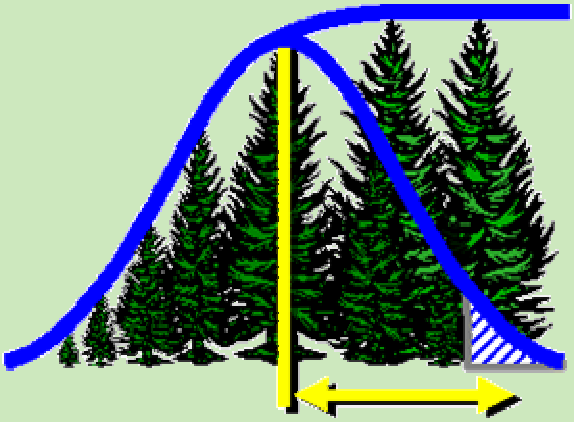
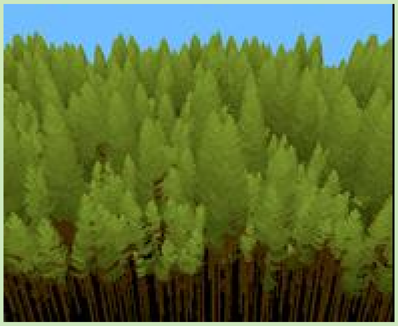
Genetics and Growth Modeling Workshop

Proceedings of a workshop organized by the

Pacific Northwest Tree Improvement Research Cooperative
USFS Pacific Northwest Research Station
Northwest Tree Improvement Cooperative
Stand Management Cooperative
Department of Forest Science, Oregon State University
Port Blakely Tree Farms

November 4 - 6, 2003
Vancouver, Washington





Oregon State University OSU College of Forestry

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Edited by Marilyn L. Cherry and Glenn T. Howe

Organizing committee:

Glenn Howe[1], Marilyn Cherry[1], Brad St. Clair[2], Keith Jayawickrama[1], David Briggs[3], David Marshall[4], Greg Johnson[5], Paul Anderson[2], David Walters[6], Mike Mosman[7]

[1] *Department of Forest Science, Oregon State University, 321 Richardson Hall, Corvallis, OR, 97331-5752*
[2] *USDA Forest Service, 3200 Jefferson Way, Corvallis, OR, 97331*
[3] *College of Forest Resources, University of Washington, Box 352100, Seattle, WA, 98195-2100*
[4] *USDA Forest Service, 3625 SW 93rd Ave., Olympia, WA, 98512-9193*
[5] *Weyerhaeuser Company, P.O. Box 9777, WTC 1A3, Federal Way, WA, 98063*
[6] *Roseburg Resources, Old Hwy 99, P.O. Box 1088, Roseburg, OR, 97470*
[7] *Port Blakely Tree Farms, L.P., 8133 River Drive SE, Tumwater, WA, 98501*

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Introduction

A primary objective of growth and yield models is to predict wood volume on an area basis at rotation age. In the Pacific Northwest, these models have historically been based on data from naturally regenerated, evenaged stands, incorporating factors such as competition and mortality. In other regions, models have been developed for evenaged plantations as well. With the increasing reliance on plantation forestry in the Pacific Northwest, and the ever-increasing use of genetically improved planting stock, questions have been raised about whether current growth and yield models are adequate. Forest growers would like to know how genetic gains estimated at young ages translate into additional volume per area at rotation. With over 40 years of investment in tree improvement in the Pacific Northwest, foresters welcome opportunities to capitalize on their investment. If rotation-age genetic gains were known, it would be possible to increase timber valuations during land sale transactions and adjust harvest schedules to reflect the anticipated volume increases.

Current growth models do not specifically model genetically improved plantations. During this workshop, we explored how we could develop new or revised models that incorporate genetic gains. Another goal was to examine whether we can use existing data to obtain provisional answers before these new models become available. Particular emphasis was placed on coastal Douglas-fir in the Pacific Northwest.

Workshop format

The workshop had two components (see Table of Contents). The first component was a one-day series of presentations that covered (1) key concepts in tree improvement and growth modeling and (2) ideas for incorporating genetic improvement into growth models. These presentations were prepared for a target audience of broadly-trained forest managers. The second component was a two-day discussion session (Workshop Discussion) that explored genetics and growth modeling issues in much greater depth (Table 1). The participants in the Workshop Discussion consisted of individuals with specific experience and interest in these topics (see Appendix 1).

Workshop goals

The goals of the workshop were to:

1. Promote discussion among forest geneticists and growth modelers
2. Promote discussion among researchers who have specifically studied the impacts of genetics on growth and yield models
3. Develop specific recommendations for incorporating genetic gain into Douglas-fir growth and yield models
4. Develop a list of research priorities to better understand the effects of genetics on growth and yield models
5. Inform foresters about the potential effects of genetics on growth and yield models
6. Evaluate the role of process and hybrid models in forest management and research

Desired outcomes

Our desired outcomes included: (1) a description of models currently in use, (2) short-term recommendations on how to incorporate genetic gain into growth projections and harvest yields of improved plantations (i.e., to bridge the gap until existing models can be revised, or new models can be developed), (3) a description of existing data and studies that can provide future information on how to incorporate genetic gain into growth models, and (4) a list of longer-term research priorities. Future goals and tasks that were formulated during the workshop are presented in Table 2.

Table 1. Questions addressed during the *Genetics and Growth Modeling Workshop Discussion Sessions* on November 5-6, 2003. The main conclusions drawn from these discussions are incorporated into the workshop Summary.

Overview

- Which questions and knowledge gaps do we need to address to incorporate genetics into growth models?

Modeling approaches and issues

- Which components of growth models should we adjust to account for genetic improvement?
- How should we modify growth models in the short-term? Long-term?

Experimentation and data needs for the Pacific Northwest

- Will interactions between genotypes and silvicultural treatments (G x S interactions) dramatically affect growth modeling?
  - *What is the evidence for important G x S interactions?*
  - *How important is it to design experiments to measure these interactions?*
- What are the existing and planned Douglas-fir experiments in the Pacific Northwest?
  - *Are new large-plot experiments needed?*
  - *Are existing and planned Douglas-fir experiments adequate?*
  - *If not, what types of experiments are needed?*
- Can we use operational planting programs to obtain the data needed to incorporate genetics into growth models?
- Can we use existing progeny tests to obtain the data needed to incorporate genetics into growth models? If so, which analytical approaches seem promising?

Using growth models to improve tree breeding

- Can we use growth models to improve tree breeding?
- Which traits should be the focus of genetic improvement to increase stand productivity (i.e., in contrast to individual-tree growth)?

Other improvements to growth models

- Can we improve growth models by incorporating better site information (e.g., soils, habitat type)?
- Can we improve growth models by incorporating climatic and weather information?

Conclusions

- What are the most important **goals** and **tasks** for incorporating genetics into growth models?

Table 2. Goals and tasks formulated during the *Genetics and Growth Modeling Workshop Discussion Sessions* on November 5-6, 2003.

GOALS

- Incorporate genetic improvement into existing growth models.
- Continue to improve existing growth models.
- Develop the next generation of growth models for the Pacific Northwest incorporating the effects of genetic improvement.
- Use operational planting programs to outplant a large number of experimental/demonstration trials of genetically improved vs unimproved stands.
- Link experiments throughout the region by using standardized methods for calculating breeding values.
- Link experiments throughout the region by including standard genetic reference populations.

TASKS

Tasks that focus on incorporating genetic improvement into growth models

- Use existing progeny test information to calculate growth multipliers for genetic improvement.
- Develop 'operational' planting guidelines for experimental/demonstration trials of genetically improved vs unimproved stands.
- Create standard genetic reference populations and plant them throughout the region.
- Standardize the calculation of breeding values.
- Develop a seedlot certification system for the Pacific Northwest.

Tasks that focus on making other improvements to growth models

- Use existing tree lists (or create new ones) to enter into ORGANON at age 15.
- Investigate whether better site characterization can be used to improve growth models.
- Make recommendations on the appropriate frequency and type of measurements for growth plots.
- Modify ORGANON (or link to other models) to start at age zero.
- Investigate whether climate/weather data can be used to improve growth models.
- Investigate hybrid models as alternatives to existing growth models.

Why incorporate genetics into growth models?

Plantations throughout the world are being established with improved tree varieties that have different growth characteristics than those used to develop current growth models. New growth models are needed to conduct realistic financial analyses and to guide tree improvement programs (Foster, p. 69).

Wade Harrison surveyed growth model users from the forest industry, TIMOs (timberland investment management organizations), and consulting firms in the U.S. and New Zealand (Harrison, p. 86). Most respondents said that it is important to incorporate genetic improvement into growth models, and that this need will only increase in the future. They generally felt that incorrect decisions will be made unless genetic improvement is incorporated into growth models, and some believe that genetics is the "last great untapped advantage for U.S. timberland investing."

Many of those surveyed are accounting for genetics by using simple assumptions based on either empirical data or gut feelings to choose model inputs or make model adjustments. They have a low comfort level about the way genetic improvement is currently incorporated into growth models, feel that their assumptions are too simplistic, and feel that more data are needed to support firm conclusions. They also worry that the estimates of genetic gain are overly optimistic.

Most respondents felt that genetically improved trees are needed to capture the full potential of advanced silvicultural regimes, and that intensive silviculture is needed to capture the full potential from genetic improvement. The respondents tend to have complex views and use unsupported assumptions about how genetic improvement will interact with other silvicultural improvements. Furthermore, these views and assumptions are often not reflected in the growth models. The point was made that models available in the public domain will have more credibility than proprietary models.

How do geneticists identify superior genotypes and estimate genetic gain?

In Douglas-fir, first-generation genetic gains of 10-30% are expected in height, diameter, and volume growth at age 10 to 15. But how do gains of 10-30% at age 10 to15 translate to rotation age (e.g., 40-70 years)? This question, which was posed by Randy Johnson (p. 37), is the focus of this workshop.

Randy Johnson and Sam Foster described the basic quantitative genetic approaches needed to predict genetic gain, including the concept of heritability—the proportion of observable, or 'phenotypic', differences among individuals that results from corresponding differences in genetic makeup (i.e., genotype) (R. Johnson, p. 23). Both speakers also highlighted the breeder's central dogma, 'phenotype = genotype + environment,' which is key to understanding tree improvement.

The approaches that geneticists use to select superior genotypes and estimate genetic gains are usually inadequate for predicting growth superiority at rotation age. These approaches include the use of small plots (mostly single-tree plots in the Pacific Northwest), selection of superior genotypes at an early age (perhaps ¼ rotation age), and incomplete sampling of field environments (R. Johnson, p. 38). Although these approaches work well for ranking genotypes at an early age and (presumably) maximizing genetic gain per year, suppression of slow-growing genotypes in single-tree plots, imperfect age-age genetic correlations, and genotype by site interactions can affect estimates of heritabilities and genetic gains. The methods used by tree breeders are highly efficient, but large-plot genetic experiments must also be established (R. Johnson, p. 30).

Sam Foster reviewed the scientific literature for studies that (1) provide estimates of genetic gain and provide relevant data for deciding how to incorporate genetics into growth models (Table 3) and (2) actually incorporated genetics into the growth models used to calculate stand volume (Table 4).

How do biometricians model tree and stand growth?

Growth models are mathematical representations of the natural dynamics of a forest (Marshall, pp. 41-42). Bob Monserud described seven classes of forest models: forest yield models, ecological gap models, ecological compartment models, process/mechanistic models, hybrid models, landscape models, and global vegetation distribution models (p. 160).

Growth models may describe the growth of individual trees or stands, or may combine both scales into disaggregative models (Marshall, pp. 46-48). Individual-tree models may have a spatial component (e.g., distance-dependent models) or they may be distance-independent. Process/mechanistic models are based on growth processes at the physiological, physical, and biochemical levels, but are not predictive (Landsberg, pp. 151-158; Monserud, p. 161). Hybrid models are a complementary merging of well-understood processes and reliable tree/stand empirical elements (Marshall, pp. 50-52; Monserud, pp. 162-163). Landsberg proposed that the most rapid progress in tree improvement will occur if physiologists and process modelers worked together with tree breeders and statisticians.

Table 3. Compilation of scientific literature, by trait, useful in resolving modifications to growth and yield models due to forest genetics.

Trait	Species	Reference
Individual tree volume	*Pinus taeda*	Buford and Burkhart 1987
	Pinus elliottii	Tankersley et al. 1983
Height-diameter function	*Pinus taeda*	Buford and Burkhart 1987
	Pinus taeda	Buford 1986
	Populus deltoides	Knowe et al. 1998
Bole taper	*Pinus taeda*	Buford and Burkhart 1987
	Pinus taeda	Schmidtling and Clark 1988
Diameter frequency distribution	*Pinus radiata*	Carson and Hayes 1998
	Pinus taeda	Janssen and Sprinz 1987
	Pinus taeda	Nance and Bey 1979
	Populus deltoides	Knowe et al. 1994
	Pinus elliottii	Spirek et al. 1981
Site index (SI); height/age curve	*Pinus taeda*	Raley et al. 2003
	Pinus taeda	Schmidtling and Froelich 1993
	Pinus taeda	Knowe and Foster 1989
	Pinus taeda	Buford and Burkhart 1987
	Pinus taeda	Nance and Wells 1981
	Pinus taeda	Sprinz 1987
	Pinus taeda	Lowe and van Buijtenen 1991
	Pinus taeda	Sprinz et al. 1989
	Pinus radiata	Carson and Hayes 1998
	Pinus radiata	Carson et al. 1999
	Pinus pinaster	Magnussen and Kremer 1993
	Cunninghamia lanceolata	Tang et al. 2001
	Populus deltoides	Knowe et al. 1998
	Larix leptolepis	Magnussen and Park 1991
Stand density vs average individual-tree size	*Pseudotsuga menziesii*	Stonecypher and McCullough 1981
	Pinus taeda	Nance et al. 1983
	Pinus taeda	Land and Nance 1987
	Pinus taeda	Schmidtling and Froelich 1993
	Pinus taeda	Schmidtling 1988
	Pinus taeda	Buford 1989
	Populus hybrids	Panetsos 1980
	Eucalyptus tereticornis x *grandis*	Bouvet 1997
Stand density vs mean plot traits	*Pinus taeda*	Buford 1989
	Pinus taeda	Land et al. 2004
	Pinus radiata	Carson et al. 1999
Basal area	*Pinus radiata*	Carson et al. 1999
	Pinus taeda	Schmidtling and Froelich 1993
	Populus trichocarpa x *deltoides*	Stanton 2001
	Populus deltoides	Knowe et al. 1994
	Cunninghamia lanceolata	Tang et al. 2001
Biomass traits	*Pinus taeda*	McCrady and Jokela 1996
	Pseudotsuga menziesii	St. Clair 1993

Table 4. Scientific literature reporting growth and yield models that incorporate genetic effects into the calculation of stand volume.

Species	Approach	Reference
Chamaecyparis obtusa	Modeled improved populations	Kurinobu and Shingai 1987
Pinus monticola	Modeled improved populations vs unimproved populations	Rehfeldt et al. 1991
Pinus ponderosa	Modeled improved populations	Hamilton and Rehfeldt 1994
Pinus radiata	Derived growth rate multipliers for height, basal area, and calculated volume increase	Carson, Garcia, and Hayes 1999
Pinus radiata	Modeled growth of seedlots	Goulding 1994
Pinus radiata	Modeled seedling vs rooted cutting stands	Holden et al. 1995
Pinus taeda	Modeled pure family stands	Knowe and Foster 1989
Pinus taeda	Simulation modeling of pure family and mixed family stands	Nance 1982
Pinus taeda	Simulation modeling of improved vs woods run seedlots	Nance and Bey 1979
Pinus taeda	Modeled pure provenance stands	Nance and Wells 1981
Populus deltoides	Modeled pure clone and mixed clone stands	Foster and Knowe 1995
Populus deltoides	Modeled improved clonal stands	Cao and Durand 1991

Growth models differ in the elements that drive the models and in their data input requirements. Crown shape is a component of many growth models (e.g., Goudie p. 96), but is rarely measured in progeny tests—even if it is an important factor in sawlog quality (but not pulpwood production).

Most growth models are designed for stands greater than 10 to 15 years-old (i.e., after vegetative competition has been overcome). Nonetheless, genetic tests in the Pacific Northwest are rarely measured beyond age 15. While young stand models do exist (e.g., CONIFERS and RVMM), there is a discontinuity when information from one growth model is fed into another (e.g., CONIFERS feeding into ORGANON at age 15). One conclusion from the Workshop Discussion was that it would be valuable to modify the CONIFERS model so it can be used for young Douglas-fir stands in Oregon and Washington and provide output that can be fed into ORGANON.

Models used in the Pacific Northwest

Many growth models have been used in the Pacific Northwest. In the past 20 years, there have been about 20 models developed that are applicable to the west coast (Marshall, p. 48). A few of the major models being used include TASS in British Columbia and ORGANON in Washington and Oregon. Although both of these models are individual-tree models, TASS is a distance-dependent model, whereas ORGANON is distance-independent.

The TASS model for British Columbia was described by Jim Goudie (Goudie, pp. 95-100). TASS is a stand simulator that is driven by height growth using a 1-year growth step. Other important components of the model include crown expansion, mortality, and volume increment. TASS is already incorporating genetic worth into stand projections (Goudie, pp. 100-108). Genetic worth (GW) estimates are translated into genetic gains at the selection age, and the gains are allowed to decay over time such that the percentage increase in volume at the index age is in agreement with the predicted genetic worth estimates. Genetic worth estimates at rotation are projected using age-age correlations (after Lambeth, 1980). Realized genetic gain trials are considered essential to validate and verify the performance of young genetic selections (Goudie, p. 107).

ORGANON was the main model discussed in terms of future genetic gain incorporation. The main components of ORGANON include height and diameter growth, crown recession, and mortality (Marshall, p. 53). ORGANON has a 5 year growth step and is designed so that other subcomponents can be developed and then incorporated into the main model. As mentioned above, CONIFERS and RVMM are young stand models that can provide data that may be fed into ORGANON.

As a corollary to models for the Pacific Northwest, Steve Knowe described models used in the southeastern U.S. (Knowe, p. 136). Genetic improvement is not included in these models, although the North Carolina State University model can be modified for different height-age and volume equations (e.g. family-specific height-age curves).

Geneticists and modelers view growth and genetic gain differently

The traits of interest to geneticists and growth modelers often differ. Geneticists typically focus on individual-tree traits such as tree height, diameter, volume, crown size, mortality, stem taper, branch size, etc. (G. Johnson, p. 73). Genetic variation and genetic gain have been demonstrated for each of these traits. Although these traits are consistent with the architecture of individual-tree growth models, modelers are often interested in other stand-level traits and growth functions as well—traits such as volume or basal area per hectare, dominant stand height, height and diameter frequency distributions, etc. (Foster, p. 63; G. Johnson, p. 73; Buford, p. 129). Genetic variation has also been demonstrated for some of these traits—i.e., height-diameter functions, height and diameter frequency distributions, height-age ratios, stand density versus average size of individual trees, stand density versus plot mean traits, and basal area per hectare (Foster, pp. 58-59). Alternatively, for process models, we may be interested in changes in photosynthetic or water-use efficiency, carbon allocation, or the architecture of crowns or roots (G. Johnson, p. 74).

Another distinction between geneticists and growth modelers is that geneticists often measure genetic gain at a particular point in time. From a modeling perspective, however, Greg Johnson stressed the importance of being able to measure genetic differences in the components of tree and stand growth (e.g., differences in growth curve parameters) (G. Johnson, p. 72). Given that growth differences are present, then it becomes important to know how long these differences persist (i.e., what is the duration of growth differences?). Our ability to predict future differences in volume per hectare is largely dependent on our ability to estimate these genetic differences in growth curves on a stand basis.

Whereas site index curves are generalizations over many sites, geneticists want to understand how much additional volume may be expected at rotation by planting a seedlot of a certain breeding value (generalized across a breeding zone) on a specific site. Although this goal may be unrealistic, it would require fine-scaled knowledge of genotype by site interactions. Furthermore, geneticists want to be able to model the effects of competition and stand structure, and to understand how to alter silvicultural practices in conjunction with improved planting stock to optimize yields. Geneticists and modelers should be working together to design trials and gather data that will provide information needed by both.

Genotype by silviculture interactions

Other factors that must be considered are the effects of silvicultural treatments on growth, and the interaction between genetics and silvicultural treatment. The relative performance of different genotypes may vary among management regimes—i.e., between clearcut and shelterwood regeneration systems, fertilized vs non-fertilized plantations, good vs poor vegetation control, or different stand densities. Therefore, it is valuable to know whether genotypes that are superior under one silvicultural regime will also perform better under alternative regimes. A genotype by silviculture interaction exists when two or more genotypes perform differently relative to one another under different silvicultural treatments. These differences may involve changes in rank (i.e., genotype 1 outperforms genotype 2 in treatment A, but underperforms genotype 2 in treatment B) or changes in magnitude (i.e., genotype 1 performs much better than genotype 2 in treatment A, but only a little better than genotype 2 in treatment B).

Sue Carson and Brad St. Clair noted that genetics by silviculture interactions were generally small and unimportant, including interactions between genotype and fertilizer, spacing, shading, and vegetation control. In New Zealand, realized gains trials validated these observations (Carson, p. 126). Given the dearth of evidence supporting the existence of major genotype by silviculture interactions, this does not seem to be a high priority for future research efforts.

Existing data and studies in the Pacific Northwest

Existing studies may be useful for studying the impacts of genetic improvement on tree and stand growth and yield. First, large block-plots of families or clones can be used to study stand-level growth directly. Second, it may be possible to use single-tree progeny tests to indirectly obtain estimates of stand-level growth. In contrast, row-plot progeny tests were considered generally inappropriate for estimating stand-level growth. Greg Johnson argued that modeling efforts require experiments designed specifically for that purpose. Because of their large size, long duration, high cost, and complexity, few well designed experiments have been established to specifically study the impacts of genetics on stand growth. Nonetheless, large-plot experiments are needed to fully understand the impacts of genetics on stand growth. Stand dynamics information should come from block plots that are at least 0.25 acres in size, have at least 30 to 50 observations per plot, have multiple observations in time, and sample different stand densities (Buford, p. 130).

Experiments are underway in the Pacific Northwest, including the (1) Type IV experiment being initiated by the Stand Management Cooperative (SMC) and the Northwest Tree Improvement Cooperative (NWTIC), (2) Genetic Gain Trials being conducted by the NWTIC and the USFS Pacific Northwest Research Station (PNWRS), and (3) Family Deployment Study being conducted by the PNWRS (St. Clair). These experiments were summarized by Brad St. Clair and David Briggs during the Workshop Discussion.

In New Zealand, gains predicted from tests using single-tree plot were similar to those predicted from tests using block-plots (Carson, p. 125). If plantations consist of family mixtures, rather than pure family blocks, then the variation within single-tree progeny tests should provide estimates of the variation within operational plantations, as long as there are enough individuals per family in the tests.

Although Sam Foster proposed that a series of large block-plot studies with a variety of species would produce the data needed to answer many of the outstanding questions, there was little optimism that resources would be available for experiments of this scale. The consensus among the Discussion participants was that the benefit/cost ratio of installing new large-scale experiments is not high enough to justify their implementation. Experiments in the ground should answer our most pressing questions in due time. Nonetheless, it will be valuable to include multiple varieties in future growth and yield trials, conduct retrospective analyses on existing experiments to determine why genetically superior varieties perform better, and use operational planting programs to establish simple demonstration/experimental comparisons of improved vs unimproved varieties (Foster, p. 69).

How should genetics be incorporated in growth models?

The most accurate way to incorporate genetics into growth models would be to derive entirely new models based on long-term measurements of superior genotypes in large-plot experiments (G. Johnson, p. 74). If the new models had the same form as earlier models, then it would also be possible to see how the growth functions changed in response to genetic improvement. Because there is not enough data to do this, other approaches have been used. These include (1) site index adjustment, (2) effective age adjustment, and (3) growth modifiers (G. Johnson, p. 74) ('growth modifiers' are referred to as 'growth multipliers' by Sue Carson, p. 119). Greg Johnson discussed the advantages and disadvantages of each approach using examples (pp. 75-79). Overall, the growth modifier approach seemed to be the most promising short-term solution. This would entail developing a multiplier for each component of the model (e.g., growth trait) that is correlated with the breeding value of that trait. Growth modeling software would be designed so that the major growth functions could be easily adjusted (e.g., to include growth modifiers for genetic improvement). Although site index and effective age adjustments may be more commonly used, a case was made against using the site index adjustment. Sue Carson and her colleagues used a growth multiplier approach to study the impacts of genetics on growth modeling of radiata pine in New Zealand (pp. 117-127). The success of this approach was greatly enhanced by the availability of a series of comprehensive (49-site), large-plot genetic gain experiments planted between 1978 and 1994. In general, the New Zealand results support the following conclusions: (1) growth multipliers are an effective way to incorporate genetics into growth models; (2) increases in growth rate (growth multipliers) are proportional to genetic superiority; (3) increases in growth rate are constant across stands ages, regions, and tree stocking levels (i.e., thinning regimes); (4) genetic gains estimated from progeny tests are similar to actual diameter increases in large-plot trials; and (5) diameter and height distributions do not differ among improved seedlots.

During the Workshop Discussion, Greg Johnson reported on his experience using growth modifiers to study the impacts of genetics on a Douglas-fir individual-tree growth model (ORGANON). Family growth functions were generated using data from family block plots, and then compared to growth functions from stands consisting of mixed genotypes. During the Workshop Discussion, it was suggested that multipliers could be used to fit the ORGANON model to existing progeny trials. The ideal verification situation would be to carry out a meta-analysis of family or clonal replicates that are established in both block plot and single-tree plots, where within-family variation could be sampled and the effects of stand structure compared.

Short-term solutions

To assist forest planners over the short term, the development of growth modifiers from single-tree plot progeny tests which can be fed into ORGANON was seen as an important first step for the region (Table 2). This approach should be easy to implement, and should provide short-term solutions in the near future. Development of tree lists for young stands that can be fed into ORGANON was also a priority. A case was made for standardizing the procedures used to estimate breeding values in the Pacific Northwest. The frequency of scheduled progeny test measurements may need to be adjusted. After crown closure, heritabilities are inflated by intergenotypic competition, but a growth model may be able to remove this bias.

Long-term needs

On a long-term basis, practitioners should be addressing the issue from numerous standpoints. One option is to establish large block-plot experiments of paired treatments as part of an operational planting program (Table 2). By using ongoing, operational planting programs, it should be feasible to install these experiments on a large scale across many sites. These experiments could compare one checklot and one seedlot of known genetic worth. It was also suggested that crown measurements should be incorporated into progeny test analyses. Validation of genotypic performance through large block-plot experiments was viewed as a high priority. Better site and genotype by site characterization is desirable, and could form the basis for refining operational planting guidelines for the deployment of genetically improved materials so that their genetic potential is optimized. The importance of a seedlot certification system for genetically improved seedlots was also recognized. Additionally, exploration of the potential ramifications of climate change is needed.

Modelers were encouraged to use spatial data from progeny trials in spatially explicit models, such as TASS, and simulate growth of the test stand. A genetic multiplier would be used to fit the model to existing progeny trials. Major additions that could be incorporated into current models such as ORGANON include young stand development, climate, and site characterization. Hybrid model development was also encouraged to further investigate physiological and morphological differences between genotypes as related to tree and stand growth.

Appendix 1. *Genetics and Growth Modeling Workshop Discussion Sessions*
November 5-6, 2003

On November 5-6, 2003, a group of forest geneticists and growth modelers discussed how to incorporate genetics into growth models, focusing on the needs of the Pacific Northwest. The participants included researchers and land managers from universities, governmental agencies, and forest industries from the United States, Canada, New Zealand, and Australia. This group addressed a wide range of questions from diverse perspectives—participants included both geneticists and growth modelers, and both researchers and practitioners with experience breeding and managing stands of Douglas-fir, loblolly pine, radiata pine, and eucalyptus. The main conclusions drawn from these discussions are included in the previous workshop Summary.

Participants in the *Genetics and Growth Modeling Workshop Discussion Sessions* held on November 5-6, 2003.

Participant	Affiliation
Paul Anderson	USFS Pacific Northwest Research Station
David Briggs	Stand Management Cooperative, University of Washington
Jean Brouard	Western Boreal Aspen Corp.
Susan Carson	Carson Associates
Marilyn Cherry	PNWTIRC, Oregon State University
G. Sam Foster	Mississippi State University
Jim Goudie	British Columbia Ministry of Forests
David Hann	Oregon State University
Mark Hanus	Forest Technology Group
Wade Harrison	Forest Technology Group
Scott Holmen	Olympic Resource Management
Glenn Howe	PNWTIRC, Oregon State University
David Hyink	Weyerhaeuser Company
Keith Jayawickrama	NWTIC, Oregon State University
Sally John	Isabella Point Forestry Ltd.
Greg Johnson	Weyerhaeuser Company
Randy Johnson	USFS Pacific Northwest Research Station
Joe Landsberg	CSIRO, Australia (retired)
Bailian Li	NCSU-Industry Cooperative Tree Improvement Program
David D. Marshall	USFS Pacific Northwest Research Station
Robert A. Monserud	USFS Pacific Northwest Research Station
Mike Mosman	Port Blakely Tree Farms
Tim Mullin	NCSU-Industry Cooperative Tree Improvement Program
Martin Ritchie	USFS Pacific Northwest Research Station
Andrew Robinson	University of Idaho
Brad St. Clair	USFS Pacific Northwest Research Station
Eric Turnblom	Stand Management Cooperative, University of Washington
Tongli Wang	University of British Columbia
Chang-yi Xie	British Columbia Ministry of Forests

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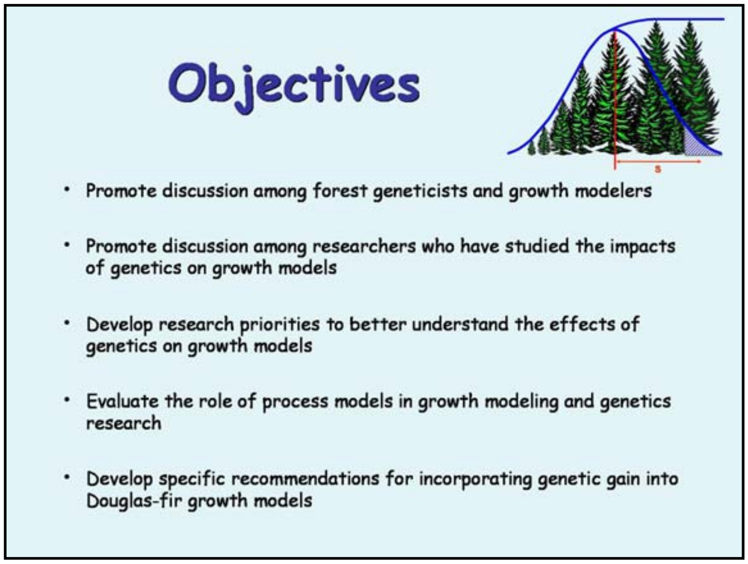
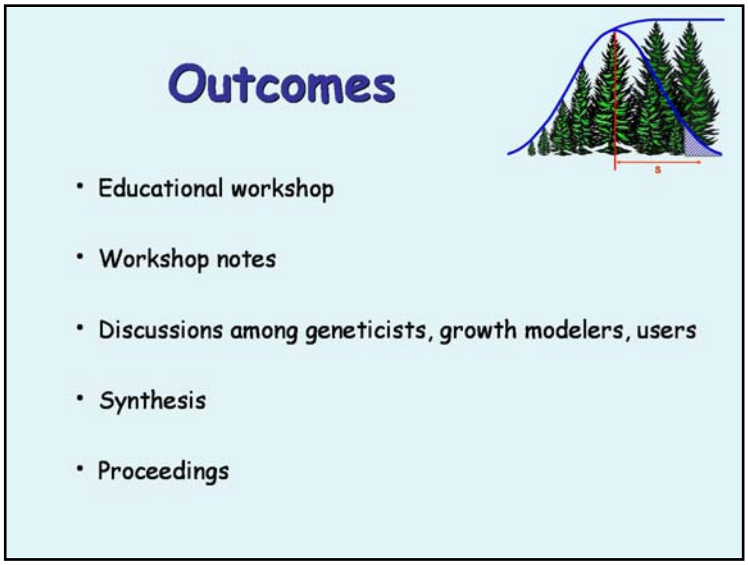
Workshop introduction

Glenn Howe
Pacific Northwest Tree Improvement Research Cooperative
Oregon State University
Corvallis, Oregon



Objectives

- Promote discussion among forest geneticists and growth modelers
- Promote discussion among researchers who have studied the impacts of genetics on growth models
- Develop research priorities to better understand the effects of genetics on growth models
- Evaluate the role of process models in growth modeling and genetics research
- Develop specific recommendations for incorporating genetic gain into Douglas-fir growth models



Outcomes

- Educational workshop
- Workshop notes
- Discussions among geneticists, growth modelers, users
- Synthesis
- Proceedings

Sponsors

- Pacific Northwest Tree Improvement Research Cooperative
- USDA Forest Service, Pacific Northwest Research Station
- Northwest Tree Improvement Cooperative
- Stand Management Cooperative
- Port Blakely Tree Farms
- OSU Department of Forest Science

Organizing Committee

- Marilyn Cherry, Glenn Howe; PNWTIRC
- Brad St. Clair, Dave Marshall, Paul Anderson; USDA PNWRS
- Keith Jayawickrama; NWTIC
- David Briggs; Stand Management Cooperative
- Greg Johnson; Weyerhaeuser
- Dave Walters; Roseburg Resources
- Mike Mosman; Port Blakely Tree Farms

Introduction to forest genetics

Randy Johnson
USFS Pacific Northwest Research Station
Corvallis Forestry Sciences Laboratory
Corvallis, Oregon

Introduction to Forest Genetics

Randy Johnson
USDA Forest Service
PNW Research Station

Goals of Tree Breeding

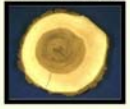
Growth

Disease resistance

Form

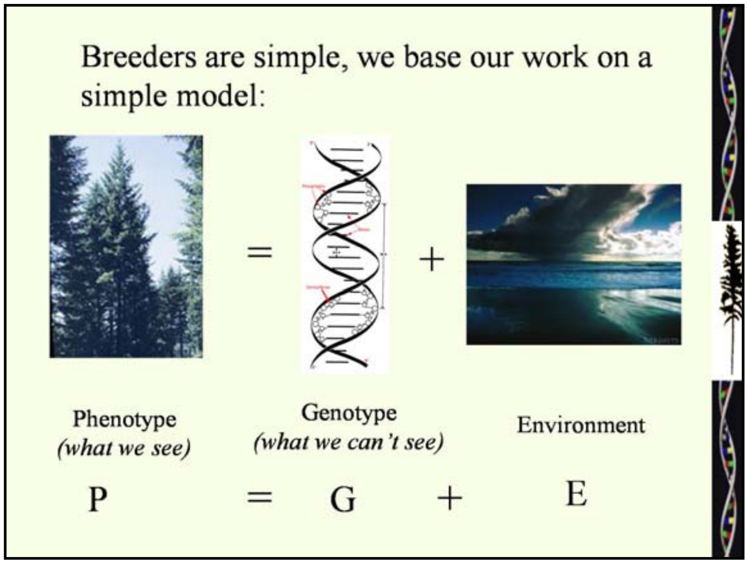
Insect resistance

Wood quality



Growth modelers think in complicated equations:

$$\ln(PAI_{2000\text{-}2001}/PAI_{1998\text{-}1999}) = 0.8903 + 0.05517 \bullet RD_{WH} + 0.1197 \bullet \ln(BA_{DF}) - 0.3864 \bullet \ln(BA_{total}) + 0.07781 \bullet \ln(FOLRET_{00})$$



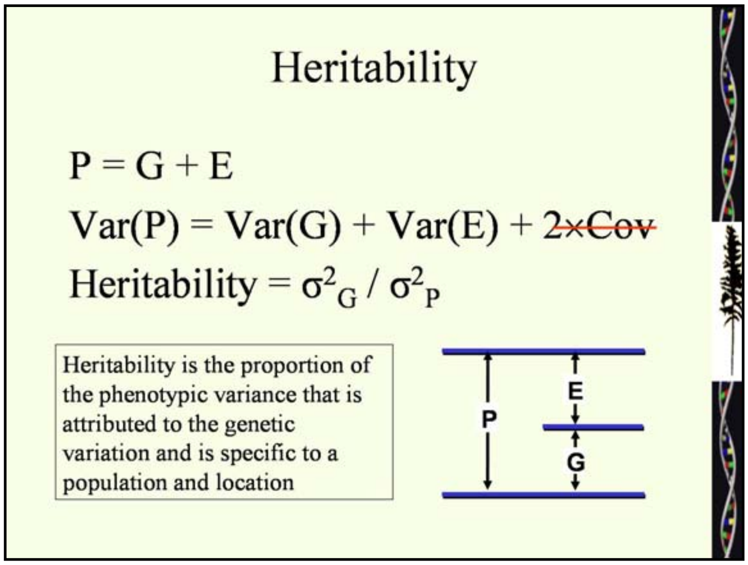
Breeders are simple, we base our work on a simple model:

Phenotype
(what we see)

Genotype
(what we can't see)

Environment

$$P = G + E$$



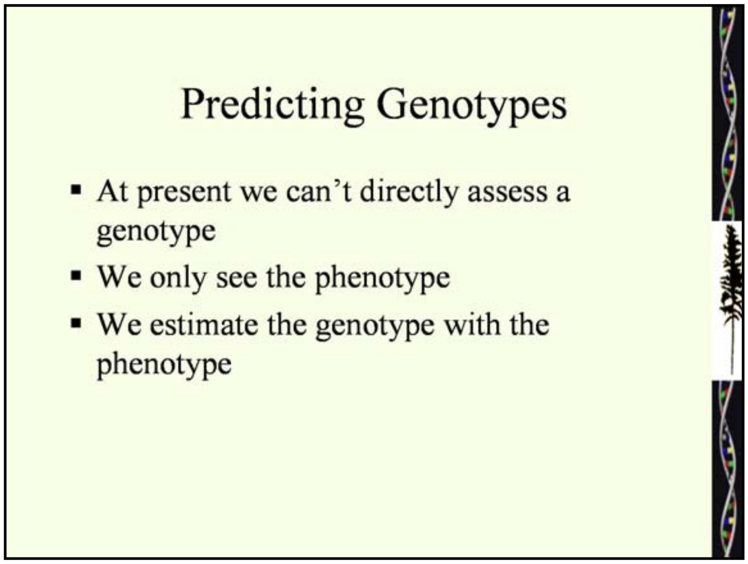
Heritability

$$P = G + E$$

$$\mathrm{Var}(P) = \mathrm{Var}(G) + \mathrm{Var}(E) + \cancel{2\times\mathrm{Cov}}$$

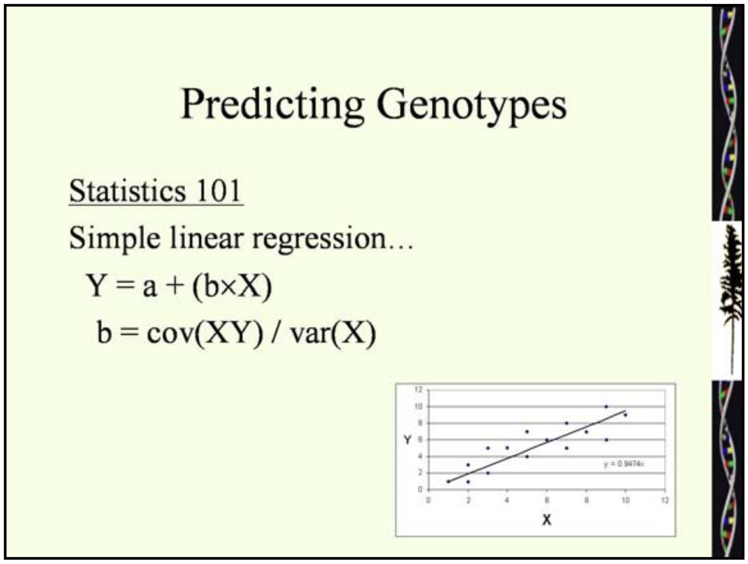
$$\text{Heritability} = \sigma^2_G / \sigma^2_P$$

Heritability is the proportion of the phenotypic variance that is attributed to the genetic variation and is specific to a population and location



Predicting Genotypes

- At present we can't directly assess a genotype
- We only see the phenotype
- We estimate the genotype with the phenotype



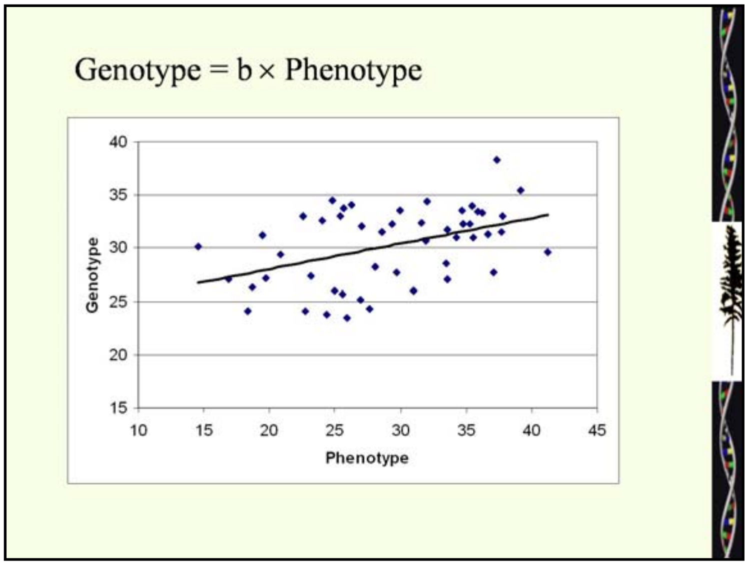
Predicting Genotypes

Statistics 101

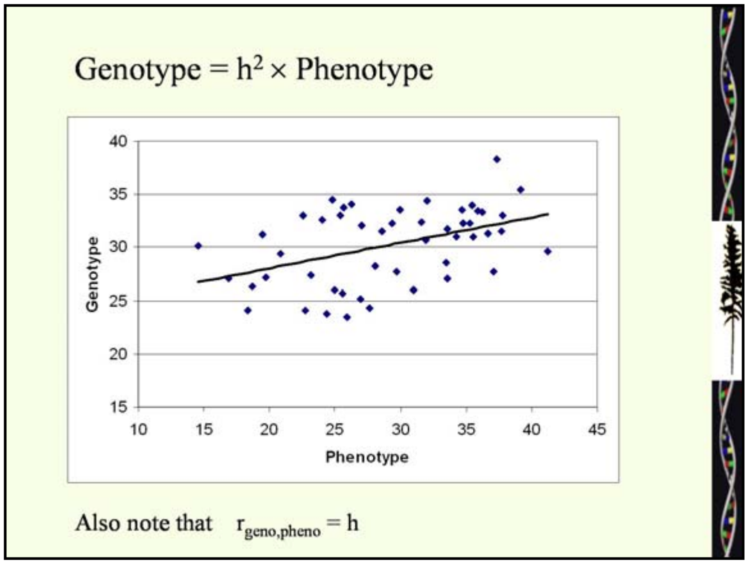
Simple linear regression…

$Y = a + (b \times X)$

$b = \mathrm{cov}(XY) / \mathrm{var}(X)$



Genotype = b × Phenotype



Genotype = h^2 × Phenotype

Also note that $r_{\mathrm{geno,pheno}} = h$

Predicting Gain

- Gain = $\text{Genotype}_{\text{selection}} - \text{Genotype}_{\text{population}}$
- Gain = $h^2 \times$ (phenotype – pop mean)
- Gain = $h^2 \times$ (selection differential)

Selection differential is the difference between the mean of the selections and the mean of the population

---

Selection differential

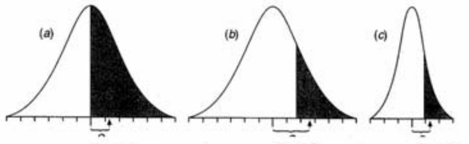


Fig. 11.2. Diagrams to show how the selection differential, S, depends on the proportion of the population selected, and on the variability of a normally distributed character. All the individuals in the stippled areas, beyond the points of truncation, are selected. The axes are marked in hypothetical units of measurement.

