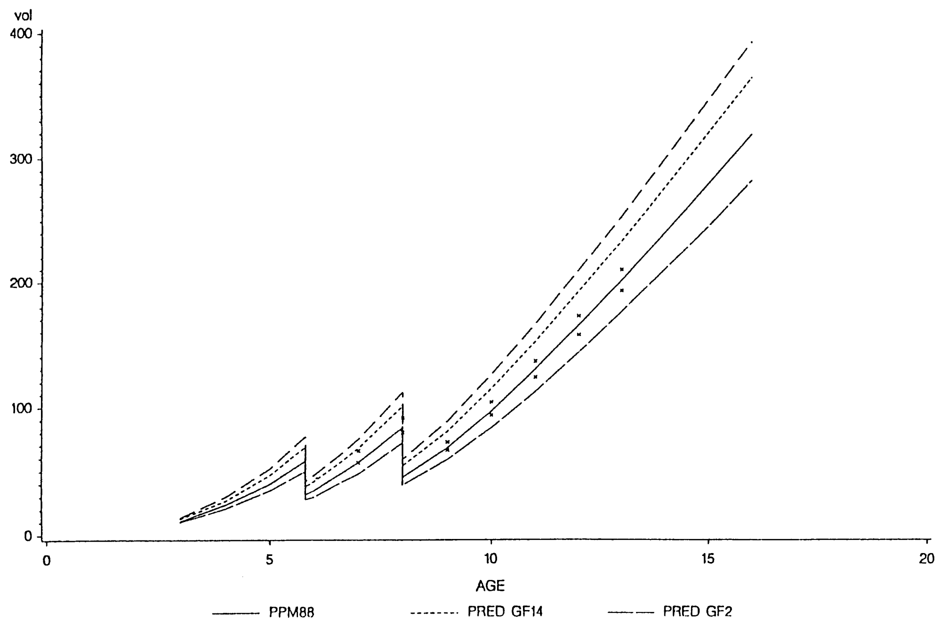
RO21033 : mean top height

Common Modifiers (Thu Apr 08 12:03:55 1993)



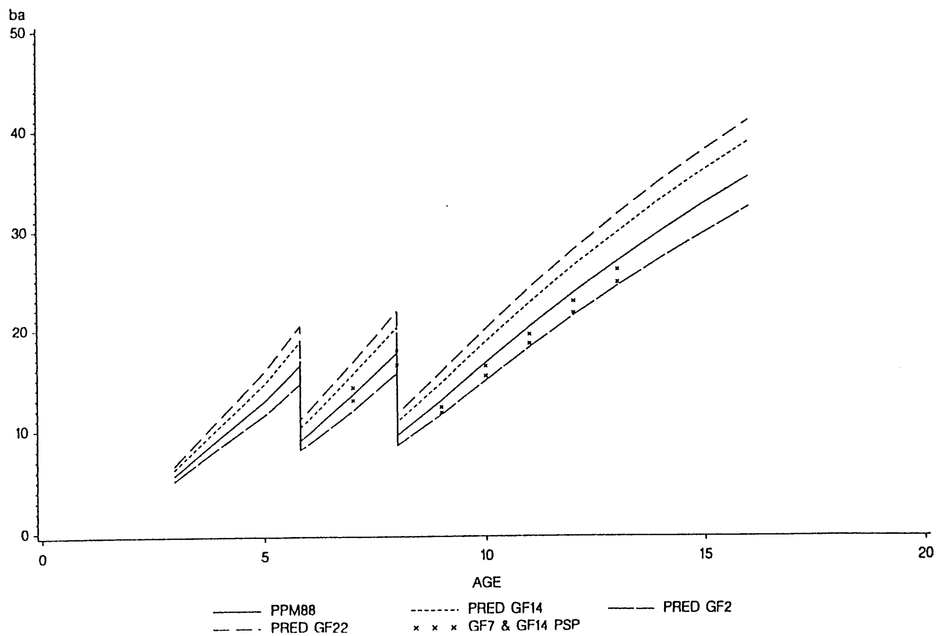
RO21033 : volume

Common Modifiers (Thu Apr 08 12:03:56 1993)



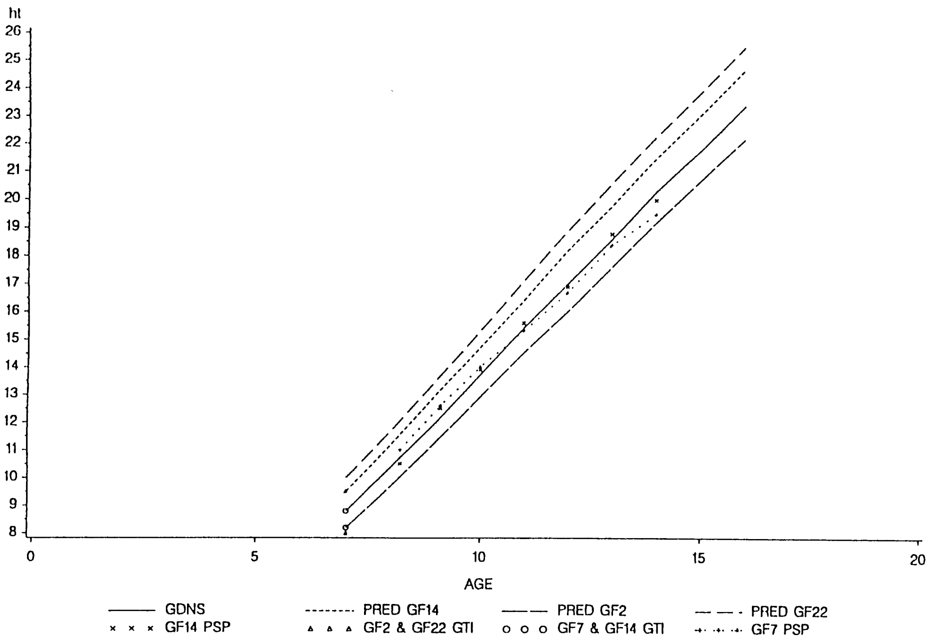
RO21033 : basal area

Common Modifiers (Thu Apr 08 12:03:53 1993)



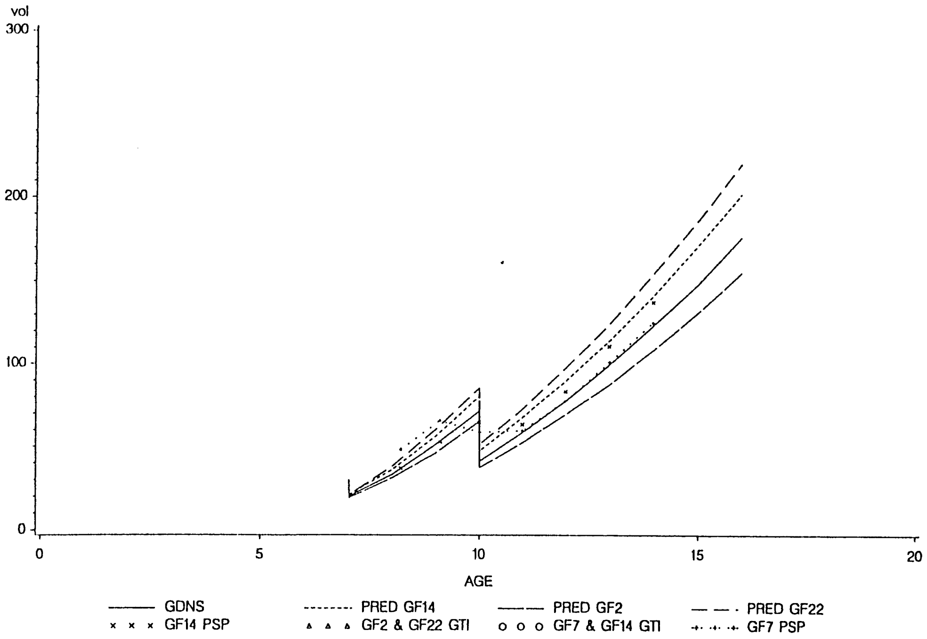
NN5302 : mean top height

Common Modifiers (Thu Apr 08 12:23:20 1993)



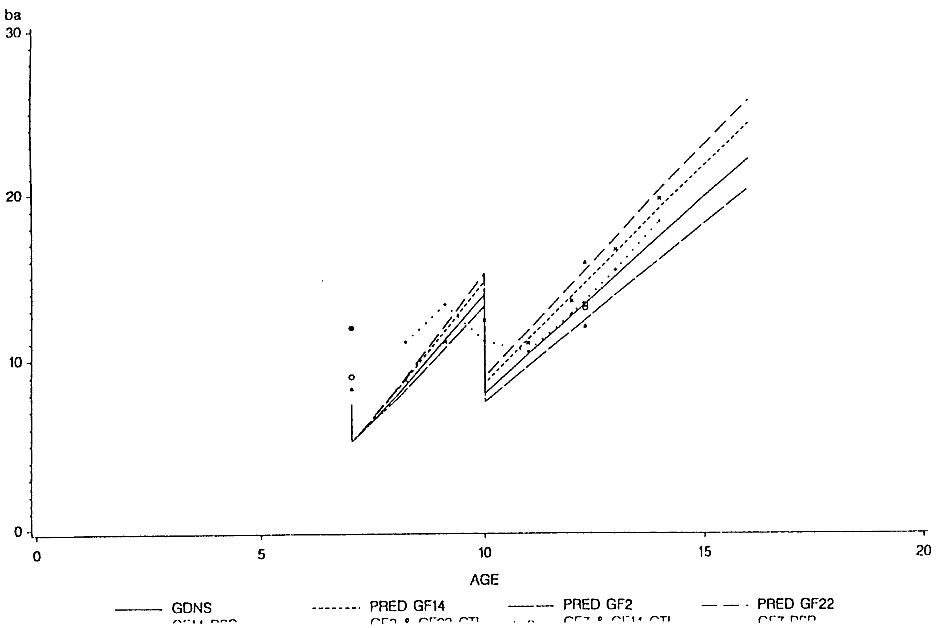
NN5302 : volume

Common Modifiers (Thu Apr 08 12:23:21 1993)



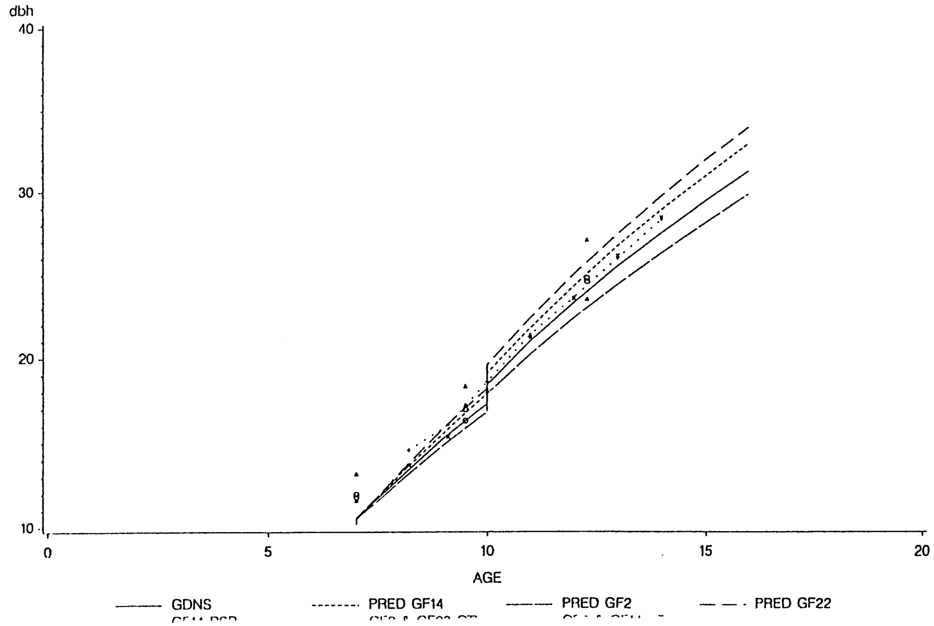
NN5302 : basal area

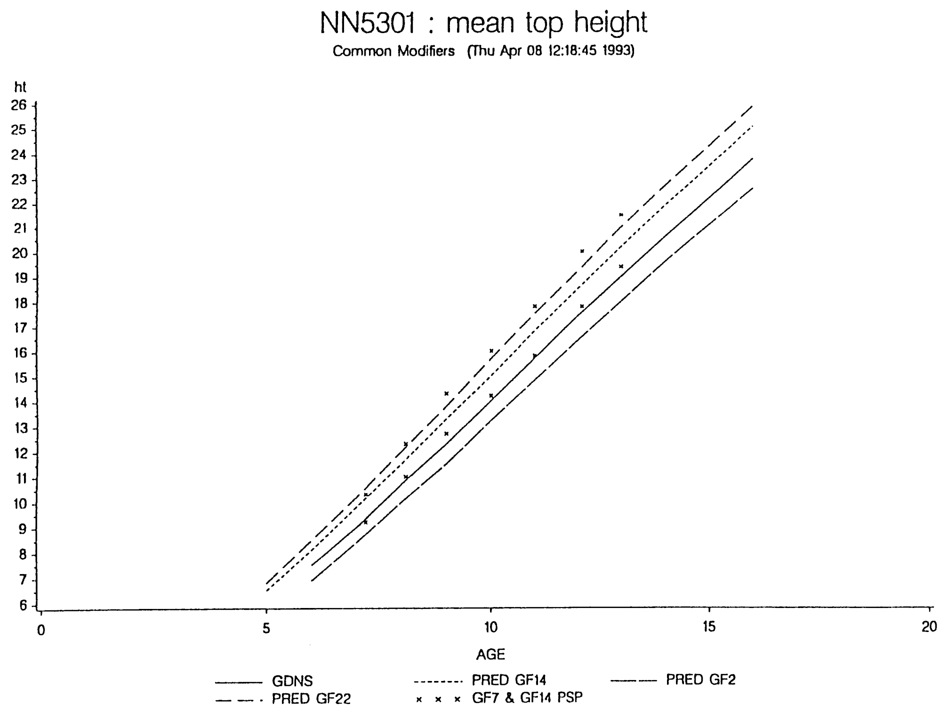
Common Modifiers (Thu Apr 08 12:23:18 1993)

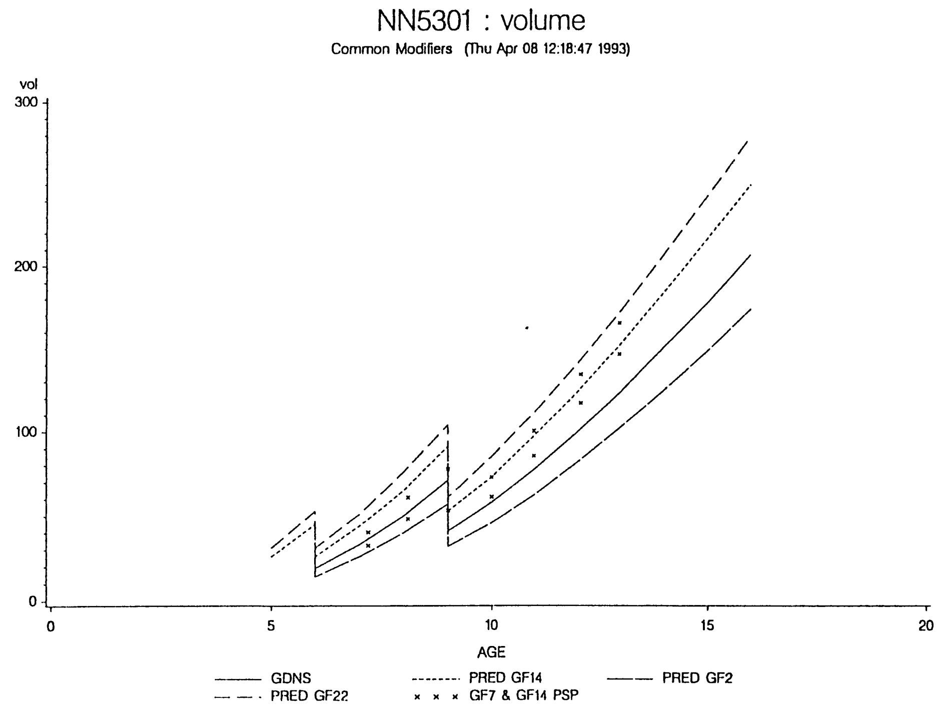


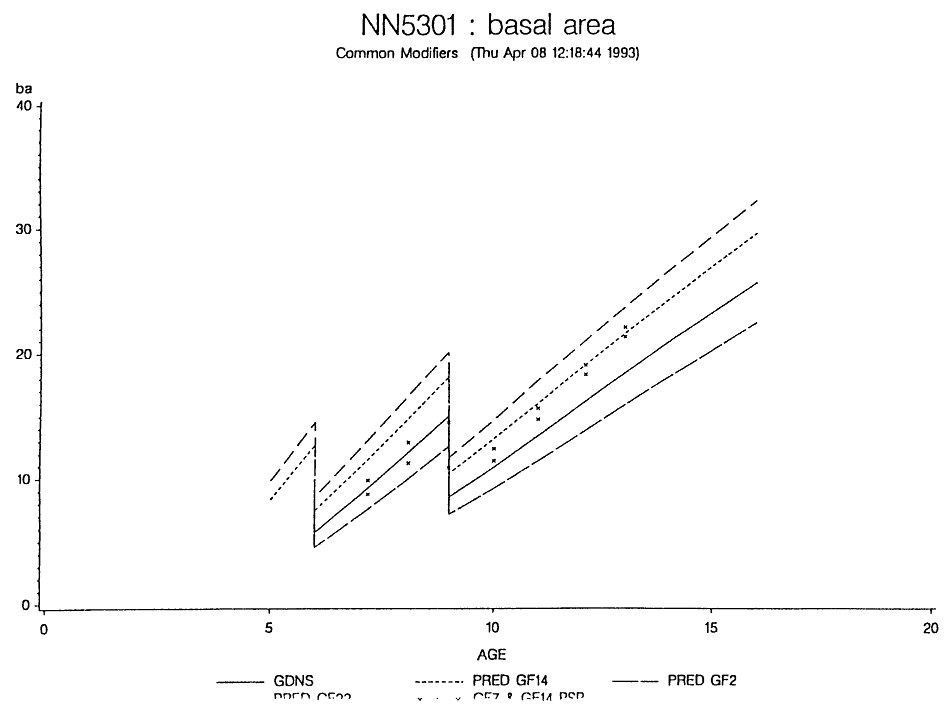
NN5302 : quadratic mean dbh

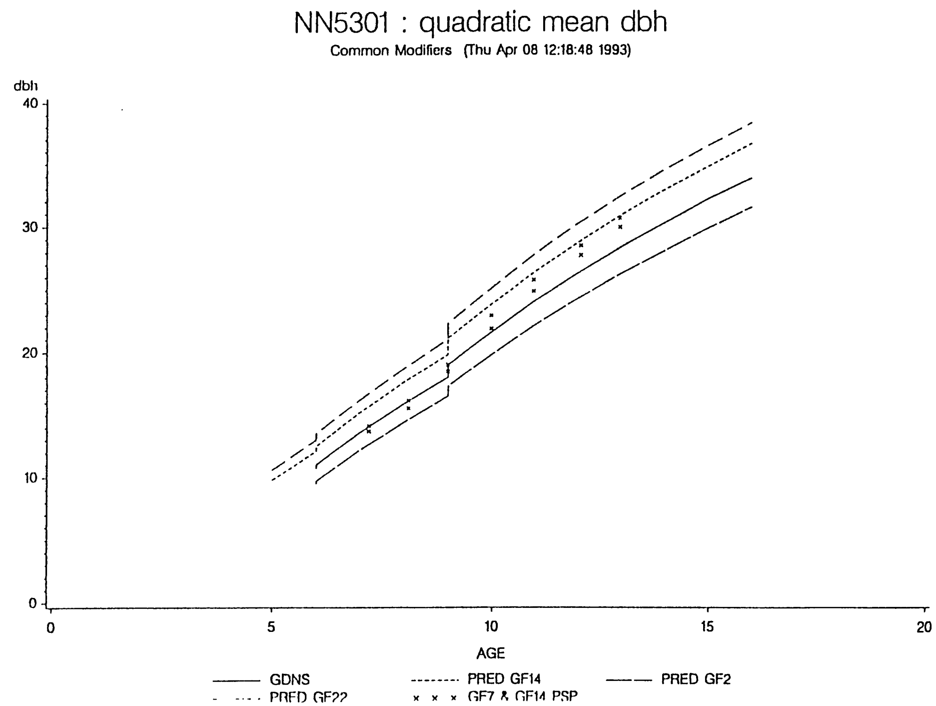
Common Modifiers (Thu Apr 08 12:23:22 1993)



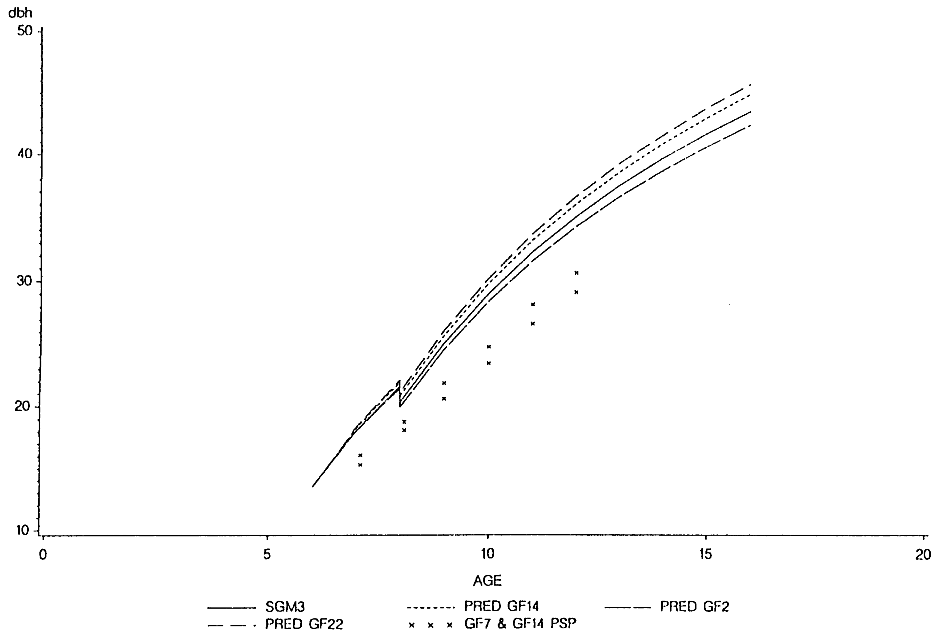

NN5301 : mean top height
Common Modifiers (Thu Apr 08 12:18:45 1993)
ht
AGE
GDNS
PRED GF22
PRED GF14
GF7 & GF14 PSP
PRED GF2


NN5301 : volume
Common Modifiers (Thu Apr 08 12:18:47 1993)
vol
AGE
GDNS
PRED GF22
PRED GF14
GF7 & GF14 PSP
PRED GF2

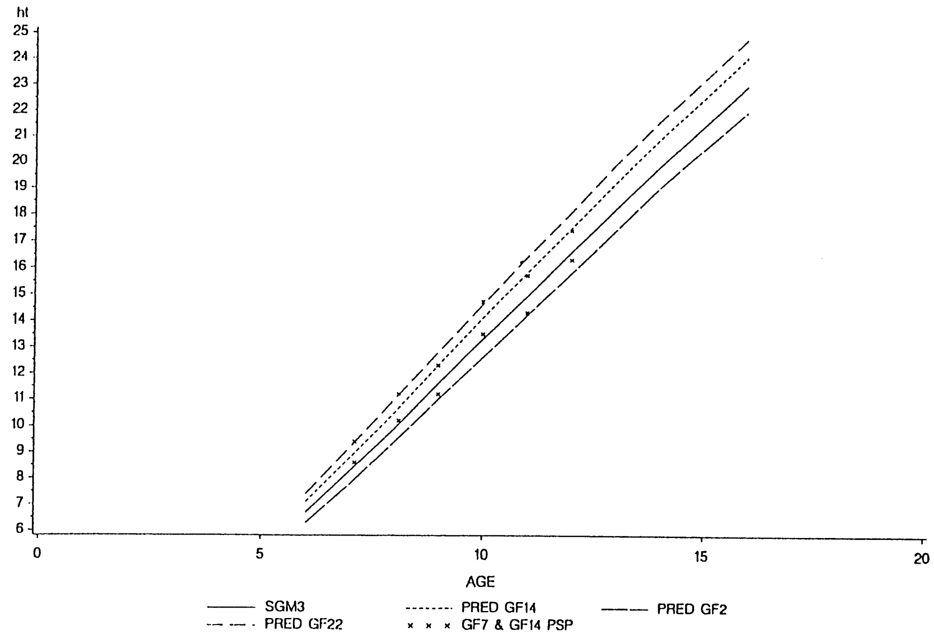

NN5301 : basal area
Common Modifiers (Thu Apr 08 12:18:44 1993)
ba
AGE
GDNS
PRED GF14
PRED GF2


NN5301 : quadratic mean dbh
Common Modifiers (Thu Apr 08 12:18:48 1993)
dbh
AGE
GDNS
PRED GF22
PRED GF14
GF7 & GF14 PSP
PRED GF2

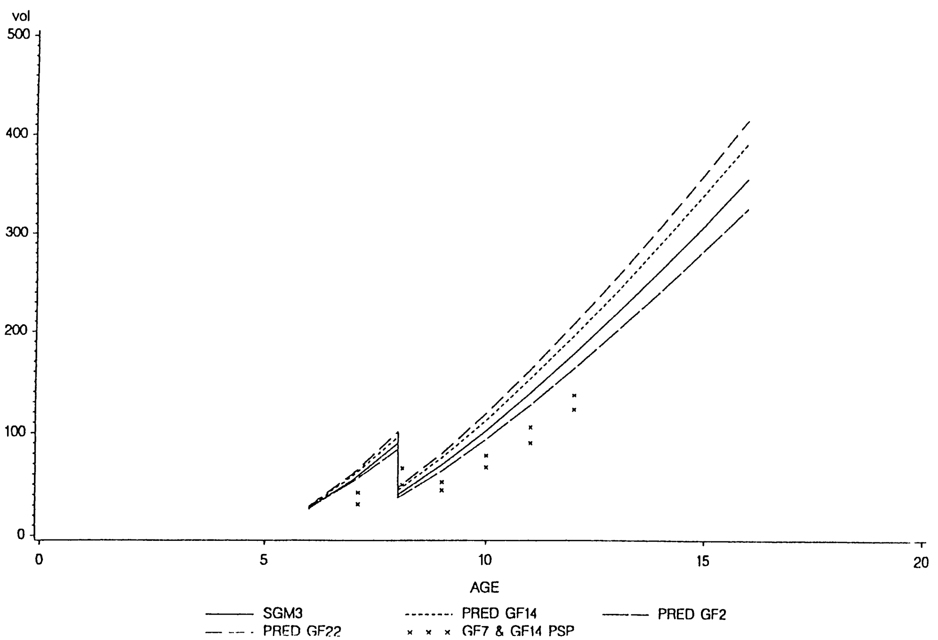
SD682 : quadratic mean dbh
Common Modifiers (Thu Apr 08 12:28:45 1993)



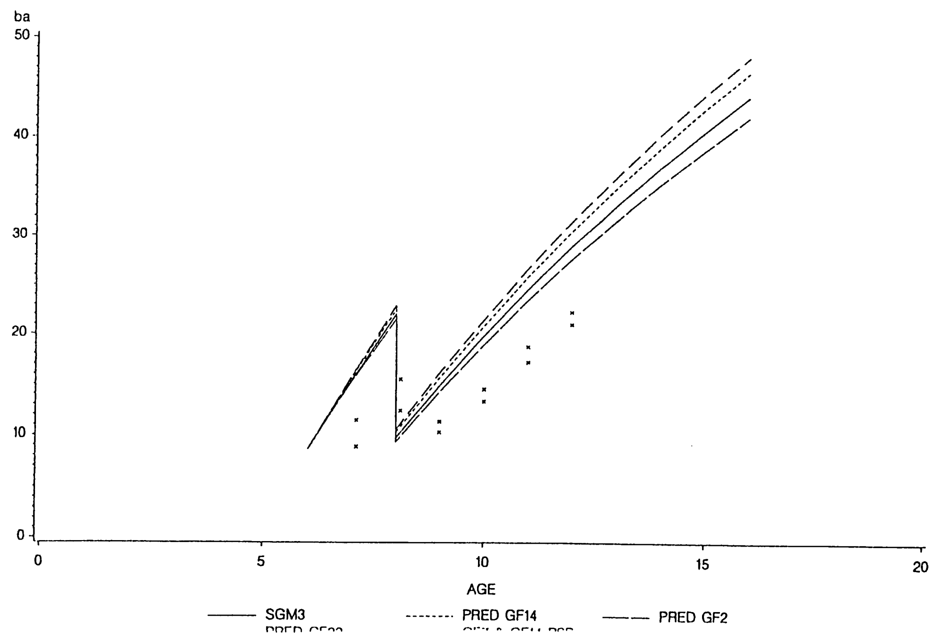
SD682 : mean top height
Common Modifiers (Thu Apr 08 12:28:42 1993)



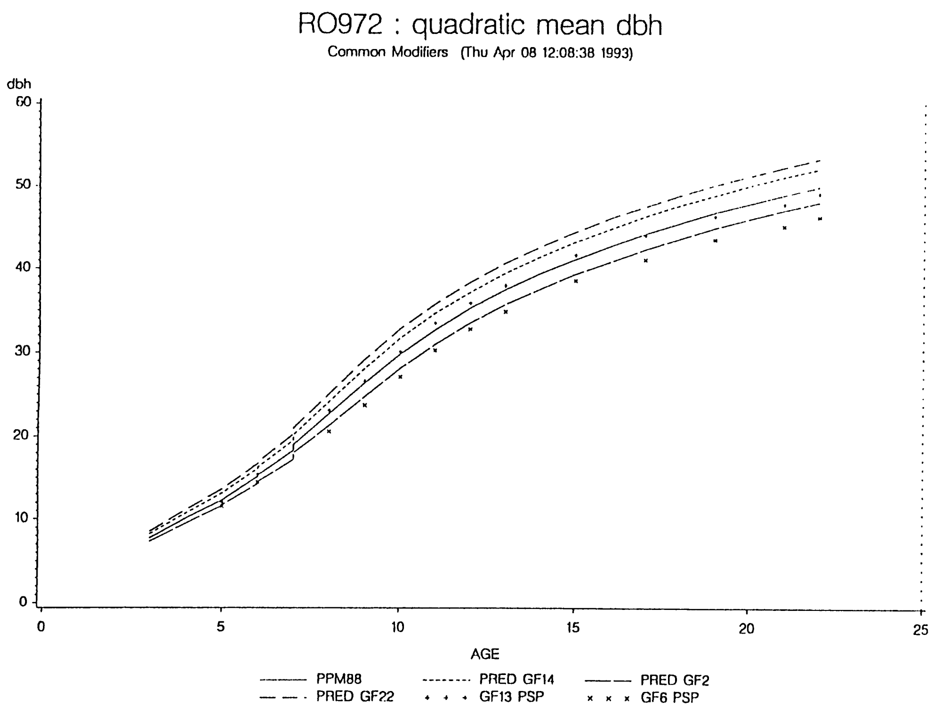
SD682 : volume
Common Modifiers (Thu Apr 08 12:28:44 1993)

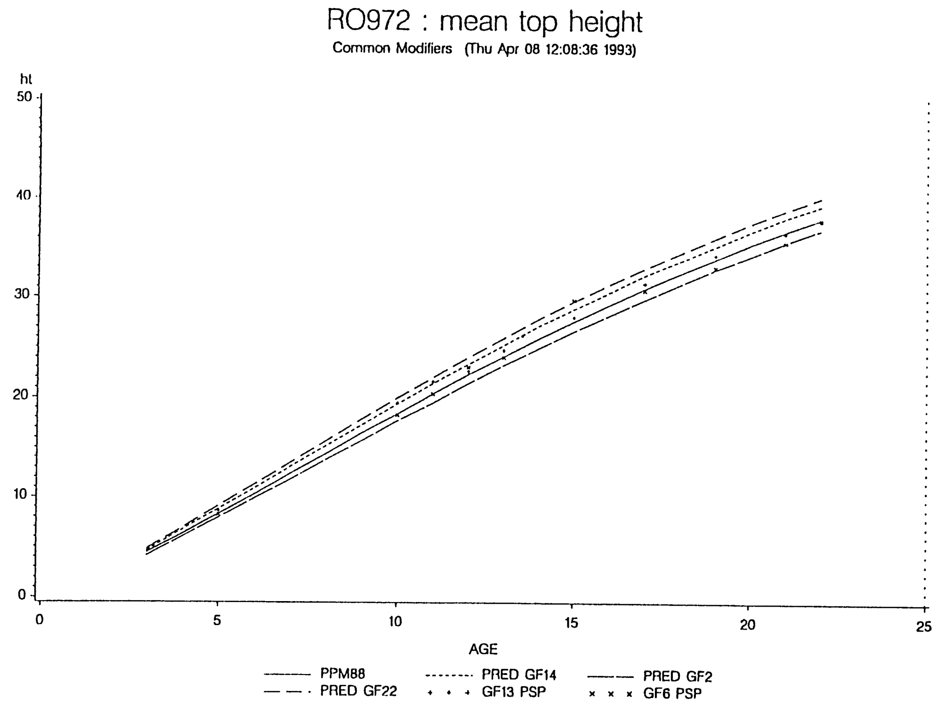


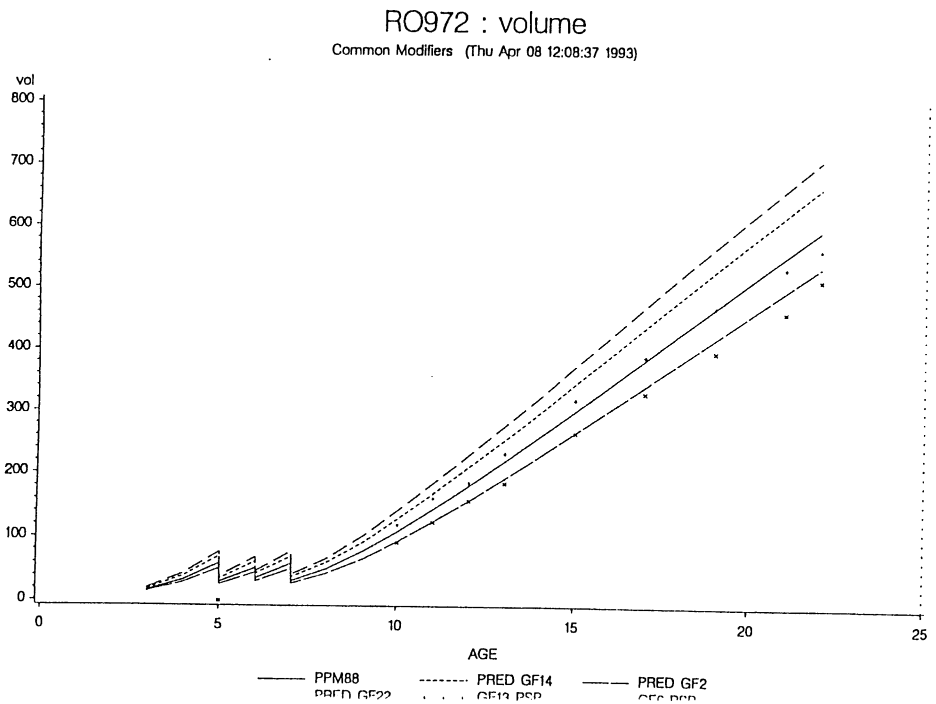
SD682 : basal area
Common Modifiers (Thu Apr 08 12:28:41 1993)

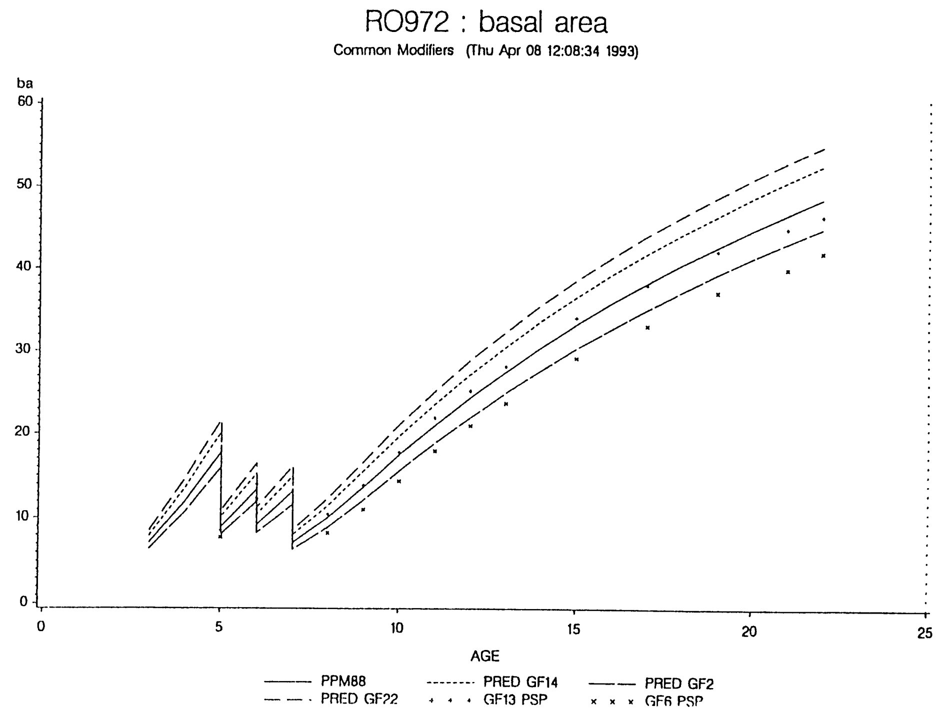


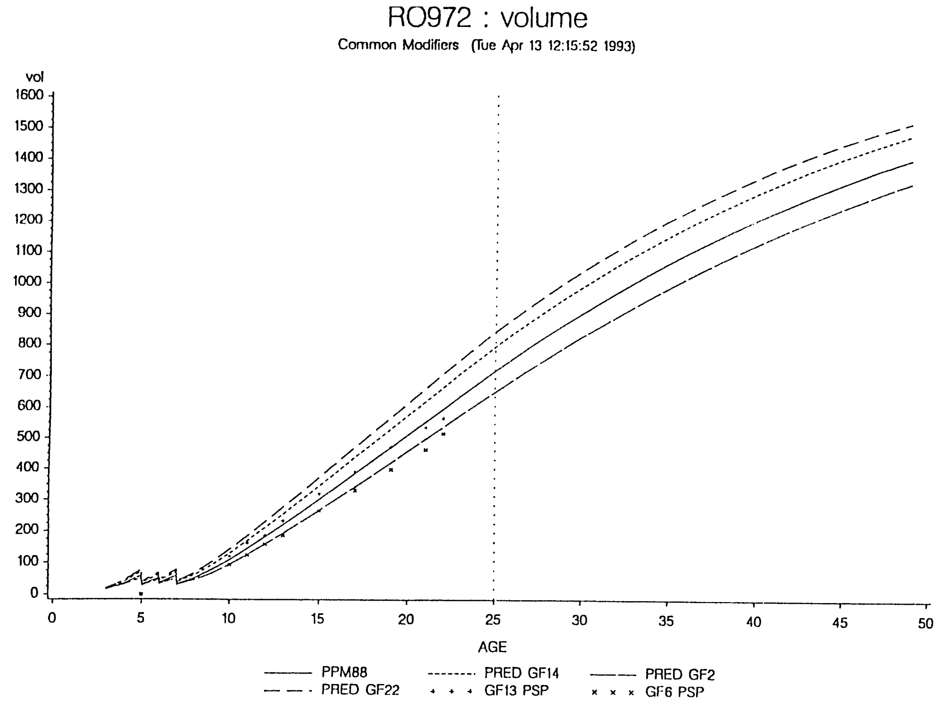
Appendix 5. Predicted and actual growth for Rotoehu initial crop stocking trial (RO972).

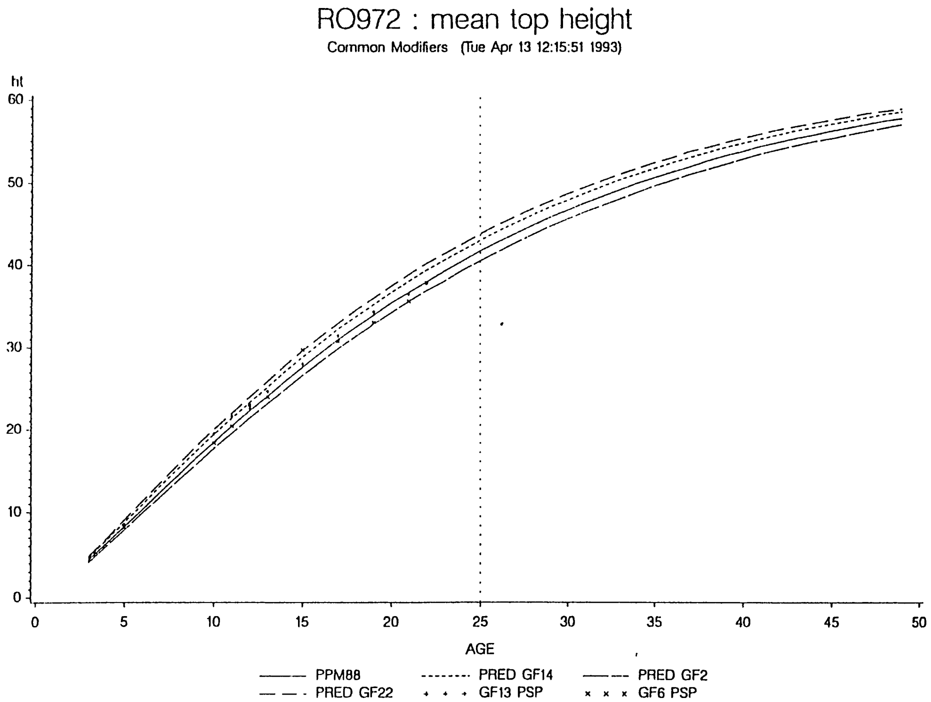

RO972 : quadratic mean dbh
Common Modifiers (Thu Apr 08 12:08:38 1993)
dbh
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF13 PSP
GF6 PSP

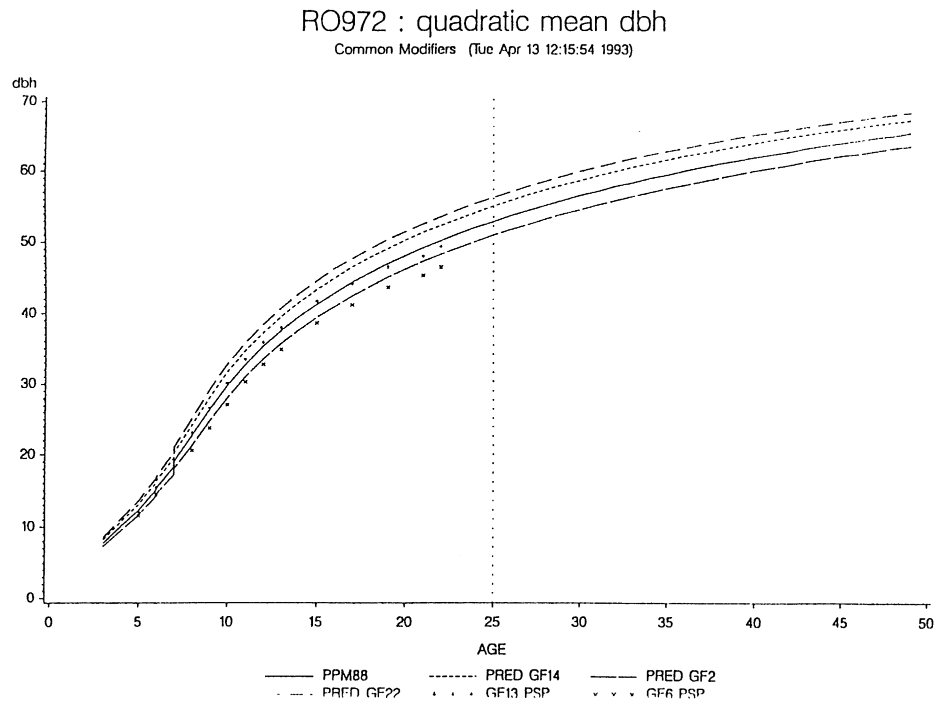

RO972 : mean top height
Common Modifiers (Thu Apr 08 12:08:36 1993)
ht
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF13 PSP
GF6 PSP