(*a*) 50 per cent selected; standard deviation 2 units: S = 1.6 units.
(*b*) 20 per cent selected; standard deviation 2 units: S = 2.8 units.
(*c*) 20 per cent selected; standard deviation 1 unit: S = 1.4 units.

(from Falconer and Mackay 1996)

Selection differential is a function of the selection intensity (i), which is related to the proportion of the population selected**, and the variability of the population (σ_P):**

Selection differential = $i\,\sigma_P$

Predicting Gain

- Gain = $h^2 \times$ (selection differential)

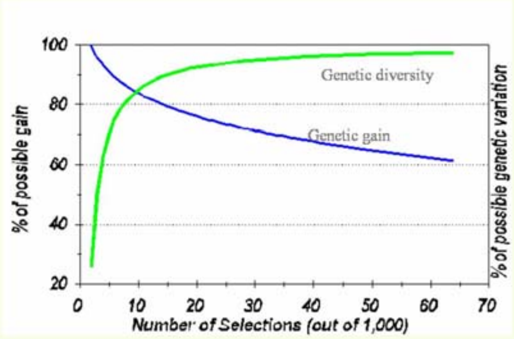
Selection differential = $i\,\sigma_P$

- Gain = $i\,h^2\,\sigma_P = i\,h\,\sigma_G$

Get more gain by selecting a smaller proportion of the population

Get more gain by controlling the environmental variation and increasing h^2

Genetic gain and genetic diversity considerations



Heritability is estimated with variance components derived from progeny tests

A typical value of h^2 is between 0.1 and 0.3

- $r_{geno, pheno}$ is between 0.3 and 0.5
- Not overly impressive accuracy
- We can't select individuals on their phenotypes very well

Selecting Families and Parents

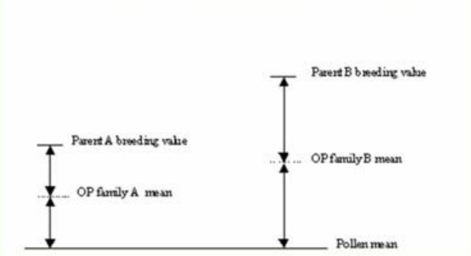
- We can select families more accurately than individuals because:
  - Multiple observations (large family sizes) reduces the environmental effect

We want to know which parents produce good kids anyway

Family mean heritabilities (h^2_{fm})

h^2_{fm} =

(among-family genetic variance) / (family phenotypic variance)

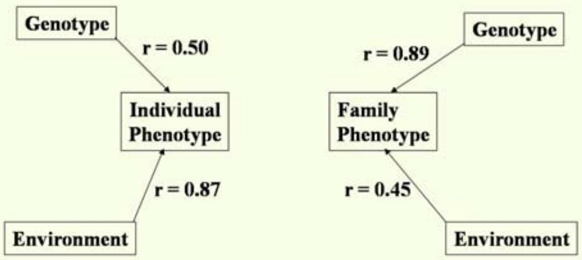


Family mean heritabilities (h^2_{fm})

- h^2_{fm} typically range from 0.6 to 0.9
- $r_{geno,\ pheno}$ is between 0.77 and 0.95
- We have good precision picking families and parents!

Path Diagrams showing the relationship between G and E with P

Individuals vs. Families



Genotype

r = 0.50

Individual Phenotype

r = 0.87

Environment

Genotype

r = 0.89

Family Phenotype

r = 0.45

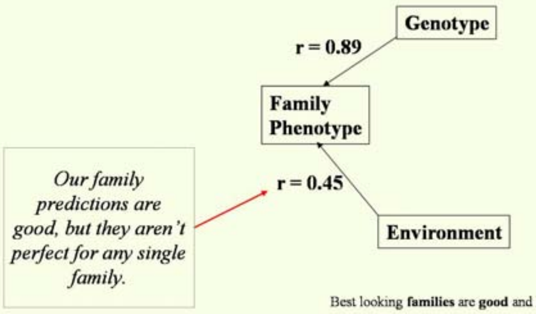
Environment

Best looking **trees** are **lucky** and good

Best looking **families** are **good** and lucky

Path Diagrams showing the relationship between G and E with P

Individuals vs. Families



Our family predictions are good, but they aren't perfect for any single family.

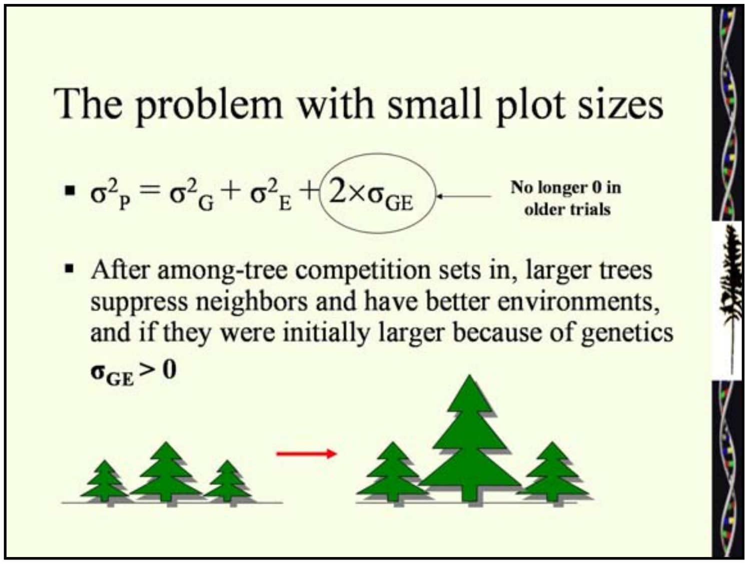
Best looking **families** are **good** and lucky

So where's the problem with predicting gain?

- We use small plots (single-trees or rows)
- We select on young traits
- Genotypes aren't perfectly stable over environments

Small plots are a necessity in tree breeding

- The breeder's primary goal is to **rank** the families.
- We must test many families in order to achieve high selection intensities.
- Single-tree plots are the most efficient for ranking families.
- We also use additional statistical tools to make good comparisons ***(alpha designs, BLUP, nearest neighbor, etc.)***



The problem with small plot sizes

- $\sigma^2_P = \sigma^2_G + \sigma^2_E + 2\times\sigma_{GE}$ ← **No longer 0 in older trials**
- After among-tree competition sets in, larger trees suppress neighbors and have better environments, and if they were initially larger because of genetics **$\sigma_{GE} > 0$**

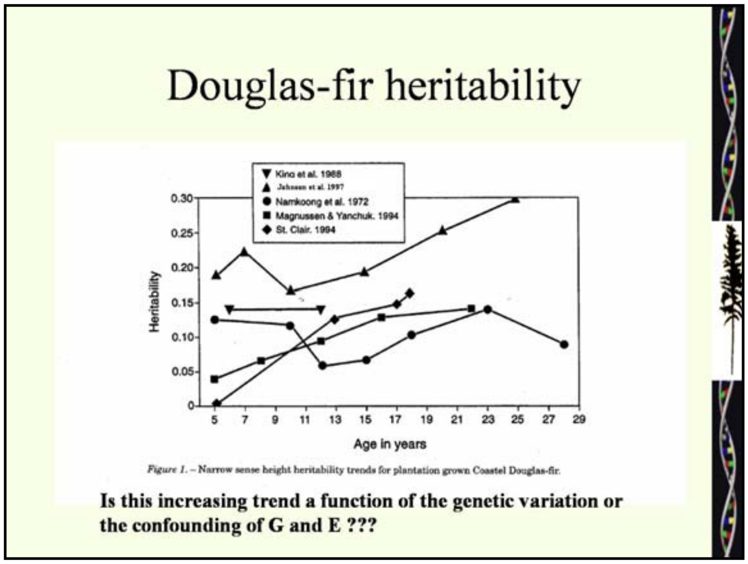
Small Plot Size

- **σ_{GE}** is confounded with **σ^2_G** in older trials

This can bias estimates of h^2 over time

and

We can't distinguish whether trees are big because of genetics alone or whether the altered environment is, in part, the reason for later improved growth



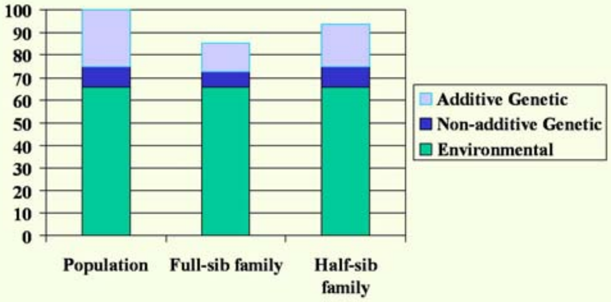
Douglas-fir heritability

Figure 1. – Narrow sense height heritability trends for plantation grown Coastel Douglas-fir.

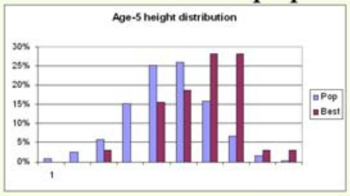
Is this increasing trend a function of the genetic variation or the confounding of G and E ???

Small Plot Size

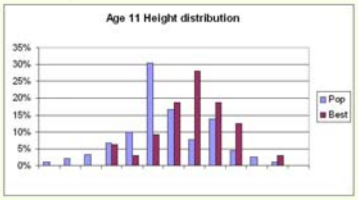
Confounding is more of a problem for individuals than families because there is considerable variation within a family



Distribution of the best family (n=32) vs. the population (n=1309)



40 families on 3 sites



Should breeders use large plots?

- Progeny tests are designed to pick the best families, this is done best with small plots.
- Progeny tests have many families (30 to 900) and there are no sites large enough to test many families in a replicated block trial
- STP trials already cost over $300,000 per series

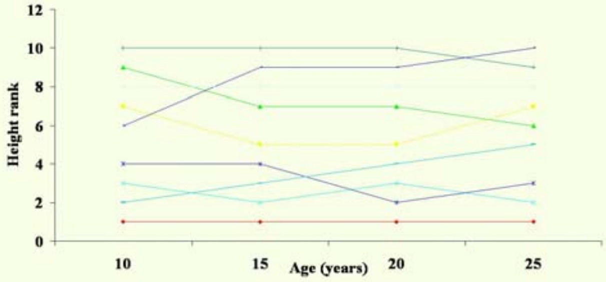
Answer

NO we shouldn’t, but someone should establish block plantings to establish genetic gains of our selected families.

Juvenile-Mature Correlations

- I'm impatient and don't want to wait 40 years to decide which family is best at rotation.
- But, the genes which influence early growth aren't necessarily the same as those that influence later growth

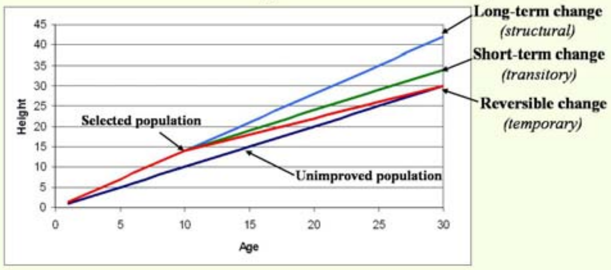
Family ranks change over time



Juvenile-Mature Correlations

- Height at early age is correlated with height at a later age.
- The real question: How is the genetics of early growth correlated with the genetics of later growth ?

Will we maintain the level of gain we see at selection age?



Family mean correlations

(a function of genes and common environment)

	r with age-20 ht	r with height inc to age 20
Age 10	0.83	0.75
Age 15	0.95	0.60

Some of the genetic effects that affect early "growth" appear to also affect later growth, but not all.

Age-age **genetic** correlations

(removing the common environment)

AGE	10	15	20	25
7	0.97	0.85	0.79	0.64
10		0.94	0.90	0.74
15			0.99	0.93
20				0.97

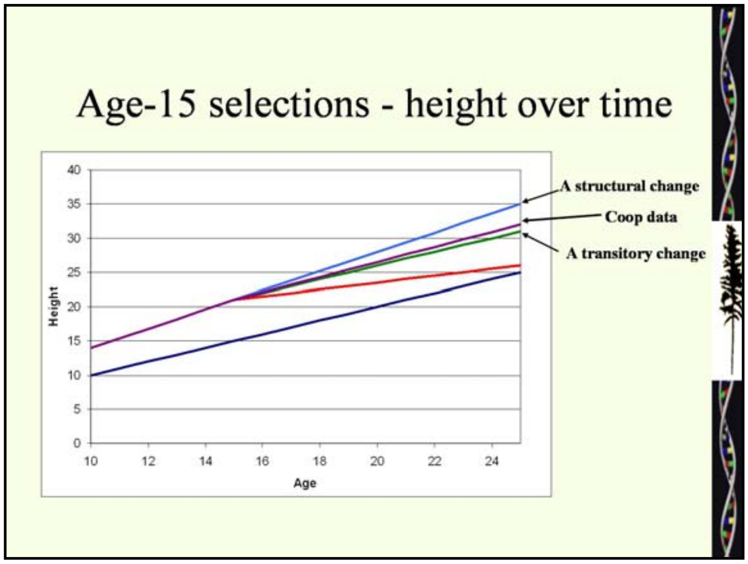
Lambeth's equation: $r = a + b \times LAR$

$LAR = \ln(age_{young} / age_{old})$

Age-15 selections – height (m)

(data averaged over 3 breeding programs)

Age	Population average	Top 10% of the families	Height difference	% increase
7	1.8	2.0	0.2	8.2
10	4.4	4.7	0.3	7.0
15	9.0	9.5	0.5	5.5
20	13.8	14.4	0.6	4.4

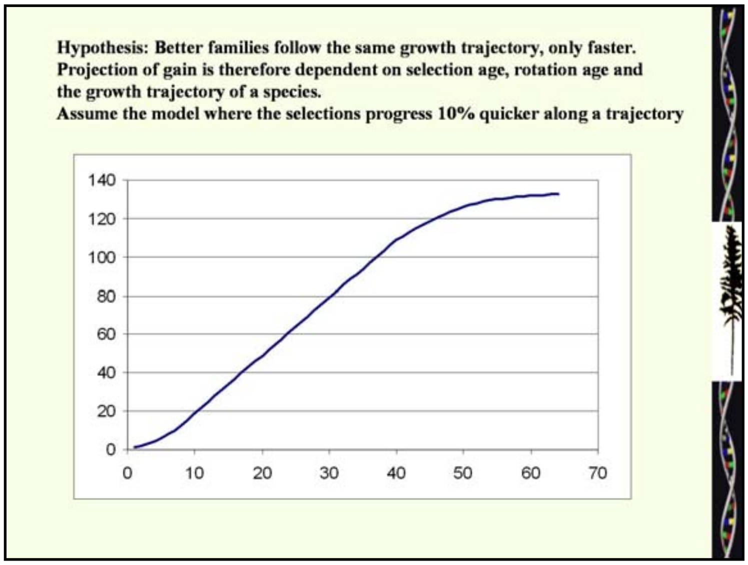


Age-15 selections - height over time

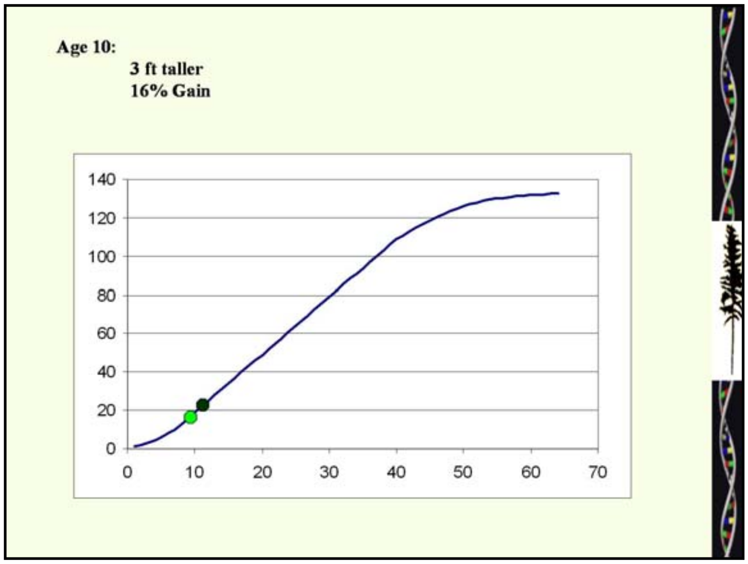
A structural change

Coop data

A transitory change

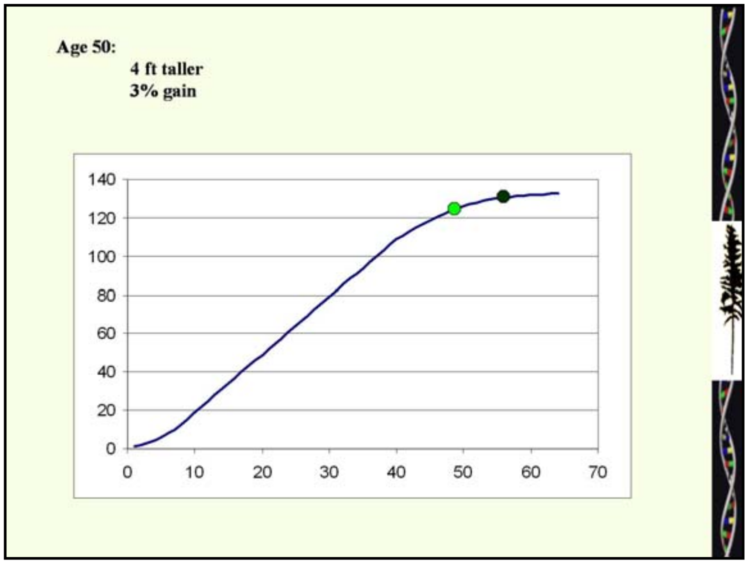


Hypothesis: Better families follow the same growth trajectory, only faster.
Projection of gain is therefore dependent on selection age, rotation age and the growth trajectory of a species.
Assume the model where the selections progress 10% quicker along a trajectory



Age 10:

3 ft taller
16% Gain

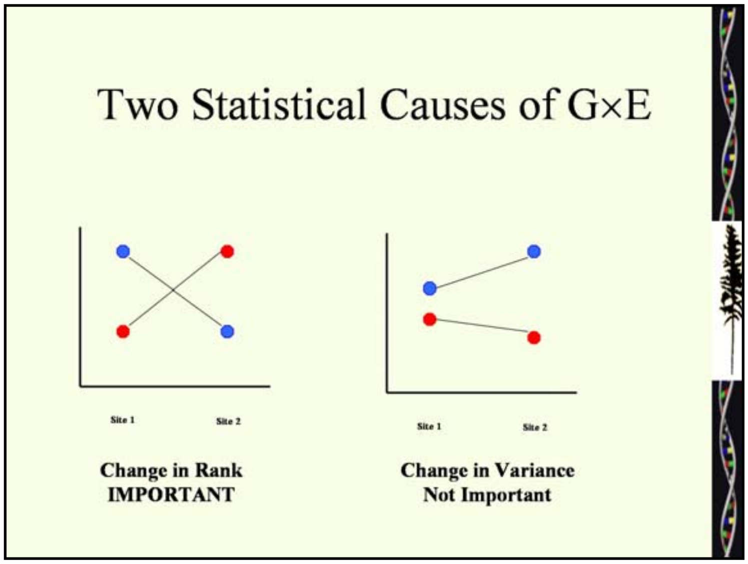


Age 50:

4 ft taller
3% gain

Genotype × Environmental Interaction

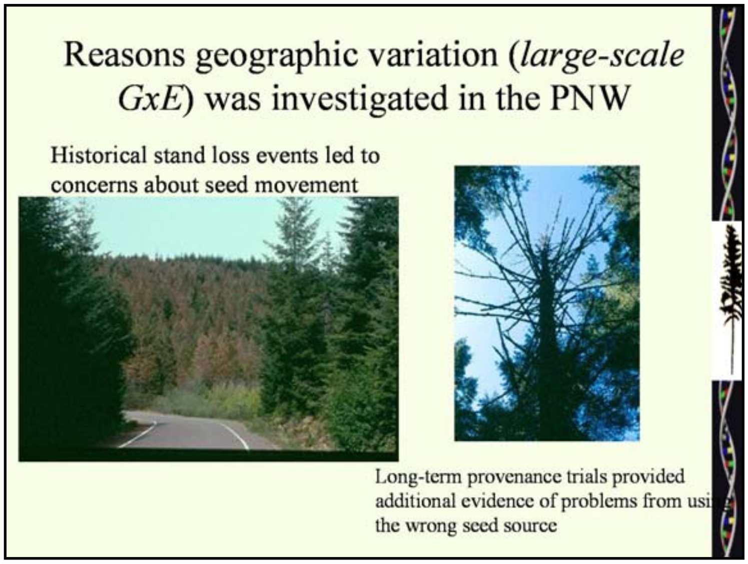
Family rankings change over sites



Two Statistical Causes of G×E

Change in Rank
IMPORTANT

Change in Variance
Not Important

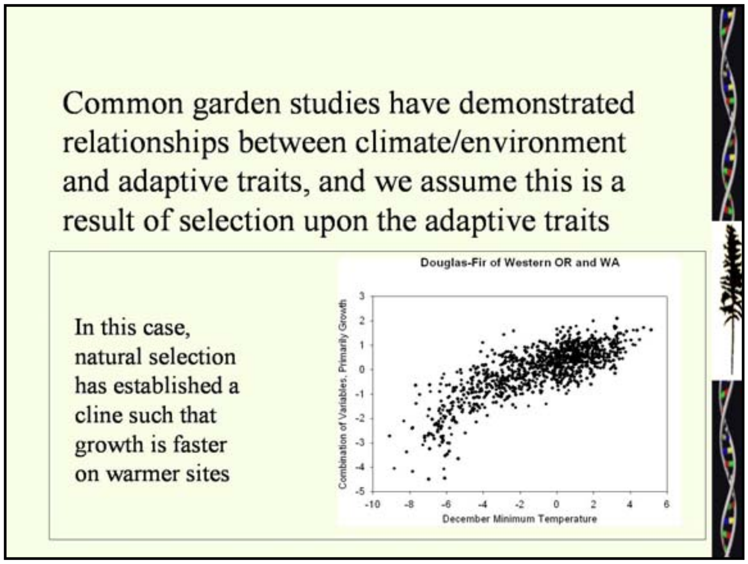


Reasons geographic variation (*large-scale GxE*) was investigated in the PNW

Historical stand loss events led to concerns about seed movement

Long-term provenance trials provided additional evidence of problems from usi the wrong seed source

This G×E wasn't so much a simple rank change, but families / seed sources completely failed



Common garden studies have demonstrated relationships between climate/environment and adaptive traits, and we assume this is a result of selection upon the adaptive traits

In this case, natural selection has established a cline such that growth is faster on warmer sites

Implications of large scale G × E

Different breeding zones are developed to ensure that selections are only used for areas where they are adapted

G × E within a breeding zone is measured in terms of the genetic correlation among sites, r_a

- Can be calculated in a number of ways:

$$r_{a(xy)} = \boldsymbol{\sigma_{xy} / \sigma_{a(x)} \times \sigma_{a(y)}}$$
$$r_{a(xy)} = \mathbf{r_{xy} / h_x \times h_y}$$
$$r_{a(xy)} = \boldsymbol{\sigma^2_{fam} / (\sigma^2_{fam} + \sigma^2_{fam*site})}$$

Genetic correlation among sites

- Typically $r_a \approx 0.7$
- What causes $r < 1$?
  - Not associated with distance between sites *(D-fir)*
  - Generally little Genotype×Silviculture found
    - ~~G×Shade~~
    - ~~G×Spacing~~
    - ~~G×Fertilizer~~
    - ~~G×Veg Control~~ *(one exception)*

Implications of G×E

- The G×E effect is confounded with the genetic effect for single-sites
- h^2 is overestimated, so gain is over estimated
- Appropriate h^2 can be estimated with a multiple-site analysis

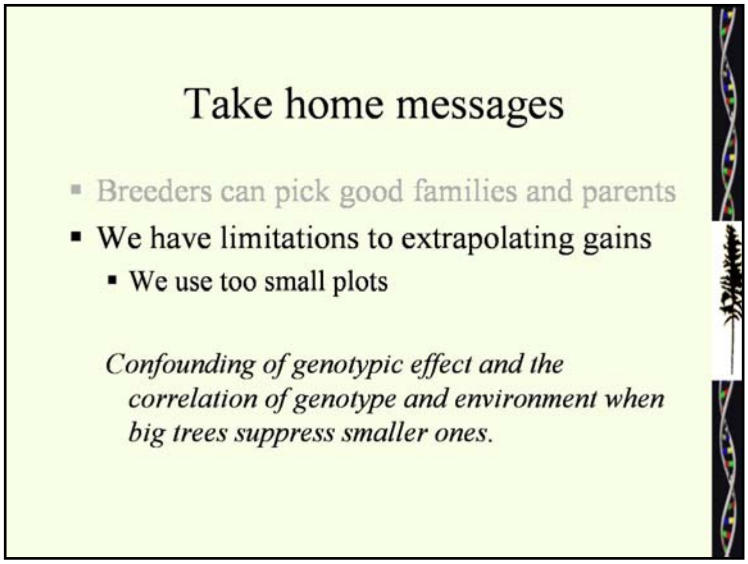
Heritabilities for multiple site analyses

- $h^2 = 4\sigma^2_{\text{family}} / (\sigma^2_{\text{family}} + \sigma^2_{\text{fam×site}} + \sigma^2_{\text{error}})$
- $h^2_{\text{fm}} = \sigma^2_{\text{family}} / [\sigma^2_{\text{family}} + (\sigma^2_{\text{fam×site}} / s) + (\sigma^2_{\text{error}} / sr)]$

Family mean heritabilities increase with additional sites by reducing the denominator (variance of family means)

Take home messages

- Breeders can pick good families and parents
  - Heritability, the ability to choose accurately, is good for families and so-so for individuals
  - Estimated height and DBH gains from 1st generation programs are between 10 and 20% for seed orchards with 20 parents
  - But, what does 10% more at age 10 or 15 really mean over a rotation?



Take home messages

- Breeders can pick good families and parents
- We have limitations to extrapolating gains
  - We use too small plots

Confounding of genotypic effect and the correlation of genotype and environment when big trees suppress smaller ones.

Take home messages

- Breeders can pick good families and parents
- We have limitations to extrapolating gains
  - We use too small plots
  - We select before rotation age (1/4 rotation age)

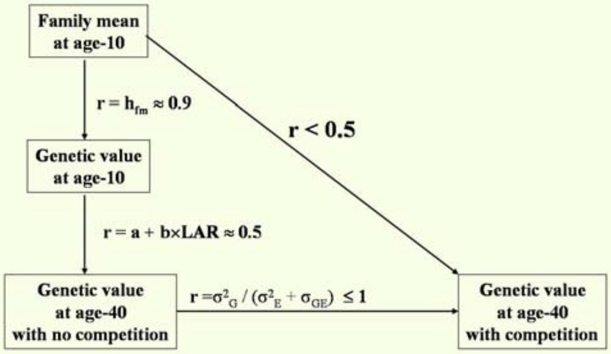
Genes that impact early growth aren't necessarily the ones affecting later growth.

Take home messages

- Breeders can pick good families and parents
- We have limitations to extrapolating gains
  - We use too small plots
  - We select before rotation age (1/4 rotation age)
  - We don't sample all sites

Gain at any one site will vary, especially when examining a single family... More stability in our estimates with family mixes and more sites.

A possible path diagram



Family mean at age-10

$r = h_{fm} \approx 0.9$

Genetic value at age-10

$r = a + b \times LAR \approx 0.5$

Genetic value at age-40 with no competition

$r = \sigma^2_G / (\sigma^2_E + \sigma_{GE}) \leq 1$

Genetic value at age-40 with competition

$r < 0.5$

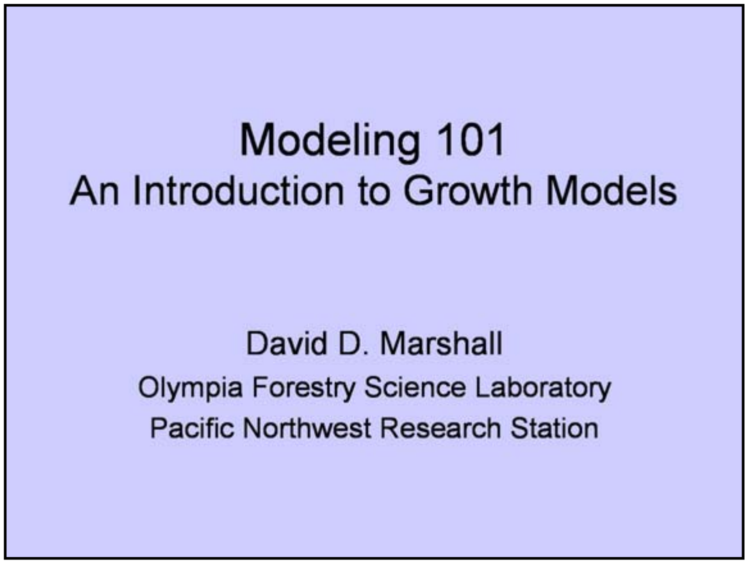
Questions?

An introduction to growth models

David D. Marshall
USFS Pacific Northwest Research Station
Olympia Forestry Sciences Laboratory
Olympia, Washington

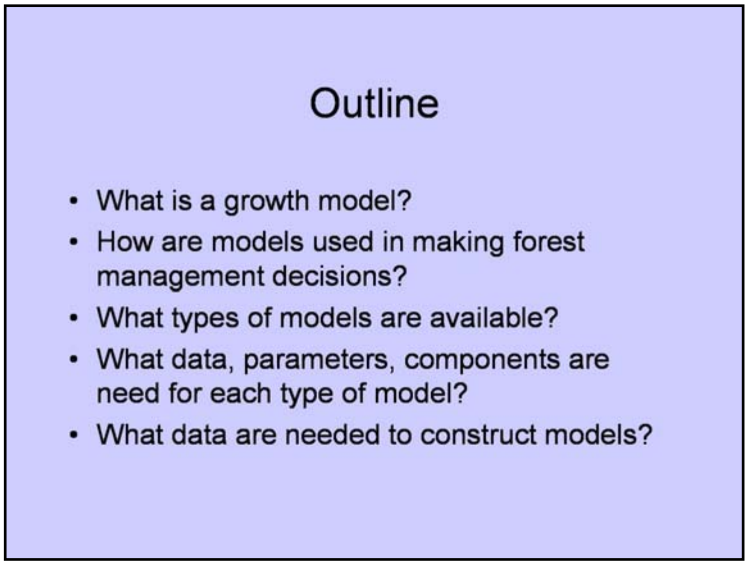
Over the last two decades, the number of forest growth models has increased at an astonishing rate due to the availability of data, better understanding of the basic processes of forest development and the power of computers. This presents the model user with a wide array, and sometimes confusing, set of choices. The eventual choice of which model to use will depend on matching the model's resolution and scale to the management decision being made, ease of use, interpretability of the output, and the accuracy of projections. A major starting point for most management decisions is the stand level inventory, which can be scaled up to provide information at the forest level and scaled down to the tree level. Most decisions that the manager is concerned about represent a time scale between the inventory cycle (5-10 years) and rotations (4-6 decades).

Models that are used for forest management decisions are generally thought of as empirical or process in nature. Empirical models are based on statistical correlations and tend to be based on large data sets of variables relevant to managers. The result is that these models tend to be accurate within the range of the data (species, treatments, geographic, and time). However, the data sets required are expensive to collect and the models may not be applicable to new or changing conditions (species, treatments, geographic areas, or climate). Of major concern are the use of site index to measure productivity and the potential impacts of changing climate. Process models may be better suited for applying to new species or conditions because they are based on basic ecophysiological processes (acquisition and allocation of carbon as affected by light regimes, temperature, water, and nutrition). While generally less data dependent, these models have generally come from a research background with a focus on understanding the processes rather than providing management information and tend to be very complex. However, much of this is changing with the development of hybrid models, which combine the best components from both empirical and process models.



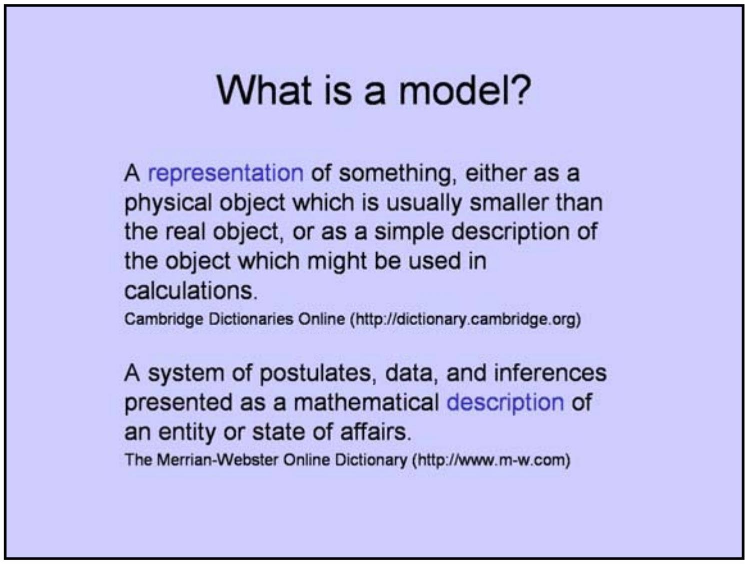
Modeling 101
An Introduction to Growth Models

David D. Marshall
Olympia Forestry Science Laboratory
Pacific Northwest Research Station



Outline

- What is a growth model?
- How are models used in making forest management decisions?
- What types of models are available?
- What data, parameters, components are need for each type of model?
- What data are needed to construct models?



What is a model?

A representation of something, either as a physical object which is usually smaller than the real object, or as a simple description of the object which might be used in calculations.
Cambridge Dictionaries Online (http://dictionary.cambridge.org)

A system of postulates, data, and inferences presented as a mathematical description of an entity or state of affairs.
The Merrian-Webster Online Dictionary (http://www.m-w.com)

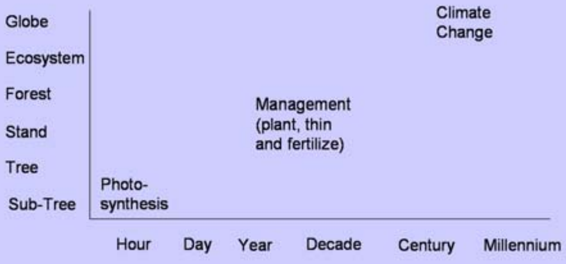
So, what is a growth model?

Vanclay (1994)

"A stand growth model is an abstraction of the natural dynamics of a forest stand …"

How are models used in making forest management decisions?

Models at different spatial and temporal scales



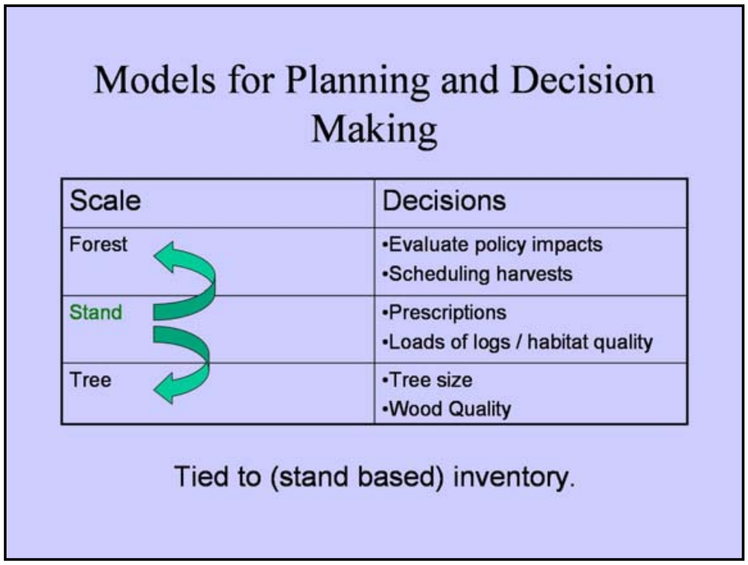
Based on Battaglia and Sands (1998)

Use of Models

- As tools for planning and decision-making.
- As a method to synthesize and describe our data, knowledge, and hypotheses about forest dynamics.

(Flewelling and others 1986)

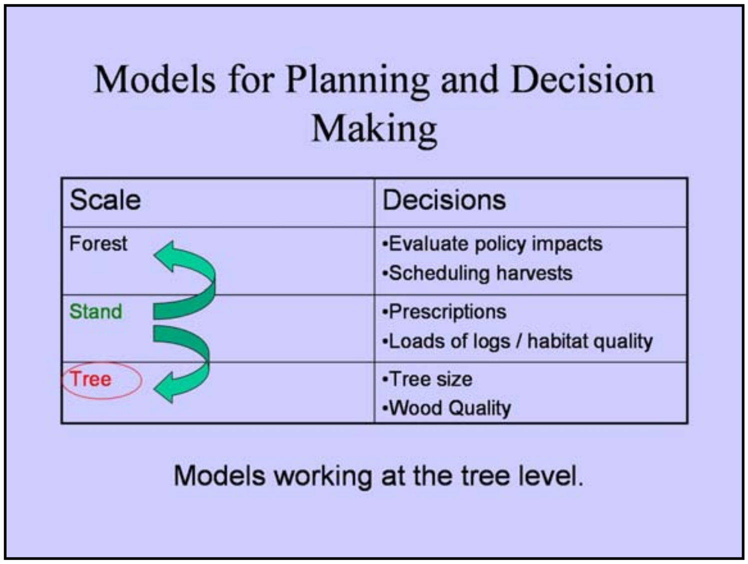
A distinction must be made between models designed for management applications and models as an integrated part of ongoing research. (Botkin and others 1972)



Models for Planning and Decision Making

Scale	Decisions
Forest	•Evaluate policy impacts •Scheduling harvests
Stand	•Prescriptions •Loads of logs / habitat quality
Tree	•Tree size •Wood Quality

Tied to (stand based) inventory.



Models for Planning and Decision Making

Scale	Decisions
Forest	•Evaluate policy impacts •Scheduling harvests
Stand	•Prescriptions •Loads of logs / habitat quality
Tree	•Tree size •Wood Quality

Models working at the tree level.