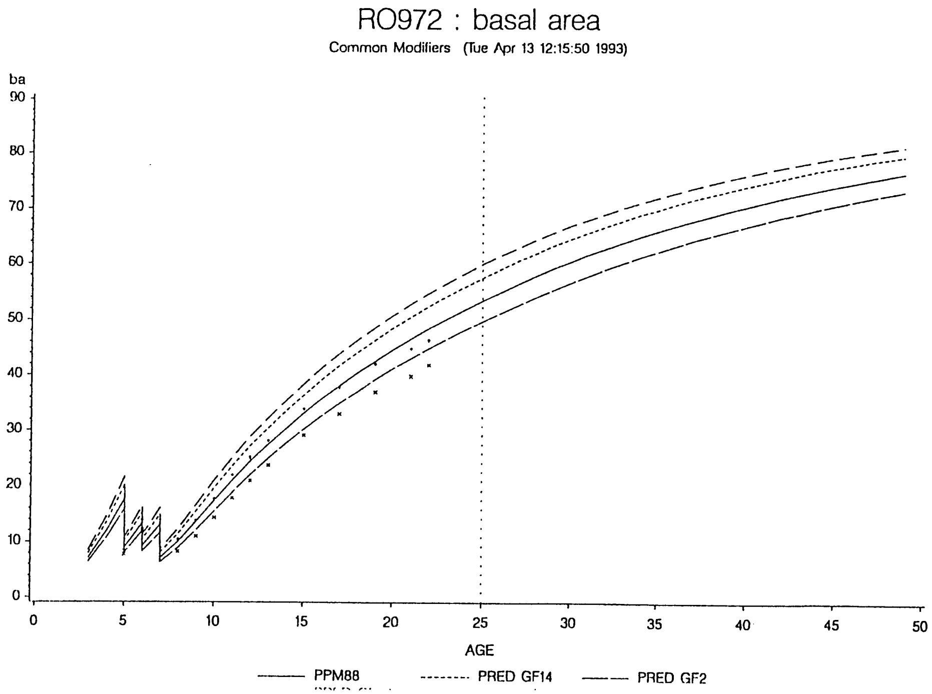

RO972 : volume
Common Modifiers (Thu Apr 08 12:08:37 1993)
vol
AGE
PPM88
PRED GF14
PRED GF2


RO972 : basal area
Common Modifiers (Thu Apr 08 12:08:34 1993)
ba
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF13 PSP
GF6 PSP


RO972 : volume
Common Modifiers (Tue Apr 13 12:15:52 1993)
vol
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF13 PSP
GF6 PSP

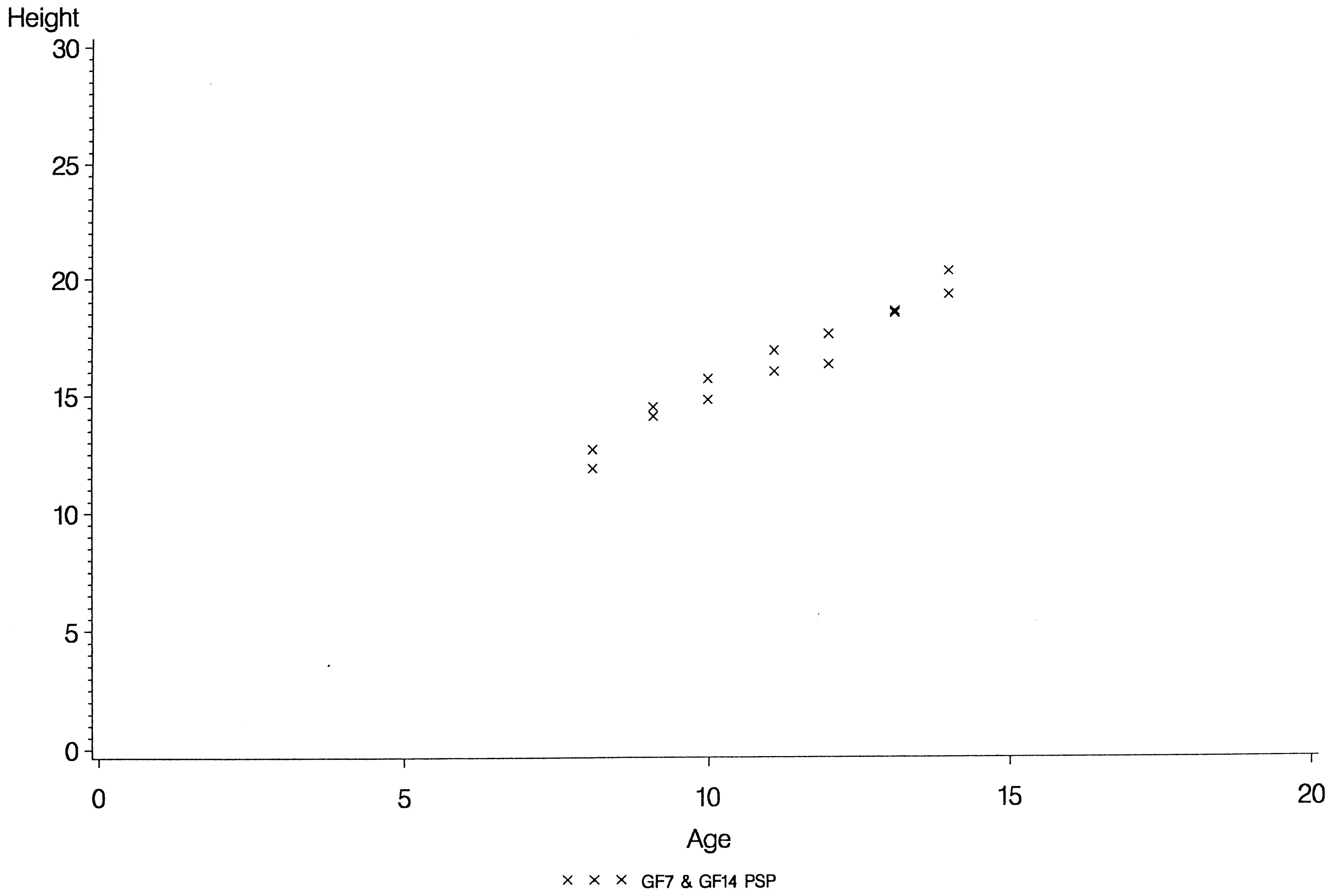

RO972 : mean top height
Common Modifiers (Tue Apr 13 12:15:51 1993)
ht
AGE
PPM88
PRED GF14
PRED GF2
PRED GF22
GF13 PSP
GF6 PSP


RO972 : quadratic mean dbh
Common Modifiers (Tue Apr 13 12:15:54 1993)
dbh
AGE
PPM88
PRED GF14
PRED GF2

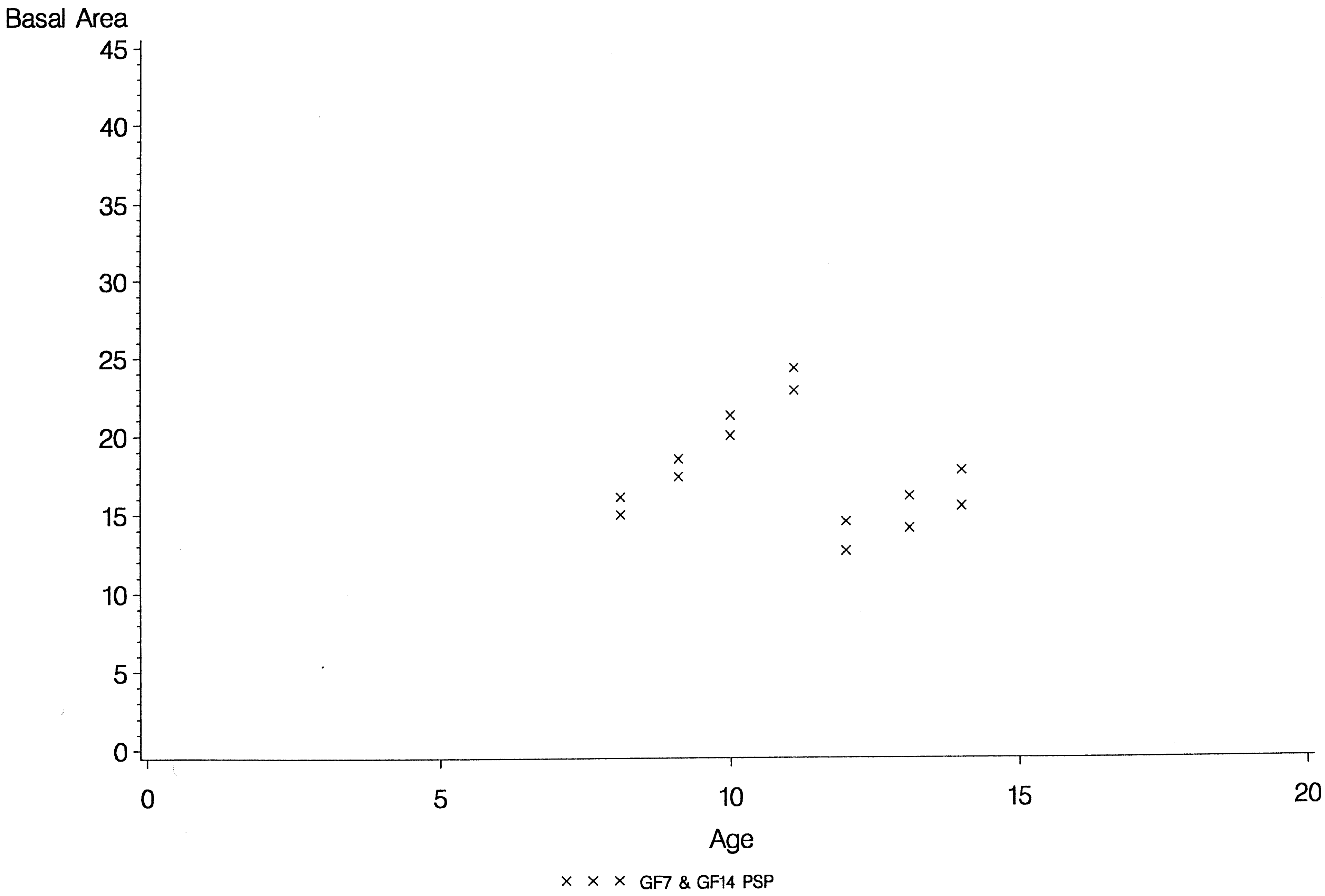

RO972 : basal area
Common Modifiers (Tue Apr 13 12:15:50 1993)
ba
AGE
PPM88
PRED GF14
PRED GF2

Appendix 6. Actual growth on two sites (AK1058 and WN377) in regions in which multiplier estimation could not be done.

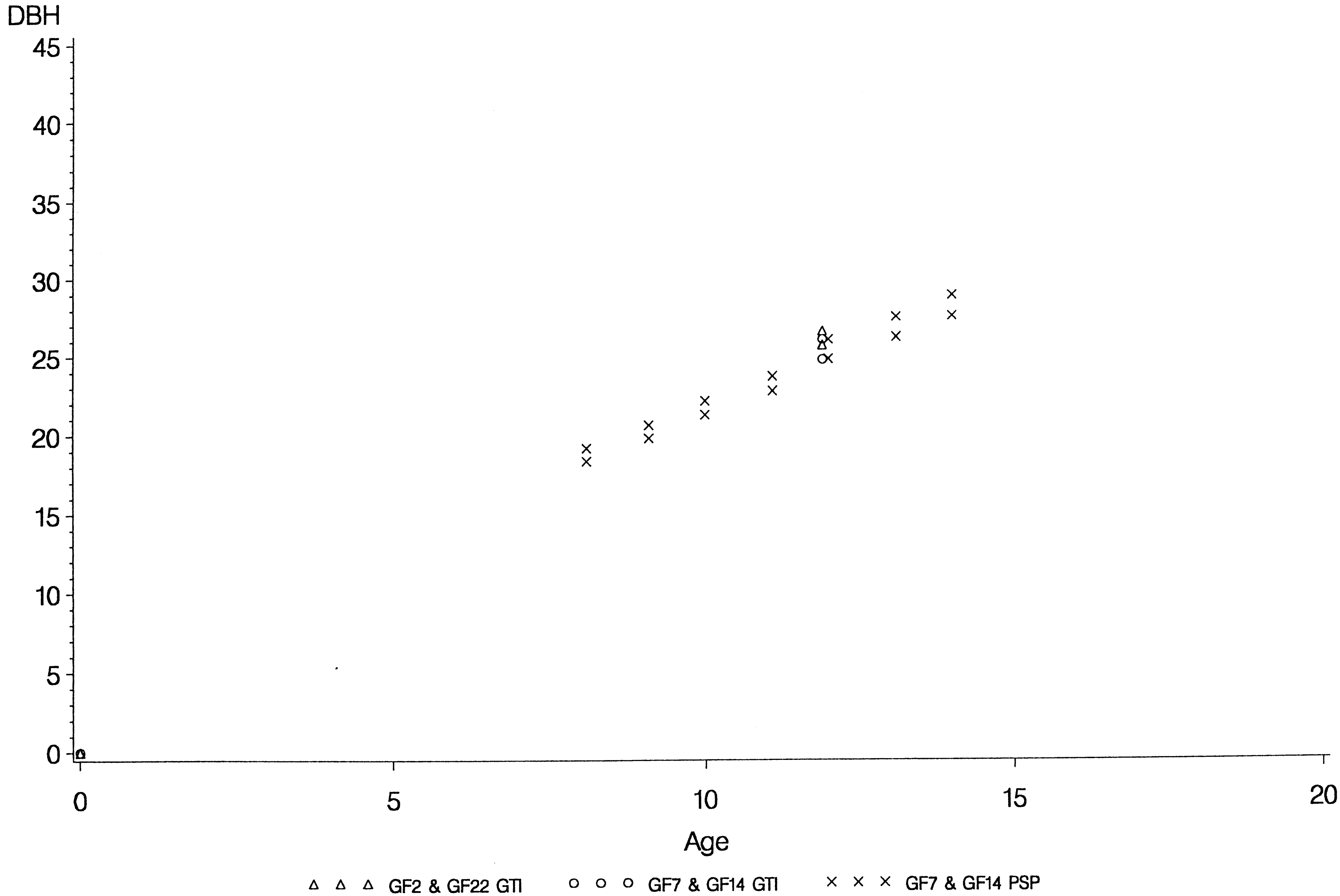
AK1058 mean top height



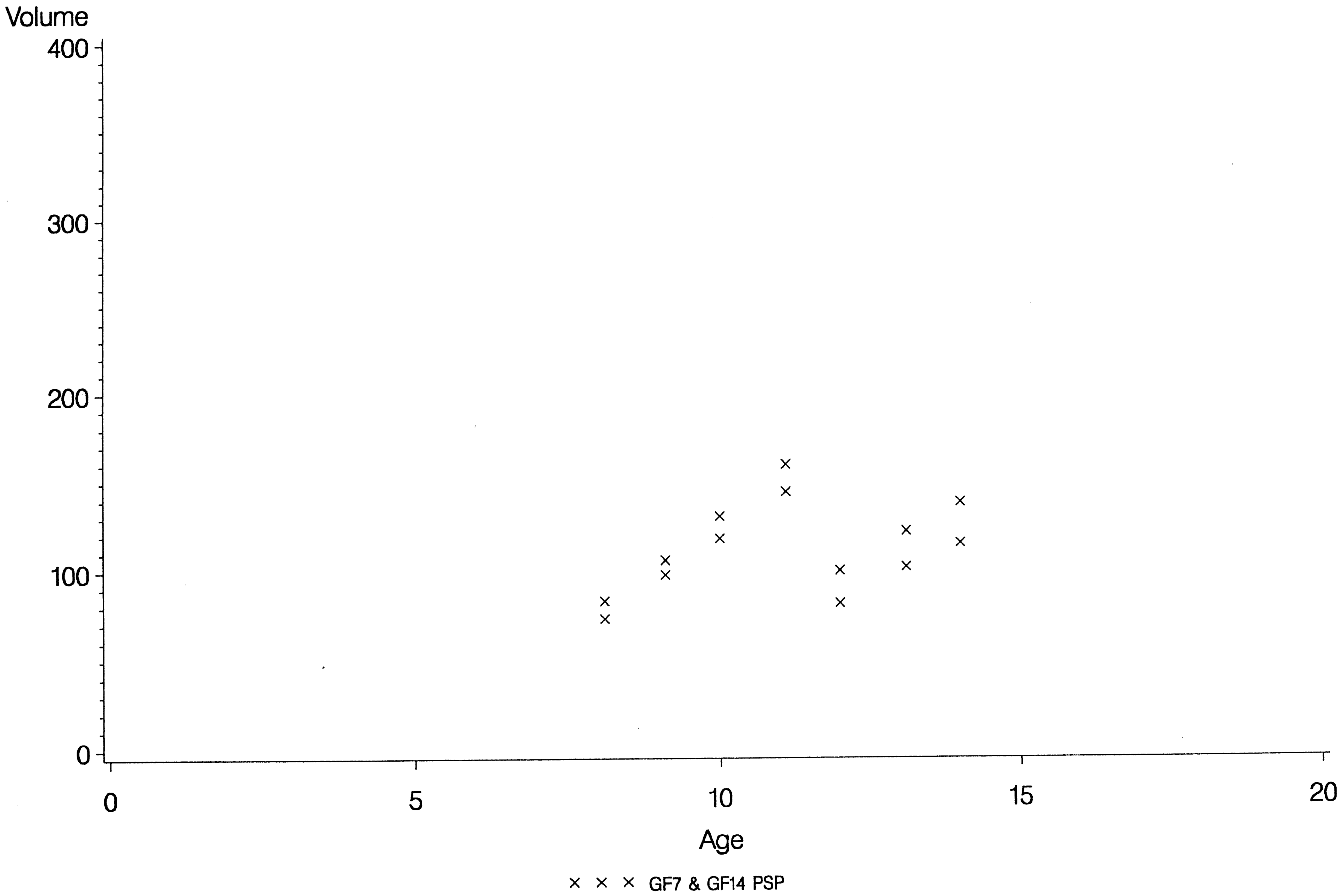
AK1058 basal area



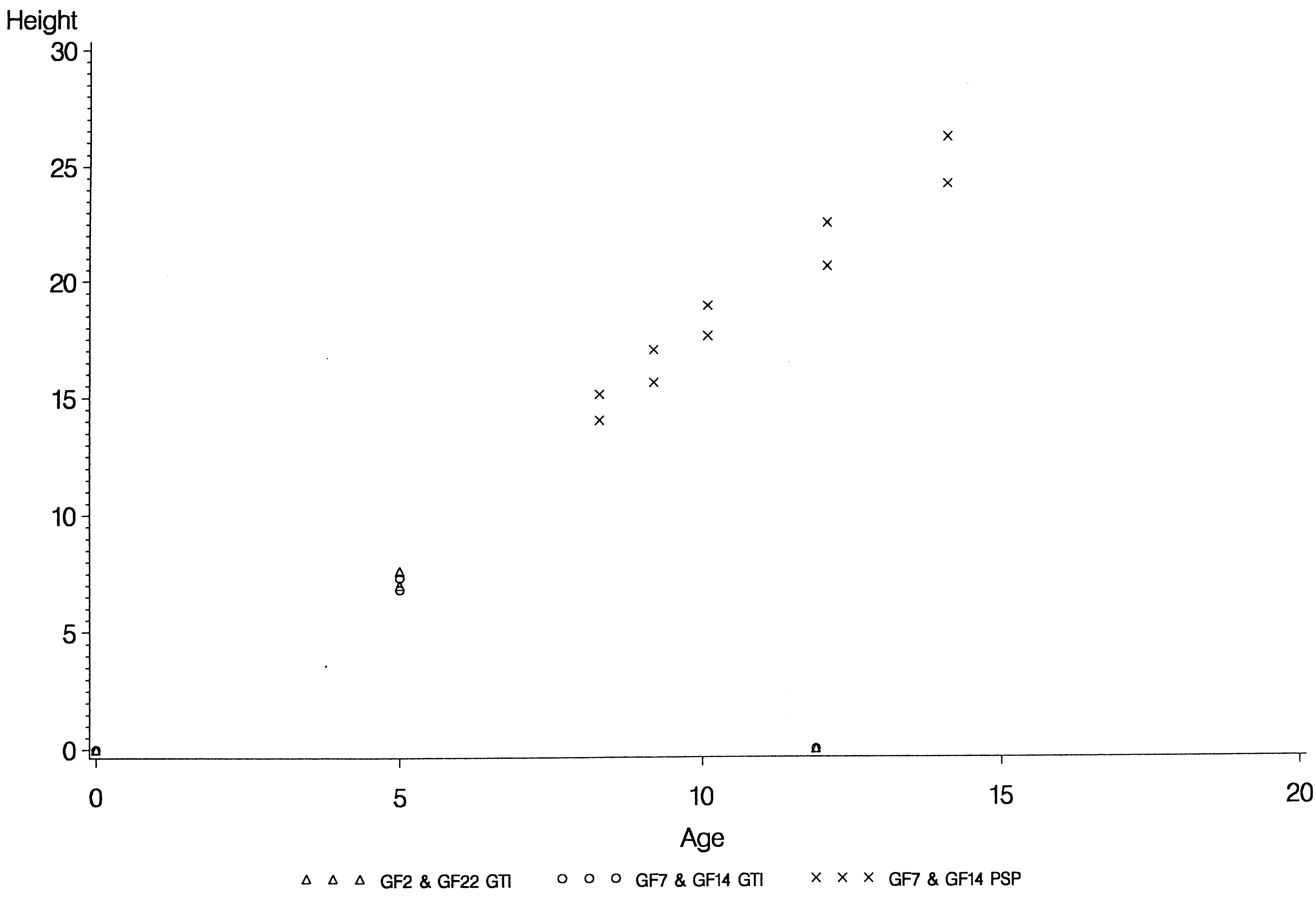
AK1058 quadratic mean diameter

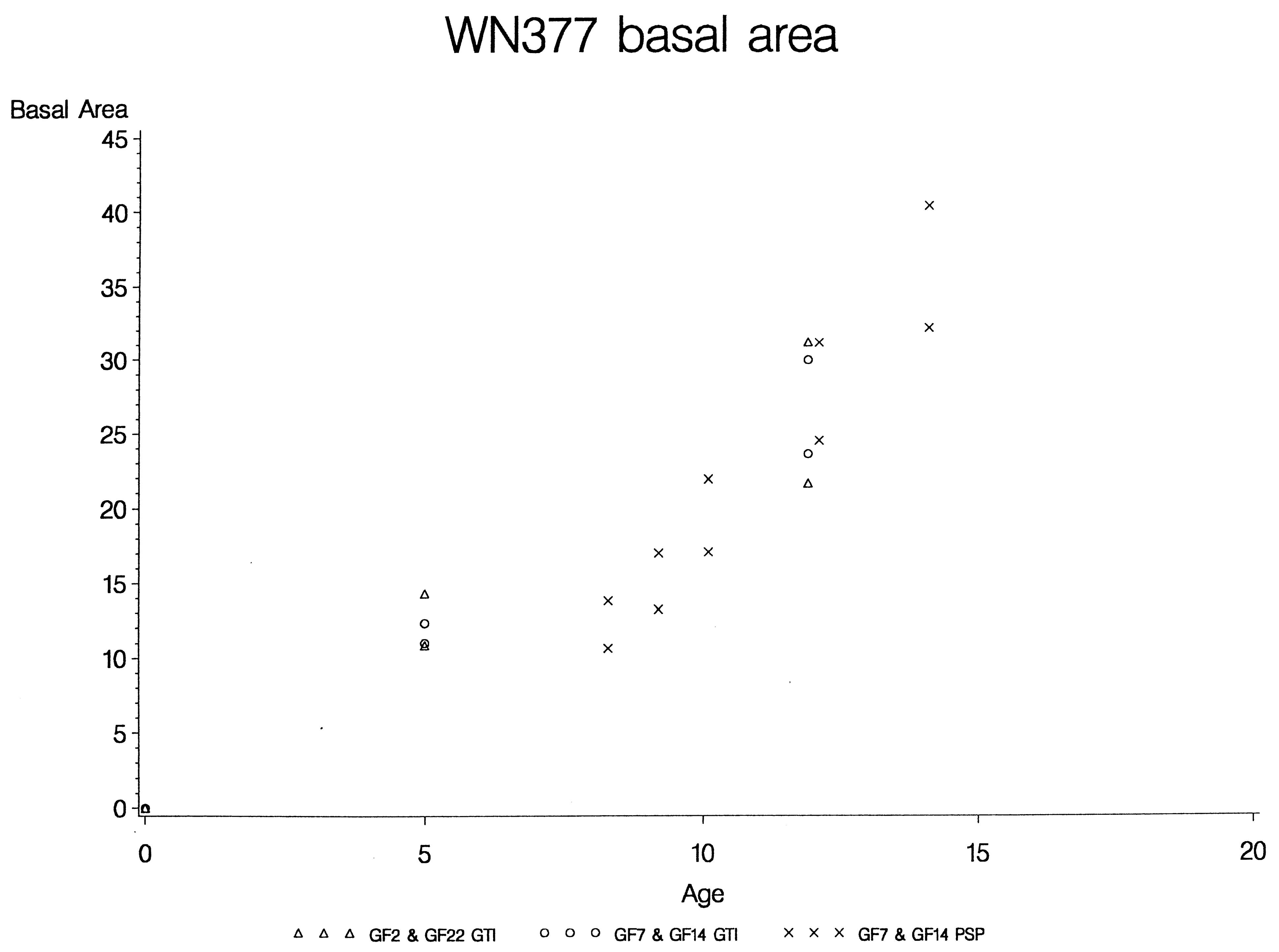


AK1058 volume

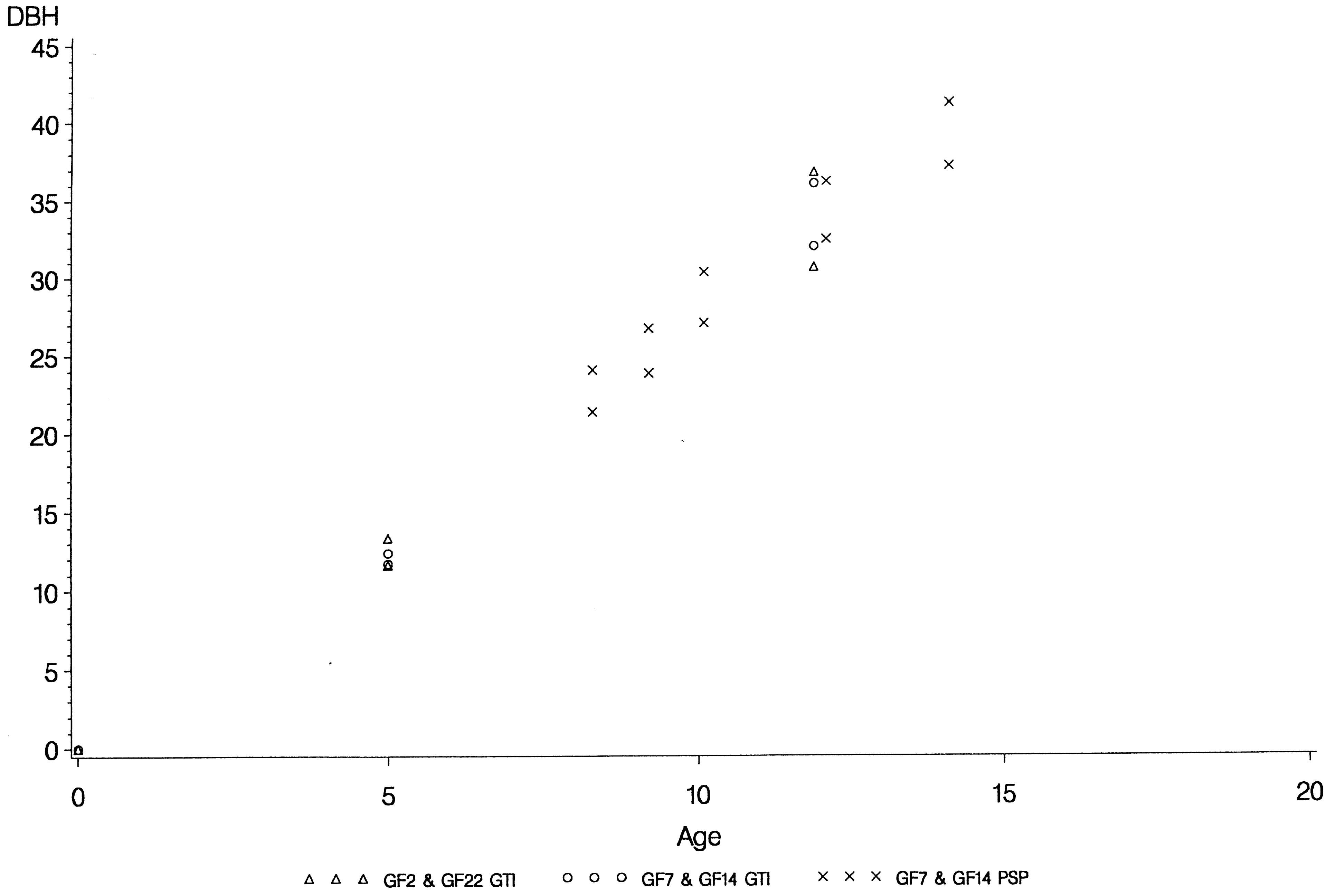


WN377 mean top height

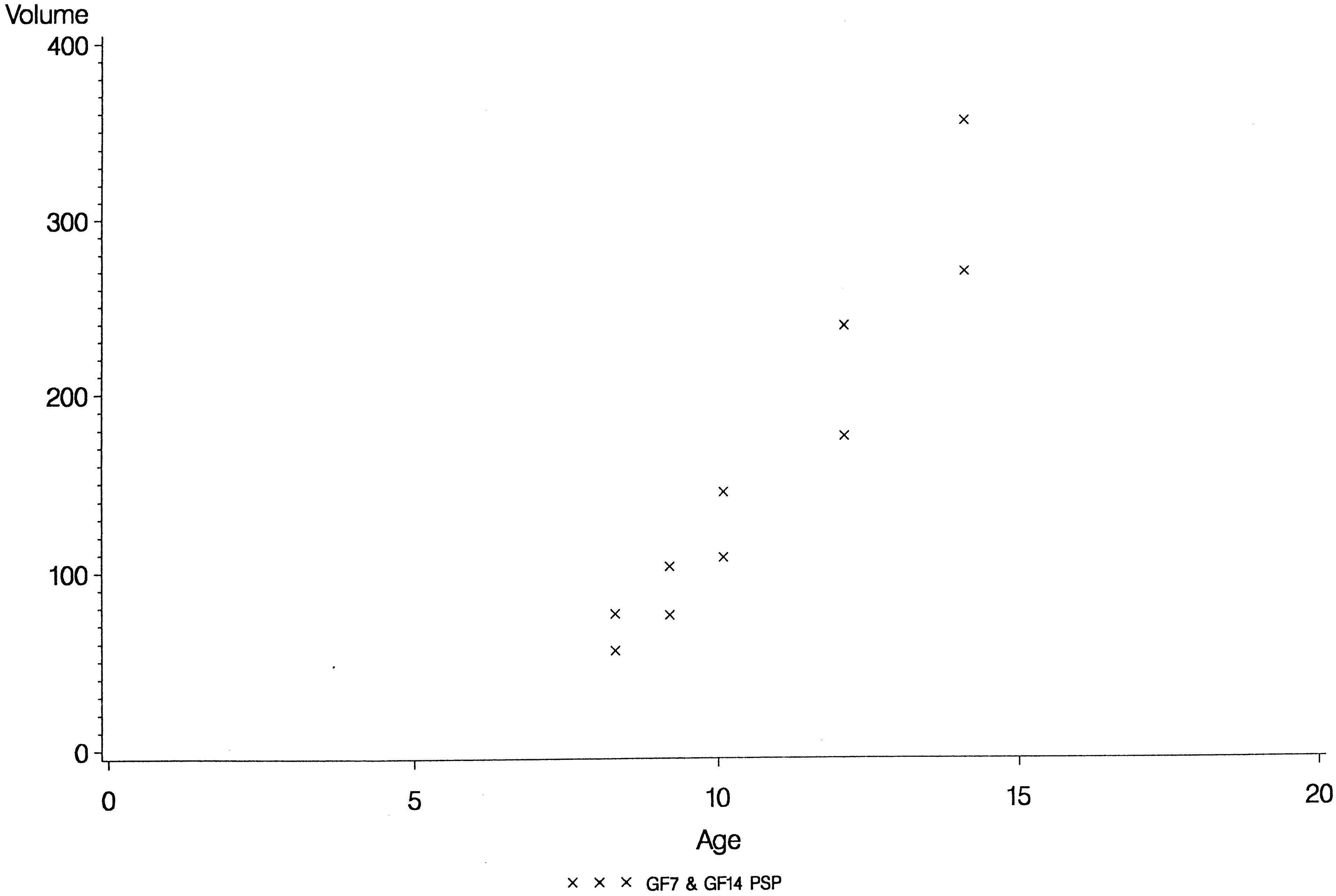



WN377 basal area
Basal Area
45
40
35
30
25
20
15
10
5
0
0
5
10
15
20
Age
GF2 & GF22 GTI
GF7 & GF14 GTI
GF7 & GF14 PSP

WN377 quadratic mean diameter



WN377 volume



Appendix 7. LI 19(GF8) genetic gain growth rate multipliers for each site and year.

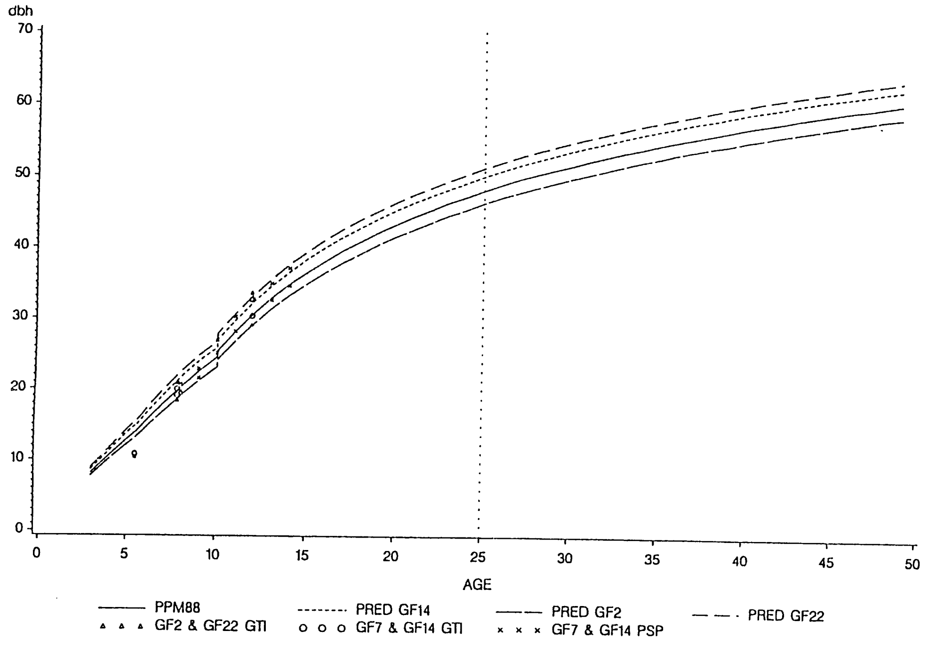
		1979 genetic gain trials					
Year	Mean	Age	RO2103/3	Age	NN530/1	Age	SD682
Growth rate multiplier for mean top height:							
1987	1.07693	8	1.05325	8	1.10061	7	-
1988	1.18747	9	-	9	1.05747	8	1.31747
1989	1.26141	10	1.26141	10	-	9	-
1990	1.03331	11	1.07693	11	1.05255	10	0.97045
1991	1.01460	12	0.87176	12	1.09069	11	1.08136
1992	1.00266	13	0.97841	13	1.02311	12	1.00647
Mean	1.06906		1.04835		1.06489		1.09394
Growth rate multiplier for basal area and stocking equations:							
1987	0.86499	8	0.78225	8	0.94772	7	-
1988	0.89760	9	-	9	0.90160	8	0.89359
1989	0.77815	10	0.77815	10	-	9	-
1990	0.84433	11	0.86981	11	0.82173	10	0.93311
1991	0.91249	12	0.94139	12	0.84110	11	0.95498
1992	0.95582	13	0.94237	13	0.95327	12	0.97182
Mean	0.89191		0.86279		0.89309		0.93838

Appendix 8. Genetic gain growth rate multipliers for each site and year for a GF14 seedlot where 39% of individuals are from half-sib matings.

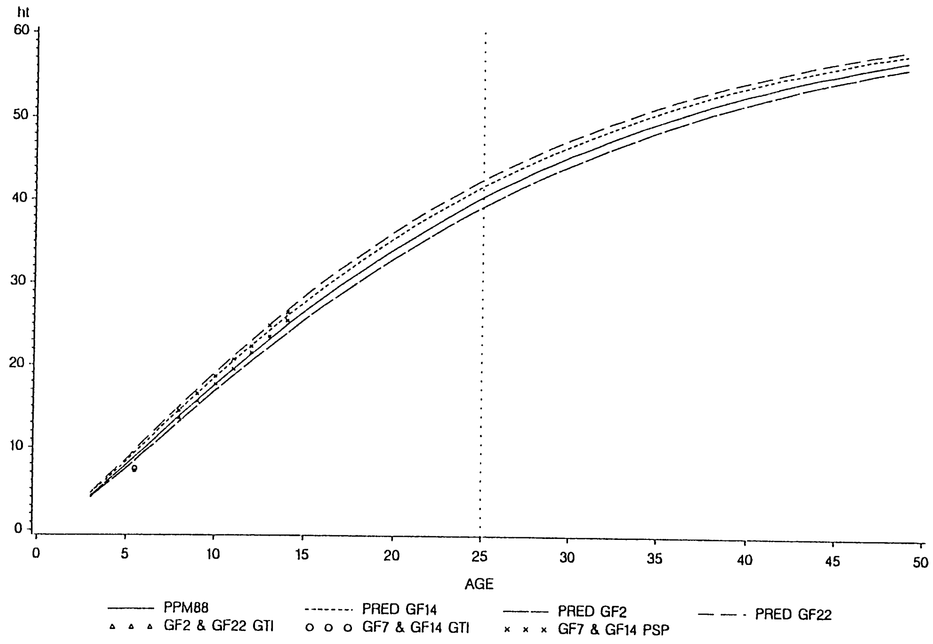
		1979 genetic gain trials					
Year	Mean	Age	RO2103/3	Age	NN530/1	Age	SD682
Growth rate multiplier for mean top height:							
1987	0.98549	8	0.97602	8	0.99495	7	-
1988	1.09974	9	-	9	1.29869	8	0.90079
1989	1.15262	10	1.15262	10	-	9	-
1990	1.10540	11	1.00709	11	1.04086	10	1.26824
1991	1.00433	12	0.99645	12	0.97466	11	1.04188
1992	-	13	-	13	-	12	-
Mean	1.05188		1.03304		1.05229		1.07031
Growth rate multiplier for basal area and stocking equations:							
1987	1.00223	8	0.99230	8	1.01215	7	-
1988	1.16235	9	-	9	0.83458	8	1.49012
1989	0.79439	10	0.79439	10	-	9	-
1990	0.84600	11	0.94325	11	0.80150	10	0.79326
1991	0.97357	12	0.97821	12	0.82755	11	1.11494
1992	-	13	-	13	-	12	-
Mean	0.97625		0.92704		0.86895		1.13277

Appendix 9. Genetic gain predictions for mean top height, basal area, diameter at breast height, and volume per ha to 50 years by site.

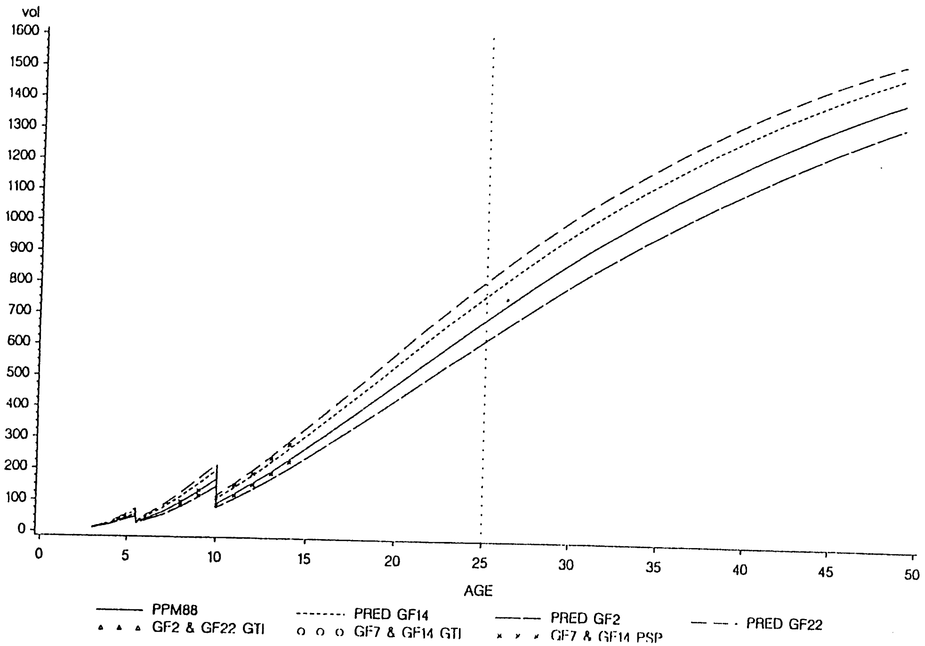
RO21031 : quadratic mean dbh
Common Modifiers (Tue Apr 13 11:57:28 1993)



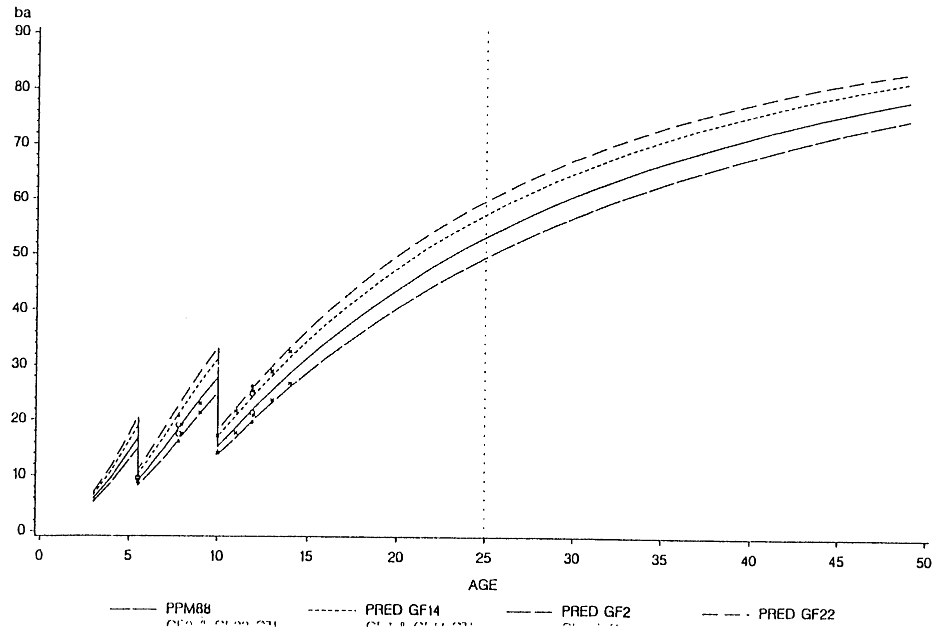
RO21031 : mean top height
Common Modifiers (Tue Apr 13 11:57:25 1993)



RO21031 : volume
Common Modifiers (Tue Apr 13 11:57:26 1993)

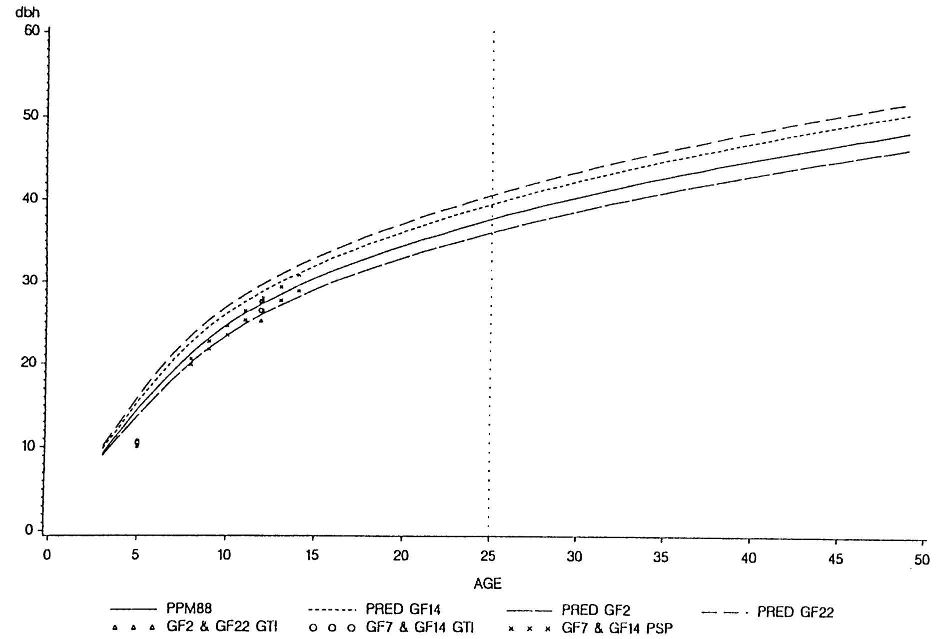


RO21031 : basal area
Common Modifiers (Tue Apr 13 11:57:23 1993)