Models for Synthesis

- Objective – to improve understanding (mechanisms and interactions between processes).
- Target – Scientists and Academics

Types of Growth Models

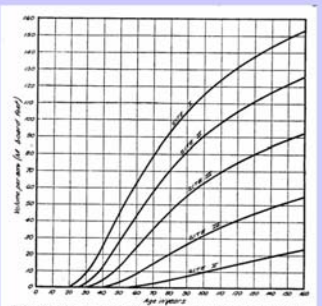
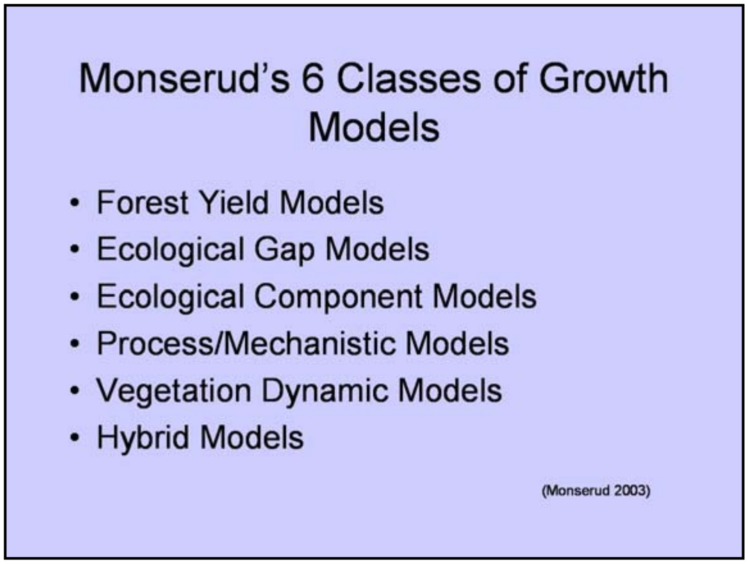


FIGURE 10.—Volume per acre in board feet by the Scribner log rule, trees 12 inches in diameter and larger

Components of a fully implemented growth model

- Estimates of Growth
- Estimates of Mortality
  - Non-catastrophic Mortality
  - Catastrophic Mortality
- Regeneration
- Management Activities
- Display of (Relevant) Results

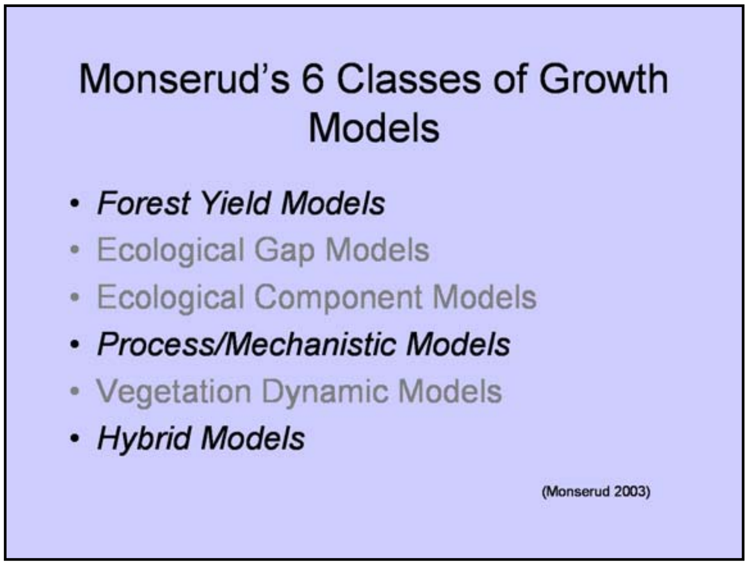
(Hann)



Monserud's 6 Classes of Growth Models

- Forest Yield Models
- Ecological Gap Models
- Ecological Component Models
- Process/Mechanistic Models
- Vegetation Dynamic Models
- Hybrid Models

(Monserud 2003)



Monserud's 6 Classes of Growth Models

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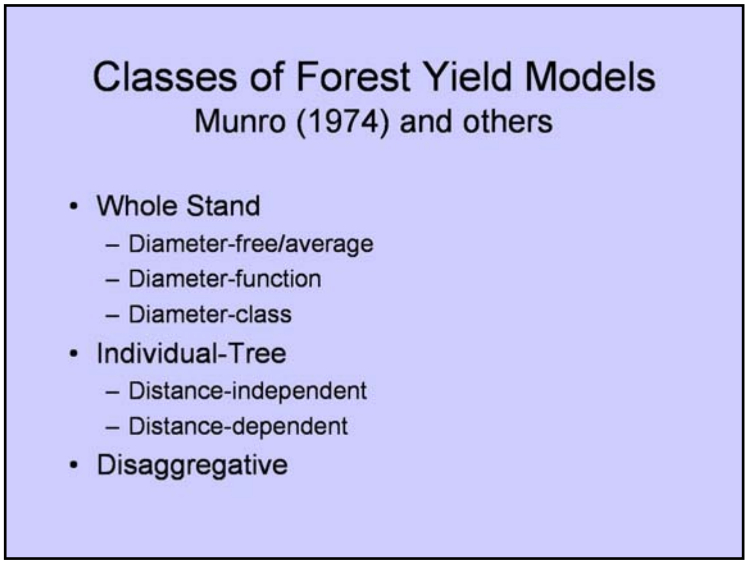
(Monserud 2003)



Classes of Forest Yield Models

Munro (1974) and others

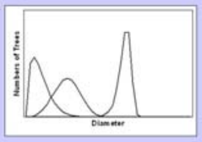
- Whole Stand
  - Diameter-free/average
  - Diameter-function
  - Diameter-class
- Individual-Tree
  - Distance-independent
  - Distance-dependent
- Disaggregative

Whole-stand/diameter-free

- Examples -- Bulletin 201, VD Yield Tables, DFSIM
- Characteristics
  - Stand level inputs (age, site index, basal area, number of trees)
  - Stand Level outputs (basal area, trees, volume)
- Advantages/Disadvantages
  - minimal input data
  - "simpler" system (stand yield)
  - no diameter distribution information
  - most applicable to even-aged, pure species

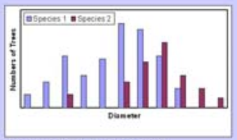
Whole-stand/diameter-function

- Examples – STEMS
- Characteristics
  - Stand level inputs (age, site index, basal area, number of trees)
  - Stand Level outputs (basal area, trees, volume)
  - Predicted/recovered diameter distribution



- Advantages/Disadvantages
  - minimal input data
  - "simpler" system (stand yield)
  - predicted diameter distribution
  - most applicable to even-aged, pure species

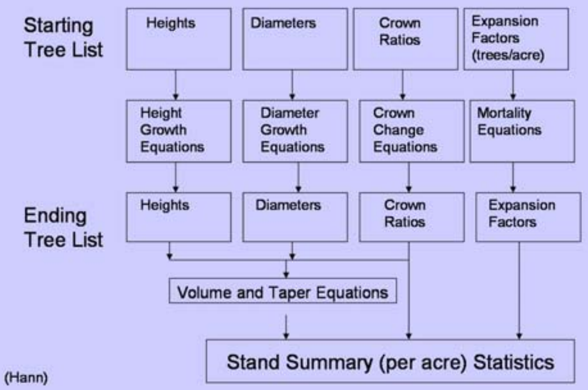
Whole-stand/diameter-class



- Examples –
- Characteristics
  - Stand level inputs (age, site index)
  - Diameter class inputs (species, number of trees, height)
  - "Move" into larger classes (diameter growth)
  - Outputs by diameter class (volume) and sum for stand

Advantages/Disadvantages
  - additional input data (classes)
  - actual diameter distribution
  - more complex (growing classes of trees)
  - applicable to even and uneven-aged, pure and mixed species

Individual Tree Models



Starting Tree List

Heights → Height Growth Equations → Heights

Diameters → Diameter Growth Equations → Diameters

Crown Ratios → Crown Change Equations → Crown Ratios

Expansion Factors (trees/acre) → Mortality Equations → Expansion Factors

Ending Tree List

Volume and Taper Equations

Stand Summary (per acre) Statistics

(Hann)

Individual-tree/distance-independent

- Examples – FVS, ORGANON, CACTOS, SPS, CONIFERS
- Characteristics
  - Stand level inputs (site index)
  - Tree list input (species, diameter, height, crown ratio, expansion)
  - Grow trees (diameter, height, crown, mortality)
  - Outputs grown trees and sum (by expansions) for stand

Advantages/Disadvantages

  - requires a tree list (added effort and expense)
  - greater complexity (growing trees -> stands)
  - provides details on single trees
  - applicable to even and uneven-aged, pure and mixed species

Individual-tree/distance-dependent

- Examples – TASS, FPS
- Characteristics
  - Stand level inputs (site index)
  - Tree list input plus spatial coordinates
  - Grow trees (diameter, height, crown, mortality)
  - Outputs grown trees and sum (by expansions) for stand
- Advantages/Disadvantages
  - requires a tree list (added effort and expense)
  - requires tree coordinates (measured or predicted)
  - greater complexity (growing trees -> stands)
  - Provides spatial information
  - provides (greater) details on single trees (especially crowns)
  - applicable to even and uneven-aged, pure and mixed species

Disaggregative models

- Examples – STEMS, LPSIM
- Characteristics
  - Stand level model
  - Tree level model
  - Grow both and rectify differences
- Advantages/Disadvantages
  - may requires a tree list (may use only stand level)
  - greater complexity (trees and stands)
  - provides consistent estimates at stand and tree level

Forest Yield Models Applicable on the West Coast (since 1980)

- Whole-Stand
  - DFSIM
  - PPSIM
  - PSME
  - DFETAL
  - SOS
- Disaggregative
  - LPSIM
  - STIM
  - RVMM

(Ritchie 1999)

- Individual Tree - DI
  - FVS
  - ORGANON
  - CACTOS
  - CRYPTOS
  - SPS
  - SYSTUM-1
  - RVMM
  - CONIFERS
- Individual Tree – DD
  - TASS
  - SPS
  - G-SPACE

Monserud's 6 Classes of Growth Models

- *Forest Yield Models*
- Ecological Gap Models
- Ecological Component Models
- *Process/Mechanistic Models*
- Vegetation Dynamic Models
- *Hybrid Models*

(Monserud 2003)

Process/Mechanistic Models

Net Production = Gross production - Respiration

Gross Production $=\alpha(\theta,N,T)\phi$

α = conversion of radiation to carbohydrates
θ = water relations
N = nutrition
T = temperature
ϕ = absorbed photosynthetically active radiation

(Landsberg 2003)

Process/Mechanistic Models Applied on the West Coast

- 3-PG
- Zelig
- FORCYTE

Monserud's 6 Classes of Growth Models

- *Forest Yield Models*
- Ecological Gap Models
- Ecological Component Models
- *Process/Mechanistic Models*
- Vegetation Dynamic Models
- *Hybrid Models*

(Monserud 2003)

Hybrid Models

Models that contain both empirical and process elements in an attempt to capitalize on the strengths of both.

Hybrid Models

Purely Empirical

Bulletin 201

ORGANON
CONIFERS
TASS

FVSBGC

3-PG
Zelig
FORCYTE

Purely Process

Hybrid Models

Purely Empirical

Bulletin 201

ORGANON
CONIFERS
TASS

FVSBGC

3-PG
Zelig
FORCYTE

Purely Process

1. Biologically meaningful
   a. sigmoid curves
   b. asymptotic
   c. reasonable maximums
   d. interpretable behavior
2. Meaningful parameters
3. Self-thinning

Hybrid Models

Purely Empirical

Purely Process

- Bulletin 201
- ORGANON
- CONIFERS
- TASS
- FVSBGC
- 3-PG
- Zelig
- FORCYTE

Productivity based on soil water holding capacity and precipitation

---

Hybrid Models

Purely Empirical

Purely Process

- Bulletin 201
- ORGANON
- CONIFERS
- TASS
- FVSBGC
- 3-PG
- Zelig
- FORCYTE

Growth based on crown volume

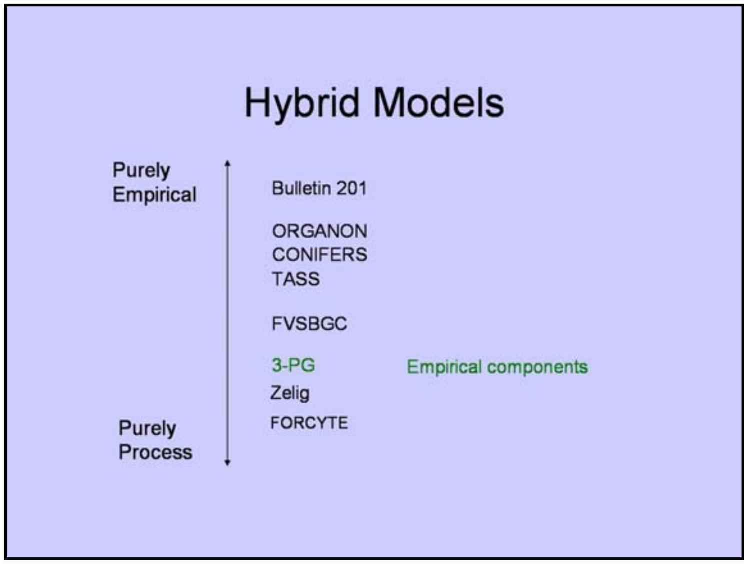
Hybrid Models

Purely Empirical

Purely Process

- Bulletin 201
- ORGANON
- CONIFERS
- TASS
- FVSBGC
- 3-PG
- Zelig
- FORCYTE

Combines empirical FVS model with process BGC model and runs both together



Hybrid Models

Purely Empirical

Bulletin 201

ORGANON
CONIFERS
TASS

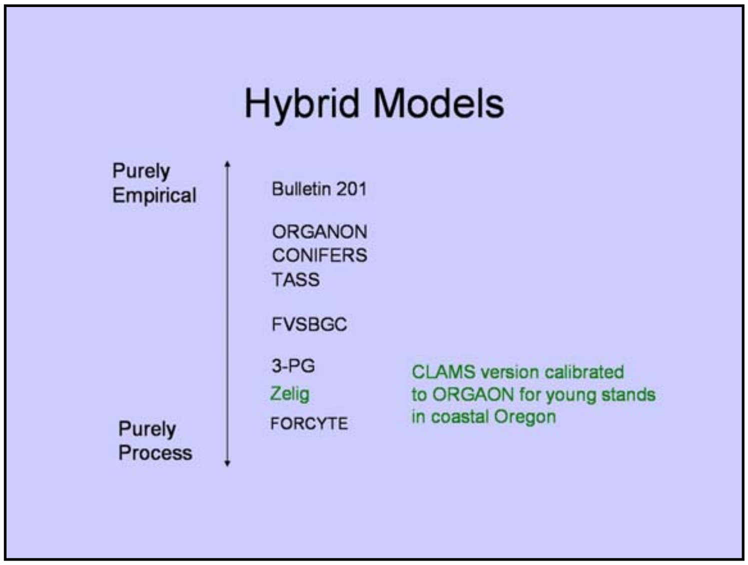
FVSBGC

3-PG — Empirical components

Zelig

FORCYTE

Purely Process



Hybrid Models

Purely Empirical

Bulletin 201

ORGANON
CONIFERS
TASS

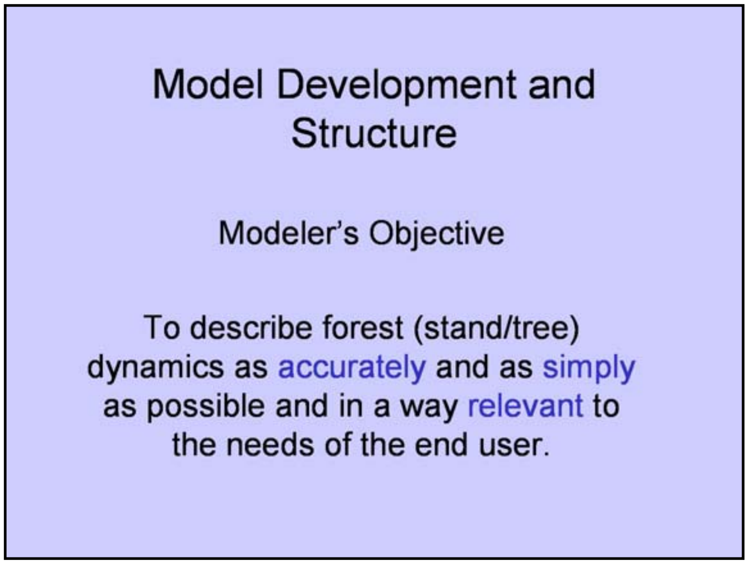
FVSBGC

3-PG

Zelig — CLAMS version calibrated to ORGAON for young stands in coastal Oregon

FORCYTE

Purely Process



Model Development and Structure

Modeler's Objective

To describe forest (stand/tree) dynamics as accurately and as simply as possible and in a way relevant to the needs of the end user.

Empirical Based Approach

Using ORGANON as an example
(individual tree/distance
dependent model)

Individual Tree Model

(ORGANON for example)

Inputs

- Site Productivity
- Sampling Scheme
- Tree List
  - Species
  - DBH
  - Height
  - Crown Ratio

Models and Parameters

- Diameter Growth
  - DBH, CR, BAL, BA, SI
- Height Growth
  - Potential: SI, HT
  - Modifier: CCH, CR
- Crown
  - HT, CCFL, BA, DBH/HT, SI
- Mortality
  - Tree: DBH, CR, BAL, SI
  - Maximum-Size Density

Individual Tree Diameter Growth

(ORGANON for example)

$$\Delta \mathrm{DBH} = \mathrm{EXP}\begin{bmatrix} a_0 + a_1 * \ln(\mathrm{DBH}+1) + a_2 * \mathrm{DBH}^2 \\ + a_3 * \ln(\mathrm{SI}-4.5) \\ + a_4 * \ln\left(\dfrac{\mathrm{CR}+0.2}{1.2}\right) \\ + a5 * \dfrac{\mathrm{BAL}^2}{\ln(\mathrm{DBH}+5.0)} + a6 * \mathrm{BA}^{0.5} \end{bmatrix}$$

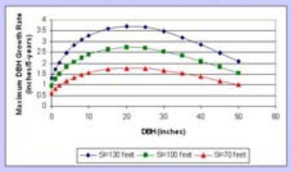
Size
Productivity

Vigor

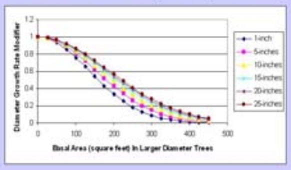
Competition

Hann and others (2003)

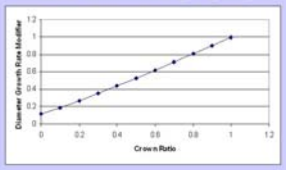
Potential Diameter Growth



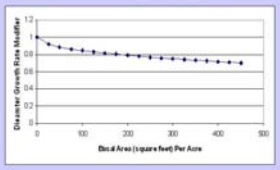
BAL Modifier (competition)



CR Modifier (Vigor)

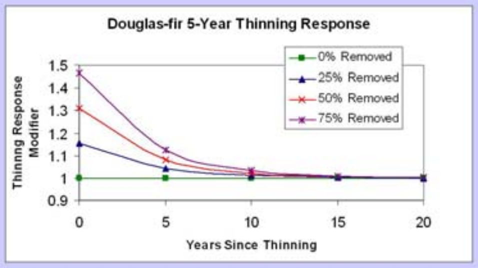


BA Modifier (competition)



Representing Treatments

$$\text{Growth}_{\text{treated}} = (\text{Growth}_{\text{untreated}})(\text{Modifier})$$



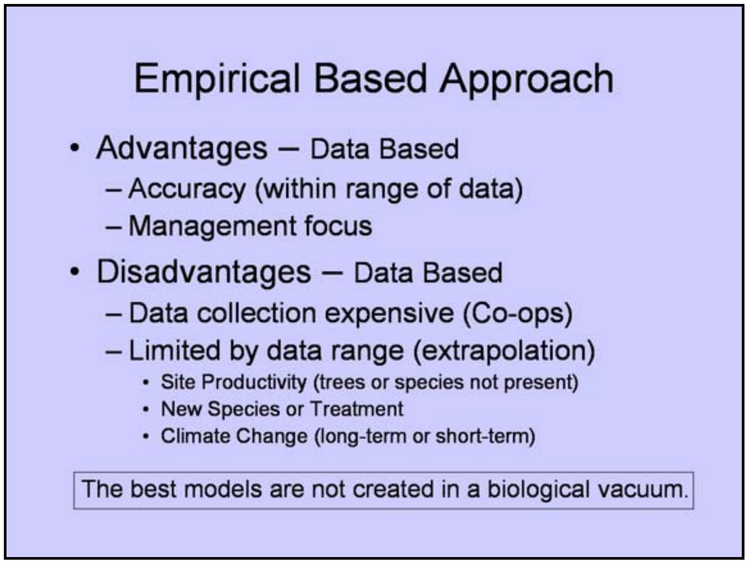
Hann and others (2003)

Empirical Model Data Sources

- Stem Analysis
- Permanent remeasured plots (coops)
- Temporary (inventory) plots

SMC Type I Installations

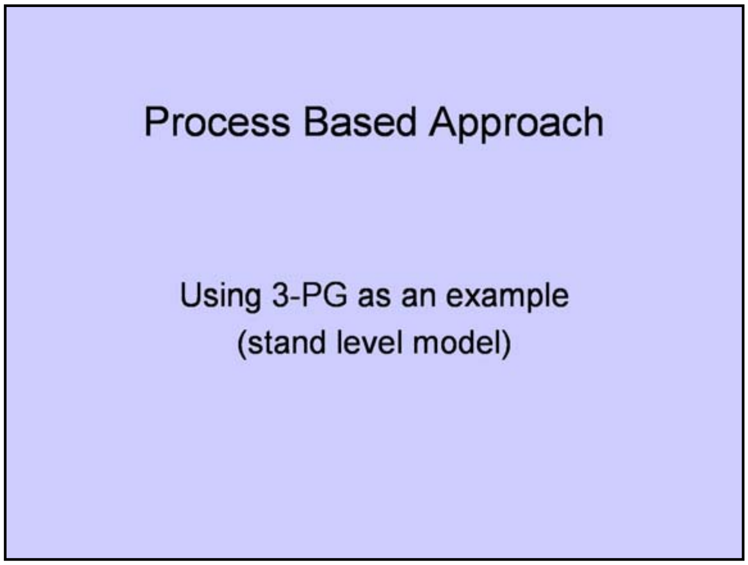
- *Most had been planted in 1970's or early 1980's*
- *Douglas-fir (30); Western hemlock (8)*



Empirical Based Approach

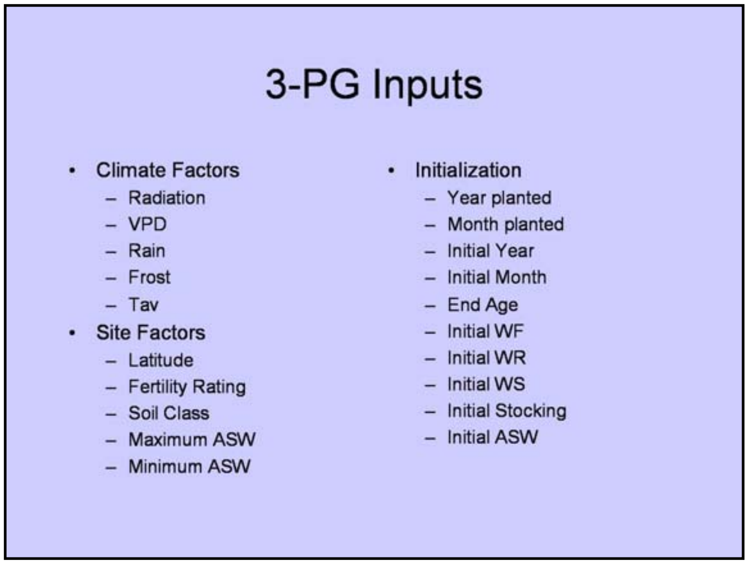
- Advantages – Data Based
  - Accuracy (within range of data)
  - Management focus
- Disadvantages – Data Based
  - Data collection expensive (Co-ops)
  - Limited by data range (extrapolation)
    - Site Productivity (trees or species not present)
    - New Species or Treatment
    - Climate Change (long-term or short-term)

The best models are not created in a biological vacuum.



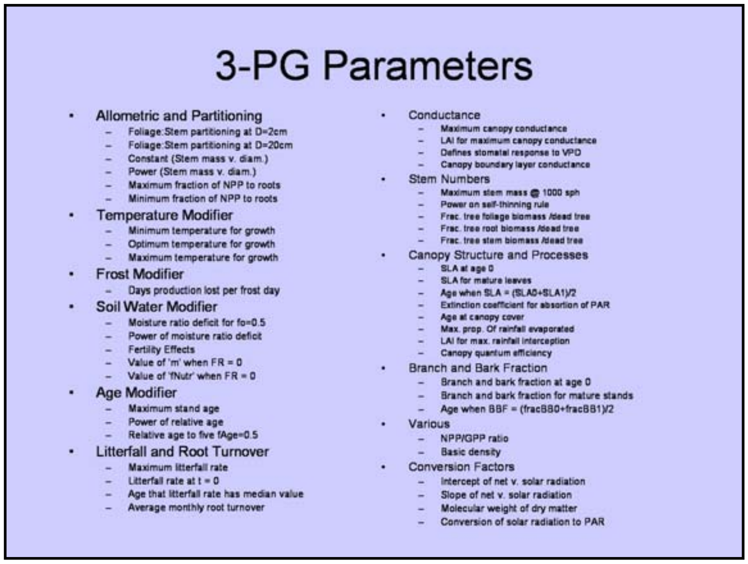
Process Based Approach

Using 3-PG as an example
(stand level model)



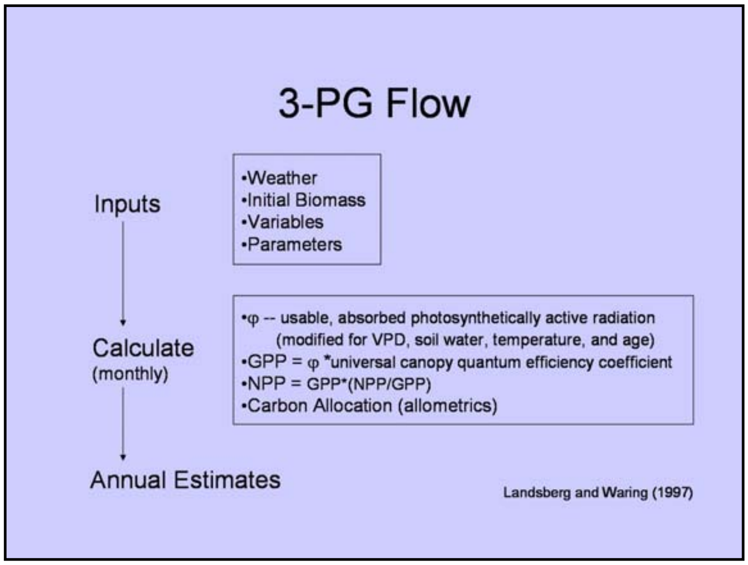
3-PG Inputs

- Climate Factors
  - Radiation
  - VPD
  - Rain
  - Frost
  - Tav
- Site Factors
  - Latitude
  - Fertility Rating
  - Soil Class
  - Maximum ASW
  - Minimum ASW
- Initialization
  - Year planted
  - Month planted
  - Initial Year
  - Initial Month
  - End Age
  - Initial WF
  - Initial WR
  - Initial WS
  - Initial Stocking
  - Initial ASW



3-PG Parameters

- Allometric and Partitioning
  - Foliage:Stem partitioning at D=2cm
  - Foliage:Stem partitioning at D=20cm
  - Constant (Stem mass v. diam.)
  - Power (Stem mass v. diam.)
  - Maximum fraction of NPP to roots
  - Minimum fraction of NPP to roots
- Temperature Modifier
  - Minimum temperature for growth
  - Optimum temperature for growth
  - Maximum temperature for growth
- Frost Modifier
  - Days production lost per frost day
- Soil Water Modifier
  - Moisture ratio deficit for fo=0.5
  - Power of moisture ratio deficit
  - Fertility Effects
  - Value of 'm' when FR = 0
  - Value of 'fNutr' when FR = 0
- Age Modifier
  - Maximum stand age
  - Power of relative age
  - Relative age to five fAge=0.5
- Litterfall and Root Turnover
  - Maximum litterfall rate
  - Litterfall rate at t = 0
  - Age that litterfall rate has median value
  - Average monthly root turnover
- Conductance
  - Maximum canopy conductance
  - LAI for maximum canopy conductance
  - Defines stomatal response to VPD
  - Canopy boundary layer conductance
- Stem Numbers
  - Maximum stem mass @ 1000 sph
  - Power on self-thinning rule
  - Frac. tree foliage biomass /dead tree
  - Frac. tree root biomass /dead tree
  - Frac. tree stem biomass /dead tree
- Canopy Structure and Processes
  - SLA at age 0
  - SLA for mature leaves
  - Age when SLA = (SLA0+SLA1)/2
  - Extinction coefficient for absortion of PAR
  - Age at canopy cover
  - Max. prop. Of rainfall evaporated
  - LAI for max. rainfall interception
  - Canopy quantum efficiency
- Branch and Bark Fraction
  - Branch and bark fraction at age 0
  - Branch and bark fraction for mature stands
  - Age when BBF = (fracBB0+fracBB1)/2
- Various
  - NPP/GPP ratio
  - Basic density
- Conversion Factors
  - Intercept of net v. solar radiation
  - Slope of net v. solar radiation
  - Molecular weight of dry matter
  - Conversion of solar radiation to PAR



3-PG Flow

Inputs

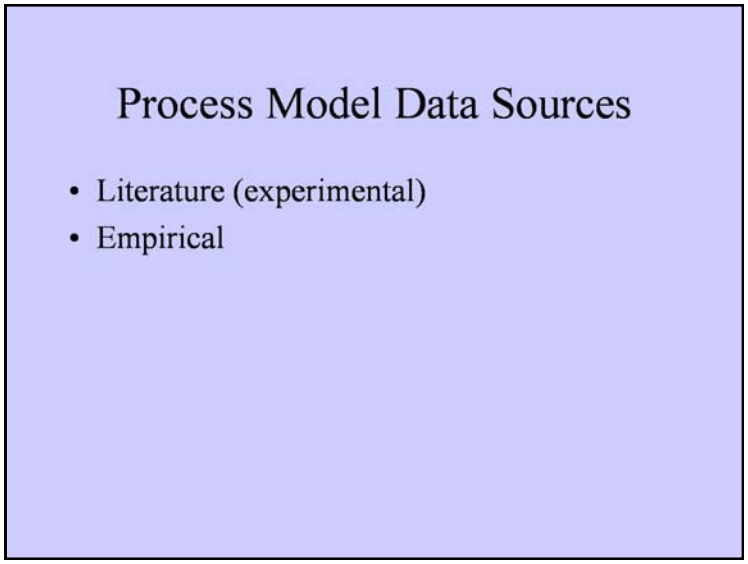
- •Weather
- •Initial Biomass
- •Variables
- •Parameters

Calculate
(monthly)

- •φ -- usable, absorbed photosynthetically active radiation (modified for VPD, soil water, temperature, and age)
- •GPP = φ *universal canopy quantum efficiency coefficient
- •NPP = GPP*(NPP/GPP)
- •Carbon Allocation (allometrics)

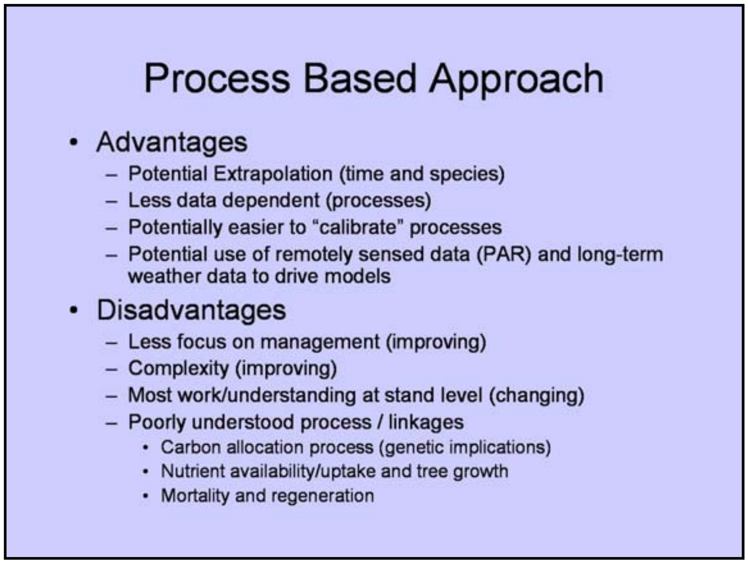
Annual Estimates

Landsberg and Waring (1997)



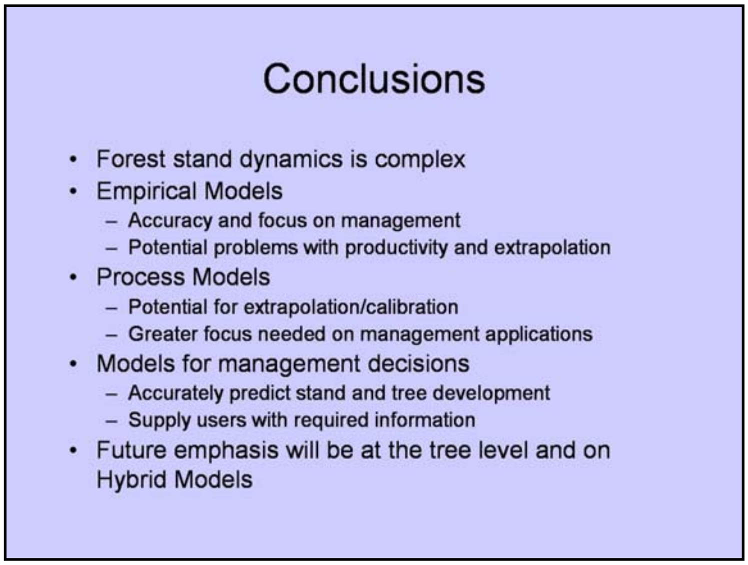
Process Model Data Sources

- Literature (experimental)
- Empirical



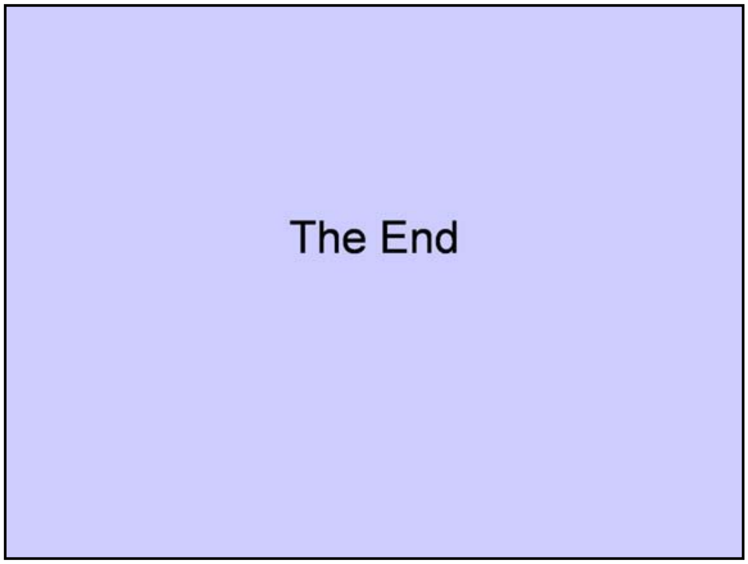
Process Based Approach

- Advantages
  - Potential Extrapolation (time and species)
  - Less data dependent (processes)
  - Potentially easier to “calibrate” processes
  - Potential use of remotely sensed data (PAR) and long-term weather data to drive models
- Disadvantages
  - Less focus on management (improving)
  - Complexity (improving)
  - Most work/understanding at stand level (changing)
  - Poorly understood process / linkages
    - Carbon allocation process (genetic implications)
    - Nutrient availability/uptake and tree growth
    - Mortality and regeneration



Conclusions

- Forest stand dynamics is complex
- Empirical Models
  - Accuracy and focus on management
  - Potential problems with productivity and extrapolation
- Process Models
  - Potential for extrapolation/calibration
  - Greater focus needed on management applications
- Models for management decisions
  - Accurately predict stand and tree development
  - Supply users with required information
- Future emphasis will be at the tree level and on Hybrid Models



The End

Incorporating genetics into growth models: a geneticist's perspective

G. Sam Foster
Mississippi State University

Tree improvement is a discipline within the general field of silviculture. From the beginning of the discipline, the three major issues were: 1) demonstrating whether traits of forest trees were inherited, 2) determining which traits to select, and 3) understanding how genetic improvement will manifest itself in forest stands. A great deal of research and development was conducted on inheritance patterns and testing and selection in the first 30 years (1950s to 1980s), while the last 20 years have seen more of an emphasis on stand level development and realized genetic gain. Unfortunately, due to the large size, complexity, cost, and long time period, relatively few studies have been established exclusively to examine the role of genetics on stand establishment and growth. Data from such studies will be needed in order to develop predictive models.

Measurement of genetic gain ultimately will be in stand productivity (i.e., volume/ha); however, the logistics of progeny test size and time period to reach rotation has caused tree breeders to seek efficiencies in both logistics and generation time. The result has been development of efficient progeny test design with small plots (1-10 trees) per variety [provenance (seed source), family, or clone] in a few blocks (5-8 per site) planted at a few sites (2-6 sites). Theoretical and empirical experiments have shown that the most efficient selection age is 5-12 years for most species and the most common traits for selection are mean individual tree height, dbh, or volume. Some tree breeders are beginning to select for dominant-codominant height or site index. Historically, tree breeders have relied on correlated response in stand volume per ha at rotation length based on direct selection for a genetically related trait such as mean height, dbh, or volume. This is a sound approach based on theoretical as well as empirical considerations. However, more and more concern is being voiced regarding the relationship between progeny test plot configuration (e.g., single-tree, row, multiple-tree non-contiguous, or block) and deployment of improved varieties. Common practice worldwide in plantation establishment is to either plant a mixture of varieties, a mosaic of pure varieties at a site, or a single variety at a site. Despite a wealth of information on intergenotypic competition in the agronomic crop literature and a few theoretical studies in forest genetics, there are only a handful of empirical studies on the effect of deployment on realized genetic gain. Much work needs to be done in this area.

Several, mostly retrospective, studies have been conducted over the past 25 years to examine the feasibility of modeling the genetic component of growth functions of forest trees. Researchers have examined genetic variation, generally with provenances or open-pollinated families, in most of the generally accepted functions of either stand level or individual tree growth and yield models. Genetic variation has been verified for functions such as: height-diameter, bole taper, diameter frequency distributions, height frequency distributions, height/age or site index, stand density versus average size of individual trees, stand density versus plot mean traits, basal area, and biomass traits. Only two studies were conducted to examine differences for individual tree volume equations and no difference was found between genetically improved versus unimproved stands. Few, if any, studies have been conducted to test for genetic differences in the survival function. Although, for single ages, survival has been shown to have a genetic basis especially on harsh sites. In at least 12 studies, these various functions, modified for genetics, have been combined in a growth and yield model, either stand level or individual tree level. Each approach has its advantages and disadvantages. For example, stand level models are generally easier to develop and certainly serve as a first approximation especially when deployment is with a single variety per stand. Individual tree models are more complex and demand additional traits such as crown dimensions and/or distances between trees (distance dependent model); but these models may work better for mixed variety stands and will lead to a more mechanistic understanding of the influence of genetics on tree and stand development.

The vast majority of the studies that have been published regarding forest genetics and growth and yield modeling were retrospective studies using provenance or progeny tests that just happened to have large plots (e.g., 49 tree plots). Few studies have been published which were designed to answer specific questions on stand growth and yield. In their paper, Nance et al. (1987) formulated ten hypotheses that were critical to understanding genetic effects on stand growth and yield. To date, several studies have been published that address many of these hypotheses. Few, if any, research results have been published to date on four of the ten hypotheses; and a single large study is proposed in the current talk that would produce data useful in testing these four remaining hypotheses. A review of the published papers in the area shows a common theme in that relatively few (e.g., 2-4) significantly different variations on model parameters result in each paper. For example, even though 11 families are tested for height/age function, there may only be two or three significantly different curves that result. A challenge to growth modelers is to develop a process which allows discrimination among varieties as early as possible as to the basic model form that they follow.

New experiments should be modified to incorporate genetics. At least a few varieties should be included in growth and yield studies, especially varieties with known growth traits (fast versus slow growth; wide versus narrow crowns; long versus short live crowns, etc.). Retrospective analyses should be conducted on existing studies to determine why (physical or physiological attribute) varieties behaved differently. Was the cause crown size, root size, water, or nutrient use efficiency, etc.? A significant effort should be initiated by university faculty or USDA Forest Service scientists with forest industry to establish plots in pure variety stands in operational plantations and use the analyses to modify regional models.

Growth and yield models must be modified as soon as possible to accommodate genetics. In many regions of the world where plantation forestry is used extensively (SE U.S., Brazil, South Africa, Chile, New Zealand, and Australia), most of the plantations are regenerated with genetically improved stock. The older growth and yield models are no longer useful. Modelers must modify their models to incorporate genetic effects if the managers are to use them. Subroutines could be incorporated that can be used to modify the major functions for genetic differences, e.g., height/age, diameter distributions, and taper functions. It is clearly time to begin delivering to forest managers, financial analysts, and landowners the modeling tools that they need to make informed decisions regarding the use and deployment of genetically improved planting stock.

INCORPORATING GENETICS INTO GROWTH MODELS

A GENETICIST'S
PERSPECTIVE

G. Sam Foster
Mississippi State University

INTRODUCTION

- Exp. Results a “long time coming”
- Reasons:
  - Few designed studies planted in 1980’s
  - Had to “make do” with existing large block studies
  - Reference Warren Nance’s and Melvin Cannell’s work in late 1970’s – early 1980”s

MEASURING GENETIC GAIN

- $G=sh^2$
  - G is genetic gain
  - s is selection differential
  - h^2 is heritability
  - $s=i(V_P{}^{1/2})$
    - i=selection intensity
    - $V_P{}^{1/2}$ = phenotypic standard deviation

  Assumes gain for measured trait and normal distribution

MEAURING GENETIC GAIN

- Traits of interest for users (silviculturists, foresters, land owners) are rotation length – vol/ha, bole str., log grades, etc.
- Dilemma is no one wants to wait for 25-50+ years for 1 cycle of genetic improvement

MEASURING GENETIC GAIN

- Breeders can select for 1 trait and calculate genetic gain (Correlated Response) in another trait if the traits are genetically correlated
- $CR_Y = i\ h_X\ h_Y\ r_G\ V_{PY}^{1/2}$
  - where X could be HT age 5 and Y could be vol/ha age 25
  - h_X and h_Y are square root of heritabilities for traits X and Y
  - r_G is genetic correlation between X and Y
  - $V_{PY}^{1/2}$ is phenotypic std. dev. for trait Y

MEASURING GENETIC GAIN

- Beginning to get critical mass of estimates of genetic parameters over a wide range of ages from a few species for: total ht, dbh, stem volume, site index, vol/ha
- Results seem promising with reasonable heritabilities and genetic correlations
- Optimum selection ages seem to be 5-12 yr.

MEASURING GENETIC GAIN

- Loblolly pine:
  - Lambeth and Dill. 2001. For. Genet. 32
- Slash pine:
  - White and Hodge. 1992. Silv. Genet. 41
- Radiata pine:
  - Cotterill and Dean. 1988. Silv. Genet. 37
- Pinus pinaster:
  - Magnussen and Kremer. 1993. Silv. Genet. 42
- Doug-fir:
  - Johnson, Sniezko, and Mandel. 1997. Silv. Genet. 46

MEASURING GENETIC GAIN

- Optimum progeny test design vs deployment of improved varieties
- Many studies have examined progeny test design and efficiency for estimating variety means and variances; recommendation:
  - Either multiple-tree plots in a non-contiguous configuration or single tree plots
  - 5-8 reps per location and at least 3 locations

MEASURING GENETIC GAIN

- Based on a survey of studies, Foster (1989) found that:
  - family ranking was stable across test design
  - genetic variances were strongly influenced by intergenotypic competition; family variance increased from block plots to row plots to non-contiguous plots

MEASURING GENETIC GAIN

- Deployment of improved varieties at a site, operationally, may be:
  - Mixtures of few to many varieties
  - Mosaics of several pure varieties
  - One pure variety
- Relationship between results from progeny test configuration and stand yield based on another configuration has been treated theoretically (Nance 1982, Foster and Knowe 1995) and experimentally (i.e., Carson, Garcia, Hayes 1999, Turner 1997)
- Intergenotypic competition among varieties may result in: overyielding, complementary, or underyielding; little experimental results are available to predict results

MEASURING GENETIC GAIN

- Common practice for tree breeders:
  - Selection based on a variety of traits including:
    - means of indiv. trees for total ht., dbh, basal area, or volume at ages 5 to 12 years
    - site index based on a family plot
    - per area volume based on a family plot

MODIFYING MODELS TO INCORPORATE GENETICS

- Stand level models, traits of interest:
  - Vol. of indiv. trees-function of ht, dbh, stem form
  - Frequency distribution of variables, i.e., dbh or ht
  - Site index: mean ht of dom.-codom. trees at a base age (e.g, 25 or 50)
  - Initial and subsequent stand density per unit area (i.e., trees per ha)
  - Tree survival over age
  - Basal area per unit area (i.e., per ha)
  - Stand density versus average tree size

MODIFYING MODELS TO INCORPORATE GENETICS

- Individual-tree level models
  - Distance dependent
  - Distance independent
- Traits of interest
  - Many of same ones as for stand level
  - Individual tree ht, dbh, crown diameter

MODIFYING MODELS TO INCORPORATE GENETICS

- Biomass models; traits of interest:
  - Bole wood
  - Branch wood
  - Amount of wood in roots
  - Biomass in leaves
  - Biomass per unit area

MODIFYING MODELS TO INCORPORATE GENETICS

- (Refer to Table 1)
- Individual tree volume
  - 2 papers: 1 Pinus taeda and 1 P. elliottii
  - No sign. diff. in tree vol. for improved vs unimproved
- Height-diameter function
  - 3 papers: 2 P. taeda and 1 Populus deltoides
  - For P. taeda prov. and fam., diff. in level of curve but not shape
  - For P. deltoides, site and clonal proportion sign.
  - For both species, level of curve related to either dom. ht or SI

MODIFYING MODELS TO INCORPORATE GENETICS

- Bole taper
  - 2 papers with P. taeda
  - sign. prov. diff. in 1 and no sign. diff. between improved vs unimproved stands in the other
- Diameter frequency distribution
  - 5 papers: 1 Pinus radiata, 2 P. taeda, 1 P. elliottii, and 1 Populus deltoides
  - no diff. in std. dev., skewness, or kurtosis for P. radiata
  - sign. diff. for shape for P. elliottii
  - slight neg. skewing of pure clones and pos. or neg. skewing for clone mixtures for P. deltoides
  - sign. fam. diff for D_{max} but not D_{min} or other parameters for P. taeda

MODIFYING MODELS TO INCORPORATE GENETICS

- Height frequency distribution
  - 1 paper P. radiata and 1 paper P. elliottii
  - No sign. diff. in std. dev., skewness, or kurtosis for P. radiata;
  - no sign. fam. diff. in any of 3 parameters for P. elliottii

MODIFYING MODELS TO INCORPORATE GENETICS

- Site index; ht/age
  - 14 papers: 8 P. taeda, 2 P. radiata, 1 Cunninghamia lanceolata, 1 Populus deltoides, 1 Pinus pinaster, and 1 Larix leptolepis
  - SI: 6 papers (3 prov., 1 fam., and 2 seedlots) had sign. diff. and 1 (prov.) had non-sign. diff.
  - Slope: 1 paper sign. and 1 non-sign. diff. (both prov.)
  - Asymptote: 3 and a part papers (all fam.) had sign. diff. and 2 (prov.) and a part (fam.) papers had non-sign. diff.

MODIFYING MODELS TO INCORPORATE GENETICS

- Site index; ht/age (continued)
  - Shape: 2 and a part (all prov.) papers had sign. diff. and 3 (2 fam. and 1 prov.) and a part (prov.) papers had non-sign. diff.
  - Rate: 3 papers (1 prov., 1 fam., and 1 clone) all had sign. diff.