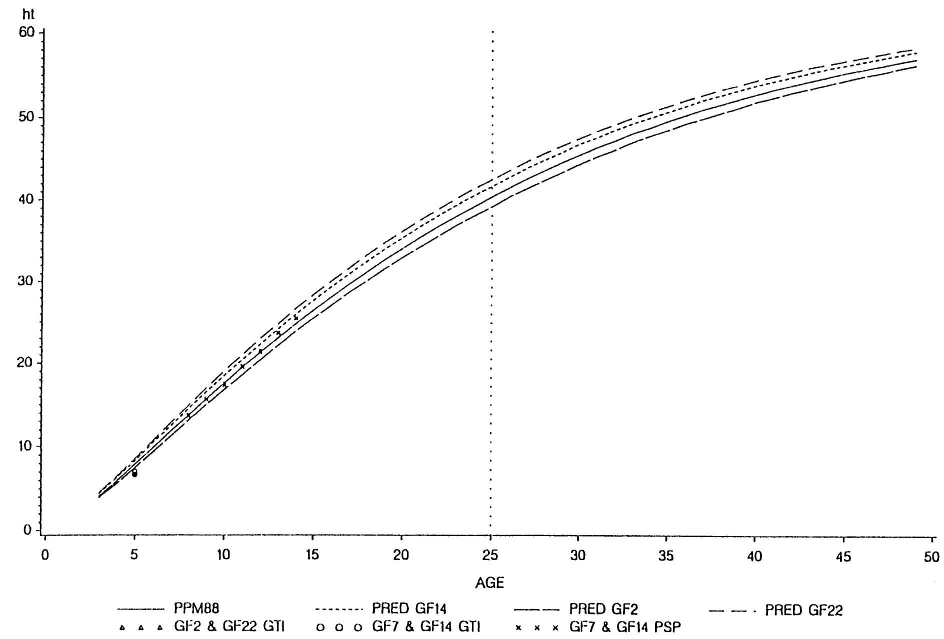
RO21032 : quadratic mean dbh

Common Modifiers (Tue Apr 13 12:03:49 1993)



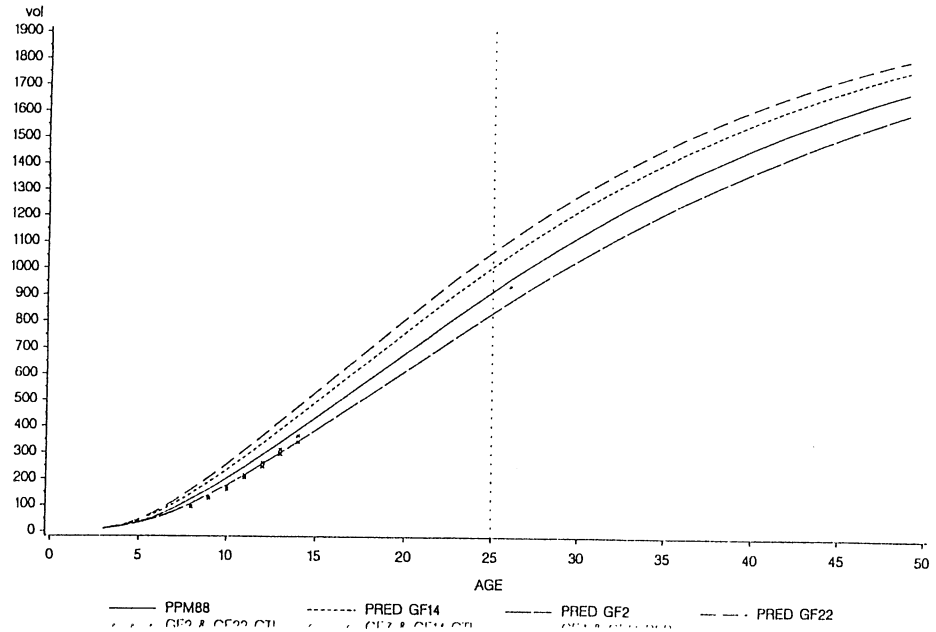
RO21032 : mean top height

Common Modifiers (Tue Apr 13 12:03:46 1993)



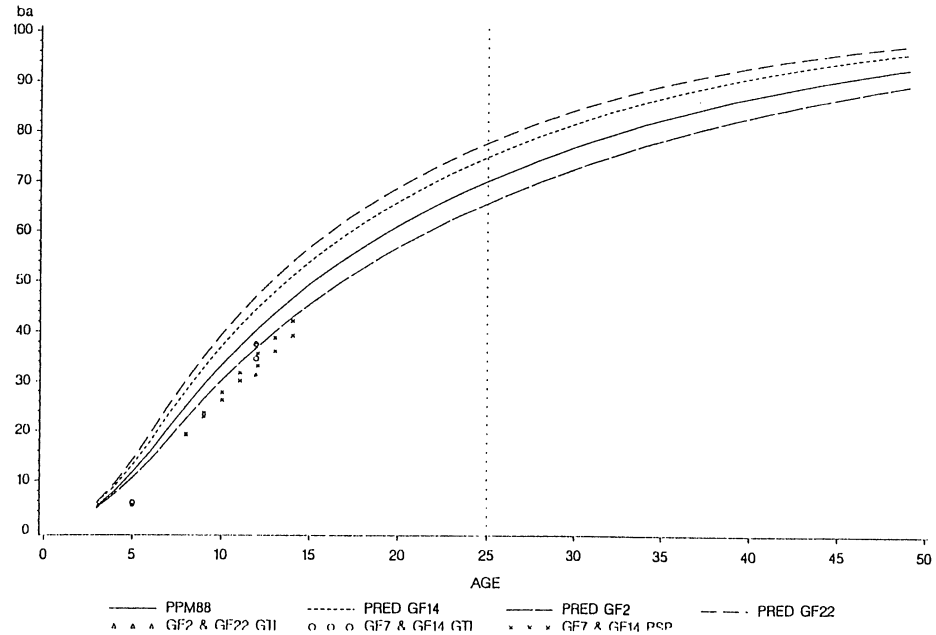
RO21032 : volume

Common Modifiers (Tue Apr 13 12:03:47 1993)



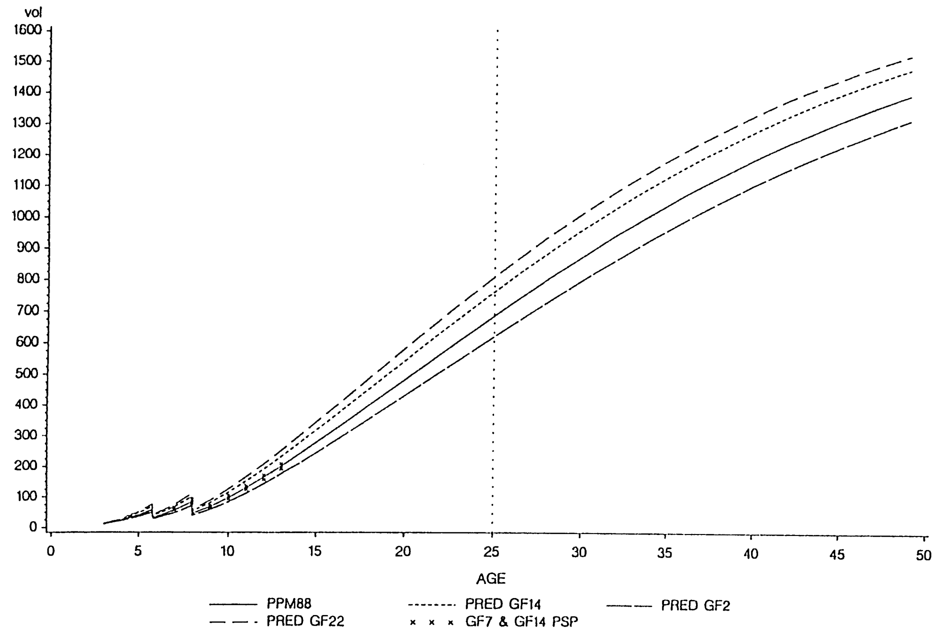
RO21032 : basal area

Common Modifiers (Tue Apr 13 12:03:45 1993)



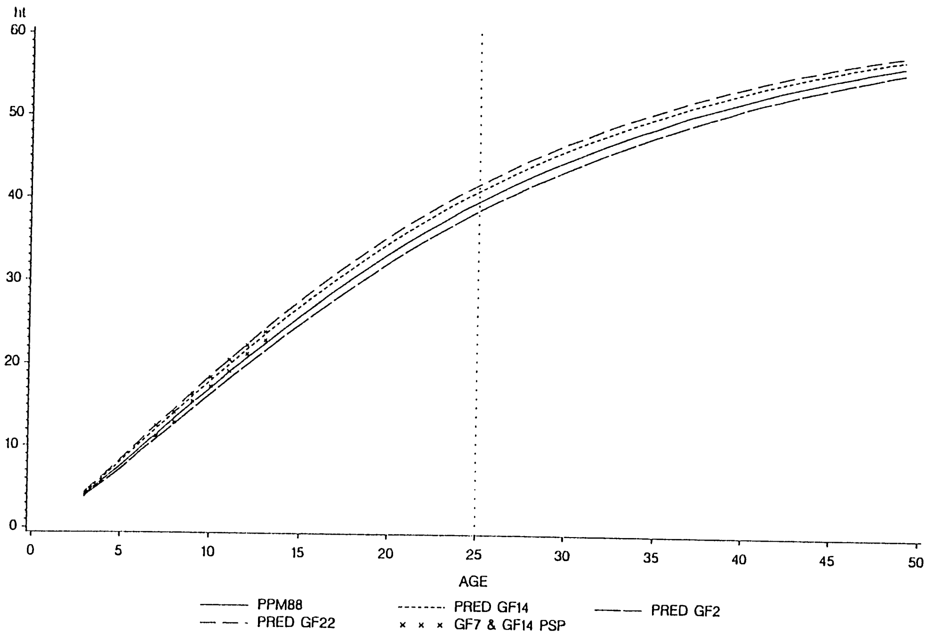
RO21033 : volume

Common Modifiers (Tue Apr 13 12:10:12 1993)



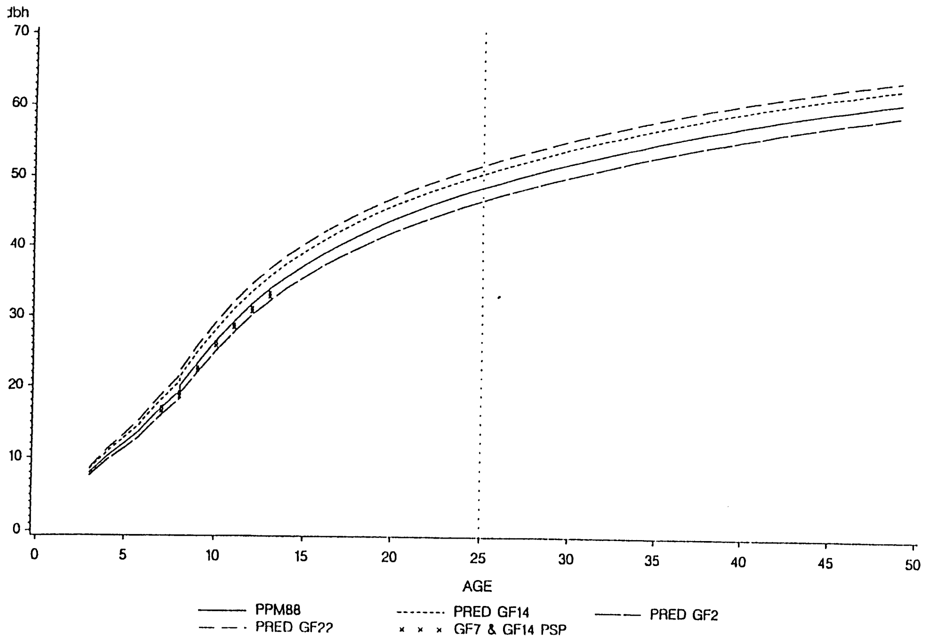
RO21033 : mean top height

Common Modifiers (Tue Apr 13 12:10:10 1993)



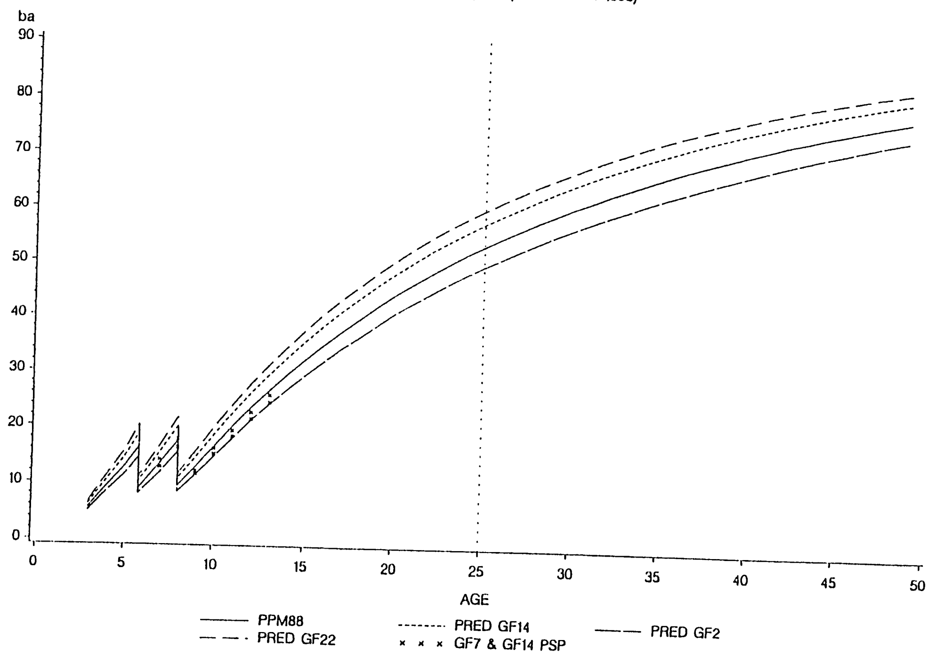
RO21033 : quadratic mean dbh

Common Modifiers (Tue Apr 13 12:10:13 1993)



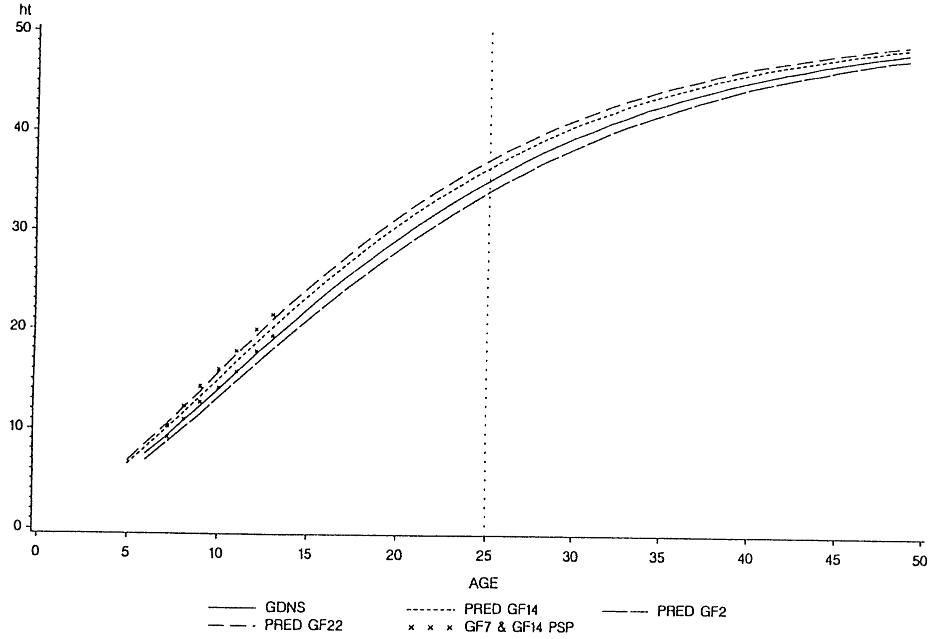
RO21033 : basal area

Common Modifiers (Tue Apr 13 12:10:09 1993)



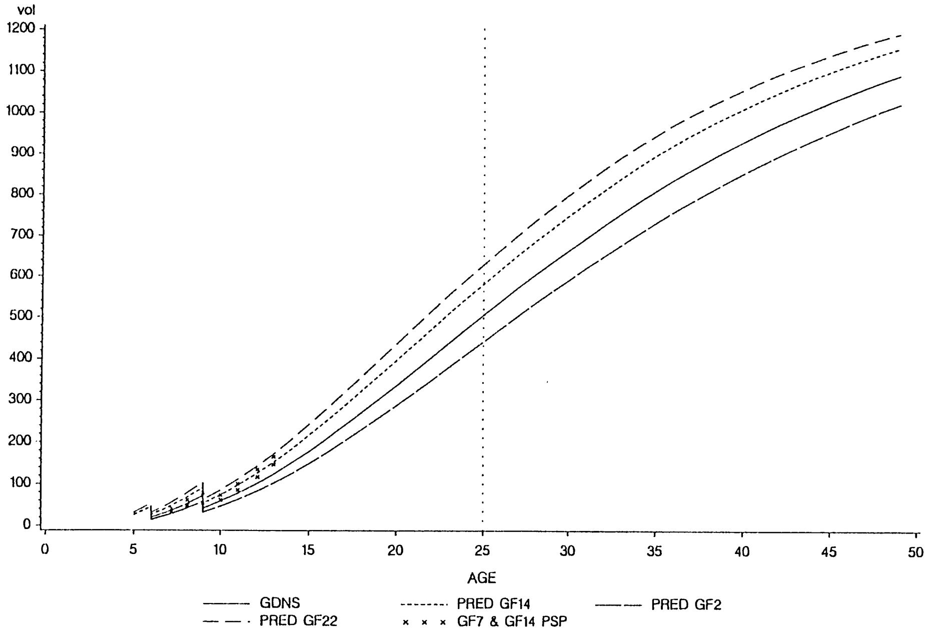
NN5301 : mean top height

Common Modifiers (Tue Apr 13 12:27:41 1993)



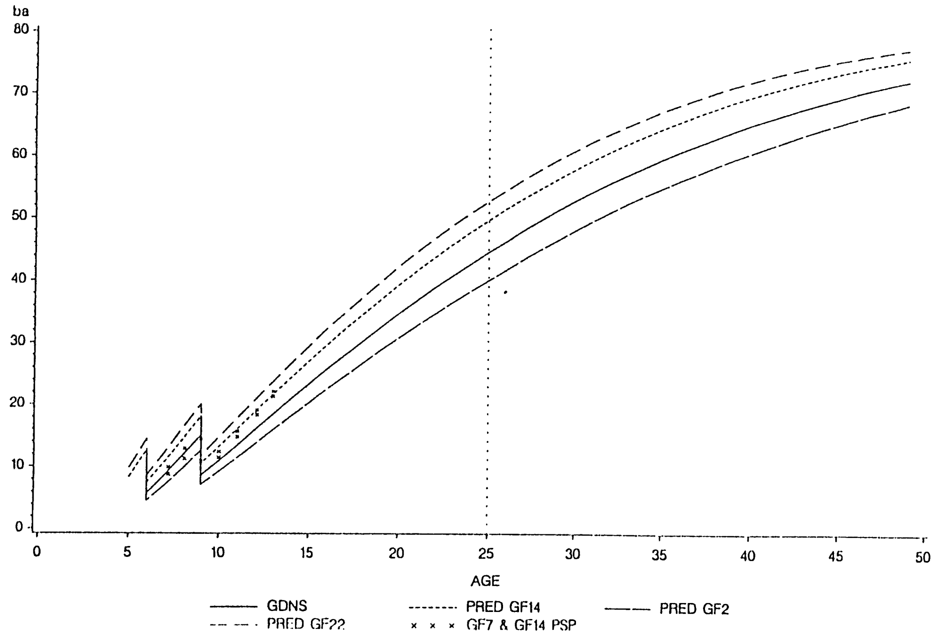
NN5301 : volume

Common Modifiers (Tue Apr 13 12:27:43 1993)



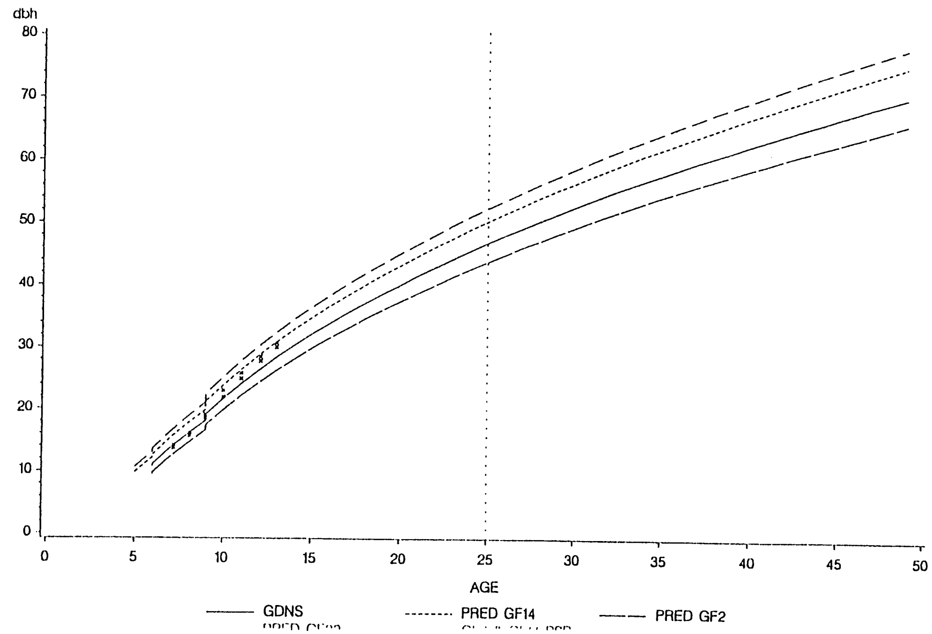
NN5301 : basal area

Common Modifiers (Tue Apr 13 12:27:40 1993)