MODIFYING MODELS TO INCORPORATE GENETICS

- Basal area
  - 5 papers: 1 P. radiata, 1 P. taeda, 2 Populus, 1 Cunninghamia lanceolata
  - Sign. variety (prov., seed lot, or clone) diff. in all papers
- Biomass traits
  - 2 papers: 1 P. taeda and 1 Pseudotsuga menziesii
  - P. taeda: sign. fam. diff. for foliage traits, biomass and LAI
  - P. menziesii: sign. fam. diff. in intercept but not slope for leaf area or leaf, branch, or bark biomass

MODIFYING MODELS TO INCORPORATE GENETICS

- G&Y models for forest stands (Table 2)
  - 12 papers totally
  - 4 papers for P. taeda
  - 3 papers for P. radiata
  - 2 papers for Populus deltoides
  - 1 paper for P. monticola
  - 1 paper for P. ponderosa
  - 1 paper for Chamaecyparis obtuse

MODIFYING MODELS TO INCORPORATE GENETICS

- Advantages and disadvantages of each approach
  - Test 3 par. SI models before using 2 par. models because 3 par. Models more flexible
  - Since deployment of improved varieties is either pure or mixed stands, G&Y or silv. studies should use similar config.; don't use row plot data for this modeling
  - Stand level models are less complex to fit and modify for genetics and work well as 1st approx.
  - Individual tree models may be better for mixed variety stands

MODIFYING MODELS TO INCORPORATE GENETICS

- Advantages and disadvantages (cont.)
  - Multiple site data sets should be used if at all possible
  - Stand level models are more empirical while individual tree models will allow more mechanistic development

DATA NEEDED TO INCORP. GENETICS INTO MODELS

- At a conf. in 1986, Nance et al. (1987) presented several hypotheses for testing re. forest genetics and G&Y (refer to Table 3)
- Research results have been published which addresses several of these
- 1 key study, with diff. species worldwide, needs to be estab./published if already estab.

DATA NEEDED TO INCORP. GENETICS INTO MODELS

- mult. fam.and check plot, block plots, mult. sites (diff. SI), diff. initial densities, mult. estab. dates to assess:
  - ht/age and SI as function of genetic, edaphic, and climatic factors (Hyp. 2.1)
  - mean size (dia., vol., or wt.) as a function of density, age, SI, genetics (Hyp. 3);
  - $V=K(SI)N^{-B(SI)}$ where V=mean tree vol., N=# surv. trees, K(SI) and B(SI) constants dependent on SI of stand (Hyp. 5, 6, 7); also modify equation such that K and B are functions of both SI and genetics

DATA NEEDED TO INCORP. GENETICS INTO MODELS

- In general, some studies are already planted and the PIs need to publish
- In many studies, a few (2-4) patterns emerge (not a diff. pattern for each variety); need to determine as early as possible which pattern a variety will follow

HOW TO MODIFY GROWTH MODELS FOR GENETICS

- Incorporate subroutines that can be used to modify the major traits for genetic differences, e.g, ht/age or SI curves, diameter distributions, taper functions, basal area, etc.

MODIFYING EXPERIMENTS TO ACCOMMODATE GENETICISTS

- Include multiple varieties in G&Y studies; esp. varieties with known growth traits
- Conduct retrospective analyses to determine why (physical or physiological attribute) varieties behaved differently, (cause=LAI, crown or root size or water or nutrient use efficiency?)
- Examine why a few varieties move up in crown class over time

MODIFYING EXPERIMENTS TO ACCOMMODATE GENETICISTS

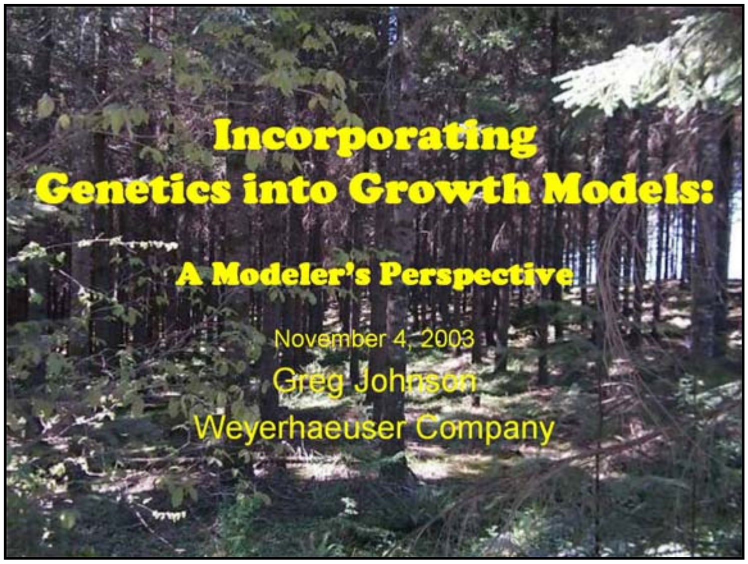
- We will never be able to conduct G&Y studies on all varieties; what are short term studies that can categorize them?
- Work with industry to establish plots in pure variety stands in operational plantations and use the analyses to modify regional models; may need check plots in some stands for baseline

SHOULD GROWTH MODELS BE CHANGED

- Yes! In some regions of the world (SE US, Brazil, S. Africa, Chile, NZ, Aust.), most, if not all, plantations are with pure or mixed improv. varieties. Older G&Y models are no longer useful! Models must be modified to incorporate genetics if managers are to use them.
- New models are critical for financial analyses
- Breeders need to use these improved models to guide tree improvement programs

Incorporating genetics into growth models: A modeler's perspective

Greg Johnson
Weyerhaeuser Company
Federal Way, Washington



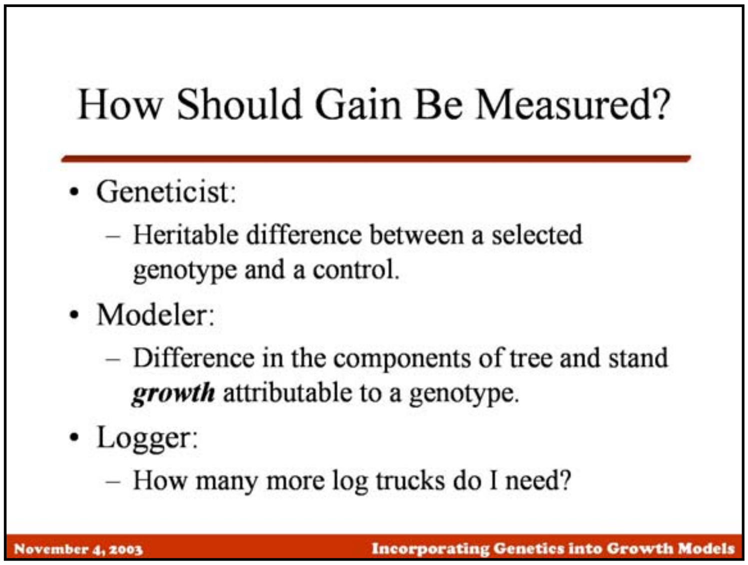
Incorporating Genetics into Growth Models:

A Modeler's Perspective

November 4, 2003

Greg Johnson

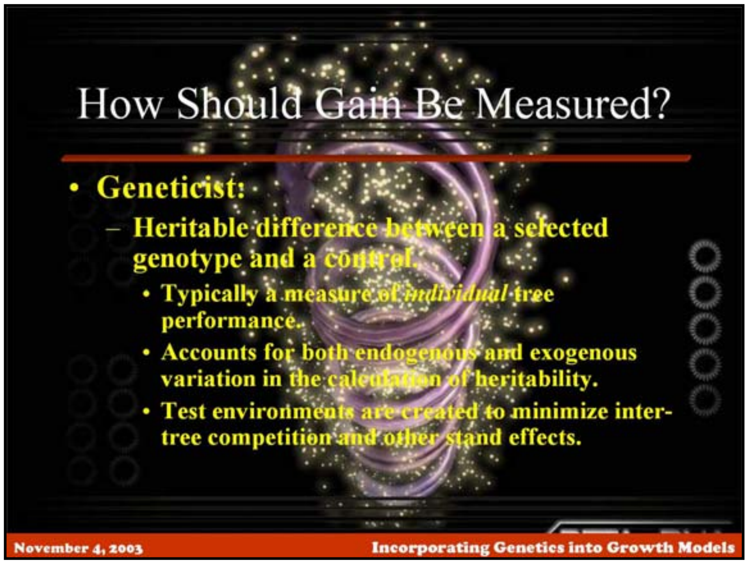
Weyerhaeuser Company



How Should Gain Be Measured?

- Geneticist:
  - Heritable difference between a selected genotype and a control.
- Modeler:
  - Difference in the components of tree and stand ***growth*** attributable to a genotype.
- Logger:
  - How many more log trucks do I need?

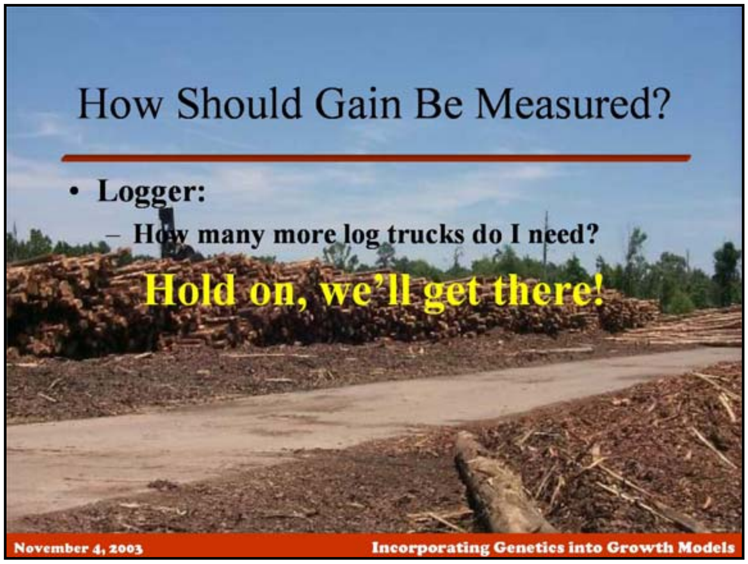
November 4, 2003 Incorporating Genetics into Growth Models



How Should Gain Be Measured?

- **Geneticist:**
  - **Heritable difference between a selected genotype and a control.**
    - **Typically a measure of *individual* tree performance.**
    - **Accounts for both endogenous and exogenous variation in the calculation of heritability.**
    - **Test environments are created to minimize inter-tree competition and other stand effects.**

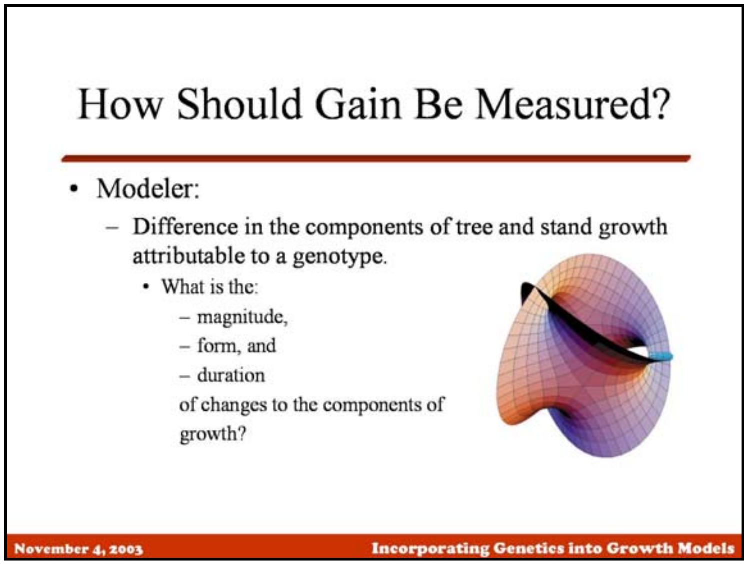
November 4, 2003 Incorporating Genetics into Growth Models



How Should Gain Be Measured?

- **Logger:**
  - **How many more log trucks do I need?**

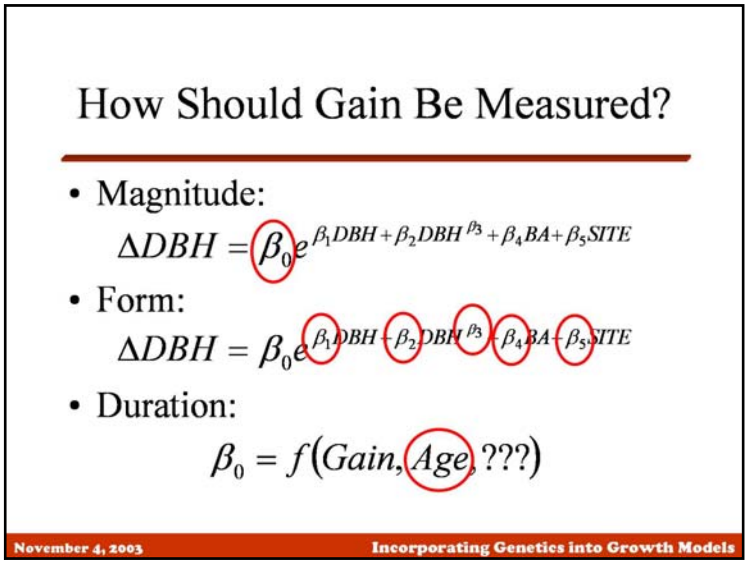
Hold on, we'll get there!



How Should Gain Be Measured?

- Modeler:
  - Difference in the components of tree and stand growth attributable to a genotype.
    - What is the:
      - magnitude,
      - form, and
      - duration

      of changes to the components of growth?



How Should Gain Be Measured?

- Magnitude:

$$\Delta DBH = \beta_0 e^{\beta_1 DBH + \beta_2 DBH^{\beta_3} + \beta_4 BA + \beta_5 SITE}$$

- Form:

$$\Delta DBH = \beta_0 e^{\beta_1 DBH + \beta_2 DBH^{\beta_3} + \beta_4 BA + \beta_5 SITE}$$

- Duration:

$$\beta_0 = f(Gain, Age, ???)$$

Gain Measurement Depends on the Model Architecture

- Model Types:
  - Whole Stand
  - Individual Tree
  - Process

Gain Measurement Depends on the Model Architecture

- Whole Stand
  - Gain in such attributes as:
    - basal area per acre growth
    - dominant height growth
    - stand-level mortality
    - average crown length
    - volume growth

DFSIM

Gain Measurement Depends on the Model Architecture

- Individual Tree
  - Gain in such attributes as:
    - diameter growth
    - height growth
    - crown length (and width)
    - individual tree mortality
    - stem taper
    - branch size

FVS
FPS
SPS
ORGANON
CRYPTOS
CACTOS

Gain Measurement Depends on the Model Architecture

- Process
  - Gain in such attributes as:
    - photosynthetic efficiency
    - water use efficiency
    - carbon allocation strategy
    - crown architecture
    - rooting strategy

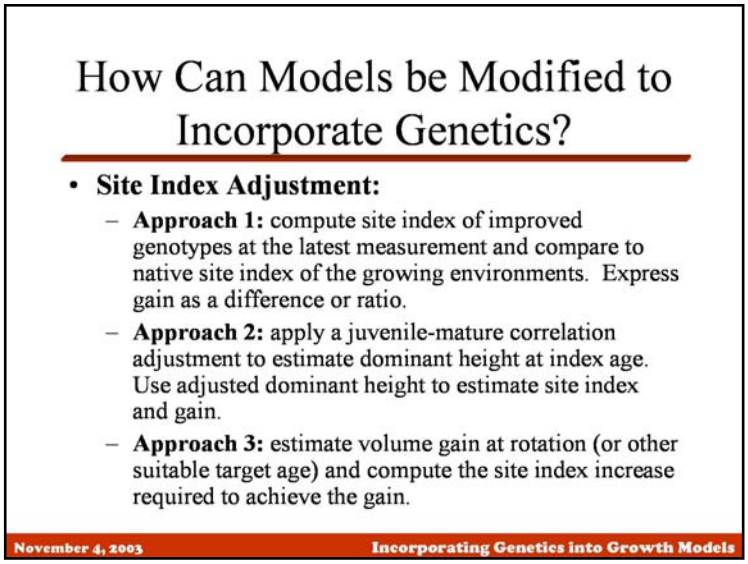
3-PG
ZELIG
FORCYTE

How Can Models be Modified to Incorporate Genetics?

- Simple answer:
  - Estimate the change/gain in each growth component of the subject model.
- Complex answer:
  - We do not have the data to make all those estimates!

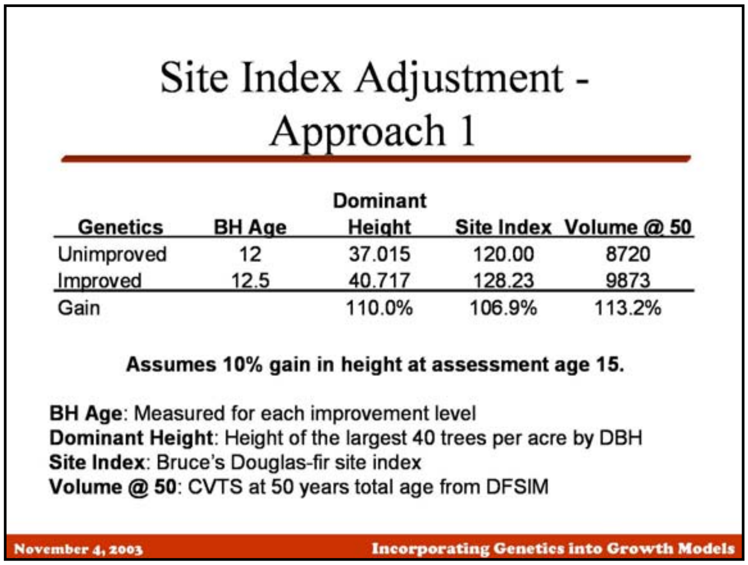
How Can Models be Modified to Incorporate Genetics?

- Given the complexity, which approaches have been used?
  - Site Index Adjustment.
  - Effective Age Computation.
  - Growth Modifiers.



How Can Models be Modified to Incorporate Genetics?

- **Site Index Adjustment:**
  - **Approach 1:** compute site index of improved genotypes at the latest measurement and compare to native site index of the growing environments. Express gain as a difference or ratio.
  - **Approach 2:** apply a juvenile-mature correlation adjustment to estimate dominant height at index age. Use adjusted dominant height to estimate site index and gain.
  - **Approach 3:** estimate volume gain at rotation (or other suitable target age) and compute the site index increase required to achieve the gain.

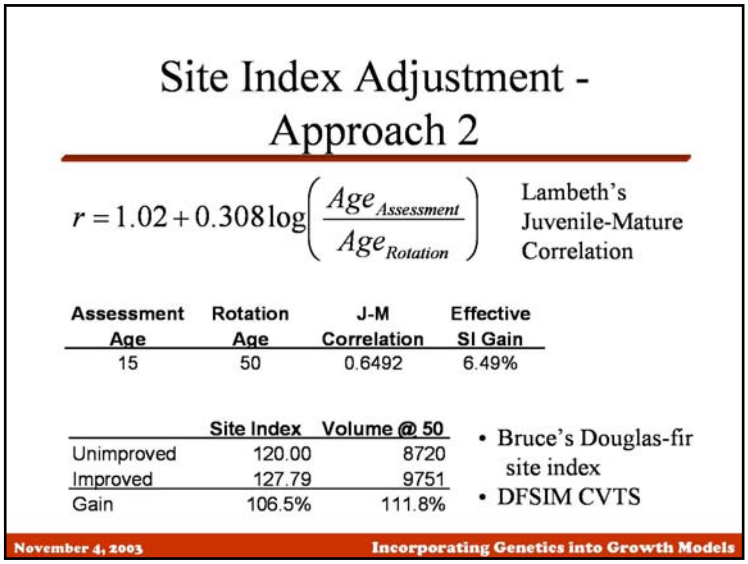


Site Index Adjustment - Approach 1

Genetics	BH Age	Dominant Height	Site Index	Volume @ 50
Unimproved	12	37.015	120.00	8720
Improved	12.5	40.717	128.23	9873
Gain		110.0%	106.9%	113.2%

Assumes 10% gain in height at assessment age 15.

BH Age: Measured for each improvement level
Dominant Height: Height of the largest 40 trees per acre by DBH
Site Index: Bruce's Douglas-fir site index
Volume @ 50: CVTS at 50 years total age from DFSIM



Site Index Adjustment - Approach 2

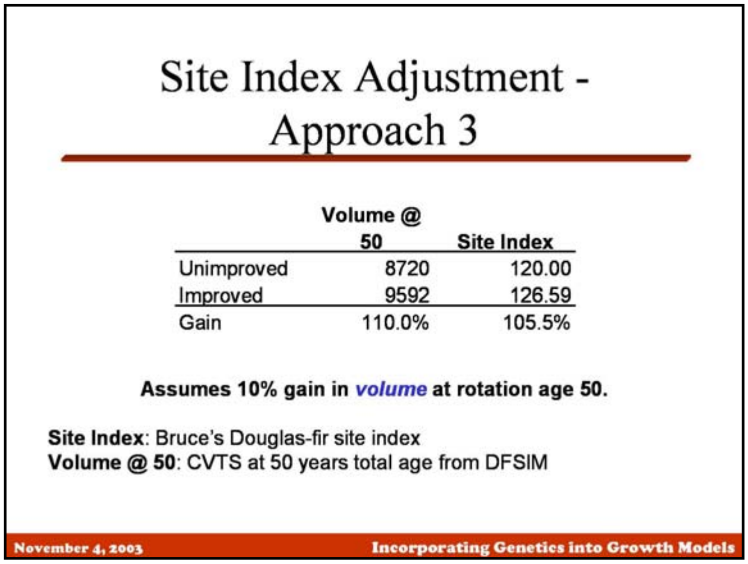
$$r = 1.02 + 0.308\log\left(\frac{Age_{Assessment}}{Age_{Rotation}}\right)$$

Lambeth's Juvenile-Mature Correlation

Assessment Age	Rotation Age	J-M Correlation	Effective SI Gain
15	50	0.6492	6.49%

	Site Index	Volume @ 50
Unimproved	120.00	8720
Improved	127.79	9751
Gain	106.5%	111.8%

- Bruce's Douglas-fir site index
- DFSIM CVTS

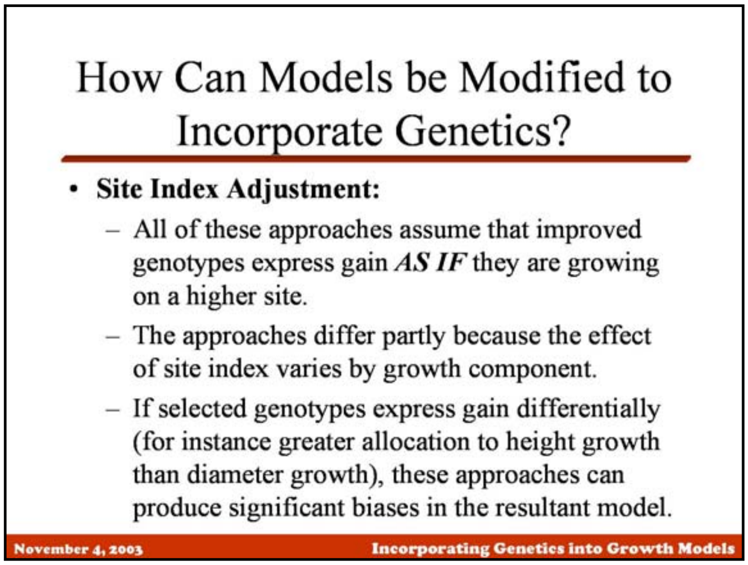


Site Index Adjustment - Approach 3

	Volume @ 50	Site Index
Unimproved	8720	120.00
Improved	9592	126.59
Gain	110.0%	105.5%

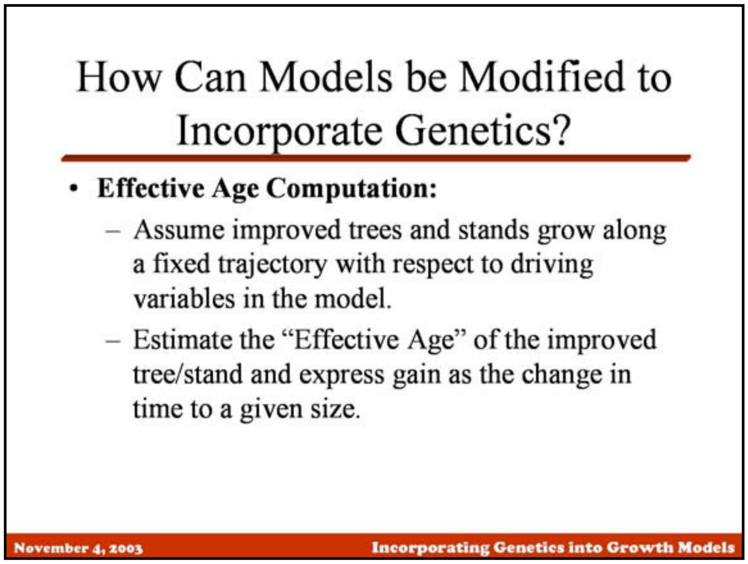
Assumes 10% gain in *volume* at rotation age 50.

Site Index: Bruce's Douglas-fir site index
Volume @ 50: CVTS at 50 years total age from DFSIM



How Can Models be Modified to Incorporate Genetics?

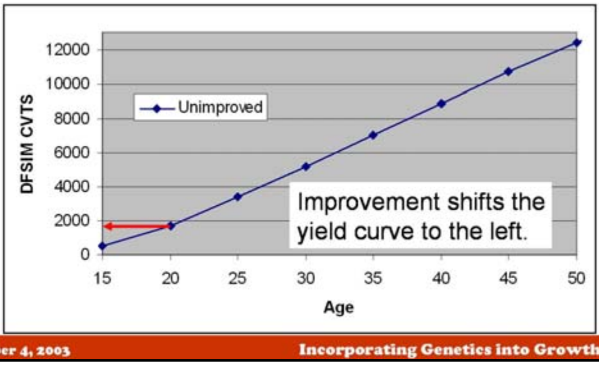
- **Site Index Adjustment:**
  - All of these approaches assume that improved genotypes express gain ***AS IF*** they are growing on a higher site.
  - The approaches differ partly because the effect of site index varies by growth component.
  - If selected genotypes express gain differentially (for instance greater allocation to height growth than diameter growth), these approaches can produce significant biases in the resultant model.



How Can Models be Modified to Incorporate Genetics?

- **Effective Age Computation:**
  - Assume improved trees and stands grow along a fixed trajectory with respect to driving variables in the model.
  - Estimate the "Effective Age" of the improved tree/stand and express gain as the change in time to a given size.

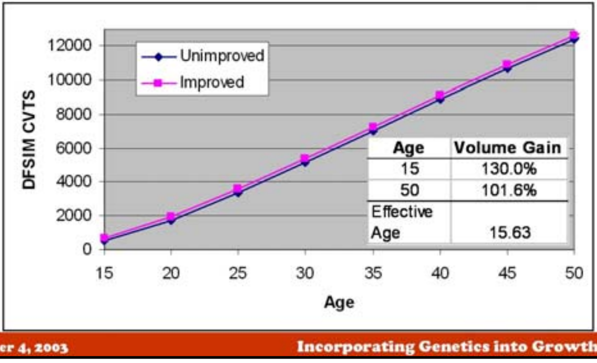
Effective Age Computation



Improvement shifts the yield curve to the left.

Effective Age Computation

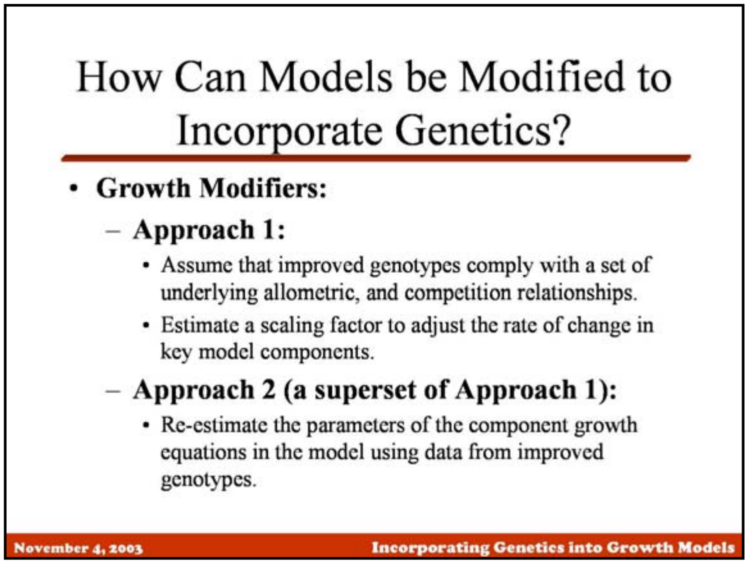
Assume a 30% gain in volume at assessment age 15.



Age	Volume Gain
15	130.0%
50	101.6%
Effective Age	15.63

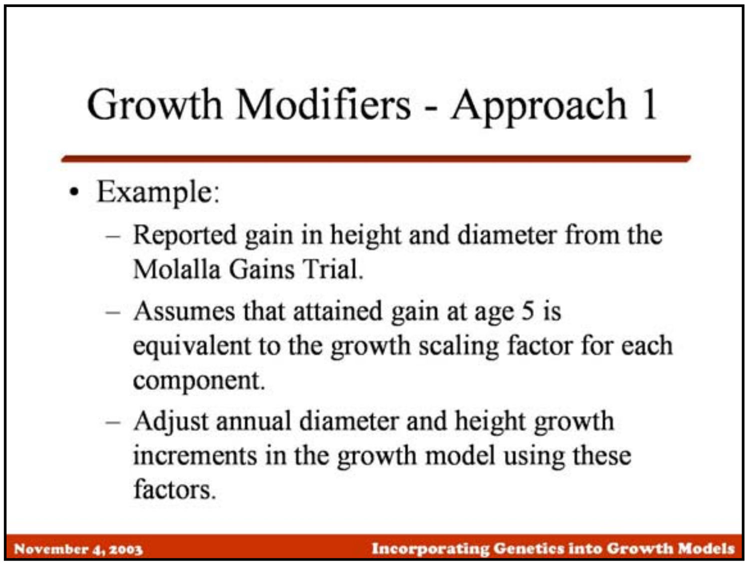
How Can Models be Modified to Incorporate Genetics?

- **Effective Age Computation:**
  - Preserves the unimproved tree and stand dynamics of the model (should have robust and reliable estimates of these properties).
  - Does not account for differential gains in the growth components.



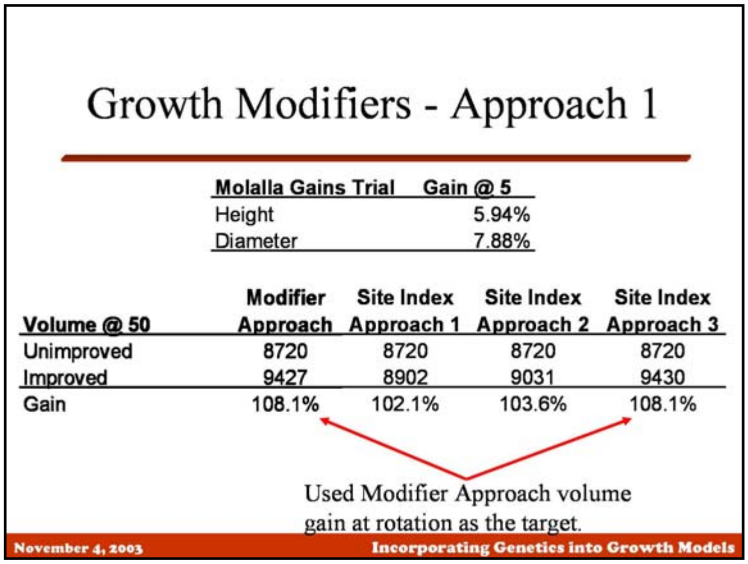
How Can Models be Modified to Incorporate Genetics?

- **Growth Modifiers:**
  - **Approach 1:**
    - Assume that improved genotypes comply with a set of underlying allometric, and competition relationships.
    - Estimate a scaling factor to adjust the rate of change in key model components.
  - **Approach 2 (a superset of Approach 1):**
    - Re-estimate the parameters of the component growth equations in the model using data from improved genotypes.



Growth Modifiers - Approach 1

- Example:
  - Reported gain in height and diameter from the Molalla Gains Trial.
  - Assumes that attained gain at age 5 is equivalent to the growth scaling factor for each component.
  - Adjust annual diameter and height growth increments in the growth model using these factors.



Growth Modifiers - Approach 1

Molalla Gains Trial	Gain @ 5
Height	5.94%
Diameter	7.88%

Volume @ 50	Modifier Approach	Site Index Approach 1	Site Index Approach 2	Site Index Approach 3
Unimproved	8720	8720	8720	8720
Improved	9427	8902	9031	9430
Gain	108.1%	102.1%	103.6%	108.1%

Used Modifier Approach volume gain at rotation as the target.

Growth Modifiers - Approach 1

Quadratic Mean Diameter @ 50	Modifier Approach	Site Index Approach 1	Site Index Approach 2	Site Index Approach 3
Unimproved	12.9	12.9	12.9	12.9
Improved	13.4	12.9	13.0	13.1
Gain	103.8%	100.5%	100.9%	102.1%

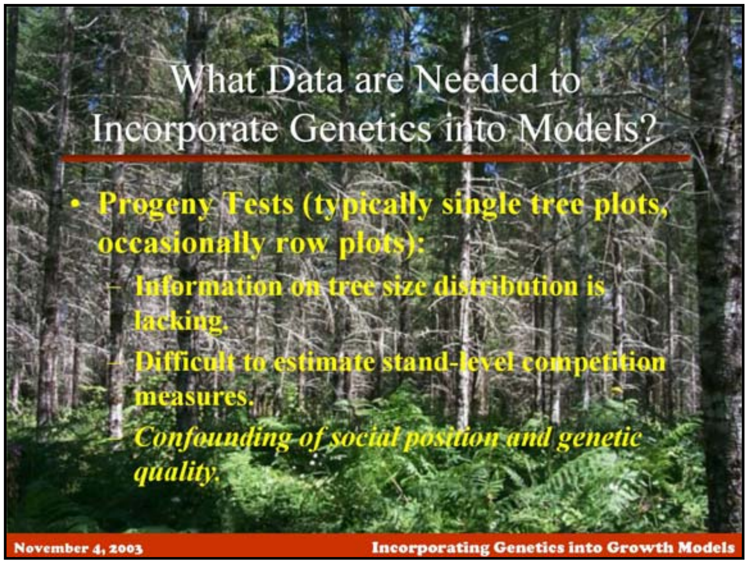
Difference in bole size is important economically, even with the same volume.

How Can Models be Modified to Incorporate Genetics?

- **Growth Modifiers:**
  - Assume that genetic gain effects are multiplicative.
  - Assume that the scaling is invariant over time.
  - Modifiers need to be estimated from ***growth*** data (a failing of the example presented here).
  - The literature has shown remarkably different effects (diameter (basal area) gain only versus height gain only).

What Data are Needed to Incorporate Genetics into Models?

- What modeling information is currently available?
  - Progeny Tests.
  - Family Blocks.
  - Realized Gains Trials.



What Data are Needed to Incorporate Genetics into Models?

- **Progeny Tests (typically single tree plots, occasionally row plots):**
  - **Information on tree size distribution is lacking.**
  - **Difficult to estimate stand-level competition measures.**
  - ***Confounding of social position and genetic quality.***

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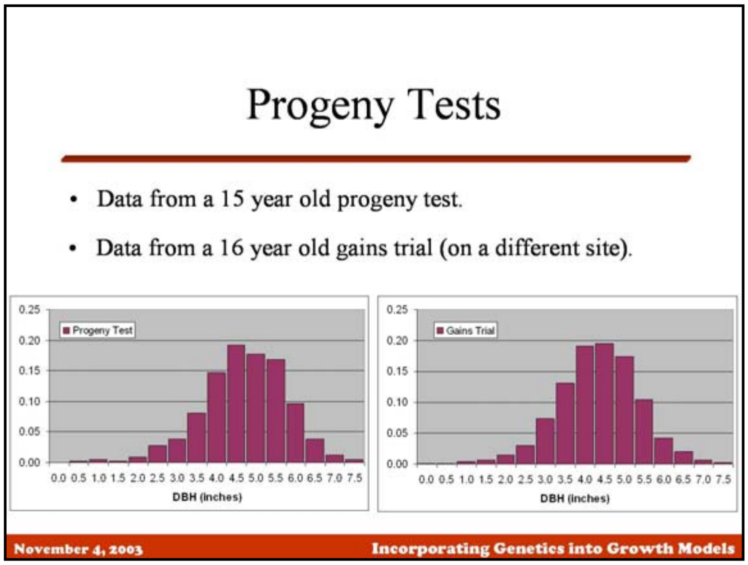

Progeny Tests

- Data from a 15 year old progeny test.
- Data from a 16 year old gains trial (on a different site).

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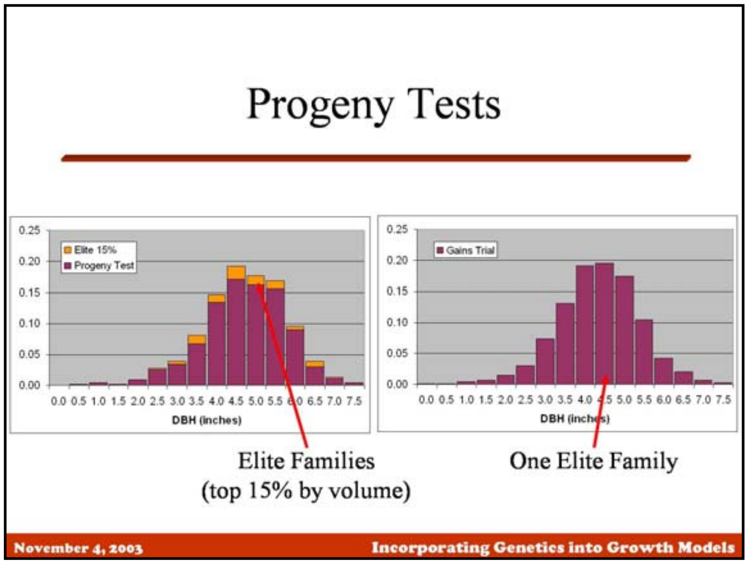


Progeny Tests

Elite Families
(top 15% by volume)

One Elite Family

November 4, 2003 Incorporating Genetics into Growth Models

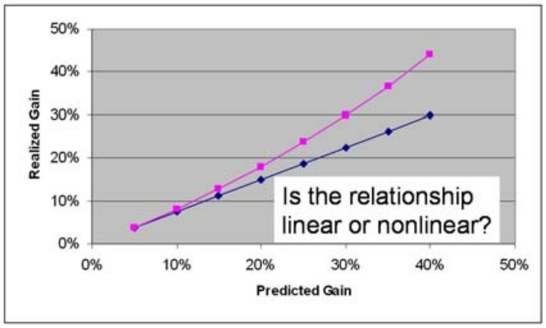
What Data are Needed to Incorporate Genetics into Models?

- **Family Blocks** (fixed area plots planted with a single genotype):
  - Typically small in size (100 tree blocks are common) and few in number.
  - Limited number of environments examined.
  - Usually planted at a fixed spacing.

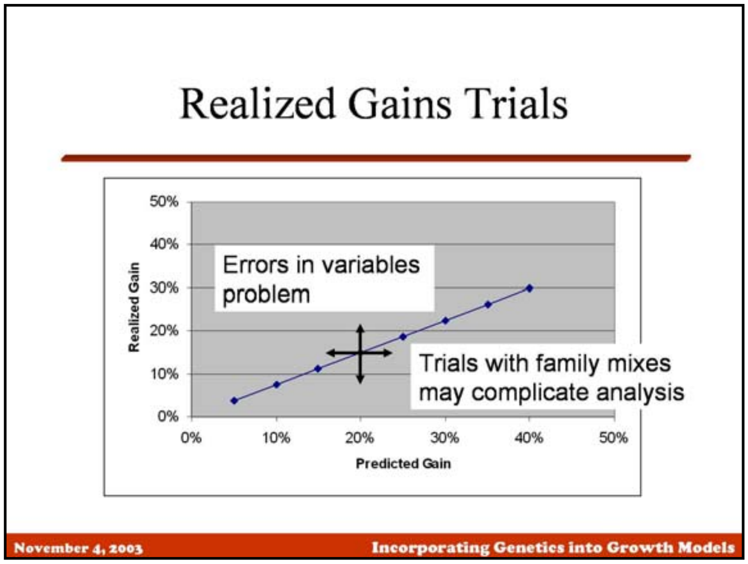
What Data are Needed to Incorporate Genetics into Models?

- **Realized Gains Trials** (large fixed area plots planted with a single genotype or known mix):
  - Can examine a broad array of environments.
  - Can be designed for rotation-length study duration.
  - Can explore effects of initial spacing.
  - Genotypic mixes complicate determining the relationship between the measured gain and the genotypes used.

Realized Gains Trials



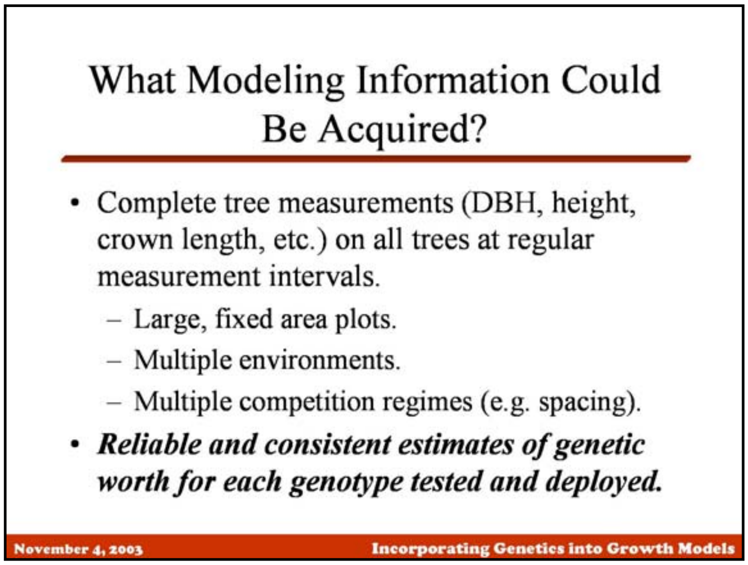
Is the relationship linear or nonlinear?



Realized Gains Trials

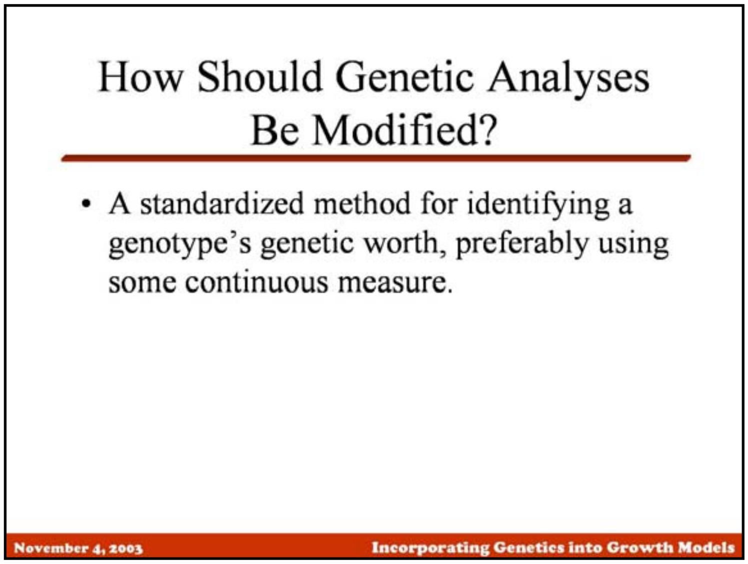
Errors in variables problem

Trials with family mixes may complicate analysis



What Modeling Information Could Be Acquired?

- Complete tree measurements (DBH, height, crown length, etc.) on all trees at regular measurement intervals.
  - Large, fixed area plots.
  - Multiple environments.
  - Multiple competition regimes (e.g. spacing).
- ***Reliable and consistent estimates of genetic worth for each genotype tested and deployed.***



How Should Genetic Analyses Be Modified?

- A standardized method for identifying a genotype’s genetic worth, preferably using some continuous measure.

How Should Genetic Experiments Be Modified?

- Genetic experiments for breeding and selection probably should be left alone -- they are efficient and effective as is for their main purpose.
- *Modeling efforts require separate experiments designed for that purpose.*

Should Breeding Programs Be Changed?

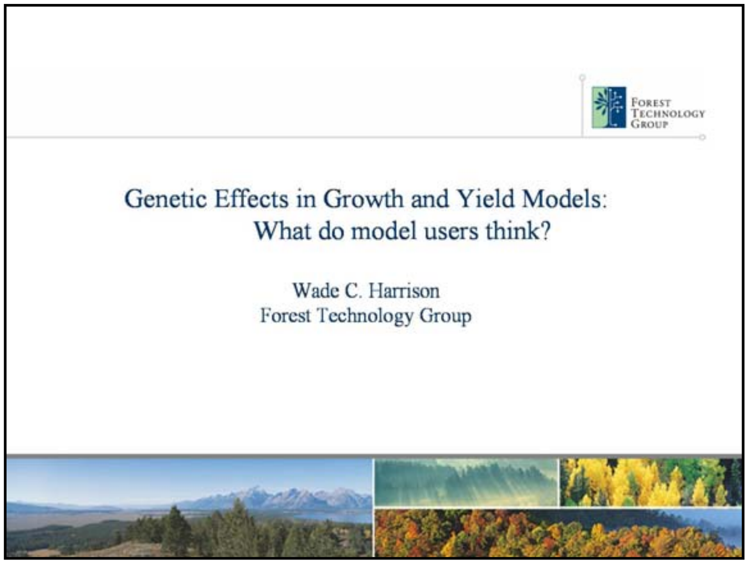
🚫

NO!

Genetic effects in growth and yield models: what do model users think?

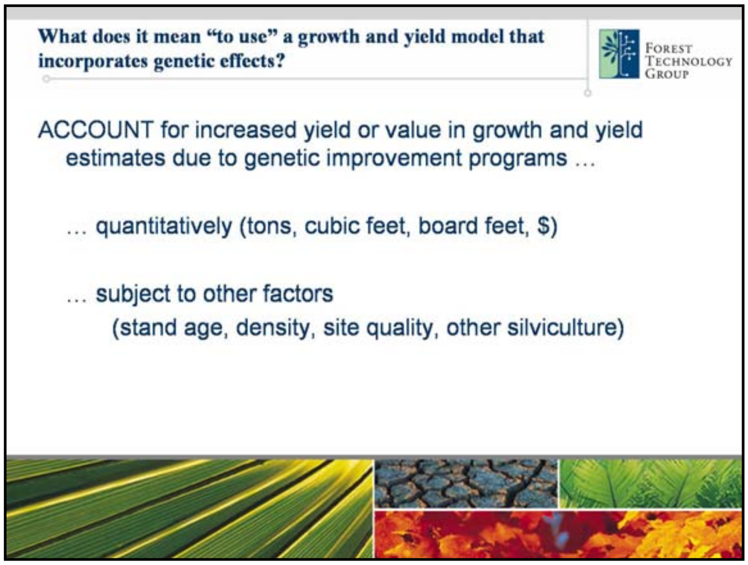
Wade C. Harrison
Forest Technology Group
Summerville, South Carolina

Users of growth and yield models are a diverse group that includes land management foresters, consulting foresters, resource planners, database managers, and researchers. Many of these users encounter model applications that require genetic or tree-improvement response in model output. Users often place considerable importance on such applications, and usually feel their importance will grow in the future. They tend to have a low comfort level in their ability to model genetic effects, and usually do so by making simplistic assumptions about model inputs (e.g. height or site index) or outputs (e.g. volume per acre). They tend to feel that expert opinion on genetic effects is optimistic, and that responses must be considered in the context of other silvicultural treatments.



Genetic Effects in Growth and Yield Models: What do model users think?

Wade C. Harrison
Forest Technology Group



What does it mean "to use" a growth and yield model that incorporates genetic effects?

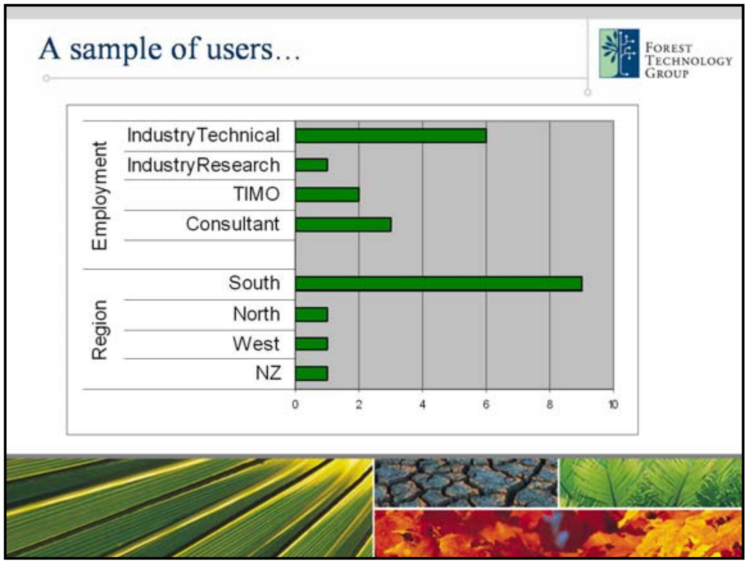
ACCOUNT for increased yield or value in growth and yield estimates due to genetic improvement programs …

… quantitatively (tons, cubic feet, board feet, $)

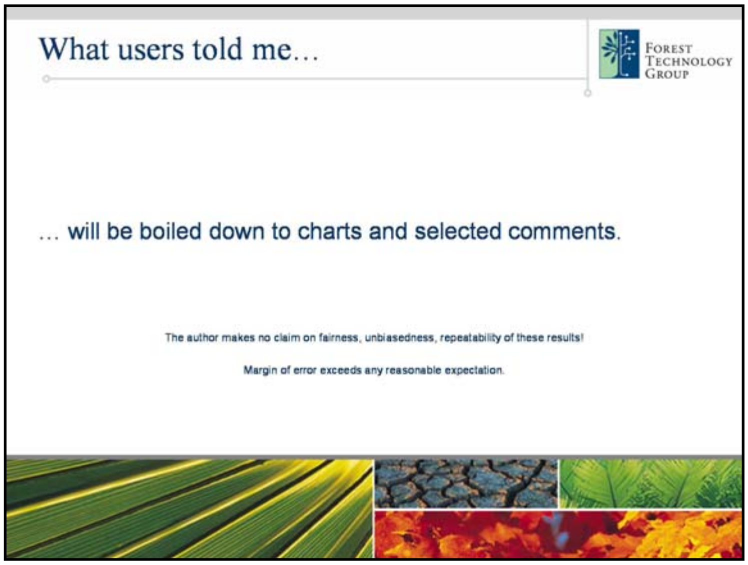
… subject to other factors
(stand age, density, site quality, other silviculture)

Who are the model users?

- Land Management Foresters
- Forestry Consultants
- Forestry IT managers/analysts/developers
- Forest Planners
- Researchers
  - Biometricians
  - Geneticists
  - Silviculturists



A sample of users…

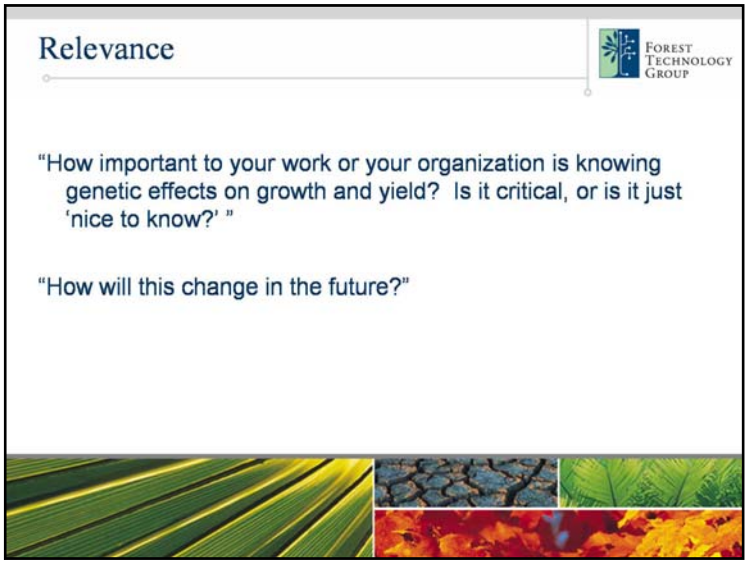


What users told me…

… will be boiled down to charts and selected comments.

The author makes no claim on fairness, unbiasedness, repeatability of these results!

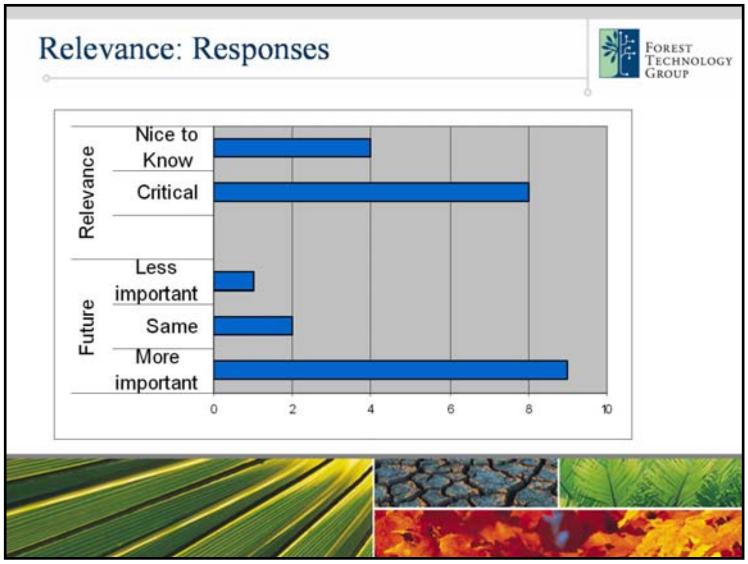
Margin of error exceeds any reasonable expectation.



Relevance

"How important to your work or your organization is knowing genetic effects on growth and yield? Is it critical, or is it just 'nice to know?' "

"How will this change in the future?"



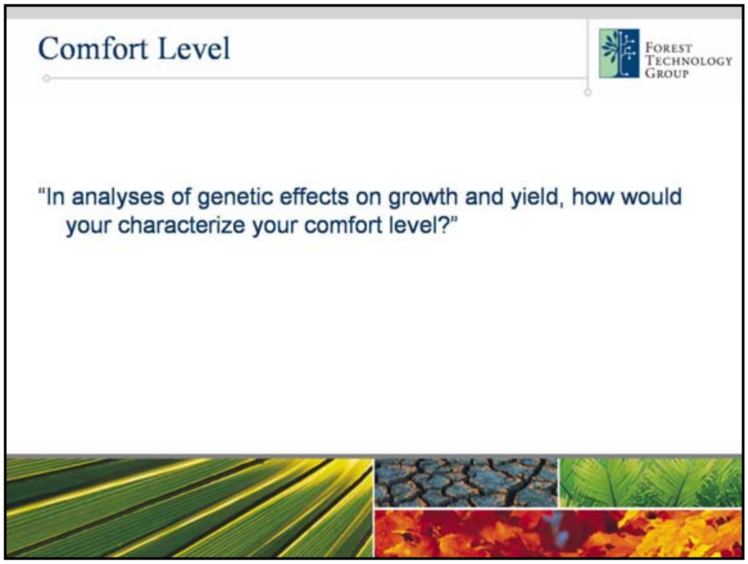
Relevance: Responses

Forest
Technology
Group

Relevance: Comments

Forest
Technology
Group

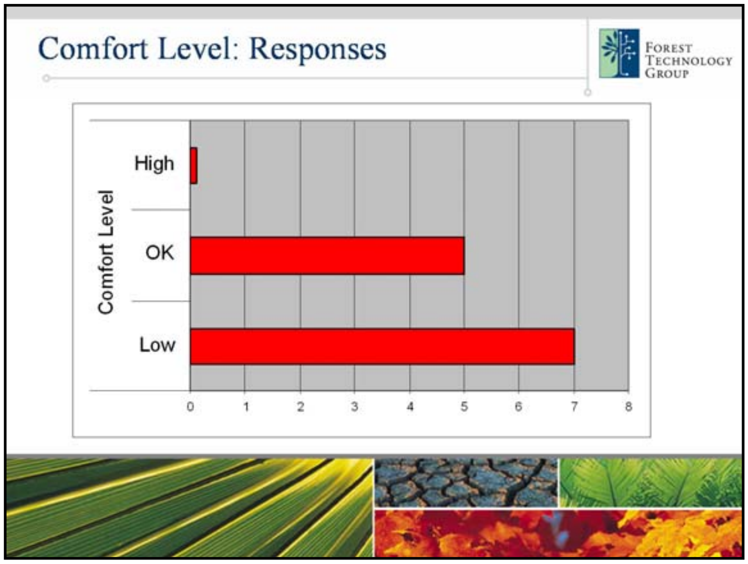
- "Very critical. The gains are so high that incorrect decisions will be made without reasonable estimates."
- "It's probably not that important if you run your models based on actual young inventory data."
- "[A timberland appraiser I talked to felt] that estimates of genetic gain are 'speculative and unproven.' He says that 'such information is proprietary and not in the public domain. Consequently it's not relevant to the appraisal process.'"
- "The decision to spend our investors money on genetics needs solid financial justification… many that think genetics is the last great untapped advantage for US timberland investing."
- "In our region, genetic improvement generally applies to exotic-species plantations, to which there is much public aversion. Consequently this issue will NOT become more important, more likely less so."



Comfort Level

Forest
Technology
Group

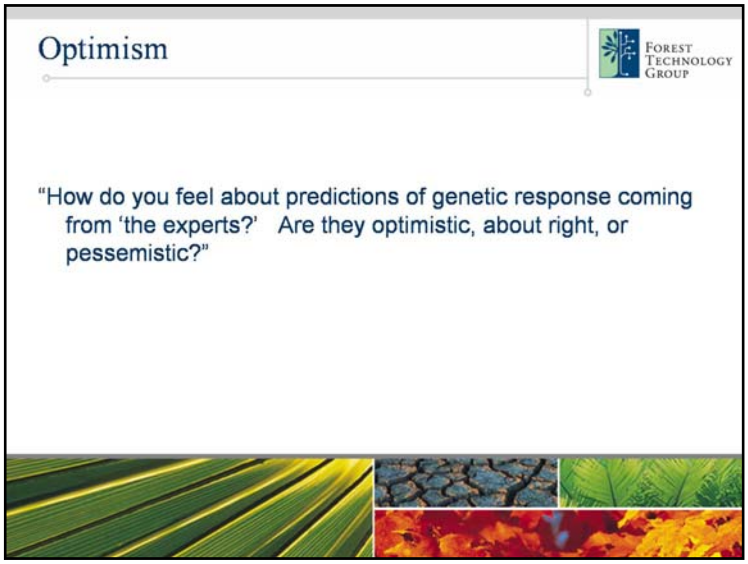
"In analyses of genetic effects on growth and yield, how would your characterize your comfort level?"



Comfort Level: Responses

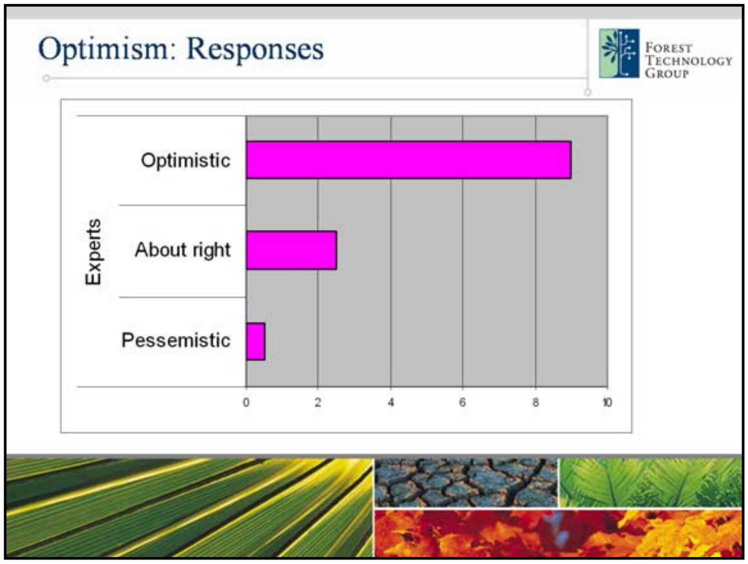
Comfort Level: Comments

- "Not very comfortable… We are changing the diameter distribution curves, reducing cull percent, talking about stands with site index levels for which we'eve not had data to develop and test our growth and yield models. The probability that average stand taper and specific gravity will be changed is good because they will be selected for."
- "Comfortable… as I have measured stands over the past 10 years, their performance seems to match the average gains seen in performance trials (but not single tree progeny tests)."

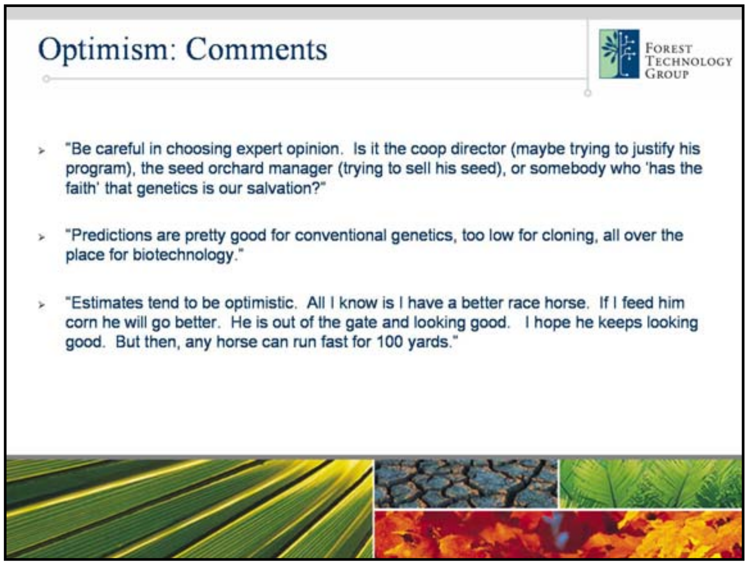


Optimism

"How do you feel about predictions of genetic response coming from 'the experts?' Are they optimistic, about right, or pessemistic?"

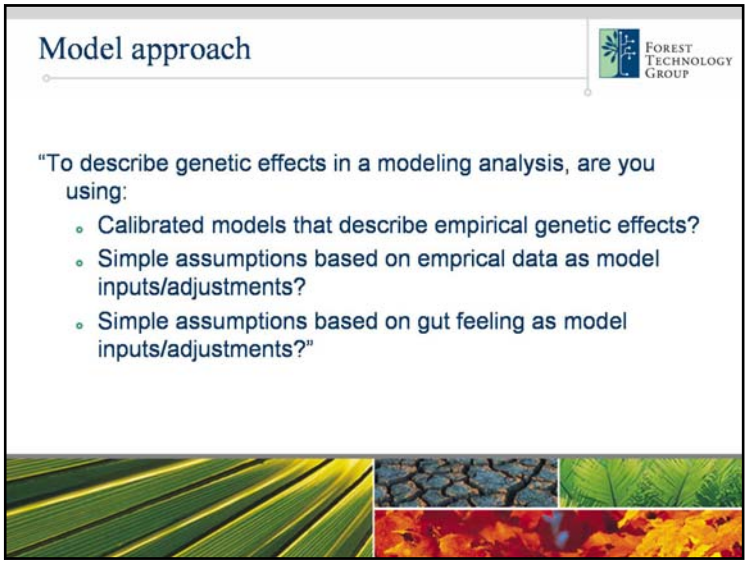


Optimism: Responses



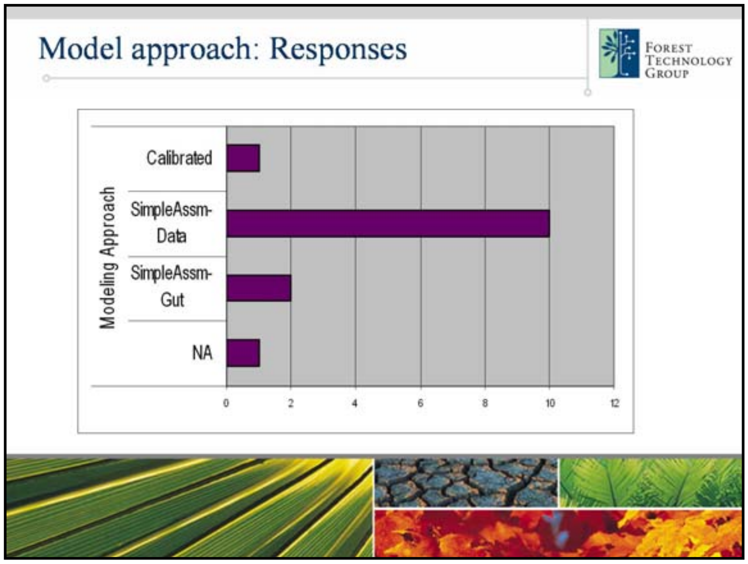
Optimism: Comments

- "Be careful in choosing expert opinion. Is it the coop director (maybe trying to justify his program), the seed orchard manager (trying to sell his seed), or somebody who 'has the faith' that genetics is our salvation?"
- "Predictions are pretty good for conventional genetics, too low for cloning, all over the place for biotechnology."
- "Estimates tend to be optimistic. All I know is I have a better race horse. If I feed him corn he will go better. He is out of the gate and looking good. I hope he keeps looking good. But then, any horse can run fast for 100 yards."



Model approach

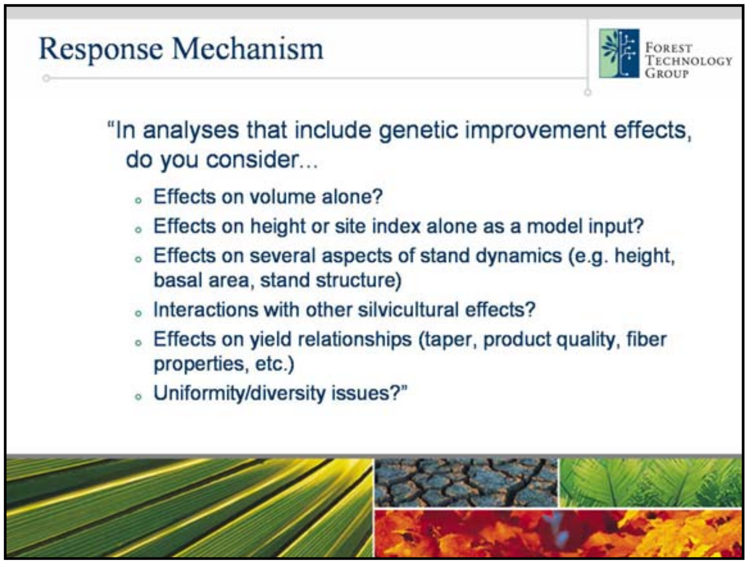
"To describe genetic effects in a modeling analysis, are you using:
- Calibrated models that describe empirical genetic effects?
- Simple assumptions based on emprical data as model inputs/adjustments?
- Simple assumptions based on gut feeling as model inputs/adjustments?"



Model approach: Responses

Model approach: Comments

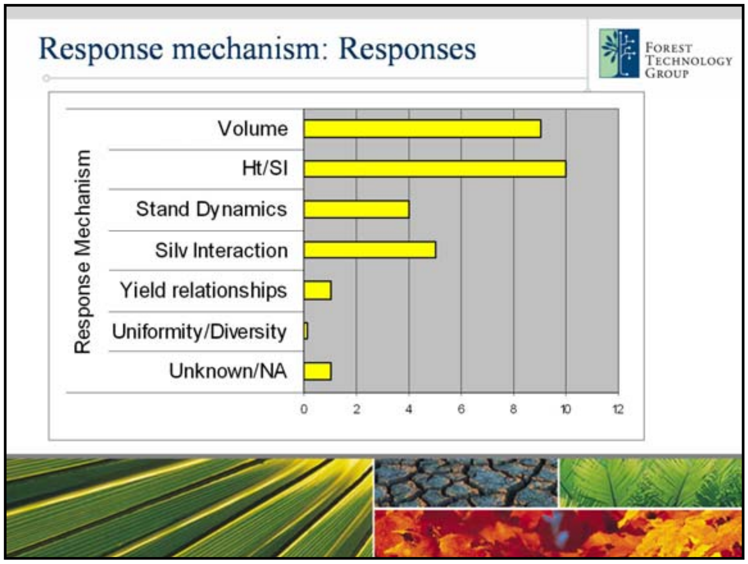
- What I've done has been pretty simple. I assume a base site quality and figure out how much it needs to be incremented in order to arrive at the percentage volume gain advertised.
- "Our growth models have genetic effects built in to a large extent as they are empirical models... We tend to measure our forests several times during a 25 year rotation so I believe we are picking up genetic effects."



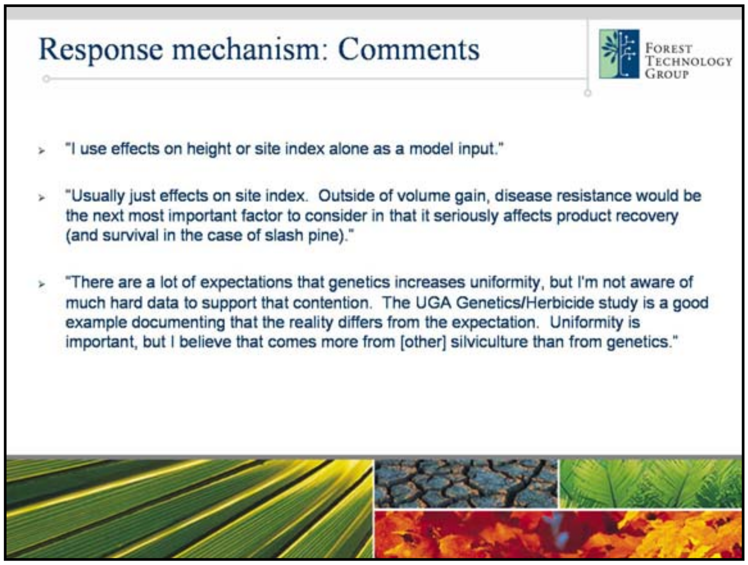
Response Mechanism

"In analyses that include genetic improvement effects, do you consider...

- Effects on volume alone?
- Effects on height or site index alone as a model input?
- Effects on several aspects of stand dynamics (e.g. height, basal area, stand structure)
- Interactions with other silvicultural effects?
- Effects on yield relationships (taper, product quality, fiber properties, etc.)
- Uniformity/diversity issues?"

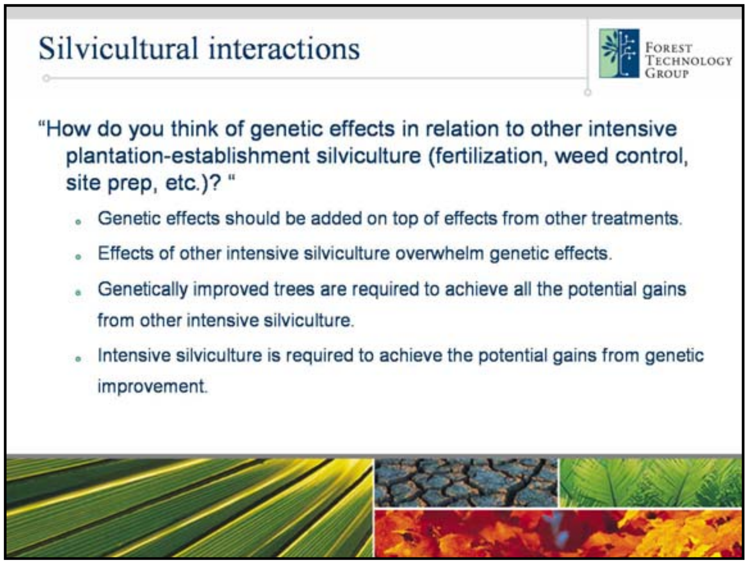


Response mechanism: Responses



Response mechanism: Comments

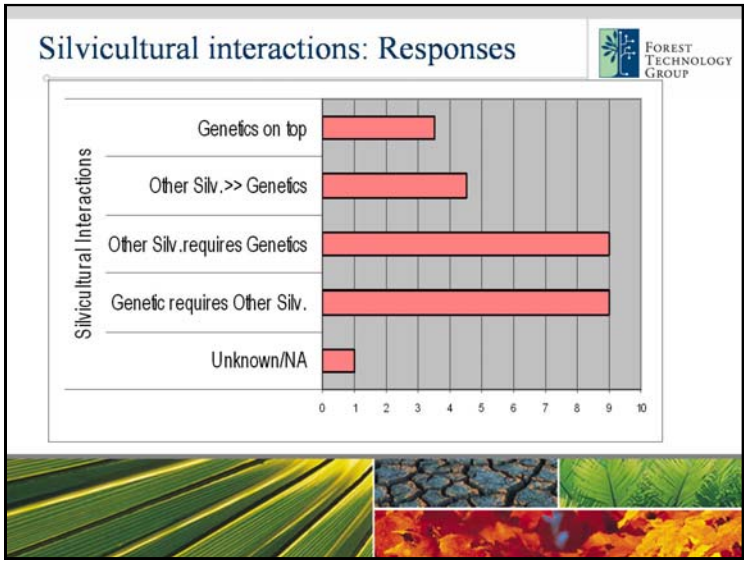
- "I use effects on height or site index alone as a model input."
- "Usually just effects on site index. Outside of volume gain, disease resistance would be the next most important factor to consider in that it seriously affects product recovery (and survival in the case of slash pine)."
- "There are a lot of expectations that genetics increases uniformity, but I'm not aware of much hard data to support that contention. The UGA Genetics/Herbicide study is a good example documenting that the reality differs from the expectation. Uniformity is important, but I believe that comes more from [other] silviculture than from genetics."



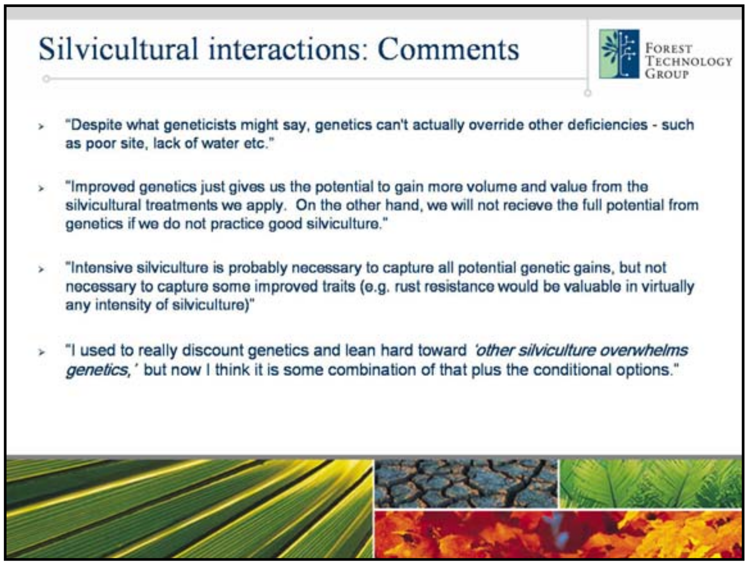
Silvicultural interactions

"How do you think of genetic effects in relation to other intensive plantation-establishment silviculture (fertilization, weed control, site prep, etc.)? "

- Genetic effects should be added on top of effects from other treatments.
- Effects of other intensive silviculture overwhelm genetic effects.
- Genetically improved trees are required to achieve all the potential gains from other intensive silviculture.
- Intensive silviculture is required to achieve the potential gains from genetic improvement.



Silvicultural interactions: Responses

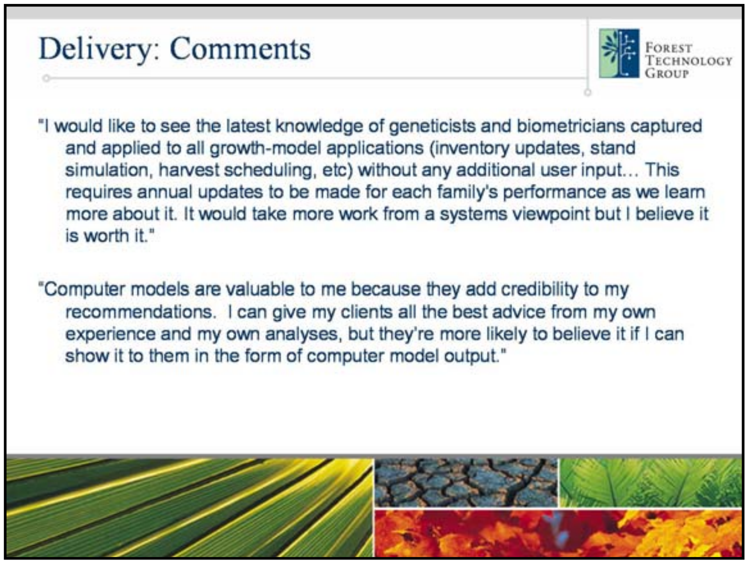


Silvicultural interactions: Comments

- "Despite what geneticists might say, genetics can't actually override other deficiencies - such as poor site, lack of water etc."
- "Improved genetics just gives us the potential to gain more volume and value from the silvicultural treatments we apply. On the other hand, we will not recieve the full potential from genetics if we do not practice good silviculture."
- "Intensive silviculture is probably necessary to capture all potential genetic gains, but not necessary to capture some improved traits (e.g. rust resistance would be valuable in virtually any intensity of silviculture)"
- "I used to really discount genetics and lean hard toward *'other silviculture overwhelms genetics,'* but now I think it is some combination of that plus the conditional options."

Delivery

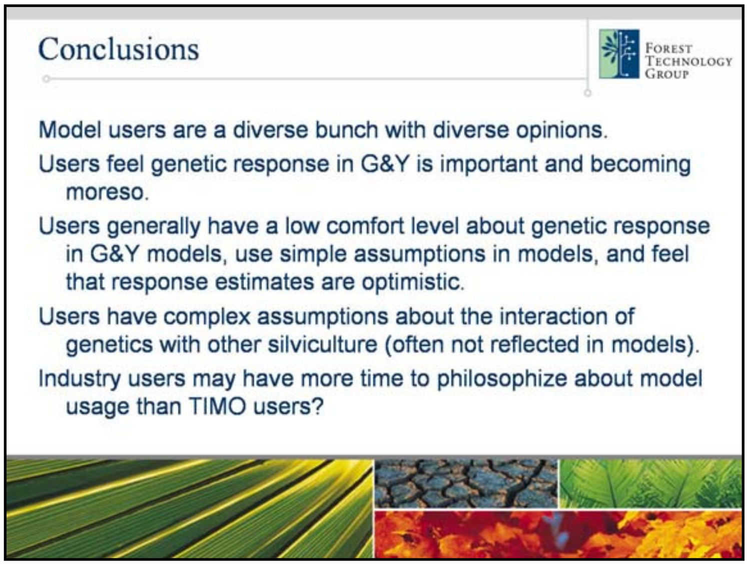
OK, we got models… how do we implement them?



Delivery: Comments

"I would like to see the latest knowledge of geneticists and biometricians captured and applied to all growth-model applications (inventory updates, stand simulation, harvest scheduling, etc) without any additional user input… This requires annual updates to be made for each family's performance as we learn more about it. It would take more work from a systems viewpoint but I believe it is worth it."

"Computer models are valuable to me because they add credibility to my recommendations. I can give my clients all the best advice from my own experience and my own analyses, but they're more likely to believe it if I can show it to them in the form of computer model output."



Conclusions

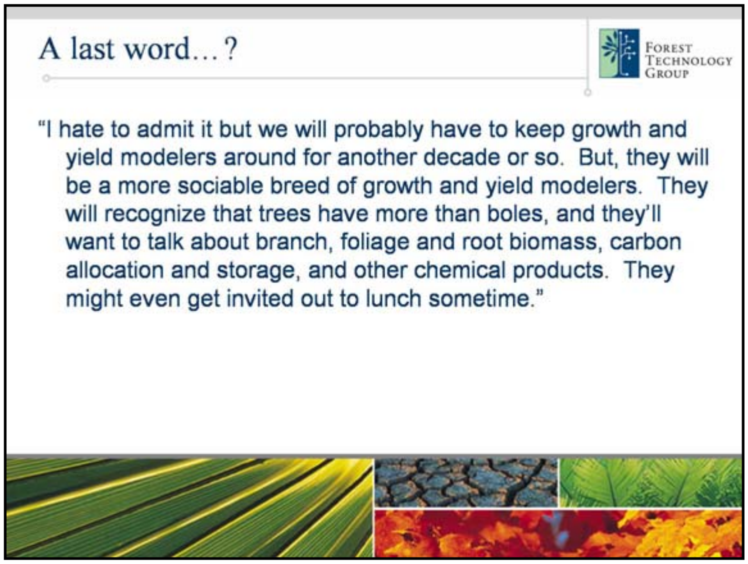
Model users are a diverse bunch with diverse opinions.

Users feel genetic response in G&Y is important and becoming moreso.

Users generally have a low comfort level about genetic response in G&Y models, use simple assumptions in models, and feel that response estimates are optimistic.

Users have complex assumptions about the interaction of genetics with other silviculture (often not reflected in models).

Industry users may have more time to philosophize about model usage than TIMO users?



A last word…?

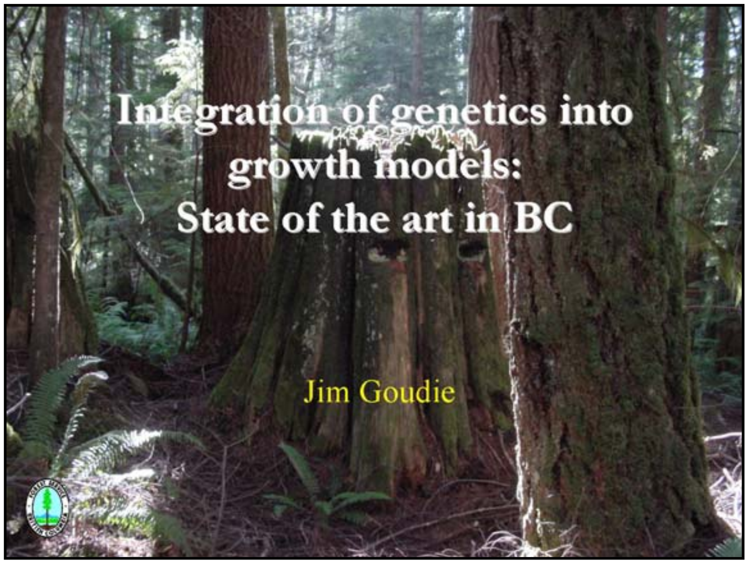
"I hate to admit it but we will probably have to keep growth and yield modelers around for another decade or so. But, they will be a more sociable breed of growth and yield modelers. They will recognize that trees have more than boles, and they'll want to talk about branch, foliage and root biomass, carbon allocation and storage, and other chemical products. They might even get invited out to lunch sometime."

Integration of genetics into growth models: state of the art in B.C.

Jim Goudie
B.C. Ministry of Forests Research Branch
Victoria, B.C.

The tree improvement program has a long, successful history in British Columbia. Extensive provenance and progeny trials typically designed as small clusters or rows of related trees followed the selection of superior phenotypes. Based on these trials, numerous seed orchards are now supplying superior, "A-grade" seedlings for most plantations. Questions arise about the impact these superior trees will have on silvicultural decisions on individual stands and timber supply at the forest level. Lacking any area-based data, at first, yield tables were simply scaled up by a fixed percentage, typically 5%. Later, site index was shifted by the amount shown in early tests but the long-term projections did not account for unknown risks. In the late 1990s, Ministry geneticists and growth and yield specialists incorporated an interim method based on a modification of the well-known research of Lambeth (1980), who predicted the correlation between early and late genetic gain.

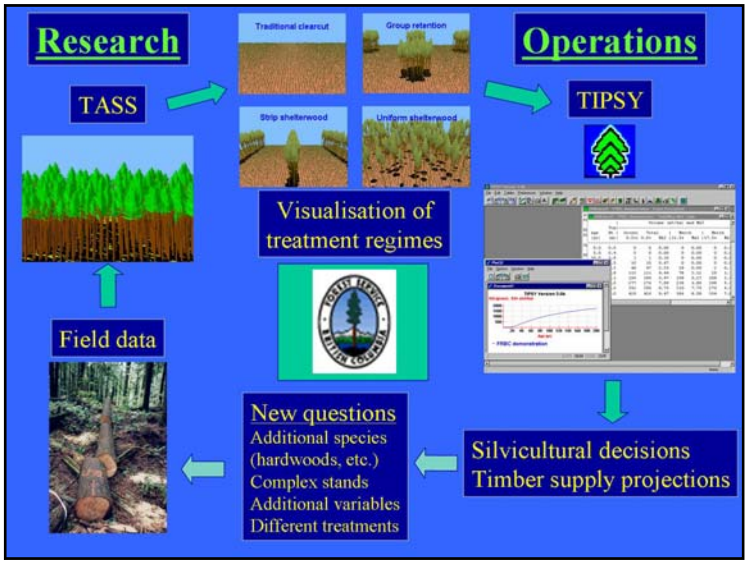
This presentation will (1) review the original research of Lambeth, (2) present the modification now incorporated into the Tree and Stand Simulator (TASS) and its associated software, TIPSY (Table Interpolation Program for Stand Yield), and (3) demonstrate the impacts of tree improvement at the stand and forest level. Also discussed will be a review of realized gain trials established in the last decade in BC that will allow both validation and development of growth models, and ancillary studies that will improve future predictions of the volume and, particularly, value of British Columbia's forests.