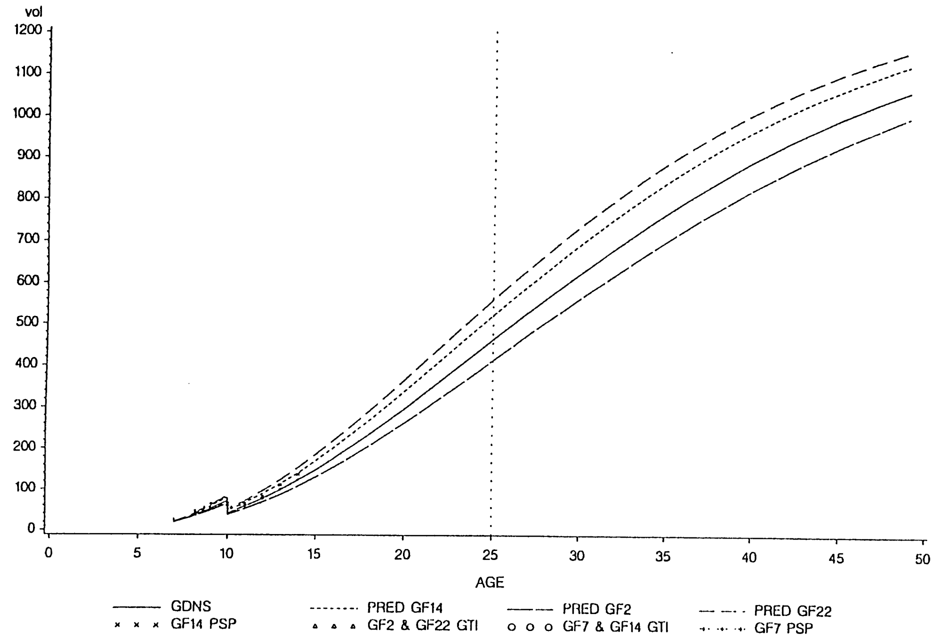


NN5301 : quadratic mean dbh

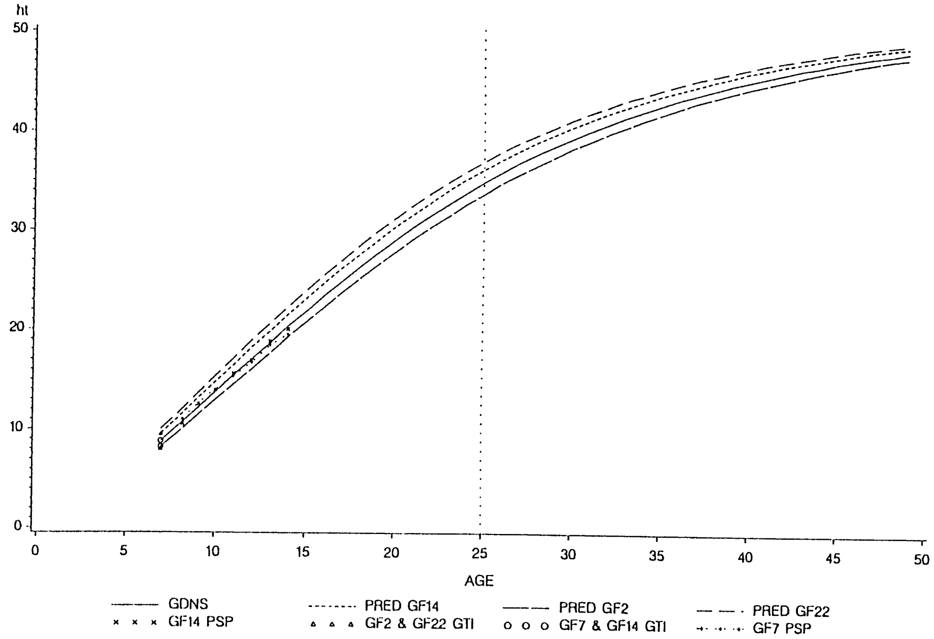
Common Modifiers (Tue Apr 13 12:27:44 1993)



Common Modifiers (Tue Apr 13 12:33:00 1993)

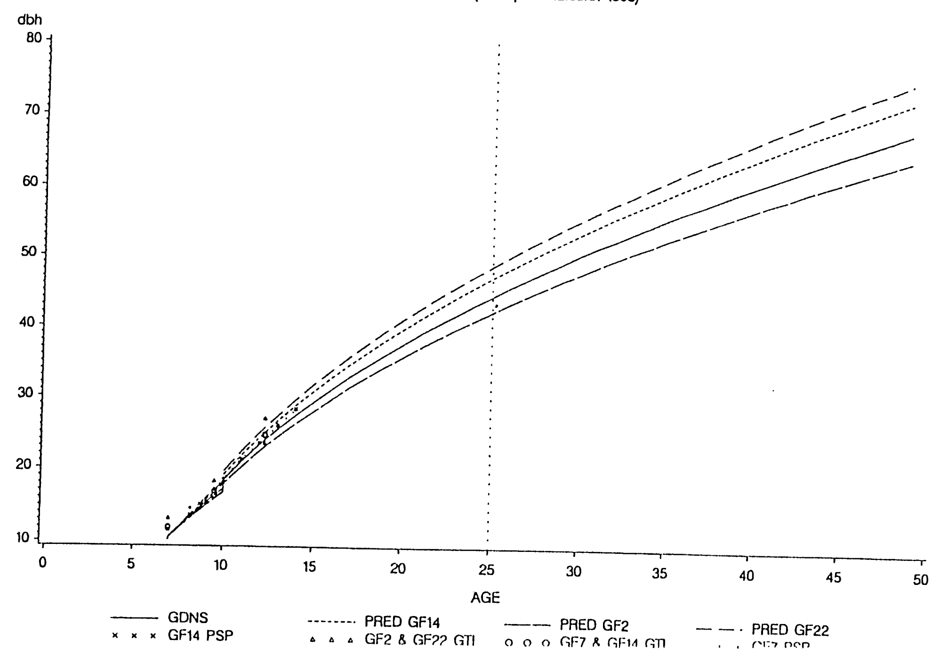


Common Modifiers (Tue Apr 13 12:32:58 1993)



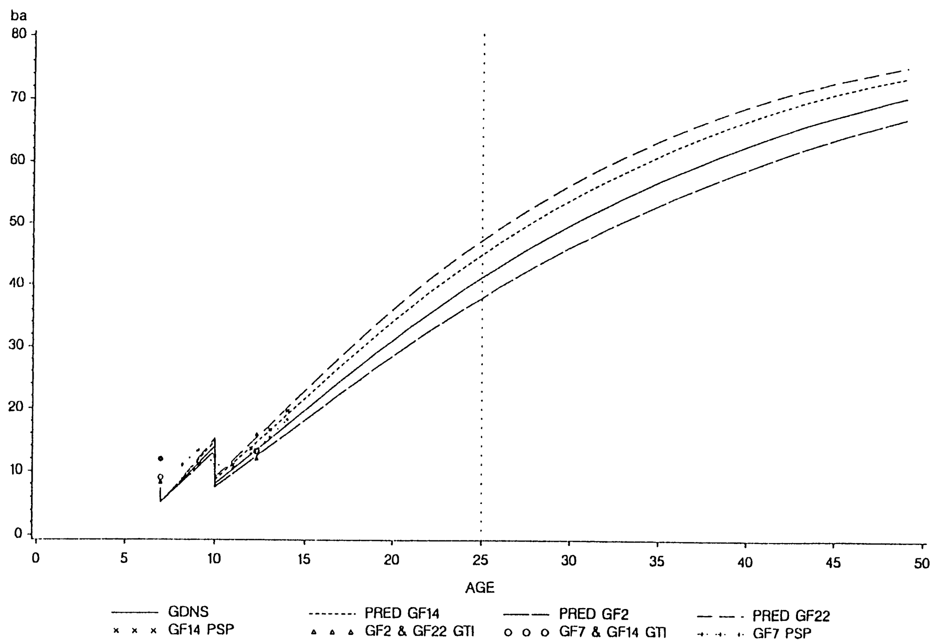
NN5302 : quadratic mean dbh

Common Modifiers (Tue Apr 13 12:33:01 1993)

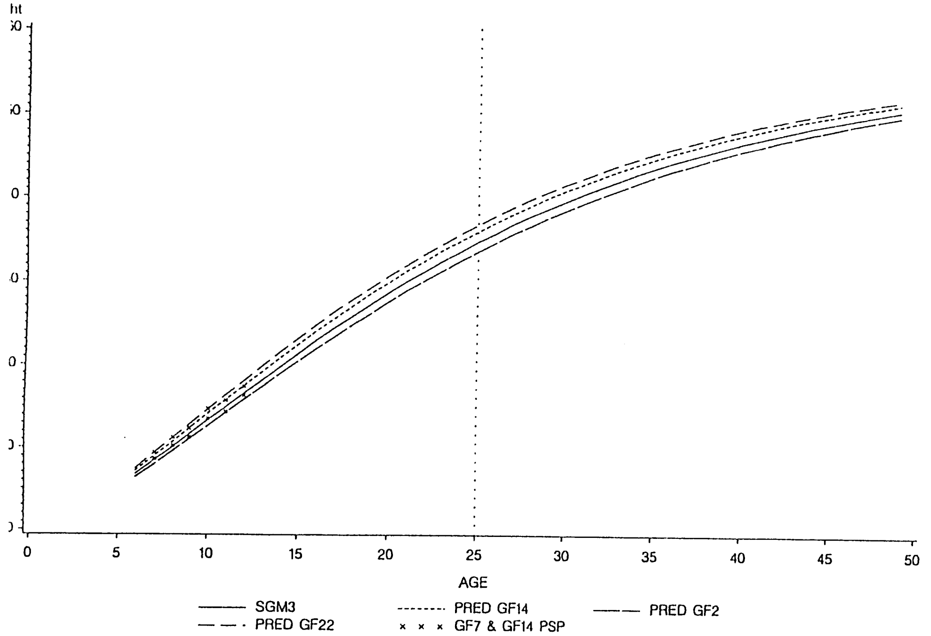


NN5302 : basal area

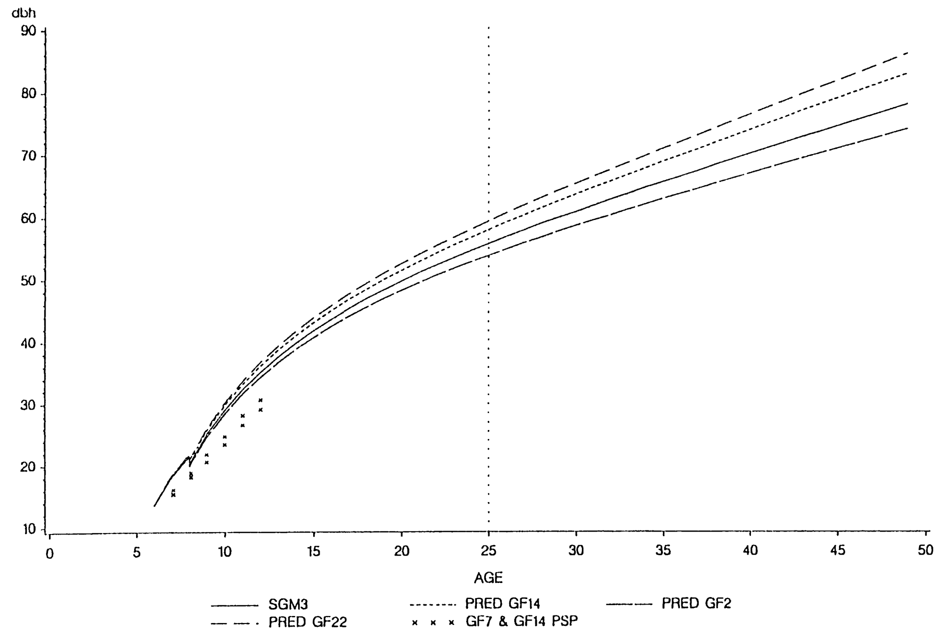
Common Modifiers (Tue Apr 13 12:32:57 1993)



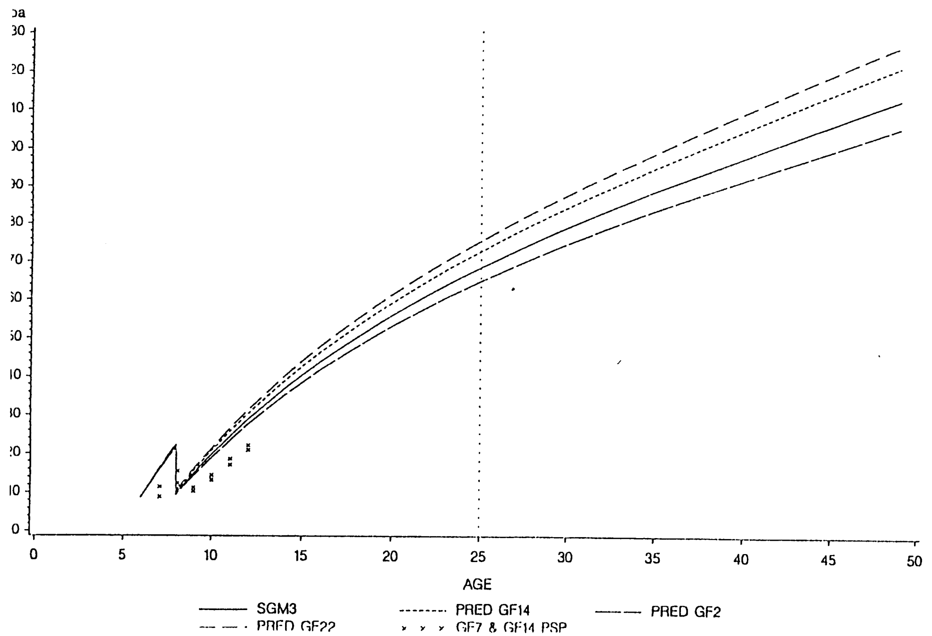
SD682 : mean top height
Common Modifiers (Tue Apr 13 12:39:10 1993)



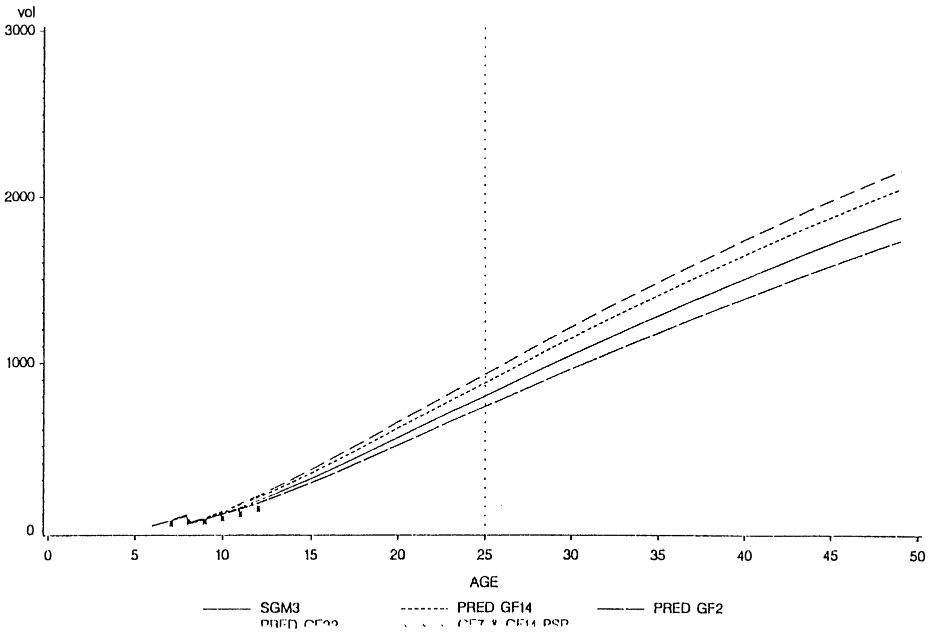
SD682 : quadratic mean dbh
Common Modifiers (Tue Apr 13 12:39:13 1993)



SD682 : basal area
Common Modifiers (Tue Apr 13 12:39:08 1993)

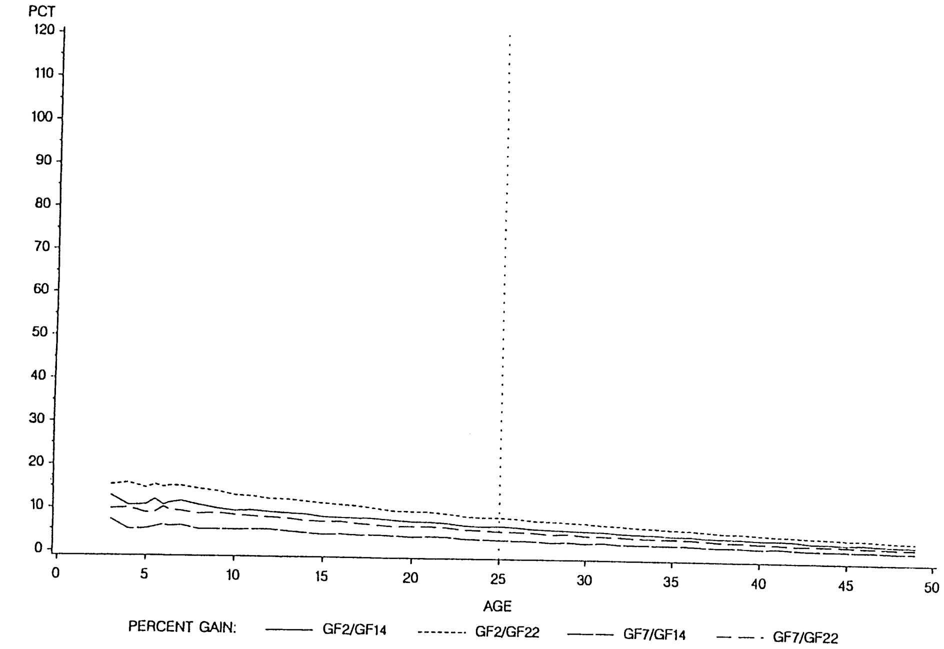


SD682 : volume
Common Modifiers (Tue Apr 13 12:39:11 1993)

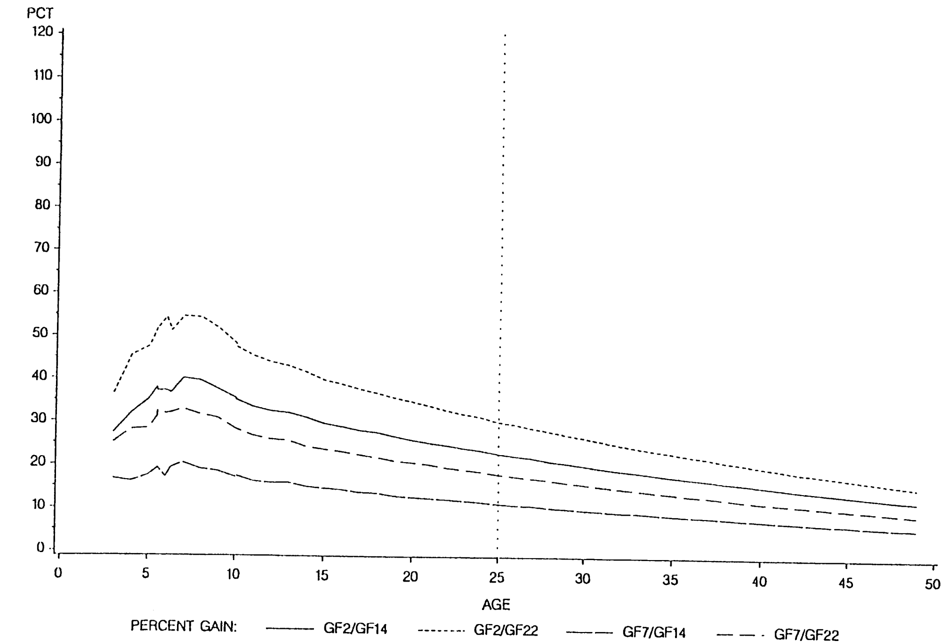


Appendix 10. Percent gain for mean top height, basal area, diameter at breast height, and volume per ha to 50 years by site

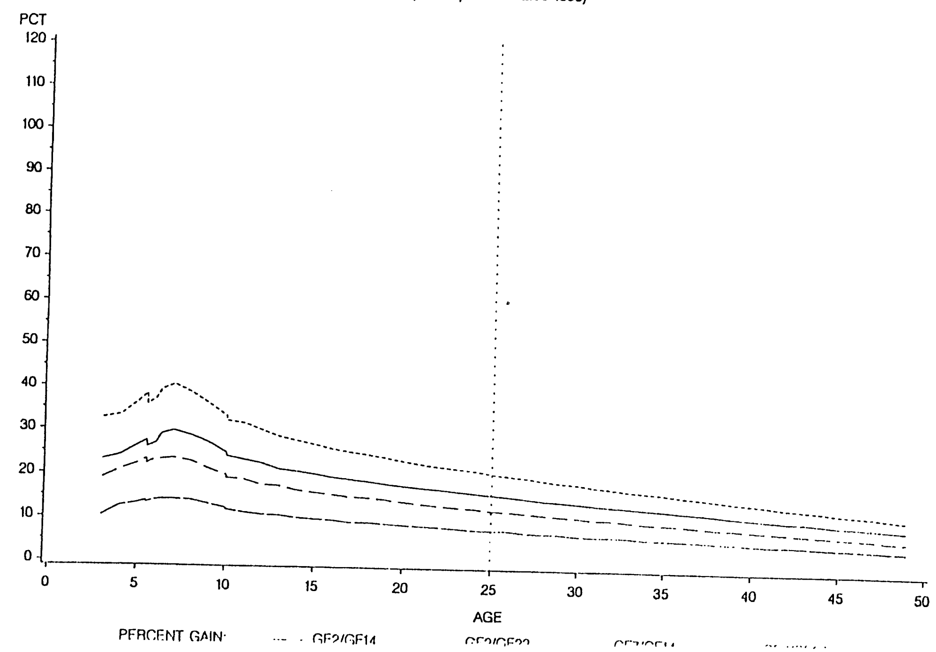
RO21031: Percent mean top height
(Wed Apr 14 13:52:59 1993)



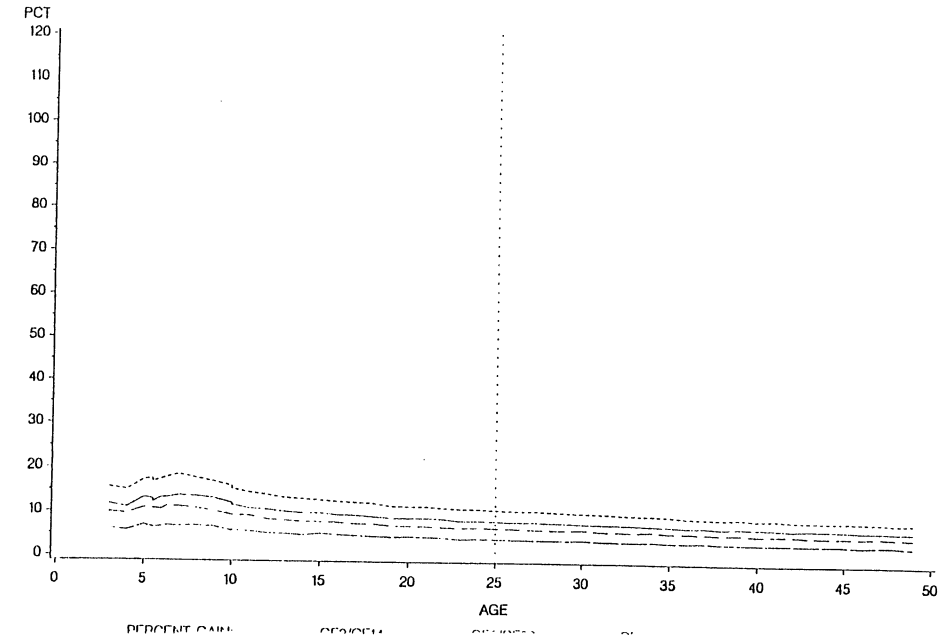
RO21031: Percent volume
(Wed Apr 14 13:53:00 1993)



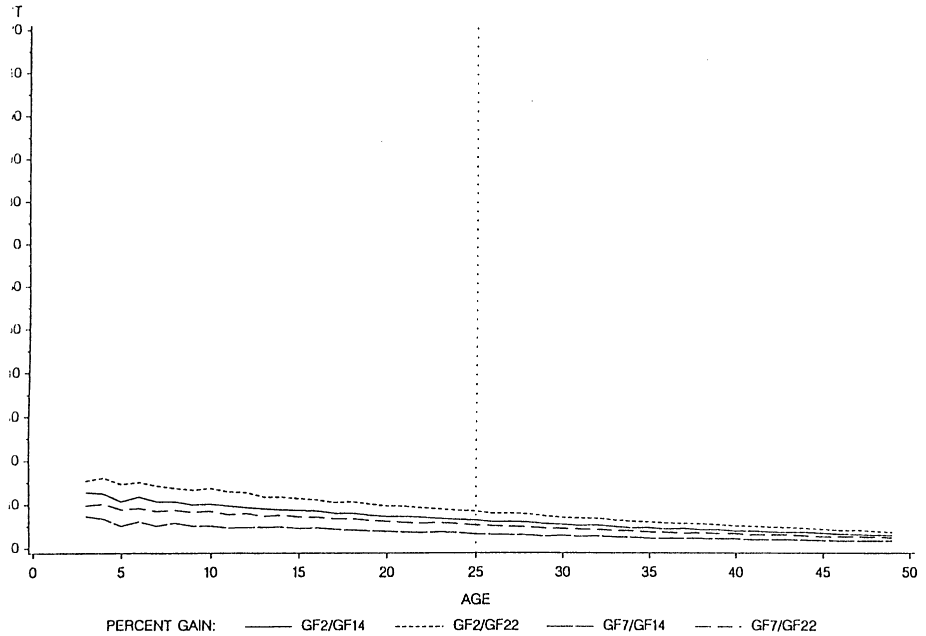
RO21031: Percent basal area
(Wed Apr 14 13:52:58 1993)



RO21031: Percent quadratic mean dbh
(Wed Apr 14 13:53:02 1993)

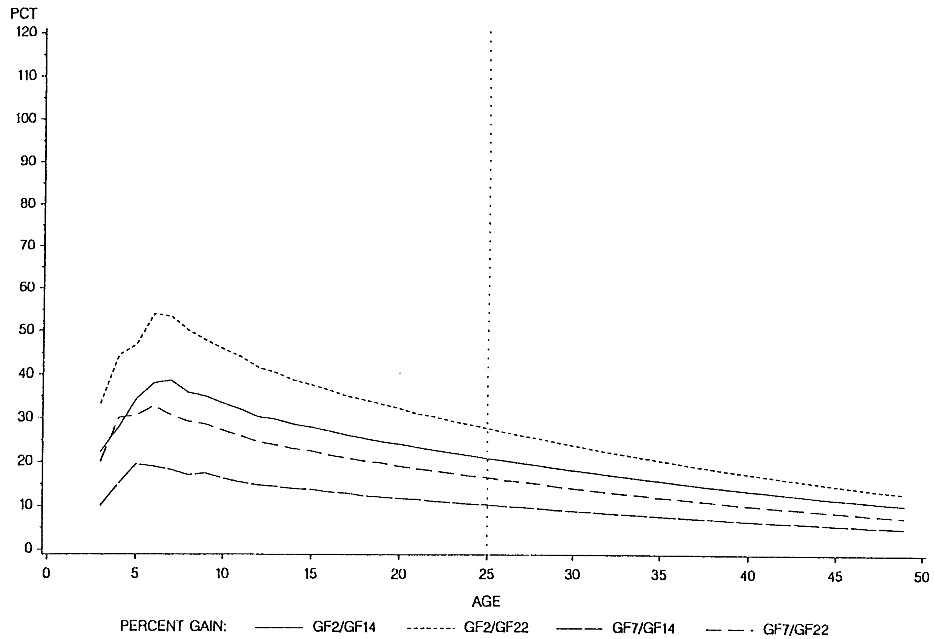


(Wed Apr 14 13:58:52 1993)



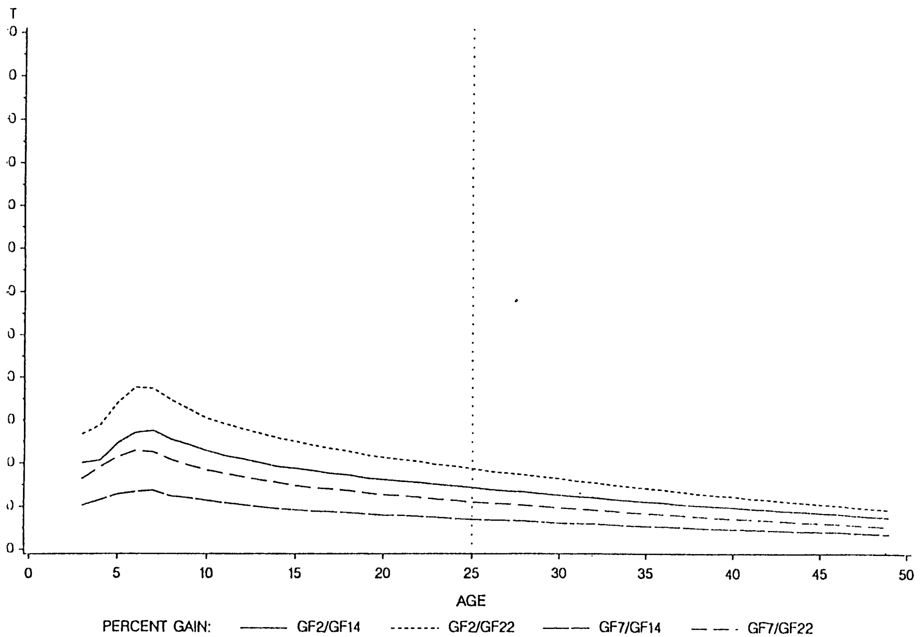
RO21032: Percent volume

(Wed Apr 14 13:58:53 1993)



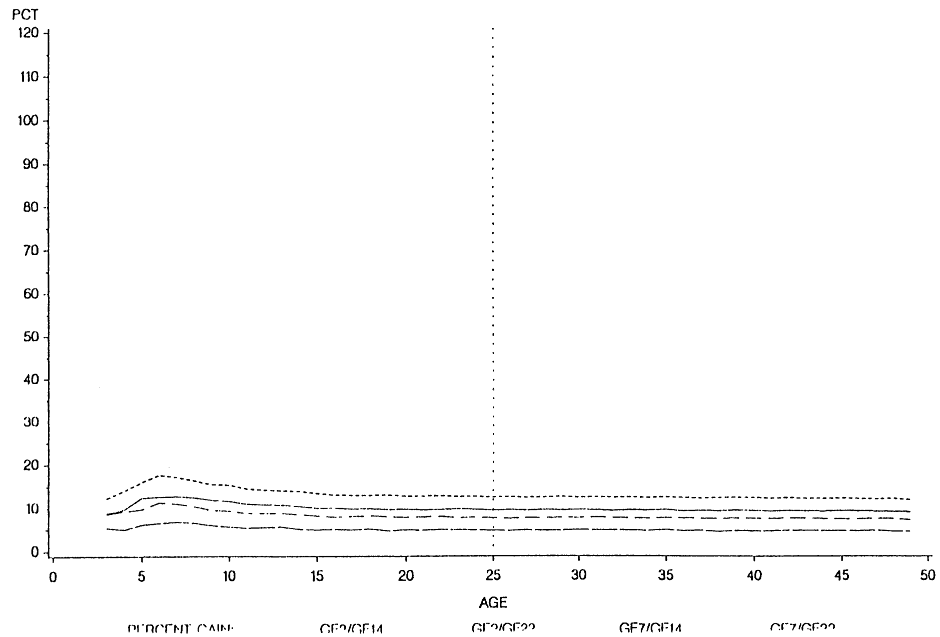
RO21032: Percent basal area

(Wed Apr 14 13:58:51 1993)

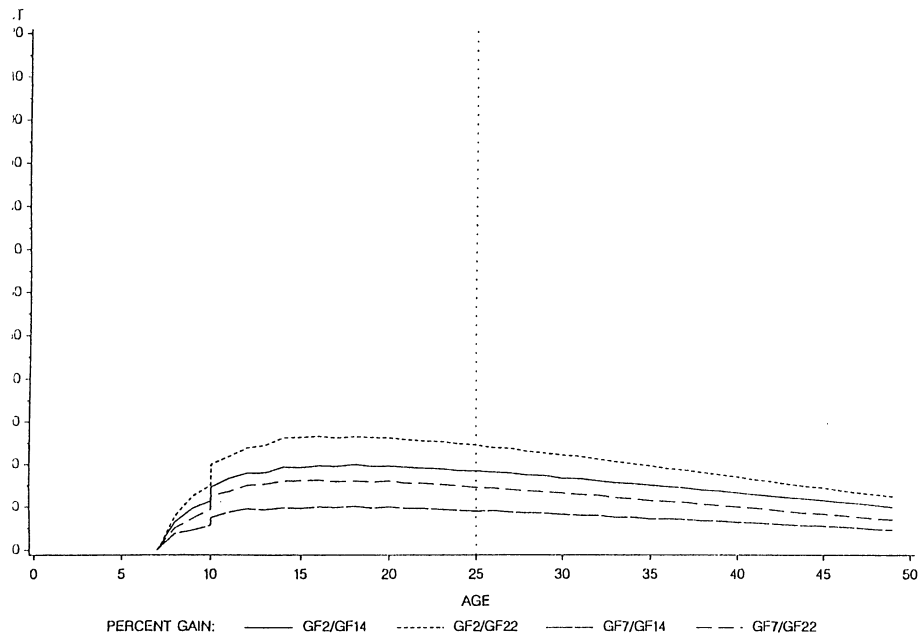


RO21032: Percent quadratic mean dbh

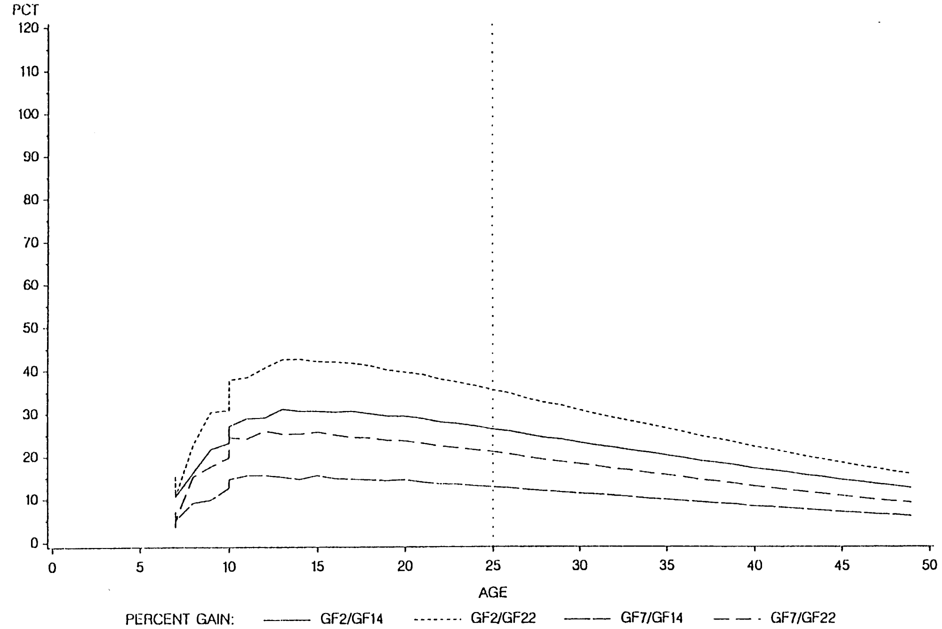
(Wed Apr 14 13:58:55 1993)



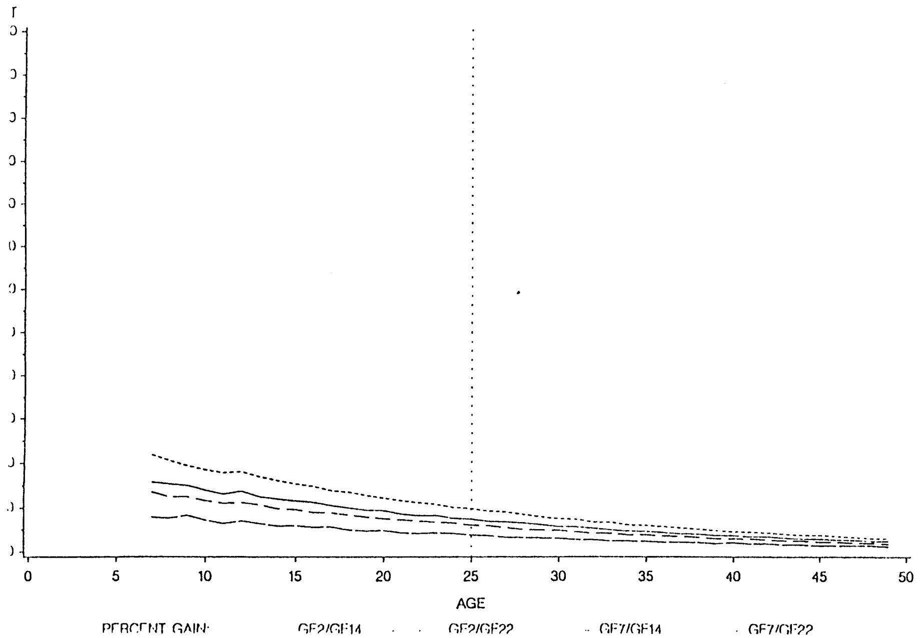
NN5302: Percent basal area
(Wed Apr 14 14:31:00 1993)



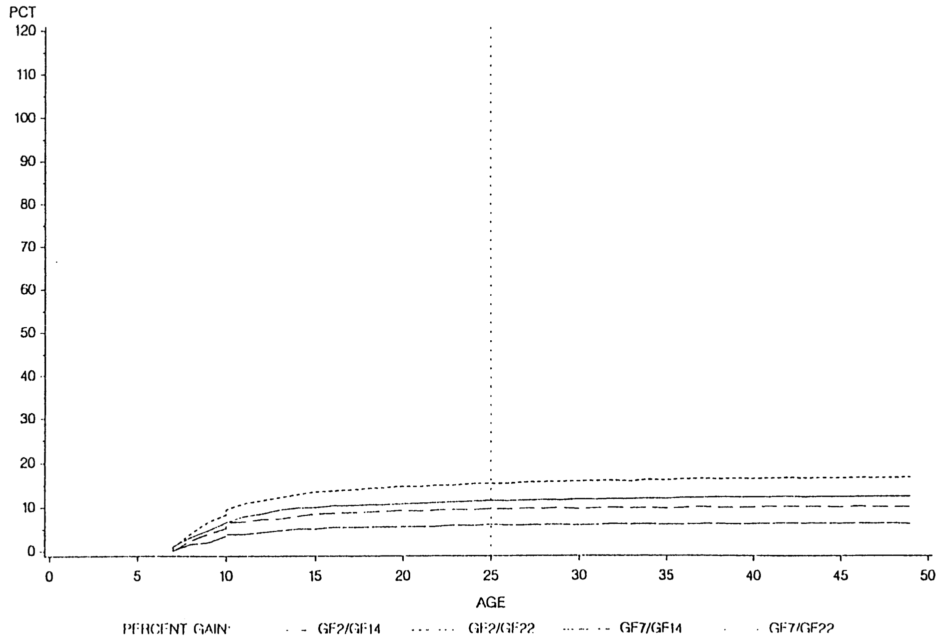
NN5302: Percent volume
(Wed Apr 14 14:31:03 1993)



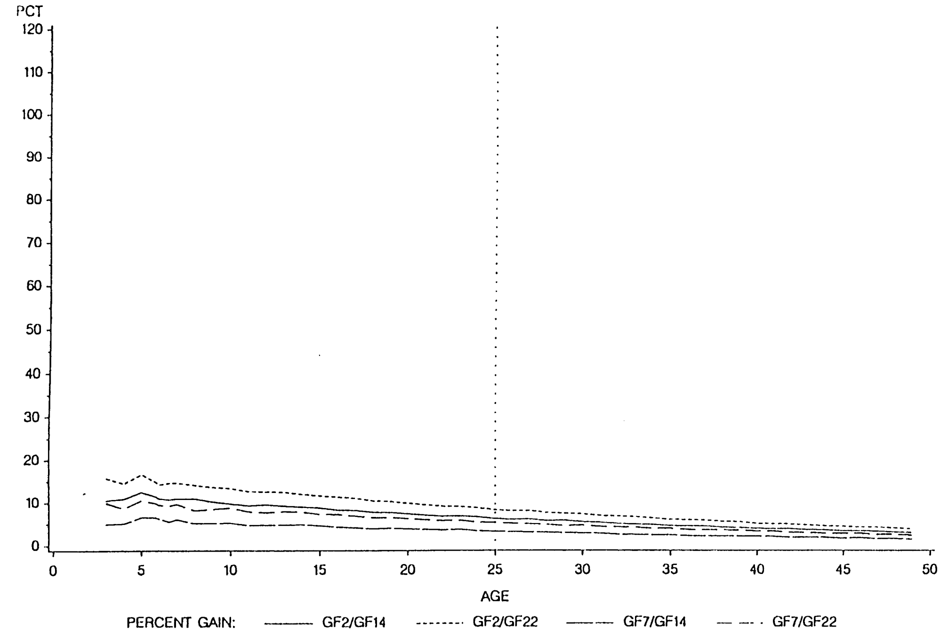
NN5302: Percent mean top height
(Wed Apr 14 14:31:01 1993)



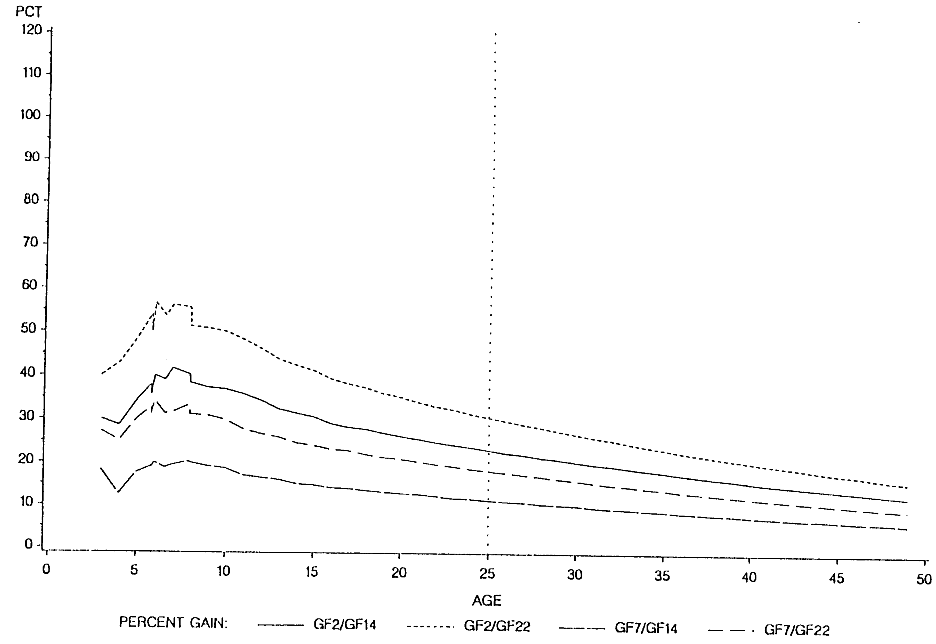
NN5302: Percent quadratic mean dbh
(Wed Apr 14 14:31:04 1993)



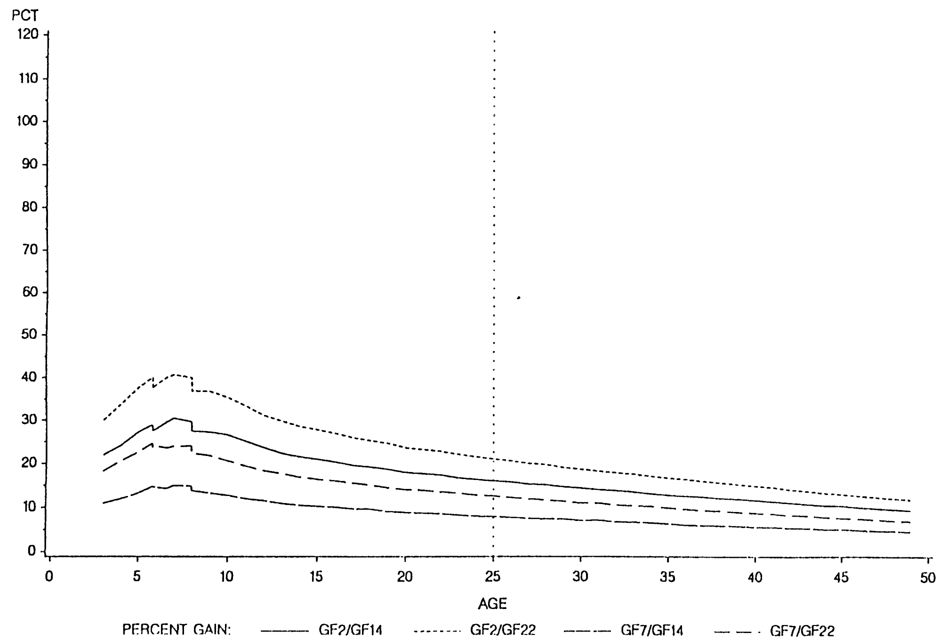
RO21033: Percent mean top height
(Wed Apr 14 14:04:54 1993)



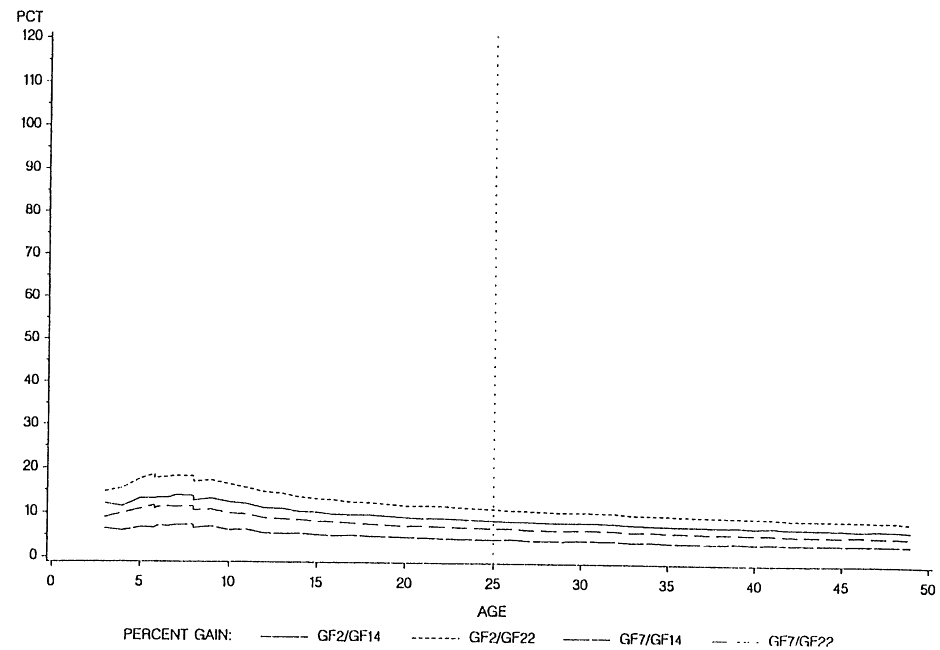
RO21033: Percent volume
(Wed Apr 14 14:04:56 1993)