Integration of genetics into growth models: State of the art in BC

Jim Goudie

Key elements of the Tree and Stand Simulator (TASS)



Research

TASS

Field data

Visualisation of treatment regimes

Operations

TIPSY

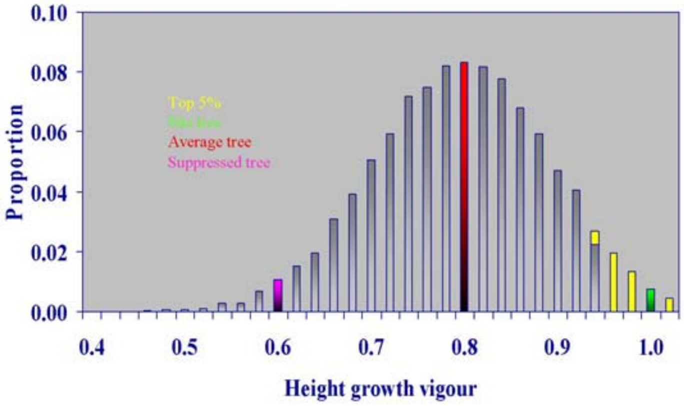
Silvicultural decisions
Timber supply projections

New questions
Additional species (hardwoods, etc.)
Complex stands
Additional variables
Different treatments

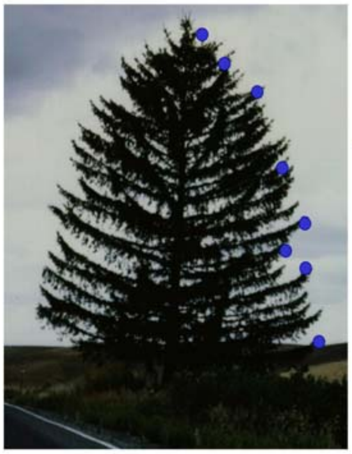
Key TASS components - **operational** version

- Height Growth = f(potential, light)
- Crown morphology
  - Branch location
  - Branch extension
  - Branch angle
  - Branch diameter
  - Foliage (biomass, leaf area)
- Competition
- Mortality
- Ring characteristics (juvenile-mature wood, size, relative density, strength, cell characteristics)
- Genetics

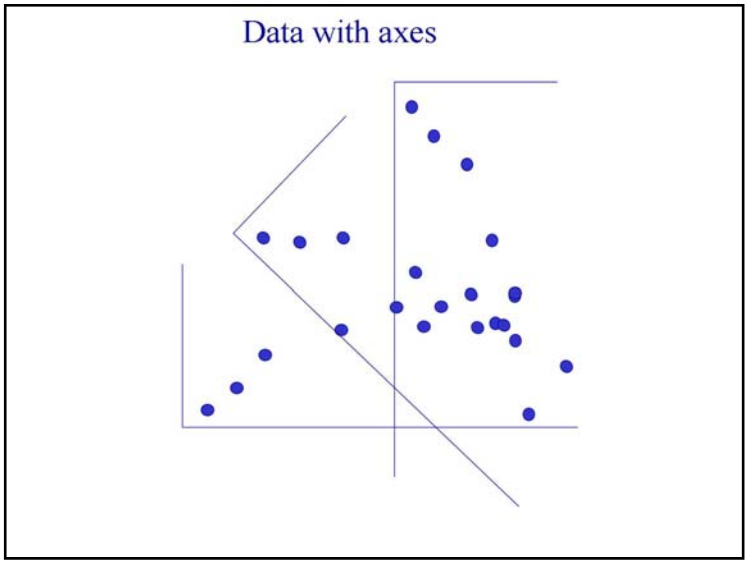
Tree-to-tree variation in relative height growth
Mean=0.8, Std.dev~0.1



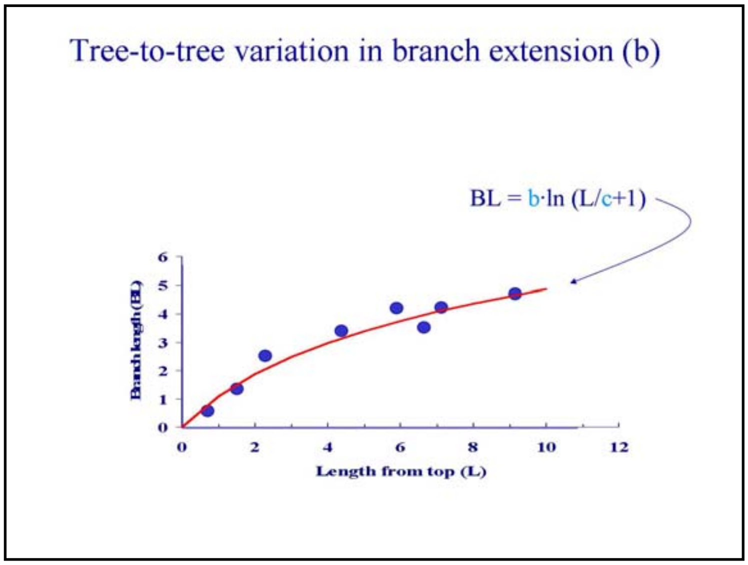
Example tree crown



With branch “data”



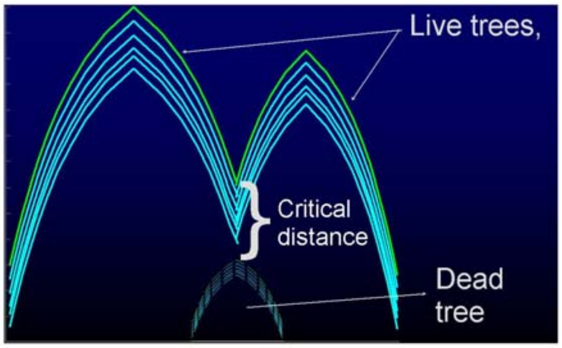
Data with axes

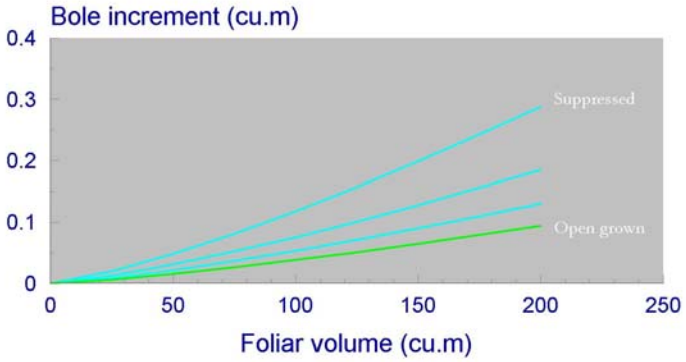


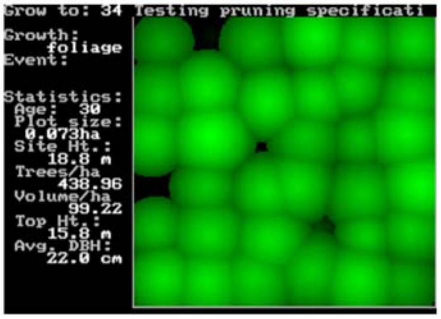
Tree-to-tree variation in branch extension (b)

$BL = b \cdot \ln(L/c+1)$

TASS - Operational version

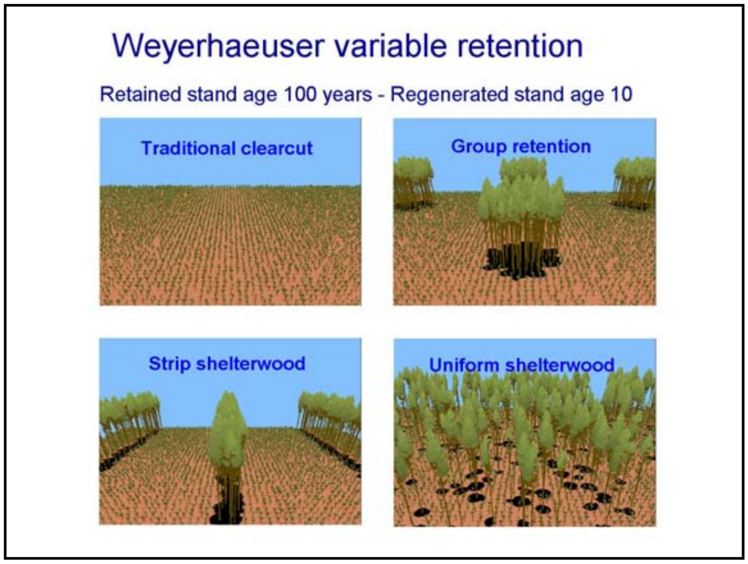






```
Grow to: 34 Testing pruning specificati
Growth:
    foliage
Event:

Statistics:
 Age:  30
 Plot size:
  0.073ha
 Site Ht.:
    18.8 m
 Trees/ha
      438.96
 Volume/ha
       99.22
 Top Ht.:
    15.8 m
 Avg. DBH:
    22.0 cm
```



Weyerhaeuser variable retention

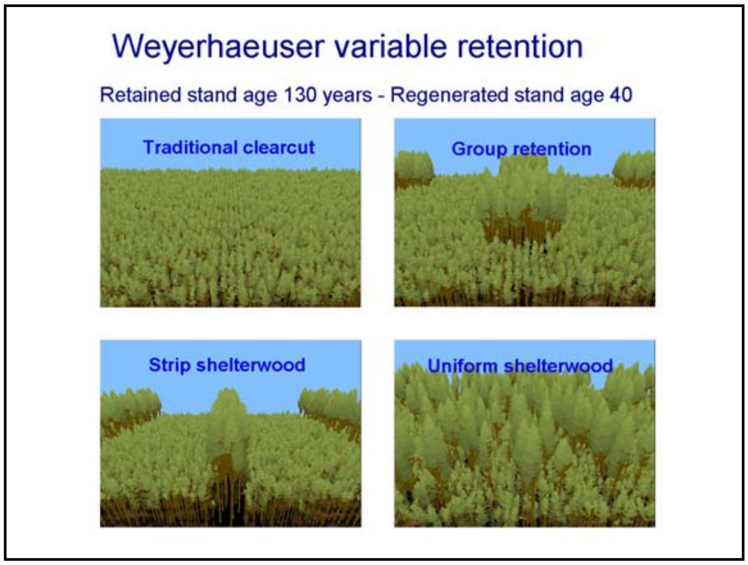
Retained stand age 100 years - Regenerated stand age 10

Traditional clearcut

Group retention

Strip shelterwood

Uniform shelterwood



Weyerhaeuser variable retention

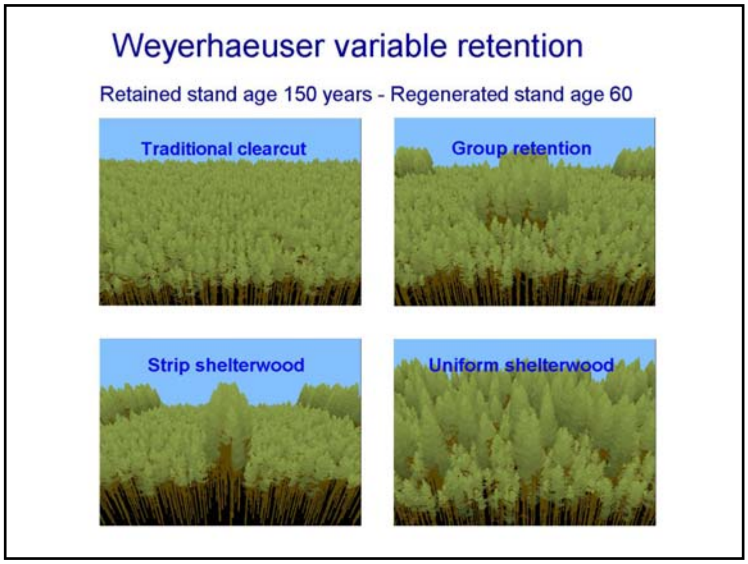
Retained stand age 130 years - Regenerated stand age 40

Traditional clearcut

Group retention

Strip shelterwood

Uniform shelterwood



Weyerhaeuser variable retention

Retained stand age 150 years - Regenerated stand age 60

Traditional clearcut

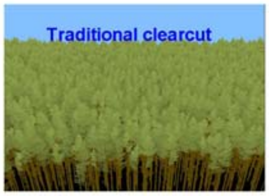
Group retention

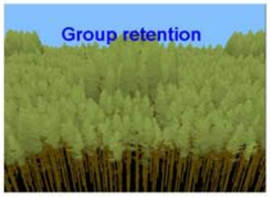
Strip shelterwood

Uniform shelterwood

Weyerhaeuser variable retention

Retained stand age 170 years - Regenerated stand age 80





TIPSY

Table Interpolation Program for Stand Yield

Change the stand specifications

A brief history of estimating the effects of genetics on stand- and forest-level yields in B.C.

- Historical approach Proportional adjustment (OAF) -
  - e.g. 5% volume increase across all ages, other statistics unaffected
- More recently -
  - Iterative change in site index to match expected gains in merchantable volume (12.5+) for a fixed initial density of 1100/ha - other statistics were altered by the change in site index and height growth;
  - TSB had problems with the magnitude of yields beyond 60 to 80 years
- New approach:
  - Allow users to input Genetic Worth (GW) estimates for seed directly into TIPSY
  - Translate that gain to the age of selection
  - Allow gains to decay with age such that the percent increase in volume at the index age agrees with genetic worth

- Genetic worth is:
  - Average breeding value of parents which make up the seed lot using Best Linear Predictor method, or, in mensurational terms,
  - the expected percent gain in merchantable volume (12.5cm+) at an index age of 60 or 80 years and is a function of:
    - species
    - observed percent gain in height growth at selection age
    - selection age
    - "index" age (60 or 80 years)
    - actual rotation age (any age to 300 in TIPSY)
- Calculated using a adaptation of the Lambeth equation

Lambeth (1980) (For.Sci.)

Gain (G_m) for selections at maturity

$$\mathbf{G_m = i_m\, h_m^2\, \sigma_{PM}} \qquad \textbf{[1]}$$

where: i_m =selection intensity

h_m^2 = heritability= $\sigma^2_{GM}/\sigma^2_{PM}$

σ^2_P =phenotypic variance

σ^2_G =additive genetic variance

Correlated Gain (CG_m) for selections well below rotation age

$$\mathbf{CG_m = i_m\, h_j\, h_m\, r_{GM} \sigma_{PM}} \qquad \textbf{[2]}$$

where: r_{GM} = genetic correlation between the juvenile and mature traits

Lambeth (1980) (For.Sci.) cont.

Assuming $\mathbf{r_{Gj,M}} = \mathbf{r_{Pj,M}}$, the calculation of CG_m becomes:

$$\mathbf{CG_m = i_m h_j h_m r_{Pj,M} \sigma_{PM}} \qquad \textbf{[3]}$$

where: $\mathbf{r_{Pj,M}}$ = phenotypic correlation between the juvenile and mature traits

A ratio of **[3]/[1]**, a little algebra and a few assumptions gives an estimate of the **efficiency** of early selection (E), that is:

$$\mathbf{E = (h_j r_{Pj,M} / h_m) \cdot (T_m / T_j)} \qquad \textbf{[4]}$$

where T = number of years to complete a breeding cycle

Assuming $\mathbf{h_j = h_m}$ then

$$\mathbf{E = r_{Pj,M} (T_m / T_j)} \qquad \textbf{[5]}$$

E can be interpreted as the **gain per year**

Lambeth (1980) (For.Sci.) cont.

Lambeth wanted to determine if $\mathbf{r_{Pj,M}}$ is predictable. (recall $\mathbf{r_{Pj,M}}$ is the phenotypic correlation between the juvenile and mature traits).

He collected realized gain data from around the world from the literature and unpublished research studies. Douglas-fir, and seven pines (ponderosa, western white, red, loblolly, slash and longleaf) were represented in the original data but only fir, ponderosa, red and slash pine data were used.

Lambeth (1980) (For.Sci.) cont

He found that it was linearly related to the natural logarithm of a ratio of any two ages involved in the age-age correlation and is also quite consistent between species, that is,

$$\mathbf{r_{Aj,M} = 1.03 + 0.306 \ln(A_m / A_j)} \qquad \textbf{[6]}$$

$$\mathbf{r^2 = 0.93}$$

He then used [6] to estimate efficiency:

$$\mathbf{E = (1.03 + 0.306 \ln(A_m / A_j)) \cdot (T_m / T_j)} \qquad \textbf{[7]}$$

As an example, he showed that selections at age 5 would yield 1.47 times more gain per year than selections at the economic rotation age of 25

Genetic worth math

Chang-yi Xie and Alvin Yanchuk (WJAF 2003) adapted the Lambeth model for use in TASS/TIPSY. Because TASS is height driven, we made the simplifying assumption that height growth response is one-half the volume response (a common approximation). That is, gain in height at index age (GH_i) is GW/2. To obtain gain in height at any yield age (GH_y) multiply by a ratio of two Lambeths. That is,

Genetic worth math

$GH_y=GH_i \cdot (R_i/R_y)$

Where:

$R_i =1.02+0.308 \cdot \ln(a_s/a_i)$ (Lambeth model, e.g. Age-age correlation between selection age and index age)

$R_y =1.02+0.308 \cdot \ln(a_s/a_y)$ (Age-age correlation between selection and yield age)

and:

a_s = selection age
a_i = index age (60 or 80 years)
a_y = age of yield estimate

Genetic worth example

Let:

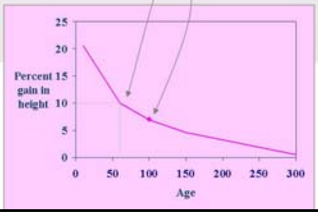
a_s = 12 years (selection age)
a_i = 60 years (index rotation age)
a_y = 100 years (harvest age)
GW= 20% (genetic worth)
GH_i= 20/2=10

Then

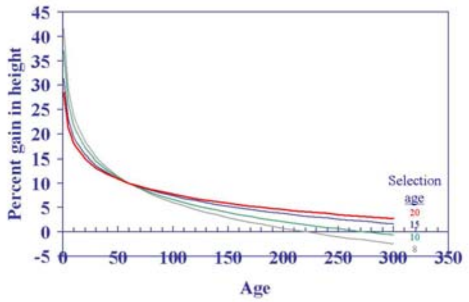
$R_i =1.02+0.308 \cdot \ln(12/60) = 0.524$
$R_y =1.02+0.308 \cdot \ln(12/100) = 0.367$
$GH_{100} = GH_i \cdot (R_i/R_y)$
$= 10 \cdot (0.367/0.524)$
$= 10 \cdot (0.700) = 7.00\%$

Additionally,

GH_{10}=20%
GH_{60}= 10%
GH_{100}= 7%
GH_{150}= 8%
GH_{300}= 3%



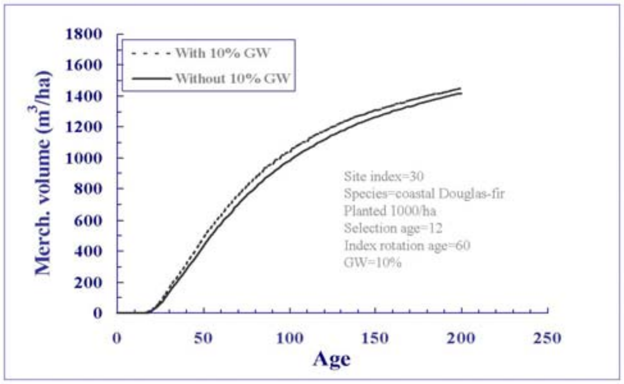
Effects of selection age on Gain in ***height growth*** for GW=20%

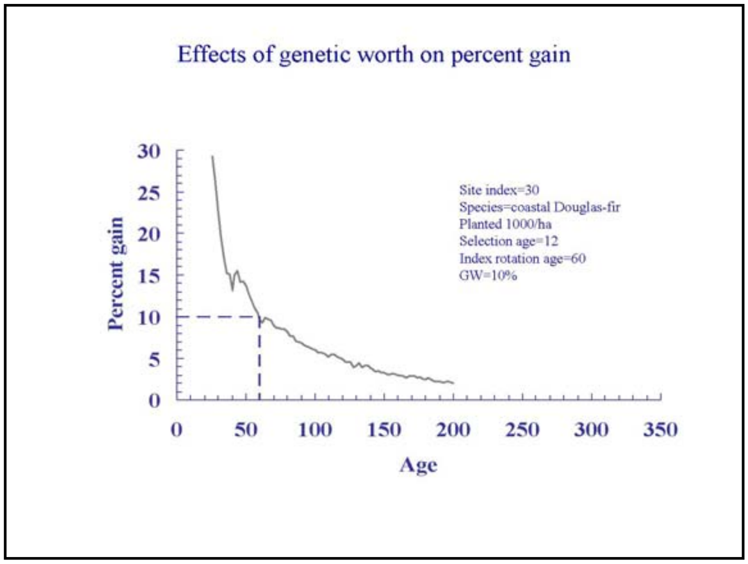


Default GW values in TIPSY

Species	Genetic worth	Selection age	Index age
	(user option)	(fixed)	(fixed)
Coast			
Douglas-fir	10	12	60
w. hemlock	10	15	60
w. redcedar	10	10	60
Sitka spruce	10	8	60
Interior			
Lodgepole pine	10	10	60
white spruce	10	15	**80**
Douglas-fir	10	10	60

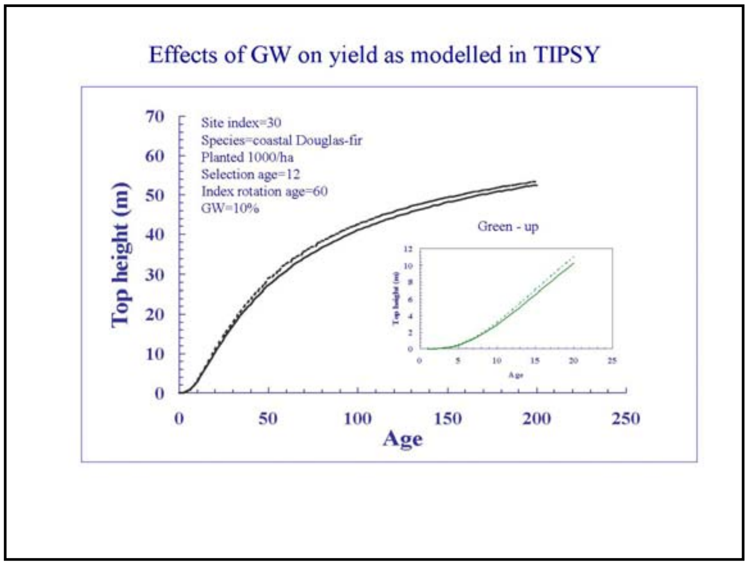
Effects of GW on yield as modelled in TIPSY





Effects of genetic worth on percent gain

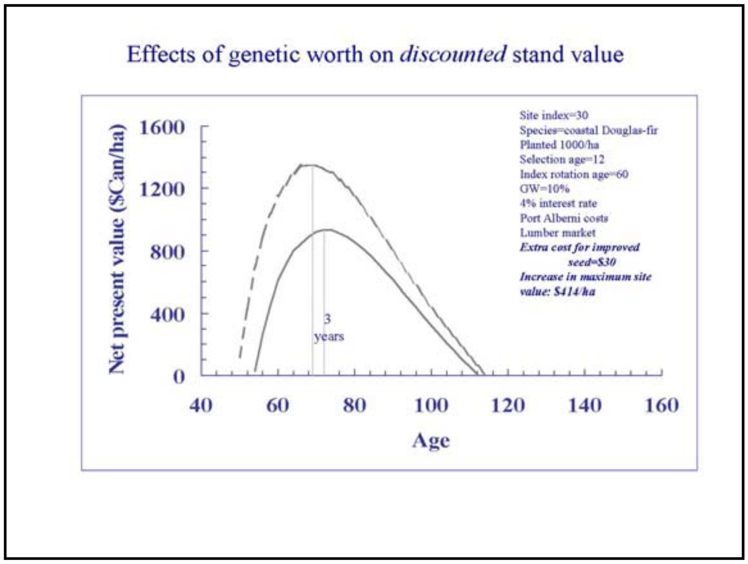
Site index=30
Species=coastal Douglas-fir
Planted 1000/ha
Selection age=12
Index rotation age=60
GW=10%



Effects of GW on yield as modelled in TIPSY

Site index=30
Species=coastal Douglas-fir
Planted 1000/ha
Selection age=12
Index rotation age=60
GW=10%

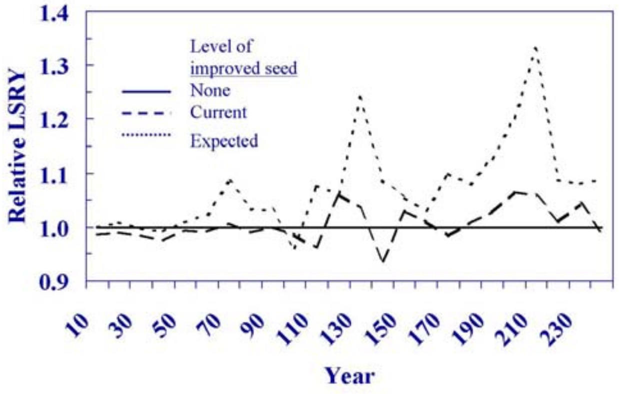
Green - up



Effects of genetic worth on *discounted* stand value

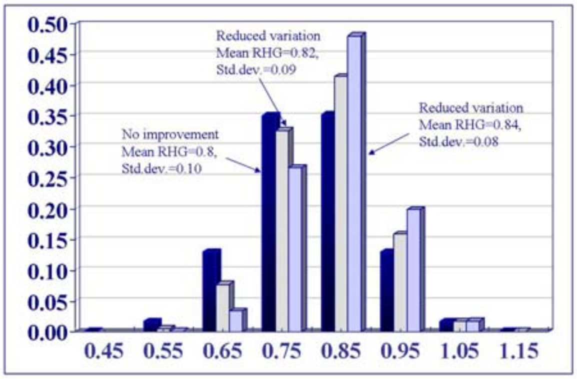
Site index=30
Species=coastal Douglas-fir
Planted 1000/ha
Selection age=12
Index rotation age=60
GW=10%
4% interest rate
Port Alberni costs
Lumber market
Extra cost for improved seed=$30
Increase in maximum site value: $414/ha

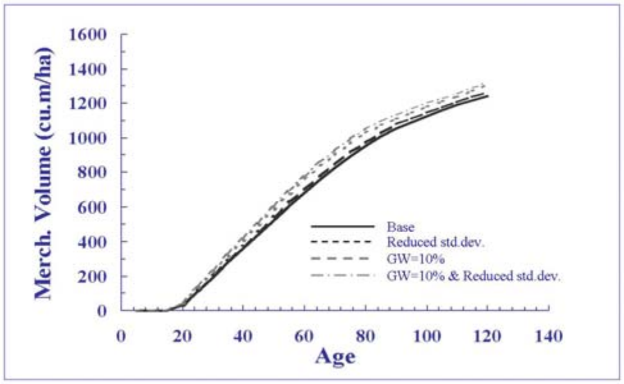
Timber supply example
Fraser TSA - Douglas-fir only



TASS “Experiment”

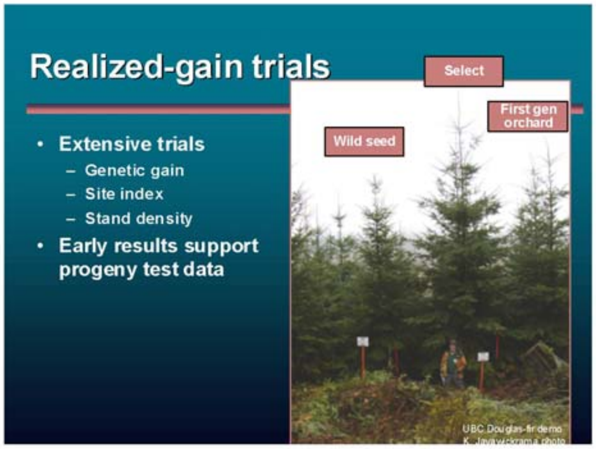
- Whatif:
  - Tree improvement doesn’t elevate height growth but reduces within-stand variation (→ HG, ↓ S_{HG})
  - Tree improvement elevates the mean height growth but keeps variation the same (↑HG, →S_{HG})
  - Tree improvement elevates the mean height growth but reduces within-stand variation (↑HG, ↓S_{HG})
  - Compare these to “control” (C)
  - All of the above differs by initial density and the amount variation is changed.





Realized Gain Trials

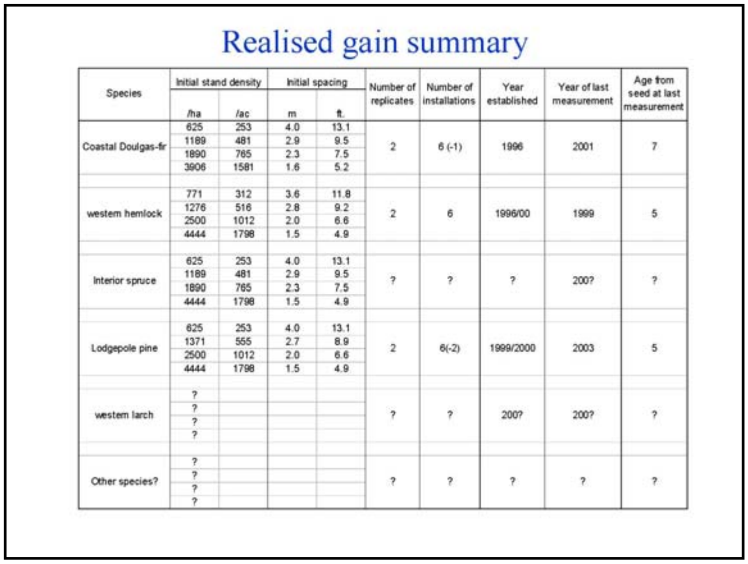
- Realized gain trials are essential to the validation and verification of young genetic selections.
- What if the part or all of the gain based on selections based on individual trees is lost when stand dynamics and competition is included in the mix?
- British Columbia has had a continuing program of establishing realized gain trials since 1991 when a preliminary set of area-based trials for Fd and Hw (but only one stand density).
- In 1994, a committee was formed to design more rigorous trials by:
  - Conduct preliminary runs of TASS to check sensitivity
  - Sow seeds in 1995
  - Establish field sites beginning in 1996



Realized-gain trials

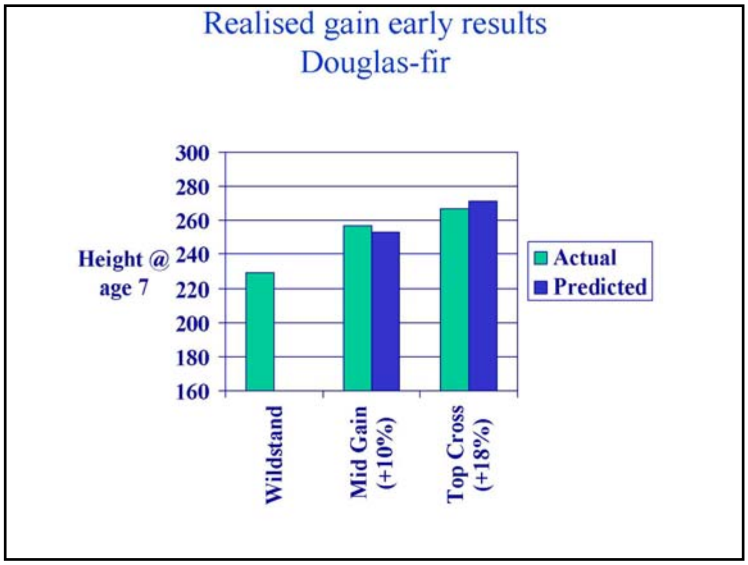
- Extensive trials
  - Genetic gain
  - Site index
  - Stand density
- Early results support progeny test data

UBC Douglas-fir demo
K. Jayawickrama photo

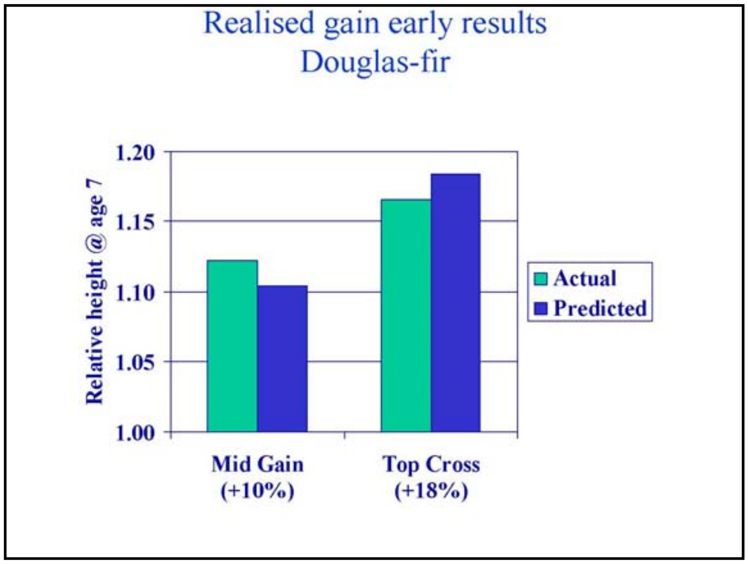


Realised gain summary

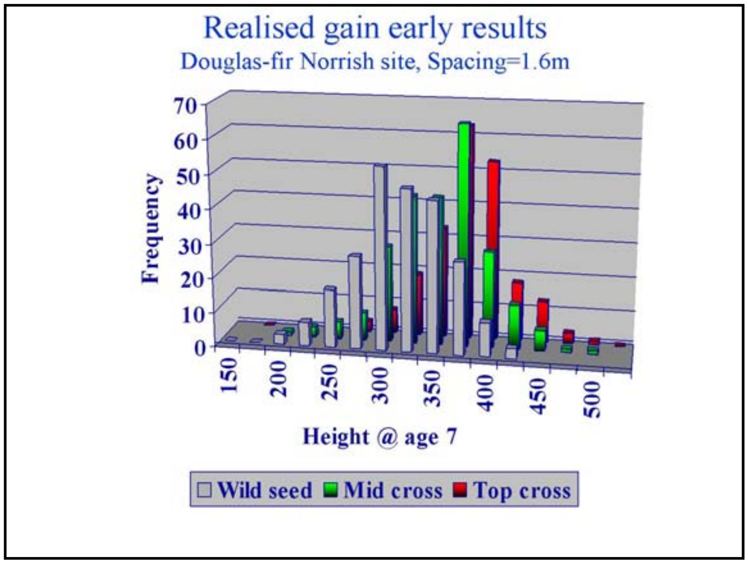
Species	Initial stand density		Initial spacing		Number of replicates	Number of installations	Year established	Year of last measurement	Age from seed at last measurement
	/ha	/ac	m	ft.					
Coastal Doulgas-fir	625	253	4.0	13.1	2	6 (-1)	1996	2001	7
	1189	481	2.9	9.5					
	1890	765	2.3	7.5					
	3906	1581	1.6	5.2					
western hemlock	771	312	3.6	11.8	2	6	1996/00	1999	5
	1276	516	2.8	9.2					
	2500	1012	2.0	6.6					
	4444	1798	1.5	4.9					
Interior spruce	625	253	4.0	13.1	?	?	?	200?	?
	1189	481	2.9	9.5					
	1890	765	2.3	7.5					
	4444	1798	1.5	4.9					
Lodgepole pine	625	253	4.0	13.1	2	6(-2)	1999/2000	2003	5
	1371	555	2.7	8.9					
	2500	1012	2.0	6.6					
	4444	1798	1.5	4.9					
western larch	?				?	?	200?	200?	?
	?								
	?								
	?								
Other species?	?				?	?	?	?	?
	?								
	?								
	?								



Realised gain early results
Douglas-fir

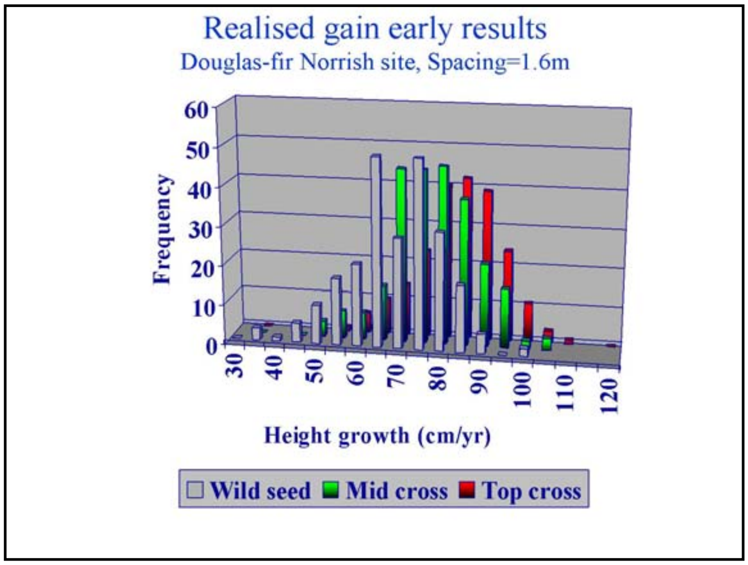


Realised gain early results
Douglas-fir



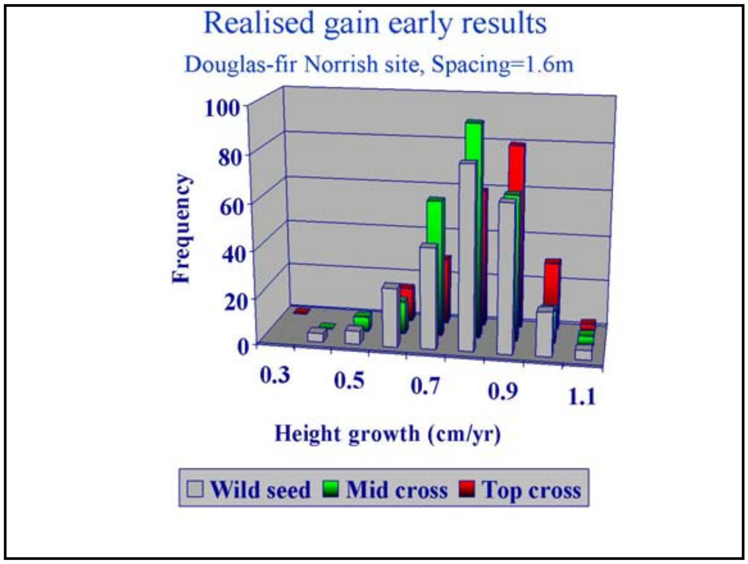
Realised gain early results

Douglas-fir Norrish site, Spacing=1.6m



Realised gain early results

Douglas-fir Norrish site, Spacing=1.6m



Realised gain early results

Douglas-fir Norrish site, Spacing=1.6m

Douglas-fir early realized gain trial results

Seed source	Relative height growth mean	Standard Deviation
Wild seed	0.6806	0.1783
Mid cross	0.7058	0.1764
Top cross	0.7027	0.1772

Ancillary studies related to genetic improvement and growth and yield

Wood Quality
Pest modelling

Modelling the impact of silvicultural activities on wood characteristics of western hemlock in British Columbia

Range of western hemlock in British Columbia

"Wild" stands
Progeny trials

---

20 year

90 year old

40 year old

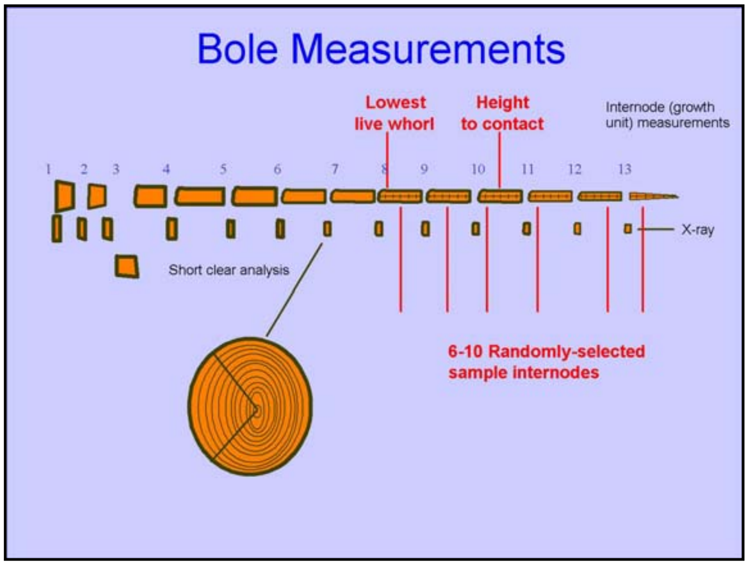
Progeny trial

Field Procedures

Stand Structure

Crown Area

Field Procedures



Bole Measurements

Lowest live whorl

Height to contact

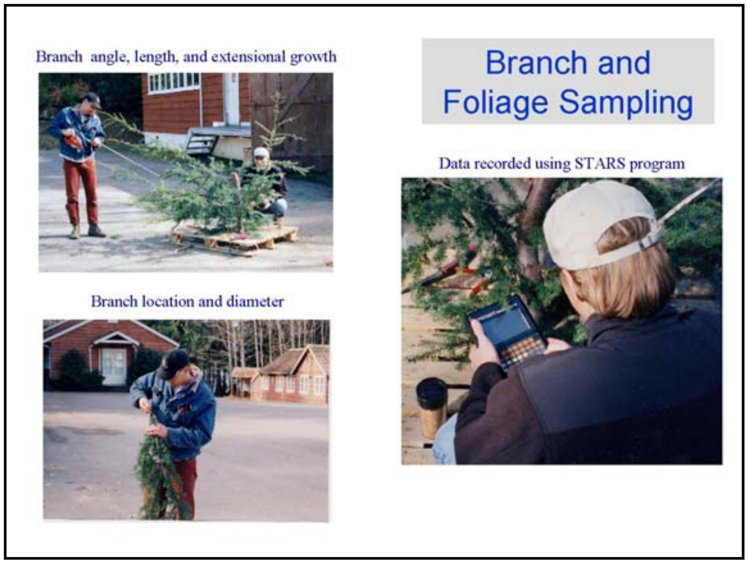
Internode (growth unit) measurements

X-ray

Short clear analysis

6-10 Randomly-selected sample internodes

Forintek Canada

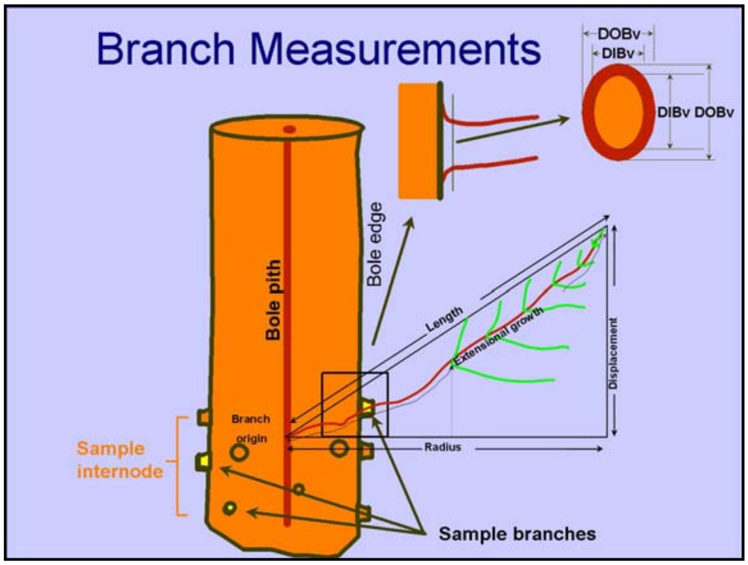


Branch and Foliage Sampling

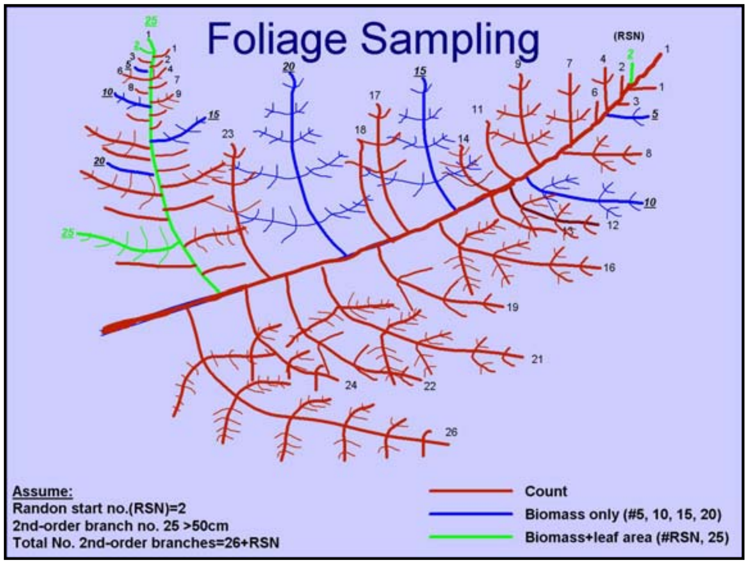
Branch angle, length, and extensional growth

Branch location and diameter

Data recorded using STARS program



Branch Measurements



Foliage Sampling

Assume:
Randon start no.(RSN)=2
2nd-order branch no. 25 >50cm
Total No. 2nd-order branches=26+RSN

🟥 Count
🟦 Biomass only (#5, 10, 15, 20)
🟩 Biomass+leaf area (#RSN, 25)

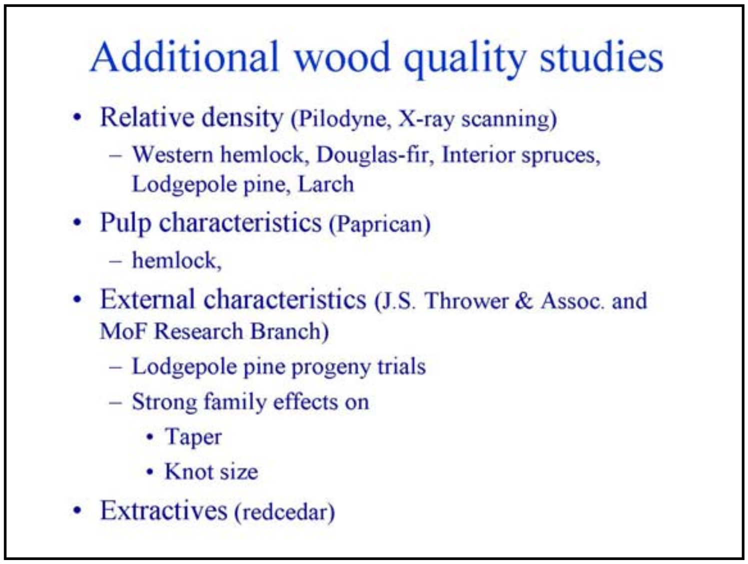
Tree Id# ____
[illegible] ____
Date ____
Branch# ____
Br. Age ____ [illegible] ____
2nd order# ____
[illegible] ____
[illegible] ____ Total # ____
Ht to Branch ____ [illegible] ____
Weight (grams) ____
Comments ____

Foliar biomass sampling

Leaf area sampling

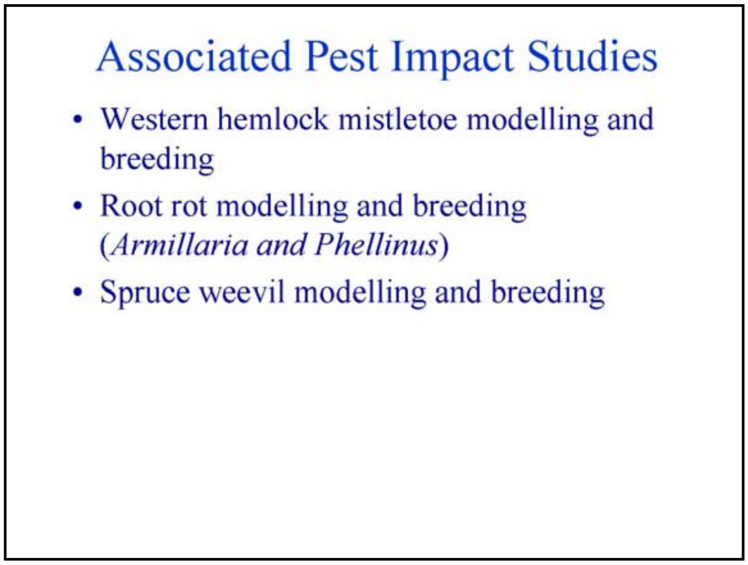
WinSEEDLE image analysis system (Regent Instruments)

SampleID,
Operator,
Date Time,
Total Projected Area
Avg. Area,
Avg. Straight Length,
Avg. Curved Length,
Avg. Straight Width,
Avg. Curved Width,
Avg. Curvature,
Cross Section Model Shape,
Cross Section Model H/W Ratio,
Avg. Volume,
Avg. Surface Area,
Avg. Half Surface Area,
Avg. W/L Ratio,
No. of Objects



Additional wood quality studies

- Relative density (Pilodyne, X-ray scanning)
  - Western hemlock, Douglas-fir, Interior spruces, Lodgepole pine, Larch
- Pulp characteristics (Paprican)
  - hemlock,
- External characteristics (J.S. Thrower & Assoc. and MoF Research Branch)
  - Lodgepole pine progeny trials
  - Strong family effects on
    - Taper
    - Knot size
- Extractives (redcedar)



Associated Pest Impact Studies

- Western hemlock mistletoe modelling and breeding
- Root rot modelling and breeding (*Armillaria and Phellinus*)
- Spruce weevil modelling and breeding

Modelling genetic gain in growth in New Zealand: 1986-2003

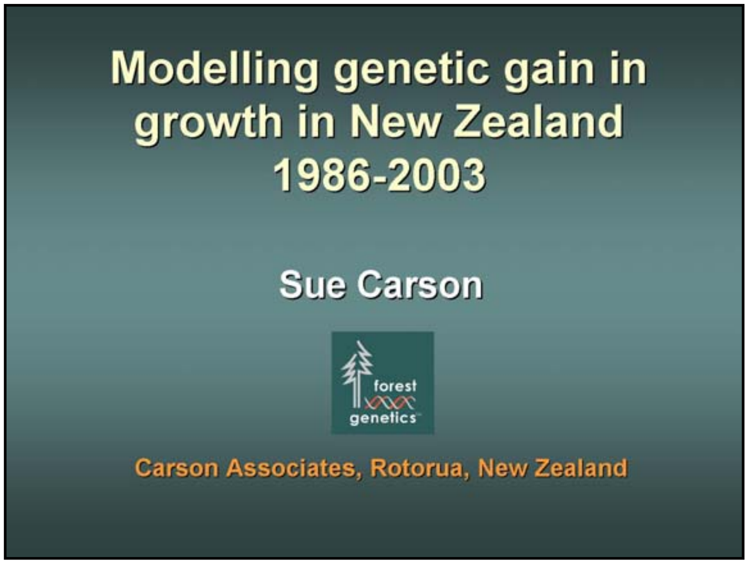
Sue D. Carson
Carson Associates Ltd.
Rotorua, New Zealand

Stand growth models in New Zealand have the capacity to predict growth of genetically improved seedlots. This has been made possible because of the extensive estate of large-plot genetic gain trials planted from 1978 to 1994, representing 49 sites and over 60 seedlots. Over half of these trials have silvicultural treatments, as well as genetically different seedlots. The over 1390 permanent sample plots (PSP) in these trials have been measured annually from age 5-8 until age 15, then bi-annually after that. Genetic gain has been observed in all trials, although occasionally a particular seedlot did not perform as expected. However, differences related to site and silviculture are 8-14 times greater than differences related to genetics.