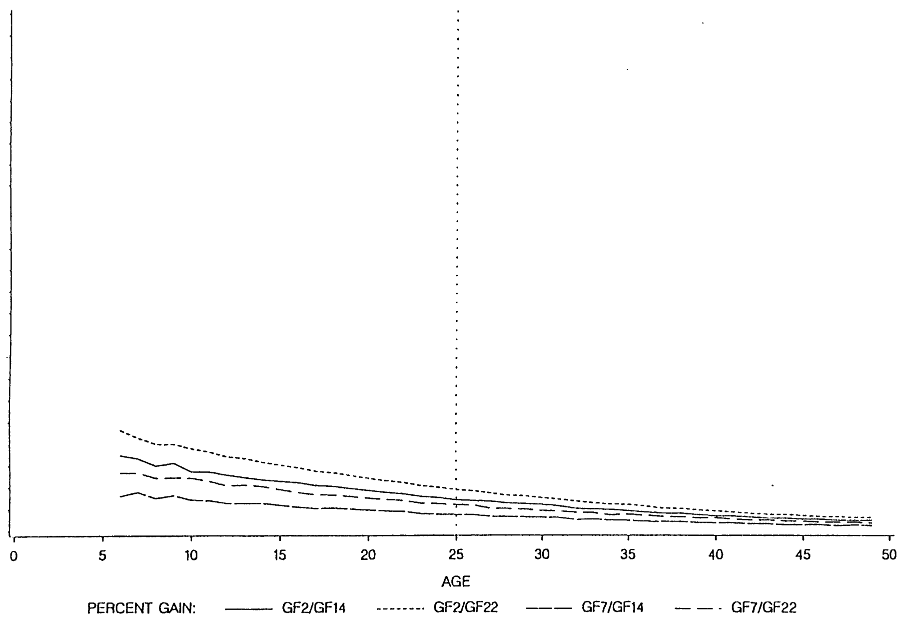
RO21033: Percent basal area
(Wed Apr 14 14:04:53 1993)



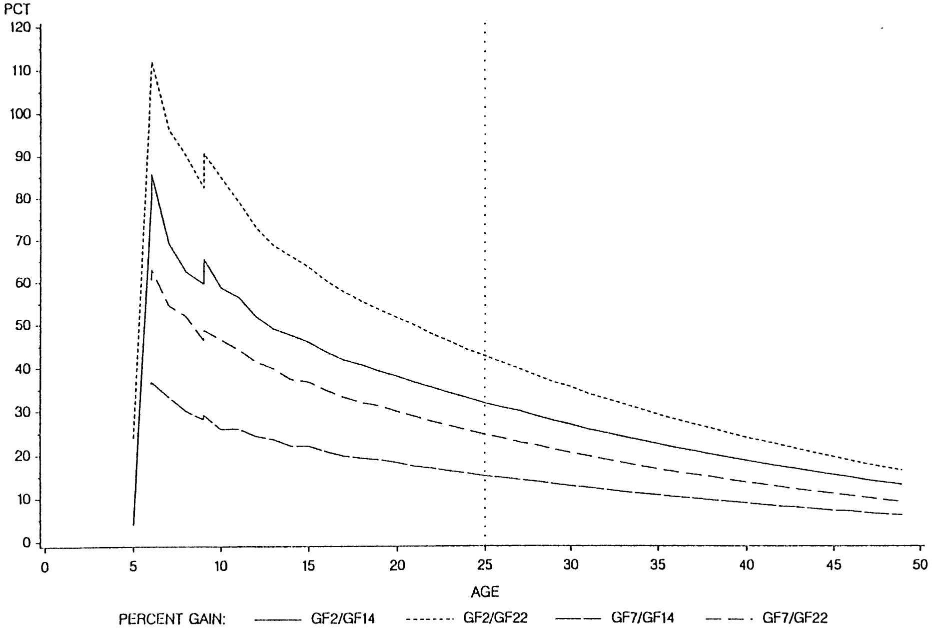
RO21033: Percent quadratic mean dbh
(Wed Apr 14 14:04:57 1993)



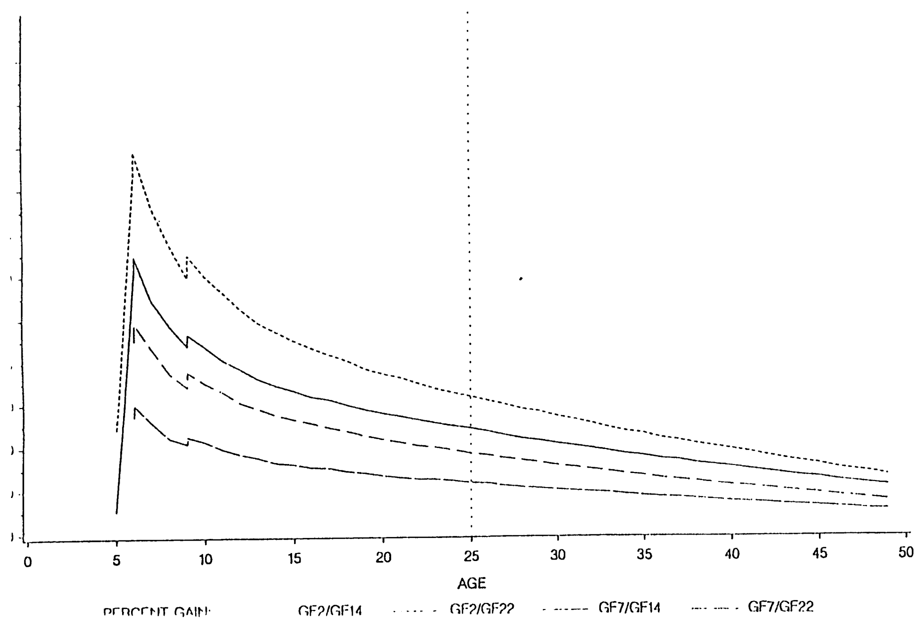
NN5301: Percent mean top height
(Wed Apr 14 14:24:22 1993)



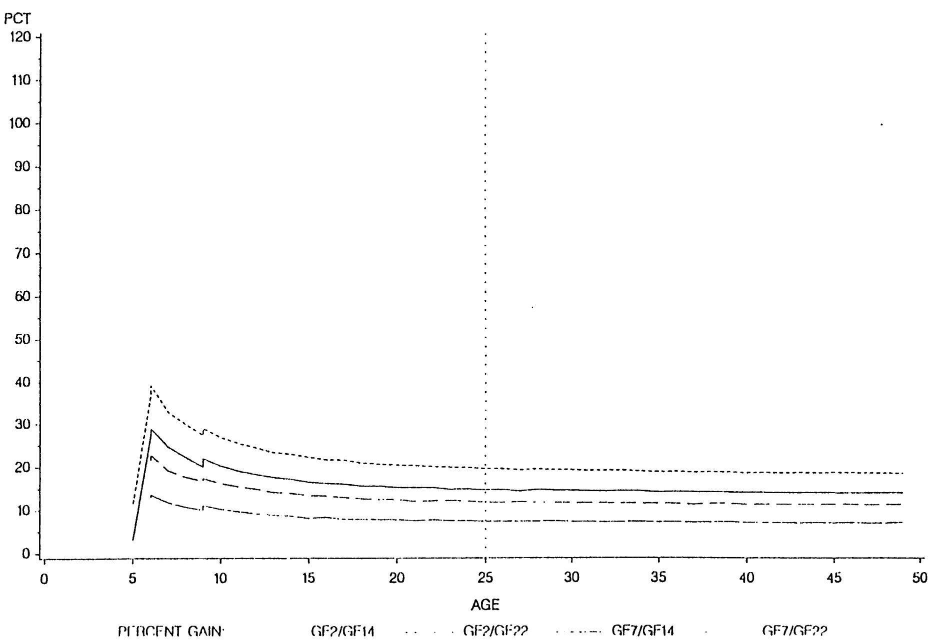
NN5301: Percent volume
(Wed Apr 14 14:24:24 1993)



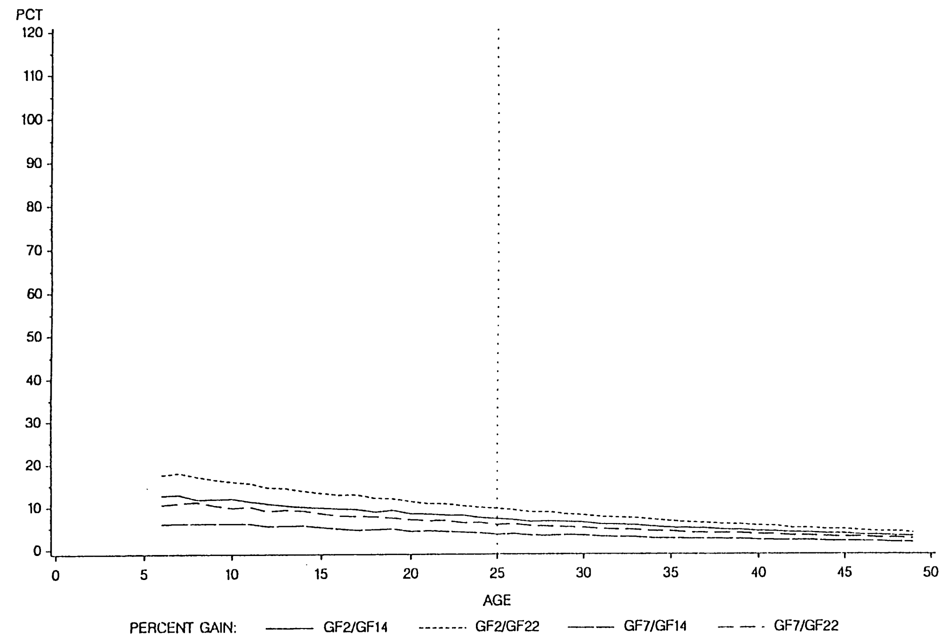
NN5301: Percent basal area
(Wed Apr 14 14:24:21 1993)



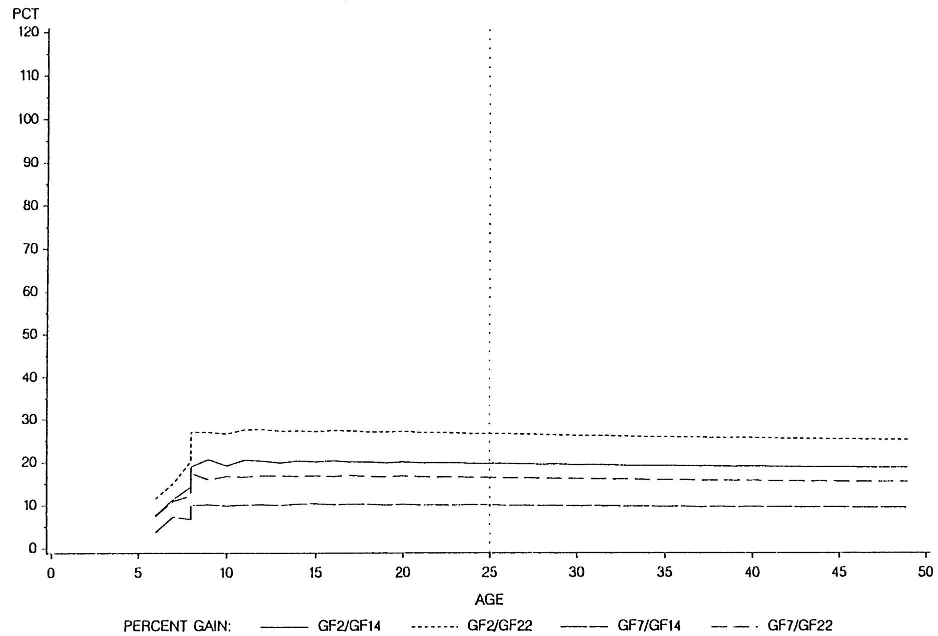
NN5301: Percent quadratic mean dbh
(Wed Apr 14 14:24:25 1993)



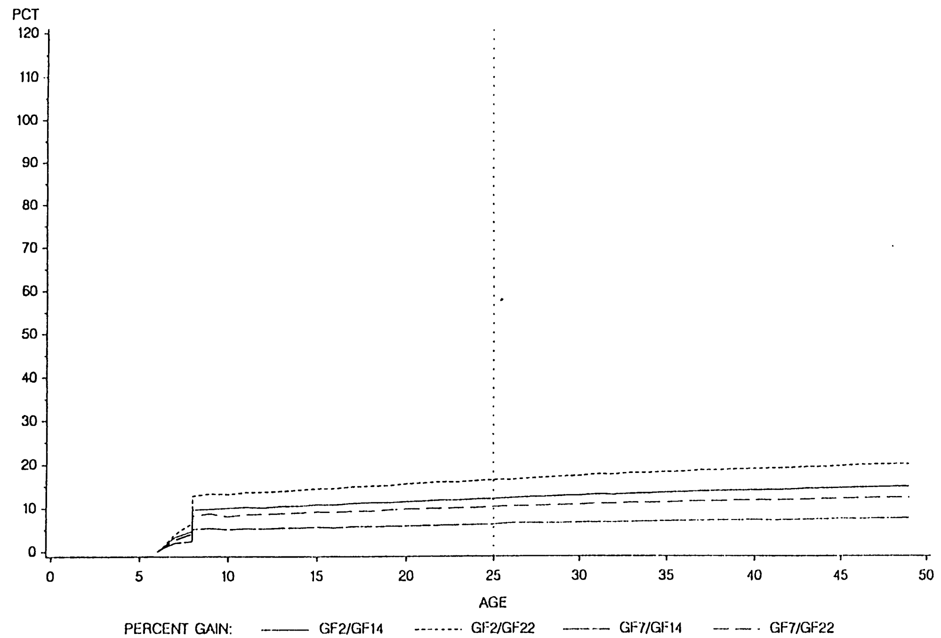
(Wed Apr 14 14:37:40 1993)



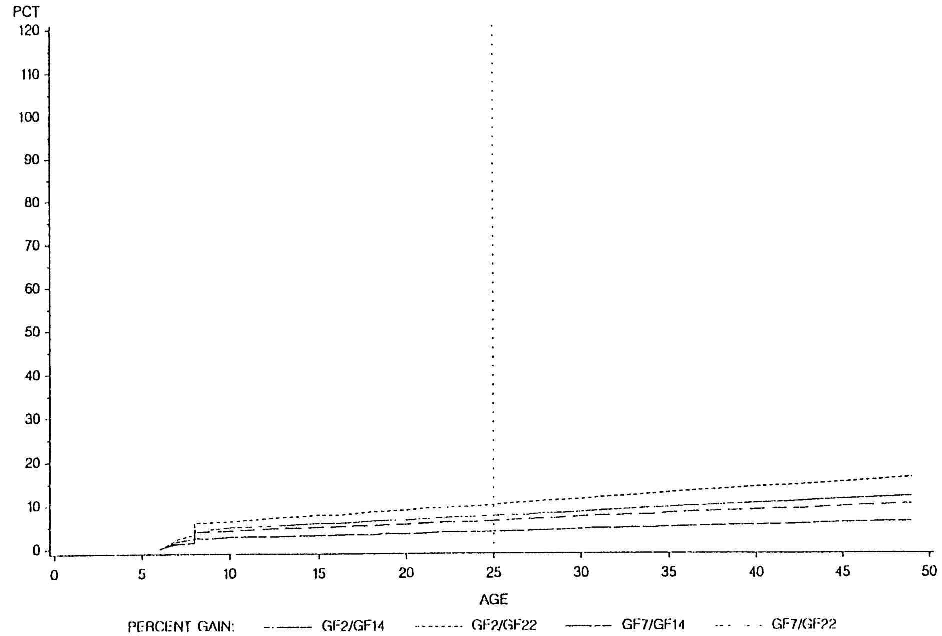
SD682: Percent volume
(Wed Apr 14 14:37:42 1993)



SD682: Percent basal area
(Wed Apr 14 14:37:39 1993)

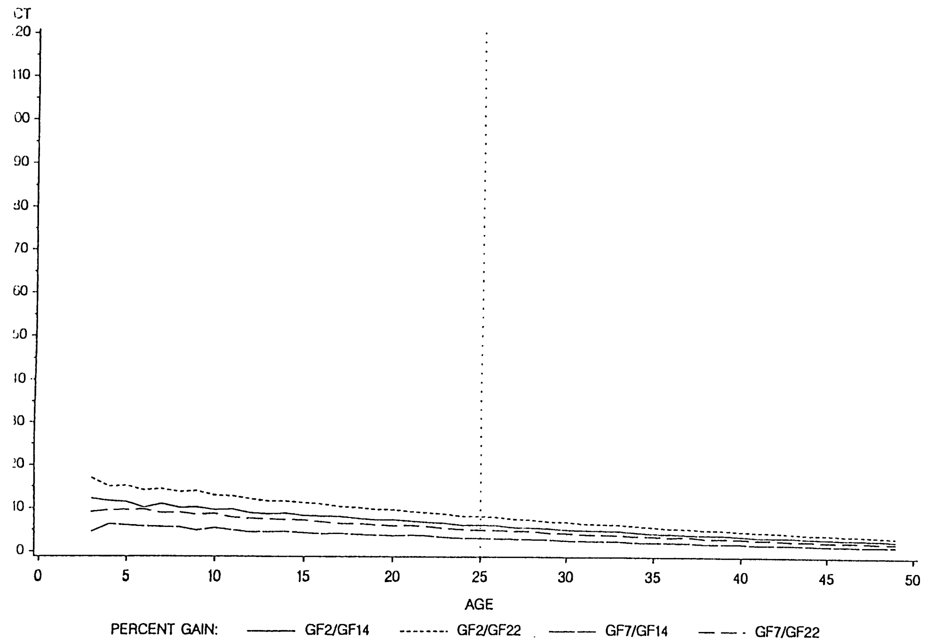


SD682: Percent quadratic mean dbh
(Wed Apr 14 14:37:43 1993)



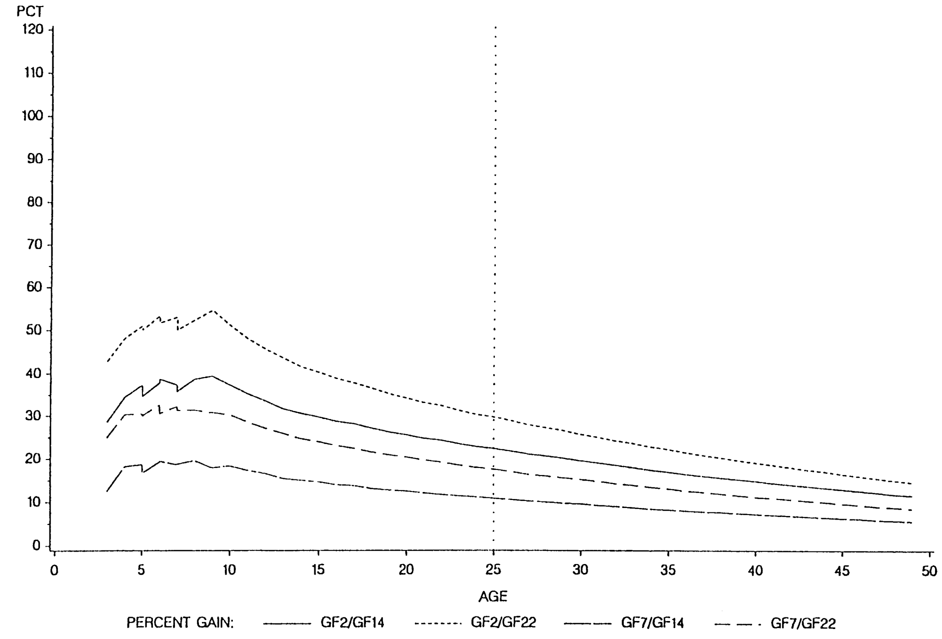
RO972: Percent mean top height

(Wed Apr 14 14:10:56 1993)



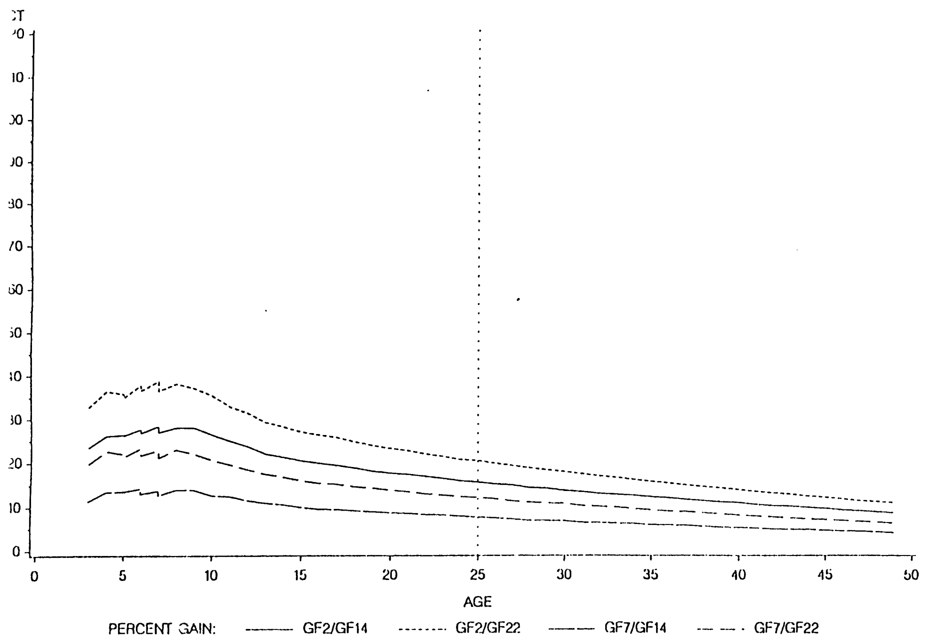
RO972: Percent volume

(Wed Apr 14 14:10.58 1993)



RO972: Percent basal area

(Wed Apr 14 14:10:55 1993)



RO972: Percent quadratic mean dbh

(Wed Apr 14 14:10:59 1993)