Genetic gain has been incorporated into growth models as a process, that is, as an increase in growth rate, termed a "growth rate multiplier" or "genetic gain multiplier". Genetic gain multipliers have been estimated using annual measurements from 18 large-plot trials with 35 seedlots and 495 PSP. Increases in rate of basal area growth are 4-5 times as great as increases in rate of height growth. Genetic gain multipliers for basal area are strongly and linearly correlated with breeding values for diameter, which were estimated from extensive single-tree plot trials. Genetic gain multipliers did not appear to differ among growth modelling regions or silvicultural treatments. Large-plot genetic gain trial data does not support the hypothesis that the benefits of genetic gain decrease as stands age.

Predictions using genetic gain multipliers were validated using growth models and data not used for estimation of the multipliers. Prediction of growth of improved seedlots using the multipliers was better than with the unmodified models. Predictions of genetic gain from progeny trials appeared, on average, to be quite accurate, although a large variation around the prediction was apparent. Prediction using genetic gain multipliers in growth models is likely to be more accurate for specific stands with a specific silviculture treatment.

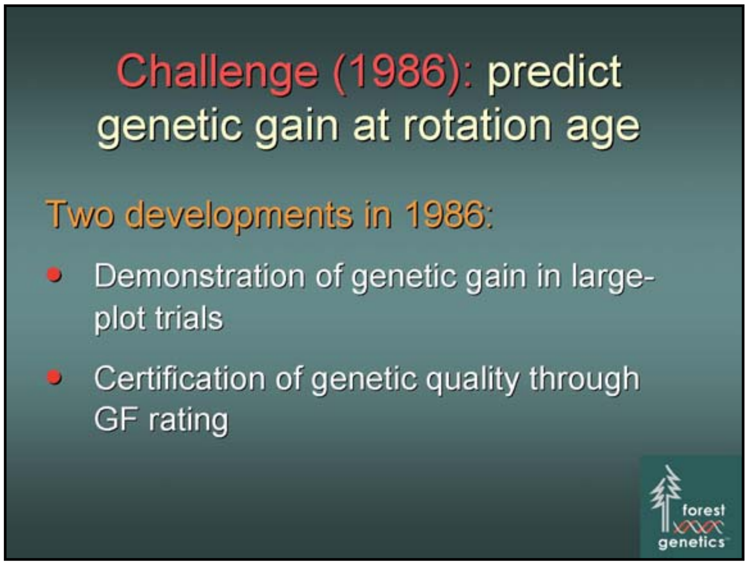
The concept of a genetic gain multiplier is robust. The approach models a process, rather than just fitting data, making it possible to extrapolate to sites, silviculture, and seedlots not represented in genetic gain trials. Similar estimates of genetic gain multipliers should be obtained regardless of growth model form, as long as both models predict growth well and a rate of increase term can be defined. In addition, estimates obtained using one form of growth model could be used in a growth model of a different form or developed using data from a different region. This would have great advantages for prediction of growth of the genetically improved seedlots in areas that do not yet have genetic gain trials.



Modelling genetic gain in growth in New Zealand 1986-2003

Sue Carson

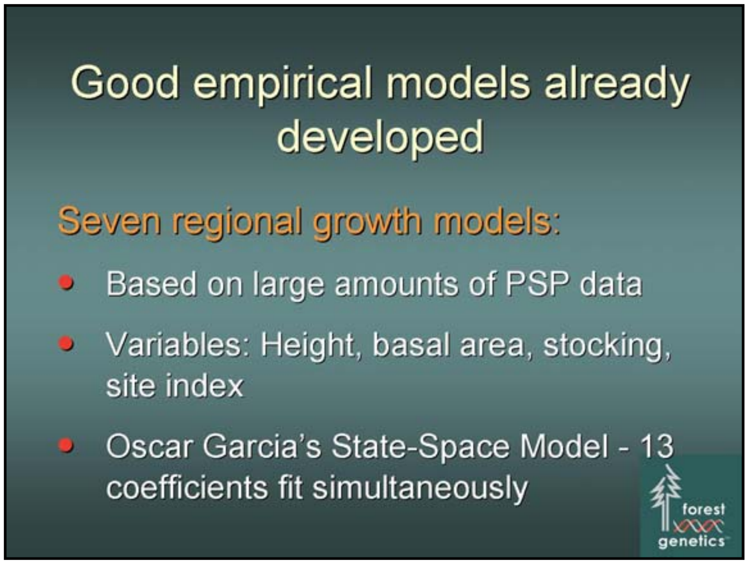
Carson Associates, Rotorua, New Zealand



Challenge (1986): predict genetic gain at rotation age

Two developments in 1986:

- Demonstration of genetic gain in large-plot trials
- Certification of genetic quality through GF rating



Good empirical models already developed

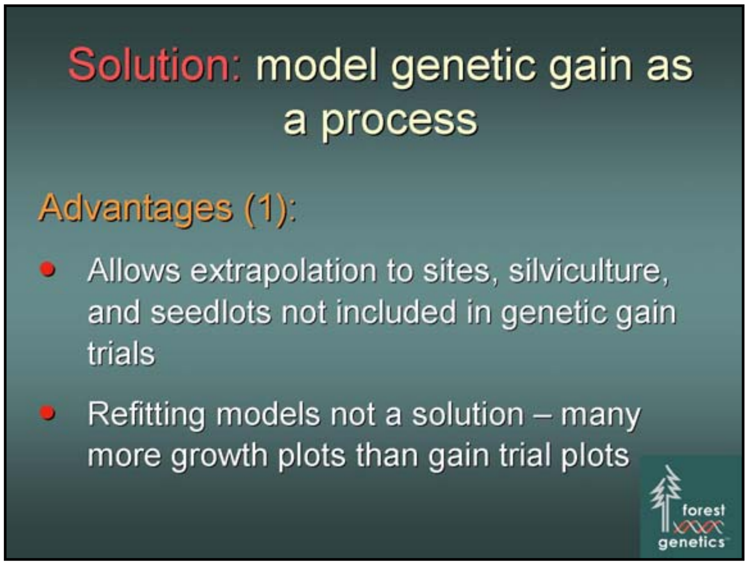
Seven regional growth models:

- Based on large amounts of PSP data
- Variables: Height, basal area, stocking, site index
- Oscar Garcia's State-Space Model - 13 coefficients fit simultaneously

Large-plot genetic gain trials available

Trials on 49 sites:

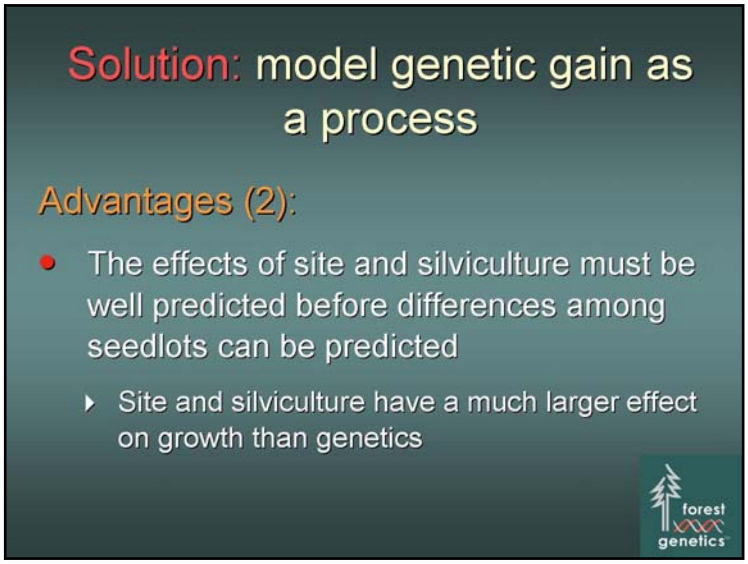
- Planted 1978-1994
- 60+ seedlots
- Final crop stocking 200-1000 sph
- ~1390+ large plots
- Annual measurements in PSP since age 5-8



Solution: model genetic gain as a process

Advantages (1):

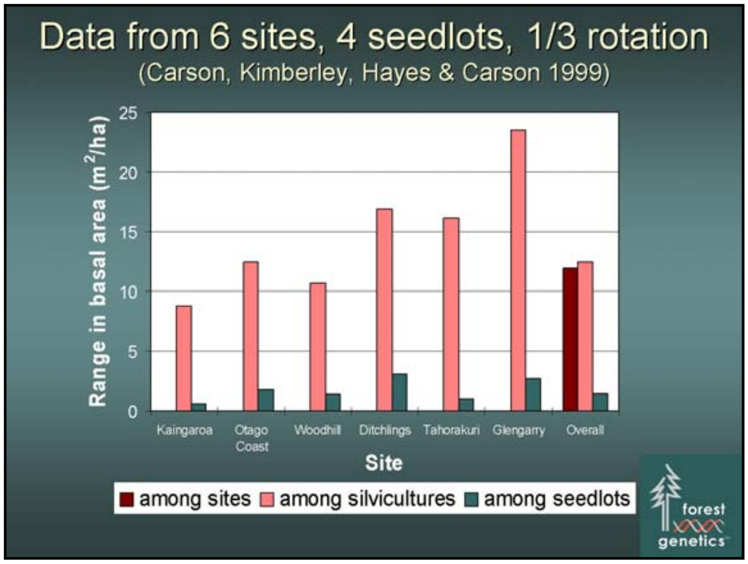
- Allows extrapolation to sites, silviculture, and seedlots not included in genetic gain trials
- Refitting models not a solution – many more growth plots than gain trial plots



Solution: model genetic gain as a process

Advantages (2):

- The effects of site and silviculture must be well predicted before differences among seedlots can be predicted
  - Site and silviculture have a much larger effect on growth than genetics



Data from 6 sites, 4 seedlots, 1/3 rotation

(Carson, Kimberley, Hayes & Carson 1999)

Solution: Growth Rate Multipliers

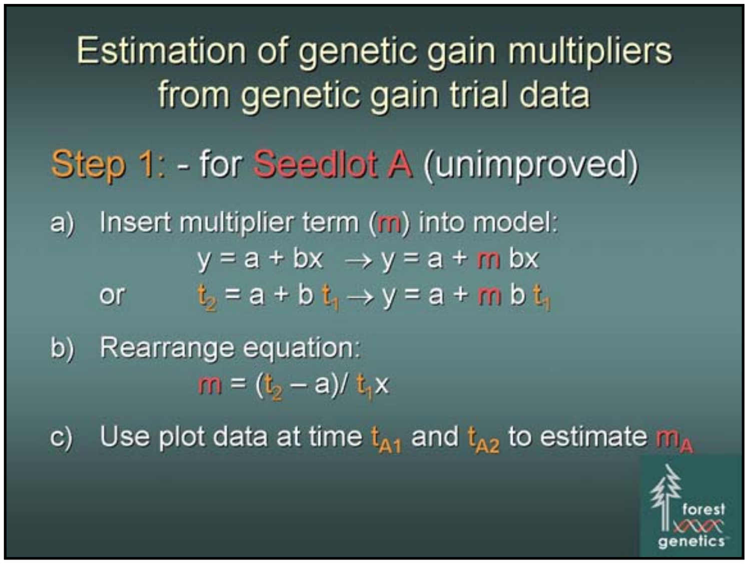
Hypotheses:

- Genetic gain is expressed as an increase in growth rate
- Increases in diameter and height growth rates are independent

Growth Rate Multipliers

Implementation of genetic gain as an increase in growth rate:

- Insert growth rate coefficient in the model
- Fit coefficient using gain trial data
- Compression of the time scale: Improved trees grow similarly to unimproved, but get there faster



Estimation of genetic gain multipliers from genetic gain trial data

Step 1: - for Seedlot A (unimproved)

a) Insert multiplier term (m) into model:

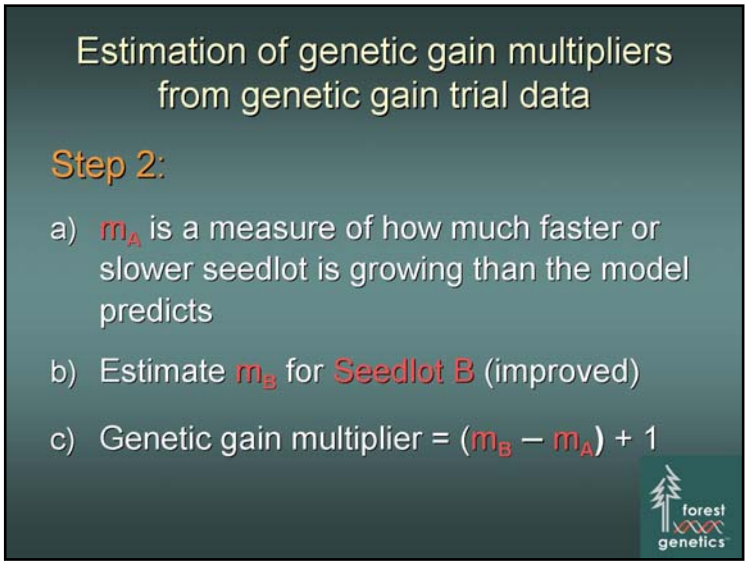
$$y = a + bx \rightarrow y = a + m\,bx$$

or $$t_2 = a + b\,t_1 \rightarrow y = a + m\,b\,t_1$$

b) Rearrange equation:

$$m = (t_2 - a)/\,t_1 x$$

c) Use plot data at time t_{A1} and t_{A2} to estimate m_A



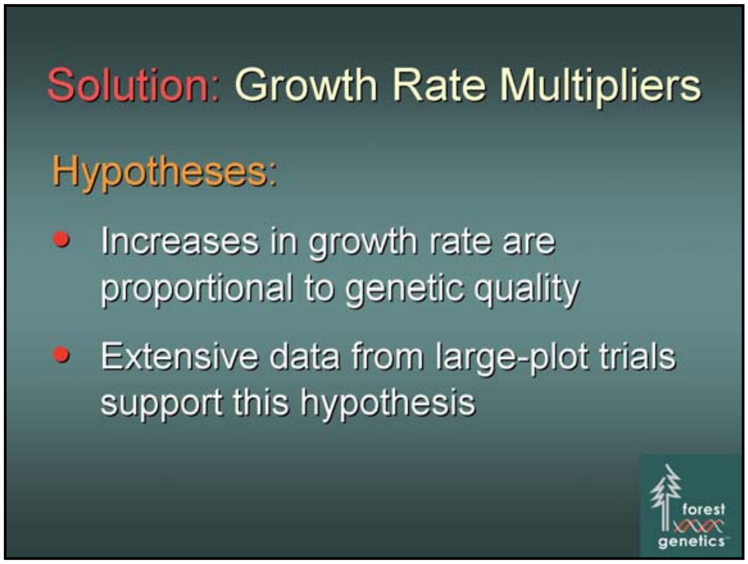
Estimation of genetic gain multipliers from genetic gain trial data

Step 2:

a) m_A is a measure of how much faster or slower seedlot is growing than the model predicts

b) Estimate m_B for Seedlot B (improved)

c) Genetic gain multiplier = $(m_B - m_A) + 1$



Solution: Growth Rate Multipliers

Hypotheses:

- Increases in growth rate are proportional to genetic quality
- Extensive data from large-plot trials support this hypothesis

Estimation of genetic gain multipliers from genetic gain trial data

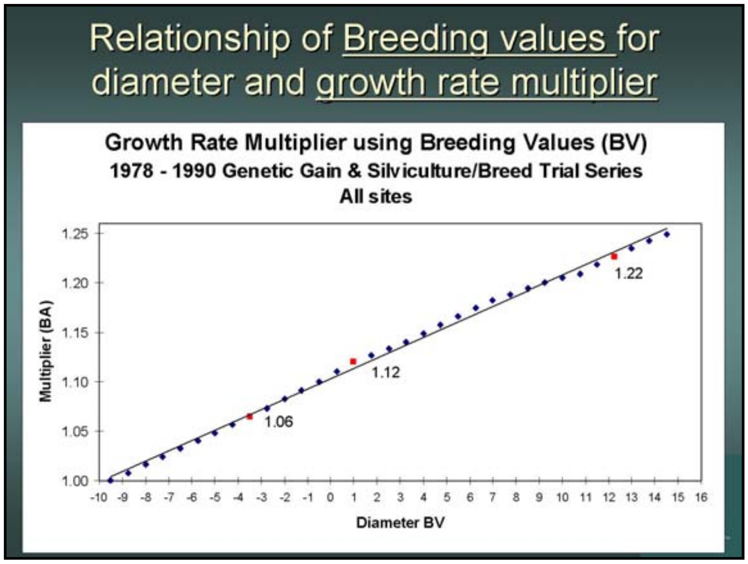
(Carson, Garcia & Hayes 1999)

	Growth rate multipliers	
Seedlot	**Height**	**Basal area**
Unimproved	0.998	0.997
Climbing select	1.000	1.000
OP seed orchard	1.051	1.130
Control pollinated	1.045	1.264

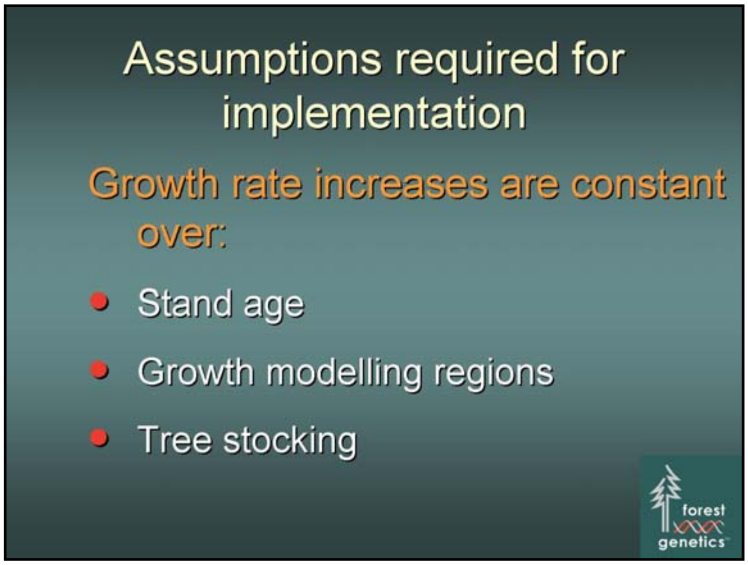
With more extensive data

Compare:

- Growth rate multipliers estimated from 18 large-plot trials with 35 seedlots and 495 plots, ages 5-19 years, and
- Breeding Values for diameter estimated from 41 single-tree plot progeny trials, 1800 parents, approx age 8 years, BLUP



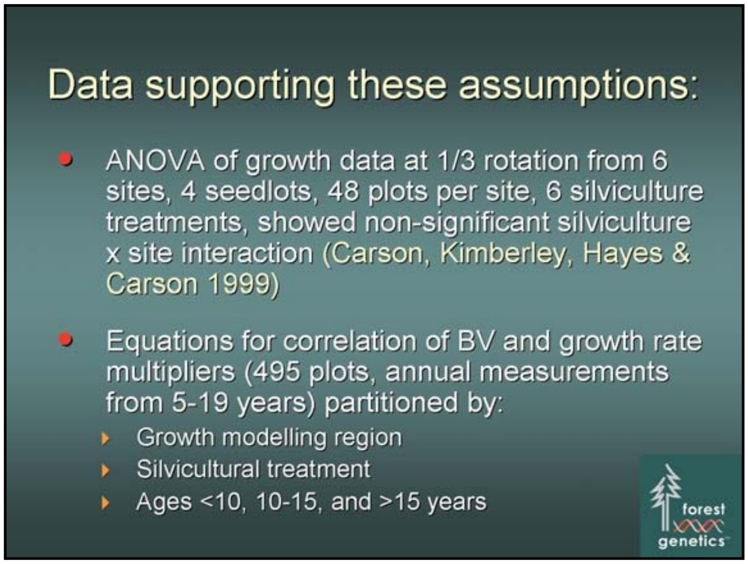
Relationship of Breeding values for diameter and growth rate multiplier



Assumptions required for implementation

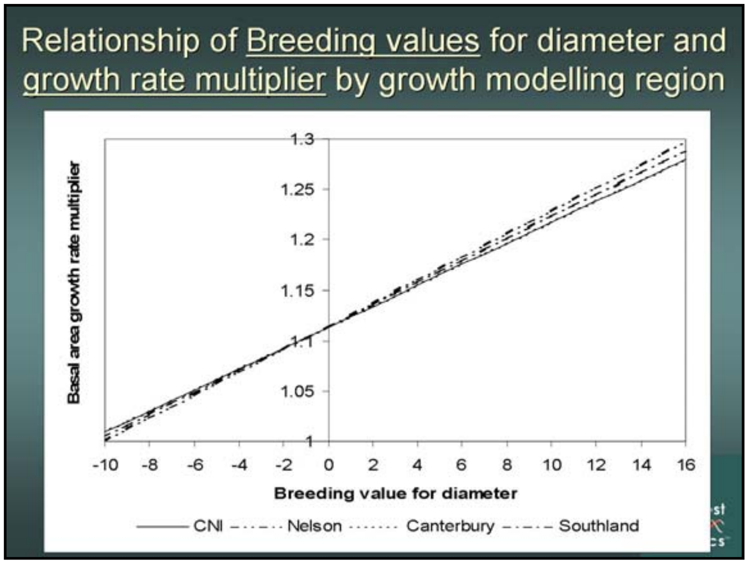
Growth rate increases are constant over:

- Stand age
- Growth modelling regions
- Tree stocking

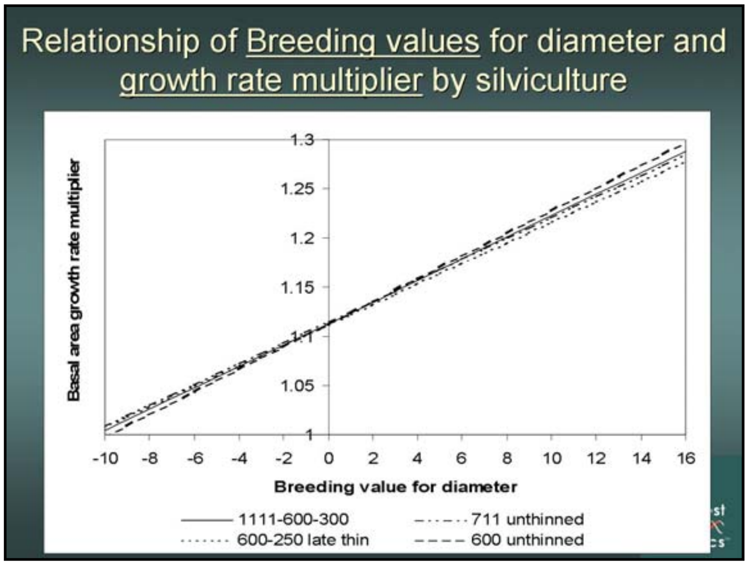


Data supporting these assumptions:

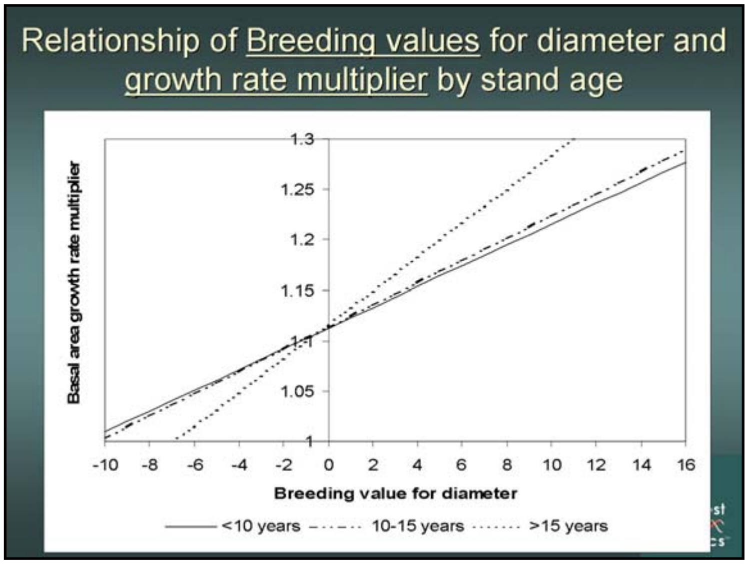
- ANOVA of growth data at 1/3 rotation from 6 sites, 4 seedlots, 48 plots per site, 6 silviculture treatments, showed non-significant silviculture x site interaction (Carson, Kimberley, Hayes & Carson 1999)
- Equations for correlation of BV and growth rate multipliers (495 plots, annual measurements from 5-19 years) partitioned by:
  - Growth modelling region
  - Silvicultural treatment
  - Ages <10, 10-15, and >15 years



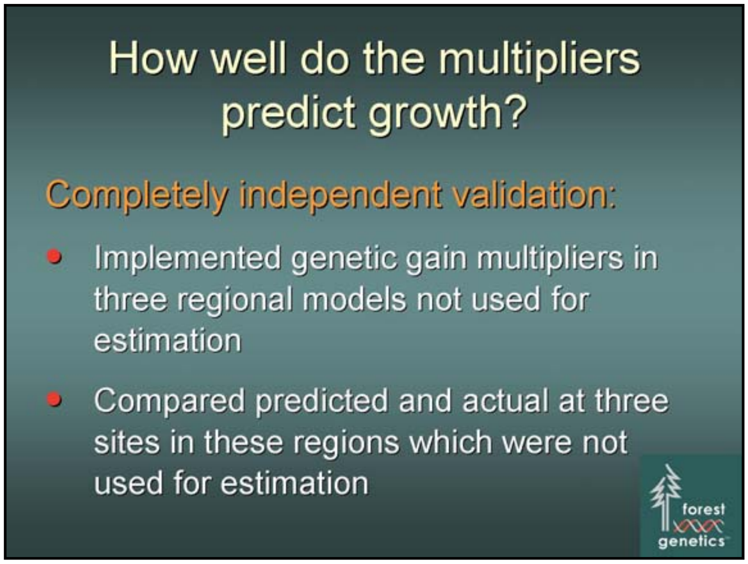
Relationship of Breeding values for diameter and growth rate multiplier by growth modelling region



Relationship of Breeding values for diameter and growth rate multiplier by silviculture



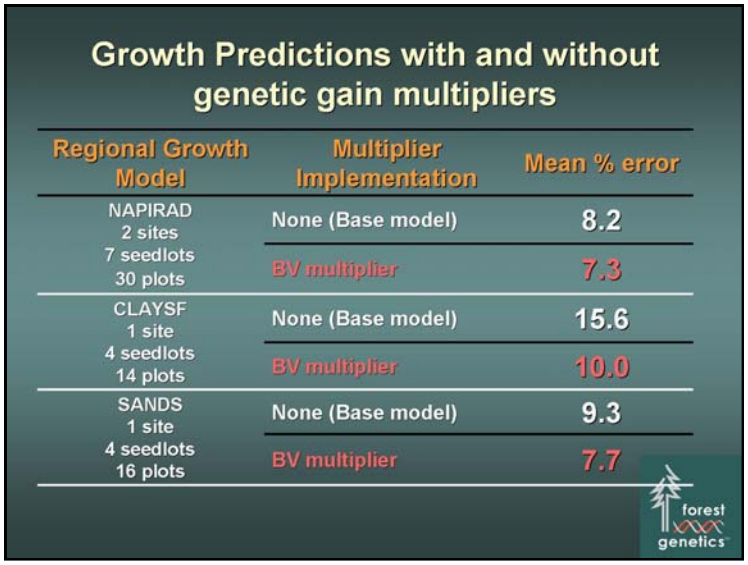
Relationship of Breeding values for diameter and growth rate multiplier by stand age



How well do the multipliers predict growth?

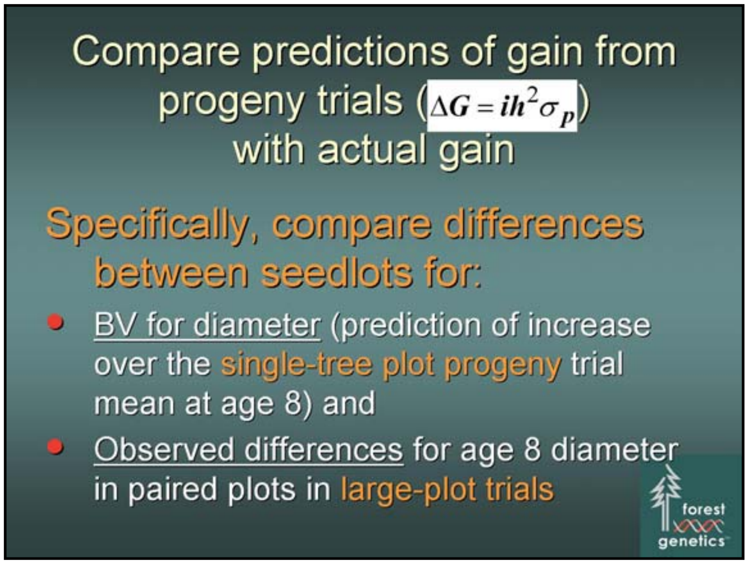
Completely independent validation:

- Implemented genetic gain multipliers in three regional models not used for estimation
- Compared predicted and actual at three sites in these regions which were not used for estimation



Growth Predictions with and without genetic gain multipliers

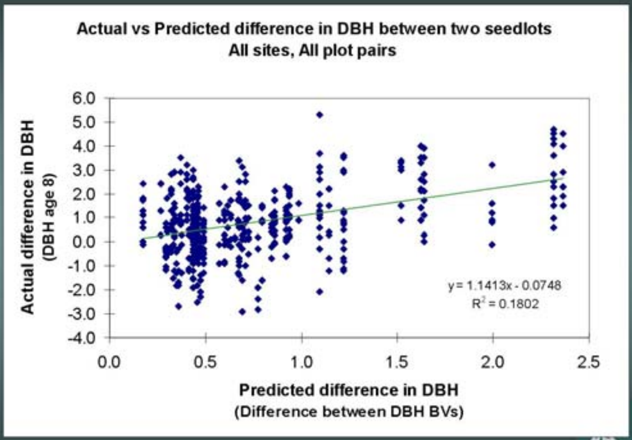
Regional Growth Model	Multiplier Implementation	Mean % error
NAPIRAD 2 sites 7 seedlots 30 plots	None (Base model)	8.2
	BV multiplier	7.3
CLAYSF 1 site 4 seedlots 14 plots	None (Base model)	15.6
	BV multiplier	10.0
SANDS 1 site 4 seedlots 16 plots	None (Base model)	9.3
	BV multiplier	7.7



Compare predictions of gain from progeny trials ($\Delta G = ih^2\sigma_p$) with actual gain

Specifically, compare differences between seedlots for:

- BV for diameter (prediction of increase over the single-tree plot progeny trial mean at age 8) and
- Observed differences for age 8 diameter in paired plots in large-plot trials



Actual vs Predicted difference in DBH between two seedlots
All sites, All plot pairs

Validity of genetic predictions from progeny tests

- Genetic predictions from progeny trials, on average, were very similar to the actual increase in diameter at the age of measurement
- However, there is a large amount of variation around the relationship
- Probably due to differences in site and silviculture

Hypotheses supported by large amount of trial data (1)

- Genetic gain was observed on all large-plot trials in all regions
- Growth is influenced much more strongly by site and silviculture than by genetics
- Genetic gain can be modeled as an increase in growth rate

Hypotheses supported by large amount of trial data (2)

- Correlation of breeding values for diameter and increases in basal area growth rate is strong and linear
- Use of genetic gain multipliers predicts actual increase in diameter better than base-line models

forest genetics

Hypotheses supported by large amount of trial data (3)

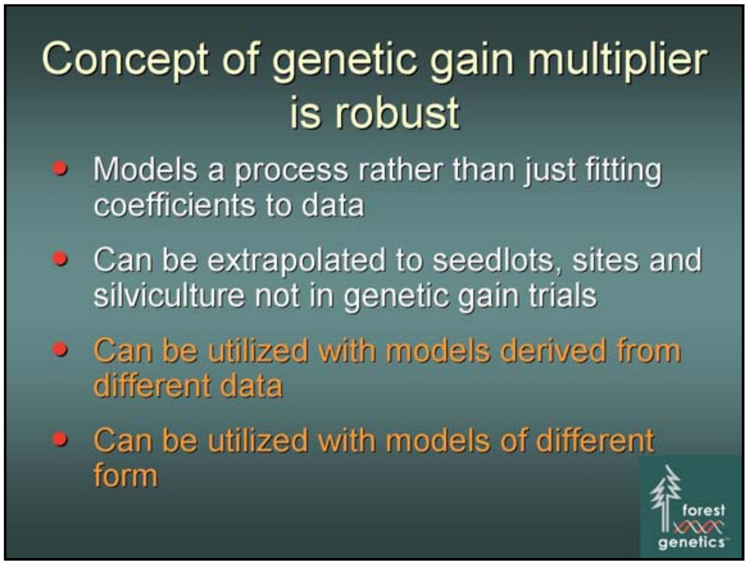
- Silviculture and growth modelling region do not effect increases in rate of growth with genetic improvement
- Increases in rate of growth with genetic improvement do not decrease as stands age

forest genetics

Hypotheses supported by large amount of trial data (4)

- Predictions of gain from progeny trials appear to be, on average, very similar to the genetic predictions at the same age
- Diameter and height distributions do not differ among improved seedlots (Carson & Dunlop 1998)

forest genetics



Concept of genetic gain multiplier is robust

- Models a process rather than just fitting coefficients to data
- Can be extrapolated to seedlots, sites and silviculture not in genetic gain trials
- Can be utilized with models derived from different data
- Can be utilized with models of different form

Incorporating genetics into growth and yield models: *stand dynamics considerations*

Marilyn A. Buford
National Program Leader for Quantitative Ecology Research
USDA Forest Service
Washington, DC

Incorporating genetics information into growth and yield models requires considering model types and their primary drivers, examining and quantifying growth patterns of genetically improved stands, and developing data appropriate for growth and yield analysis of genetically improved stock. Results from an effort to develop guidelines for incorporating the effects of genetic improvement into various types of growth and yield models for loblolly pine plantations indicate that at the seed source and family levels: 1) the shape of the height-age curve is dictated by the site, but the level of the curve is dictated by the seed source or family; 2) the shape of the height-diameter relationship at a given age is determined by the site and initial density, while the level of the relationship is determined by the seed source or family and is directly related to the dominant height of the seed source or family at that age; and 3) slopes of self-thinning trajectories do not differ by seed source, but the level of the self-thinning trajectories is strongly positively correlated with the exhibited site index of the seed source. Implications for modeling growth of genetically improved stands are: 1) genetic improvement affects the rate at which stands develop, but does not fundamentally alter the pattern of stand development from that of unimproved stands; 2) changes in genetic material on a given site will likely affect the level, but not the shape, of basic relationships such as the height-age and height-diameter curves; and 3) appropriately characterizing the height-age profile will be very important for modeling stand growth and yield of genetically improved stands.

Incorporating Genetics into Growth and Yield Models:

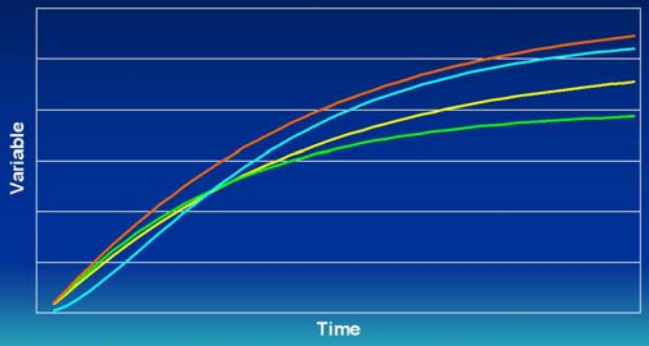
Stand Dynamics Considerations

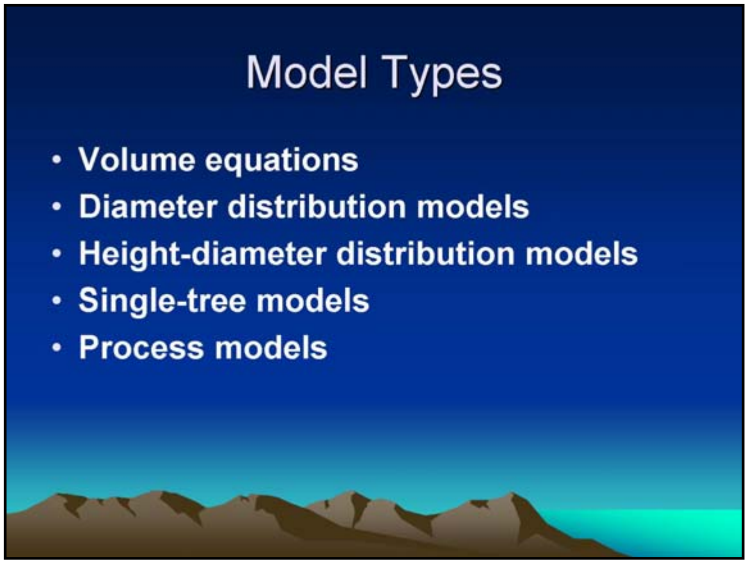
Marilyn A. Buford
USDA Forest Service
Vegetation Management and Protection Research

Stand Dynamics Considerations

- **Height-age development**
- **Density dependent growth**
- **Mortality**

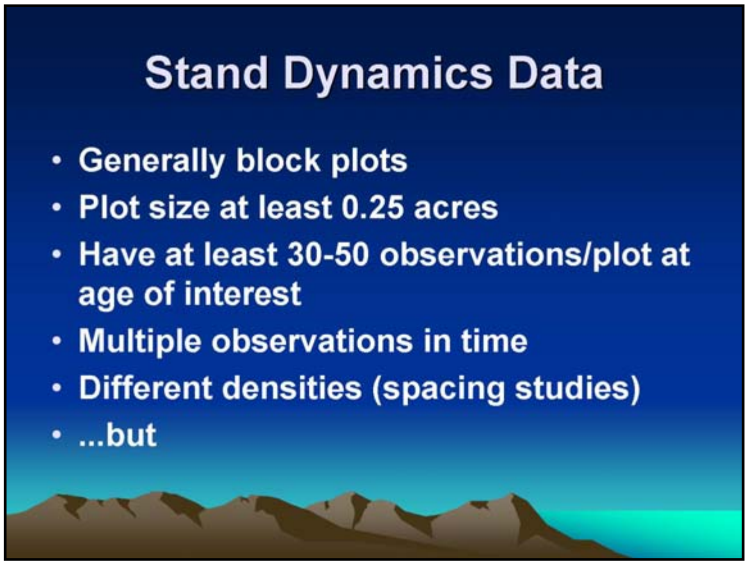
Potential Growth Curves





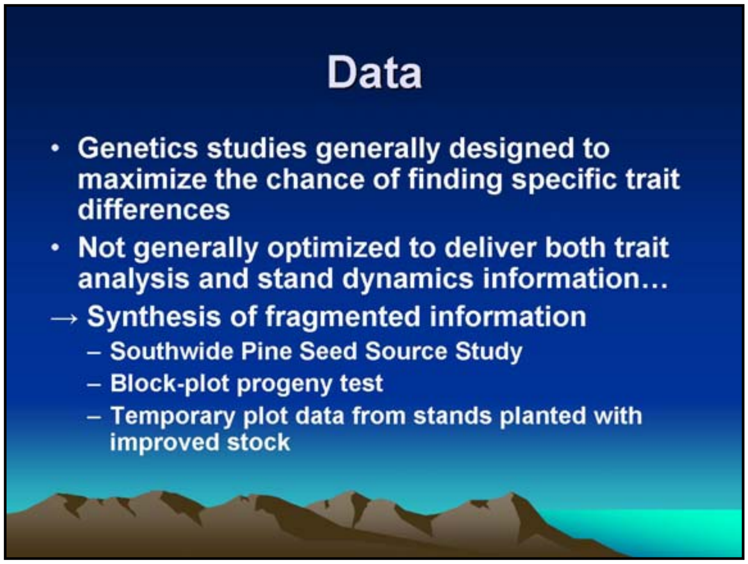
Model Types

- Volume equations
- Diameter distribution models
- Height-diameter distribution models
- Single-tree models
- Process models



Stand Dynamics Data

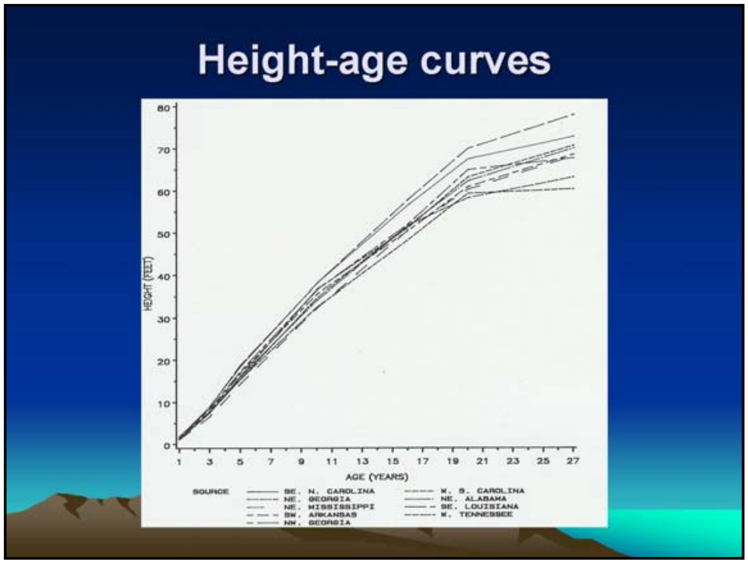
- Generally block plots
- Plot size at least 0.25 acres
- Have at least 30-50 observations/plot at age of interest
- Multiple observations in time
- Different densities (spacing studies)
- ...but



Data

- Genetics studies generally designed to maximize the chance of finding specific trait differences
- Not generally optimized to deliver both trait analysis and stand dynamics information…

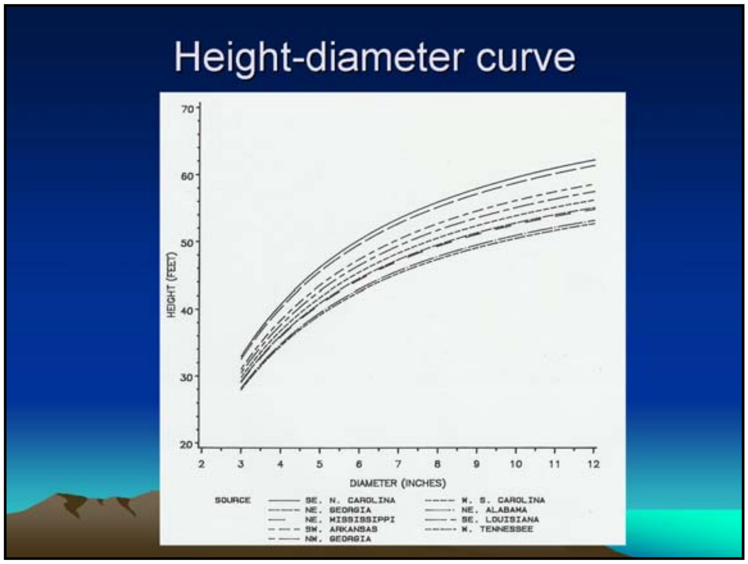
→ Synthesis of fragmented information
  - Southwide Pine Seed Source Study
  - Block-plot progeny test
  - Temporary plot data from stands planted with improved stock



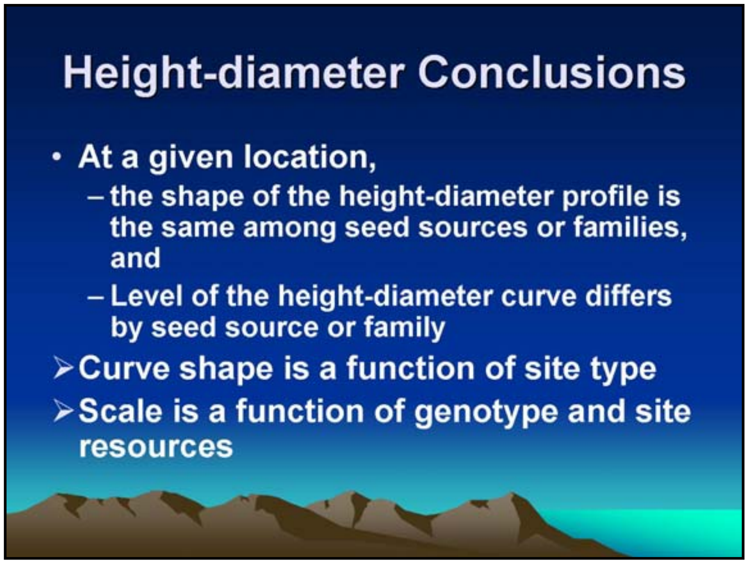
Height-age curves

Height-age Conclusions

- At a given location,
  - the shape of the height-age profile is the same among seed sources or families, and
  - Level of the height-age curve differs by seed source or family
- ➢Curve shape is a function of site type
- ➢Scale is a function of genotype and site resources

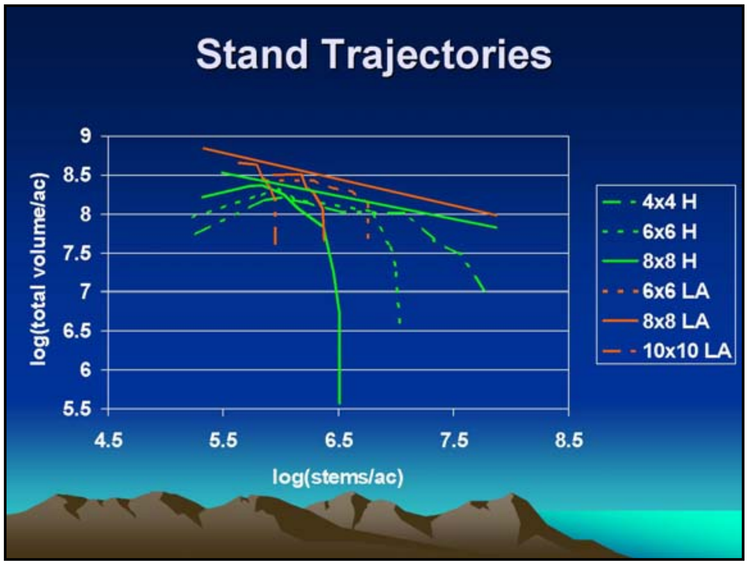


Height-diameter curve

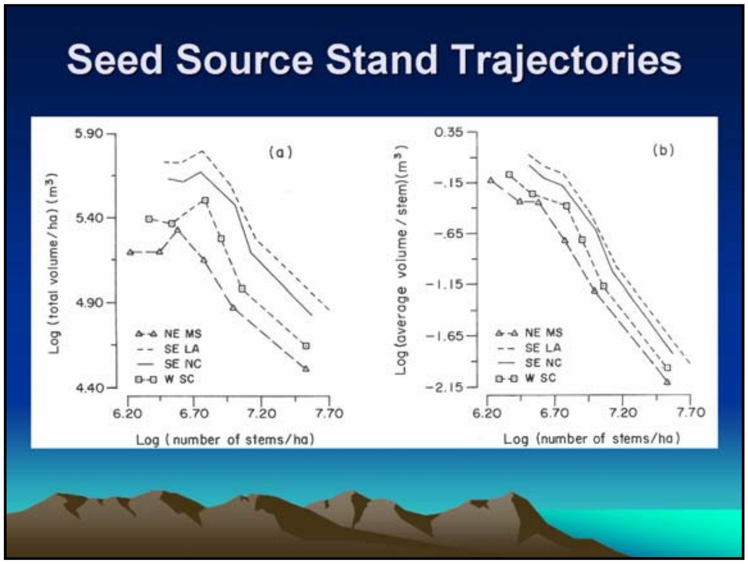


Height-diameter Conclusions

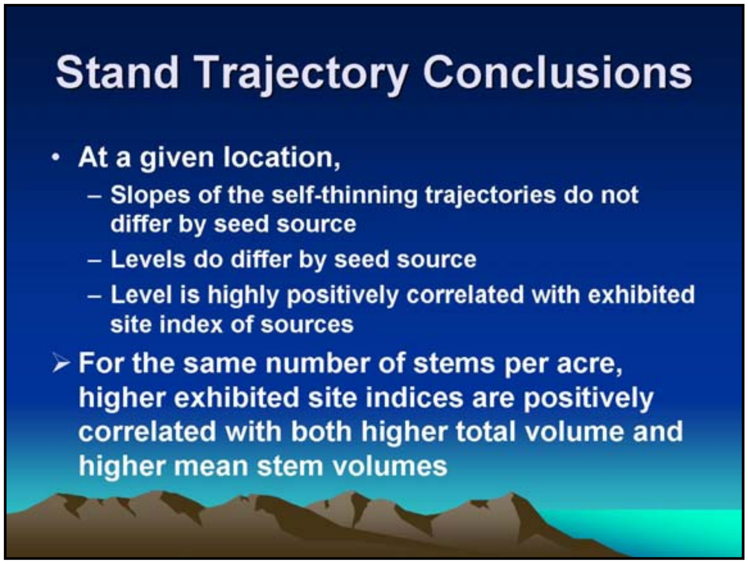
- At a given location,
  - the shape of the height-diameter profile is the same among seed sources or families, and
  - Level of the height-diameter curve differs by seed source or family
- ➢Curve shape is a function of site type
- ➢Scale is a function of genotype and site resources



Stand Trajectories

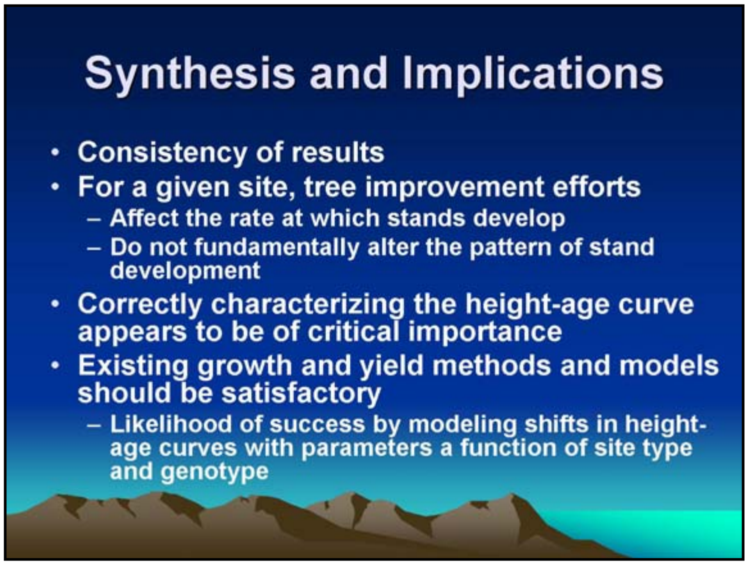


Seed Source Stand Trajectories



Stand Trajectory Conclusions

- At a given location,
  - Slopes of the self-thinning trajectories do not differ by seed source
  - Levels do differ by seed source
  - Level is highly positively correlated with exhibited site index of sources
- ➢ For the same number of stems per acre, higher exhibited site indices are positively correlated with both higher total volume and higher mean stem volumes



Synthesis and Implications

- Consistency of results
- For a given site, tree improvement efforts
  - Affect the rate at which stands develop
  - Do not fundamentally alter the pattern of stand development
- Correctly characterizing the height-age curve appears to be of critical importance
- Existing growth and yield methods and models should be satisfactory
  - Likelihood of success by modeling shifts in height-age curves with parameters a function of site type and genotype

Integration of genetics into growth models: state of the art and challenges in the southern U.S.

Steven A. Knowe
Department of Forestry, Wildlife, and Fisheries
University of Tennessee, Knoxville

Forest growth models typically used in the Southern U.S. are explicit and implicit yield systems. The explicit systems provide estimates of basal area or volume per unit area, while the implicit systems provide information on stand structure (distribution of tree diameter and height), and the components of stand structure are used to estimate yield. With few exceptions, these models do not include genetic effects. Several reasons for not including genetics are discussed.

Examples of both explicit and implicit systems that include genetic effects are presented, with emphasis on a diameter distribution approach to modeling mixtures of eastern cottonwood clones. Modifications to include interactions between specific clones and to estimate the relative contribution of each clone in mixtures are demonstrated. Two methods for incorporating genetic effects into existing forest growth models are: 1) to modify the height-age curves, thereby adjusting site index; and 2) to adjust the age. These methods are demonstrated for an explicit yield system by using data from an open-pollinated test. The best results in terms of bias, average deviation, and fit index were obtained for basal area and volume by combining family-specific height-age curves and an overall age adjustment function.

Breeding programs could be modified to provide data suitable for developing growth models. Genetically improved trees can be planted in plots that are large enough to include 70 (minimum 30) trees of each family, in both single-family plots and in mixtures of two or more families. In addition, interactions with other silvicultural treatments such as herbaceous weed control and fertilization should be included in field studies.

Integration of Genetics

Into Growth Models:

State of the Art and Challenges

In the Southern U.S.

Steven A. Knowe

University of Tennessee
Department of Forestry,
Wildlife & Fisheries

Overview

- What models are used in the Southeastern U.S.?
- Are genetic gains incorporated in these models?
  - If not, why not?
  - If so, how?
- How can the models be improved?
- What new experiments are needed to improve these models?
- How should breeding programs be modified?

Forest Growth and Yield Prediction Systems

Explicit systems-provide estimates of volume per unit area by using an equation or system of equations

- variable-density yield prediction equations

Implicit systems-provide information on stand structure (distribution of tree diameter, height, and volume), and the components of stand structure are used to estimate yield

- Stand-level: diameter-distribution prediction systems
- Distance-independent individual tree growth prediction
- Distance-dependent individual tree growth prediction
- Stand-table projection methods: hybrid

What models are used in the Southeastern U.S.?

Regional growth and yield research cooperatives:

Virginia Tech Growth and Yield Cooperative
TauYield-stand-level thinning response
TruLob-individual tree growth to thinning, fertilization, and hardwood control

Plantation Management Research Cooperative (PMRC)
Site-prepared plantations with thinning and fertilization
Explicit yield with yield breakdown functions
Implicit yield

NC State Managed Loblolly Pine Plantation Simulator
Implicit yield for thinning and hardwood competition

What models are used in the Southeastern U.S.?

Genetic effects are NOT included in these models

NCSU model can be modified for different height-age and volume equations

Why not?

Need 30+ trees/plot to develop models
Data from row plots generally not suited for model development
Rapid progression in tree improvement
Seed sources in 1960's
Half-sib open-pollinated tests in 1970's
Full-sib controlled pollinated families in 1980's
Clones in 1990's
Modern progeny tests are planted in noncontiguous blocks but still have only a few individuals of each family

---

Explicit System
Schumacher Variable-Density Yield

$$\ln(V_1) = \beta_0 + \beta_1 S + \beta_2 A_1^{-1} + \beta_3 \ln(BA_1)$$

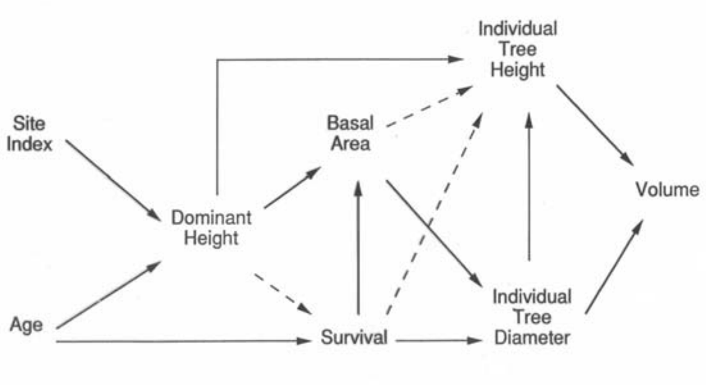
$$\ln(BA_2) = \left(\frac{A_1}{A_2}\right)\ln(BA_1) + \alpha_0\left(1 - \frac{A_1}{A_2}\right) + \alpha_1 S\left(1 - \frac{A_1}{A_2}\right)$$

$$\ln(V_2) = \ln(V_1) + \beta_2(A_2^{-1} - A_1^{-1}) + \beta_3\{\ln(BA_2) - \ln(BA_1)\}$$

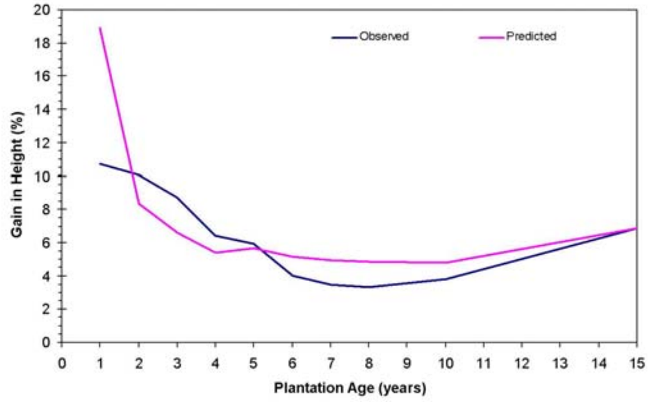
A_1= plantation age (years) at start of growth period
A_2= plantation age (years) at end of growth period
BA_1= basal area (ft^2/ac) at start of growth period
BA_2= basal area (ft^2/ac) at end of growth period
S= site index
V_1= volume (ft^3/ac) at start of growth period
V_2= volume (ft^3/ac) at end of growth period

Cao, Q.C., and Durand, K.M. 1991. A growth and yield model for improved cottonwood plantations in the lower Mississippi Delta. South. J. Appl. For. 15: 213-216.

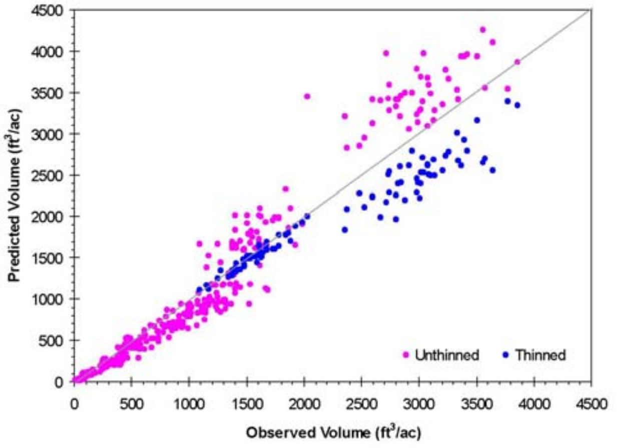
Implicit System With Interrelated Components



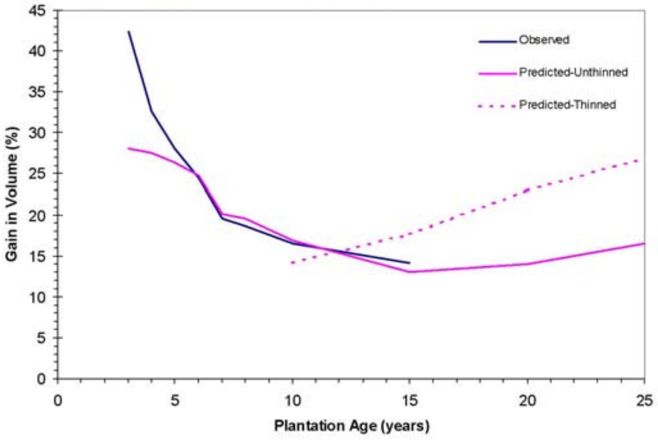
Height Gain in Loblolly Pine Open-Pollinated Test Using Family-Specific Height-Age Curves



Volume in Loblolly Pine Open-Pollinated Test Using Family-Specific Height-Age Curves in NSCU Model



Volume Gain in Loblolly Pine Open-Pollinated Test Using Family-Specific Height-Age Curves in NSCU Model



Implicit Yield: Diameter Distributions

$$p(D) = 1 - \exp\left\{-\left(\frac{D-a}{b}\right)^{c}\right\}$$

p(D) = cumulative probability of a diameter (D) less than or equal to D

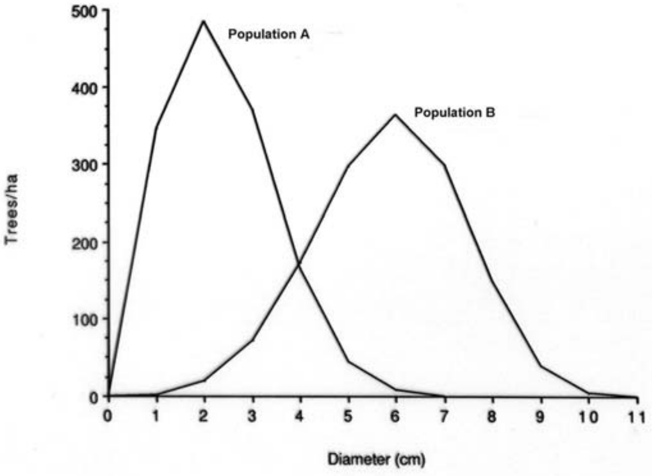
a = location parameter (minimum dbh)

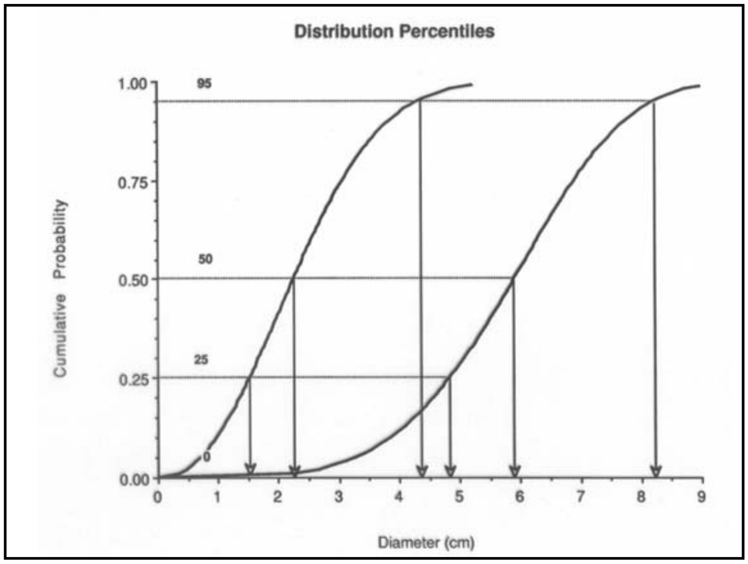
b = scale parameter (spread of distribution)

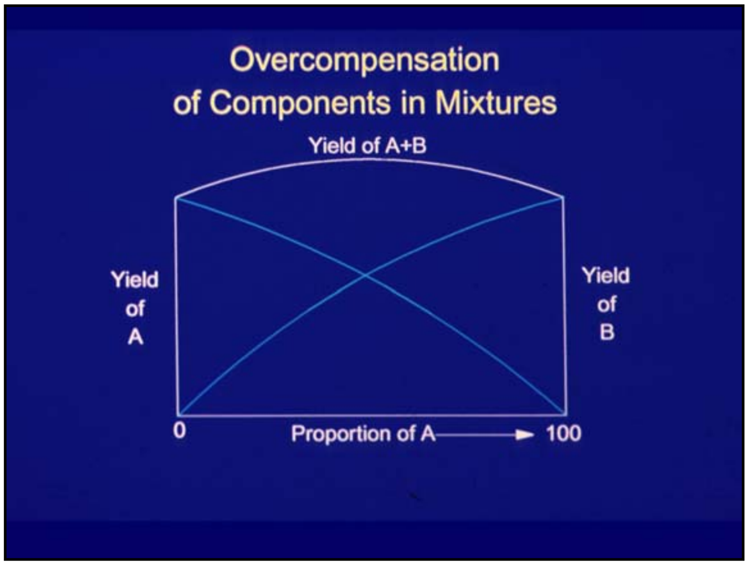
c = shape parameter (peakedness of distribution)

$$N_i = TPA\left[\exp\left\{-\left(\frac{D_L-a}{b}\right)^{c}\right\} - \exp\left\{-\left(\frac{D_U-a}{b}\right)^{c}\right\}\right]$$

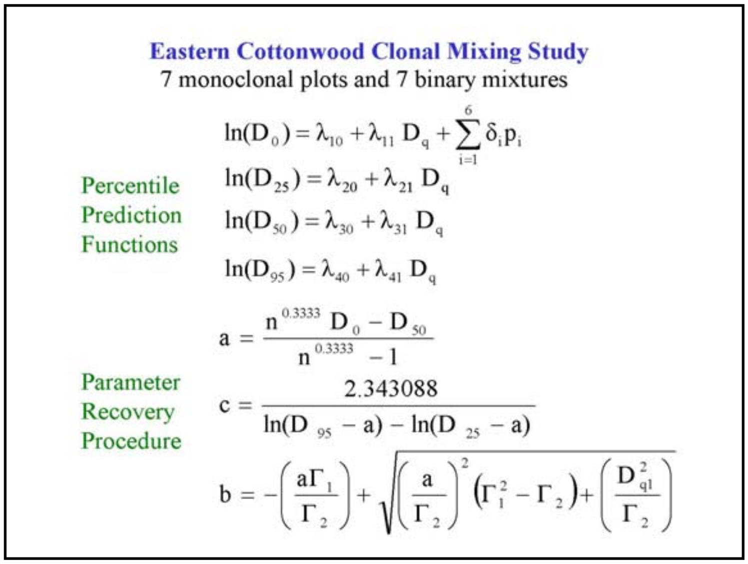
Diameter Distributions







Overcompensation of Components in Mixtures



Eastern Cottonwood Clonal Mixing Study

7 monoclonal plots and 7 binary mixtures

Percentile Prediction Functions

$$\ln(D_0) = \lambda_{10} + \lambda_{11}\, D_q + \sum_{i=1}^{6} \delta_i p_i$$

$$\ln(D_{25}) = \lambda_{20} + \lambda_{21}\, D_q$$

$$\ln(D_{50}) = \lambda_{30} + \lambda_{31}\, D_q$$

$$\ln(D_{95}) = \lambda_{40} + \lambda_{41}\, D_q$$

Parameter Recovery Procedure

$$a = \frac{n^{0.3333}\, D_0 - D_{50}}{n^{0.3333} - 1}$$

$$c = \frac{2.343088}{\ln(D_{95} - a) - \ln(D_{25} - a)}$$

$$b = -\left(\frac{a\Gamma_1}{\Gamma_2}\right) + \sqrt{\left(\frac{a}{\Gamma_2}\right)^2 \left(\Gamma_1^2 - \Gamma_2\right) + \left(\frac{D_{q1}^2}{\Gamma_2}\right)}$$

Eastern Cottonwood Clonal Mixing Study

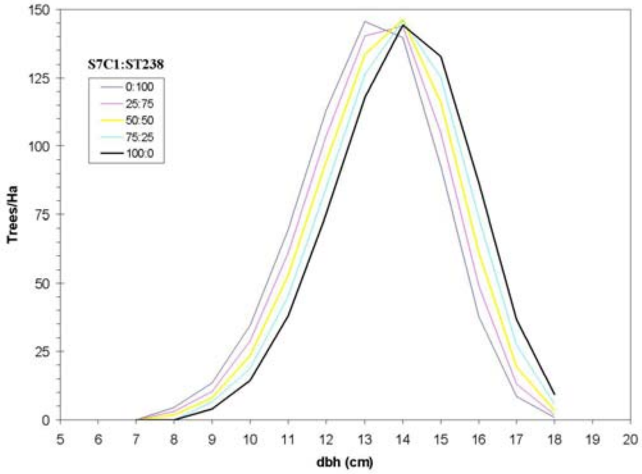
$$H_2 = H_1 \times \exp\left\{\left(\beta_0 + \beta_{01}L + \sum_{i=1}^{6}\beta_i p_i\right)\left(A_2^{-1} - A_1^{-1}\right)\right\}$$

$$BA = \alpha_0 N^{\alpha_1} H^{\alpha_2+\beta_{21}L} A^{\alpha_3} \times \exp\left\{\sum_{i=1}^{6}\theta_i p_i\right\}$$

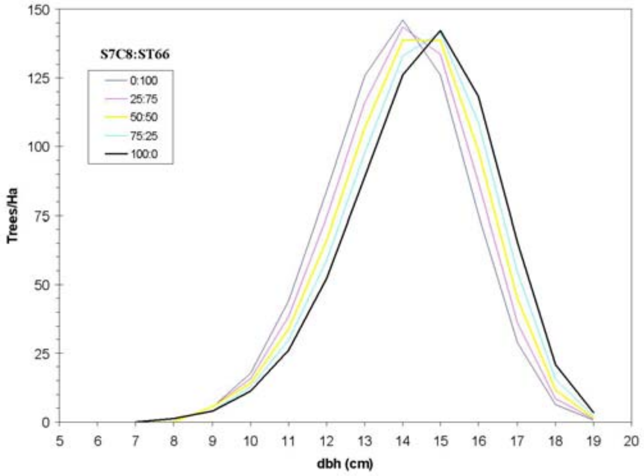
$$\text{with } 0 \le \sum_{i=1}^{6} p_i \le 1$$

Basal area model has 11 parameters
Interactions are not significant

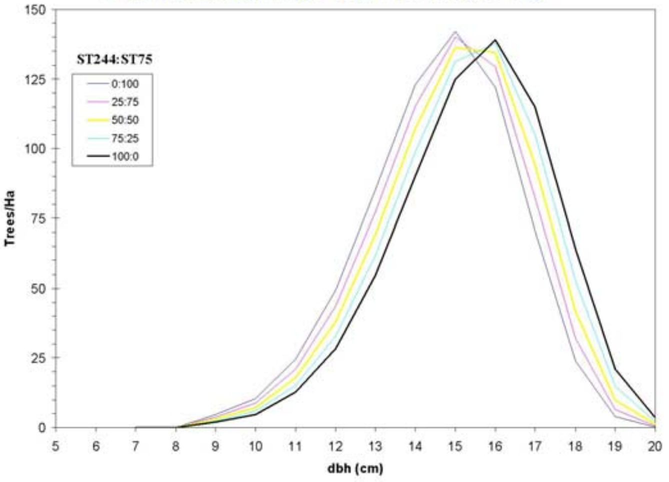
Eastern Cottonwood Clonal Mixing Study



Eastern Cottonwood Clonal Mixing Study



Eastern Cottonwood Clonal Mixing Study



Eastern Cottonwood Clonal Mixing Study

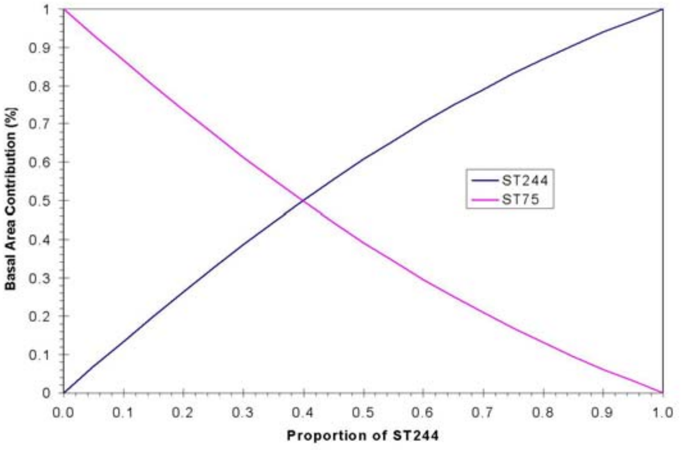
$$\text{Modifier} = \exp\left\{\begin{array}{l}\sum_{i=1}^{6}\alpha_i p_i + \sum_{j=4}^{5}(\alpha_{1j}p_j)p_1 + \sum_{k=5}^{6}(\alpha_{2k}p_k)p_2 \\ + \sum_{l=6}^{7}(\alpha_{3l}p_l)p_3 + (\alpha_{47}p_7)p_4\end{array}\right\}$$

$$= \exp\left\{\begin{array}{l}(\alpha_1 + \alpha_{14}p_4 + \alpha_{15}p_5)p_1 + (\alpha_2 + \alpha_{25}p_5 + \alpha_{26}p_6)p_2 + \\ (\alpha_3 + \alpha_{36}p_6 + \alpha_{37}p_7)p_3 + (\alpha_4 + \alpha_{47}p_7)p_4 + \\ \alpha_5 p_5 + \alpha_6 p_6\end{array}\right\}$$

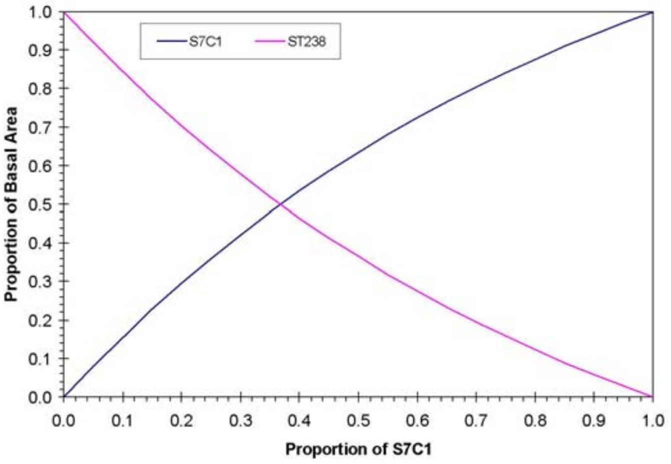
Basal area model with interactions has 18 parameters

Mixture model to provide Dewit diagrams with interactions has 4 coefficients x 7clones x2 mixtures
56 parameters

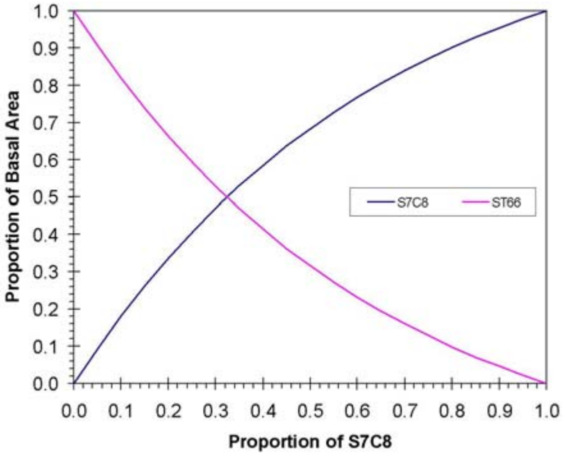
Eastern Cottonwood Clonal Mixing Study

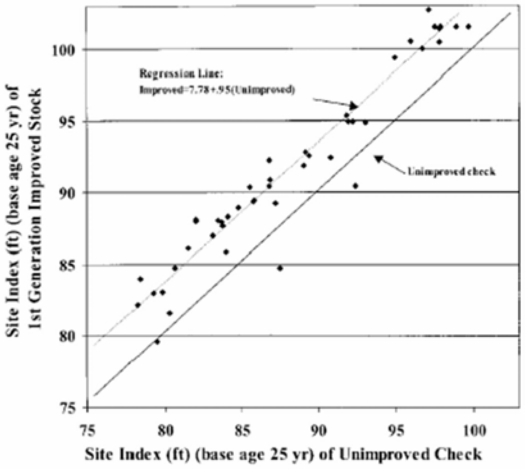


Eastern Cottonwood Clonal Mixing Study



Eastern Cottonwood Clonal Mixing Study





Lambeth, C. 2000. Realized genetic gains for first generation improved loblolly pine in 45 tests in coastal North Carolina. South. J. Appl. For. 24: 140-144.

Explicit Yield System for Loblolly Pine Open-Pollinated Test

$$H = S\{[1-\exp(-\theta_1 A)]/[1-\exp(-\theta_1 25)]\}^{\theta_2}$$

$$BA = \alpha_0 N^{\alpha_1+\alpha_{12}/A} H^{\alpha_2+\alpha_{22}/A} \exp\left\{A^{\alpha_3} + \alpha_4 \frac{A_T}{A}\frac{N_T}{N_B}\right\}$$

$$V = \beta_0 N^{\beta_1+\beta_{12}/A} H^{\beta_2+\beta_{22}/A} \exp\left\{A^{\beta_3} + \beta_4 \frac{A_T}{A}\frac{N_T}{N_B}\right\}$$

BA= basal area (ft^2/ac)
V= volume (ft^3/ac)
N= number of surviving trees/ac
A= plantation age (years)
H= dominant height (ft) and S=site index (base age 25)
A_T= plantation age (years) at time of thinning
N_T= number of trees/ac removed by thinning
N_B= number of trees/ac before thinning

Explicit Yield System for Loblolly Pine Open-Pollinated Test

Height-Age Curves

- Base: unimproved check
- Family-specific coefficients

Age Adjustment

$$Adj = +\varpi_1 A^{\varpi_2} \exp\{\varpi_3 A\}$$

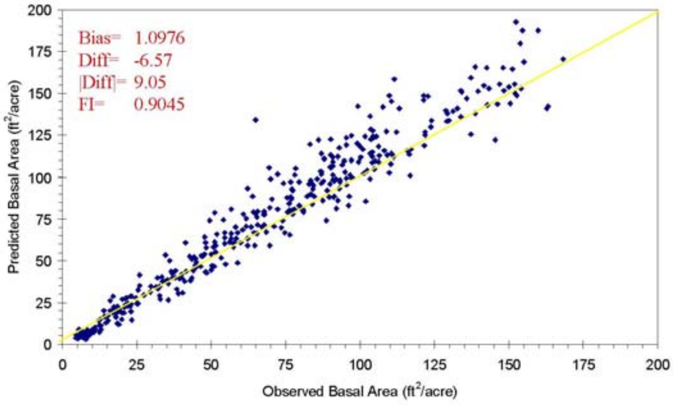
- Base: none (models fit to unimproved check only)
- All: 1 set of coefficients for all families
- Family-specific coefficients

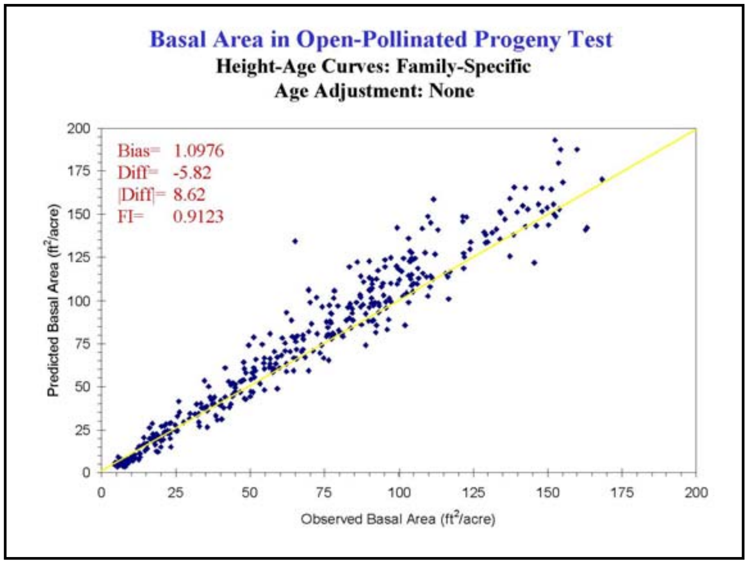
Height-Age Curves	Base	All	Family-Specific
Base	BaseSI: NoAdj	BaseSI: AllAdj	BaseSI: FamAdj
Family-specific	FamSI: NoAdj	FamSI: AllAdj	FamSI: FamAdj

Basal Area in Open-Pollinated Progeny Test

Height-Age Curves: Base (Unimproved Check)

Age Adjustment: None

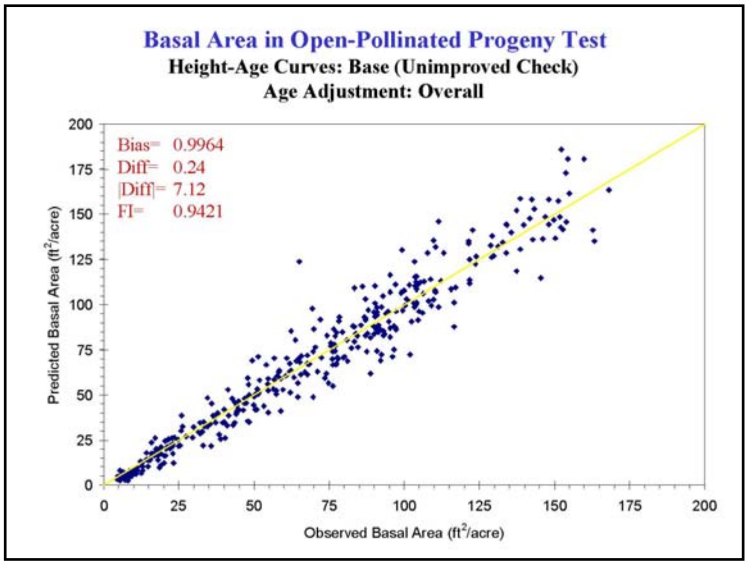




Basal Area in Open-Pollinated Progeny Test

Height-Age Curves: Family-Specific

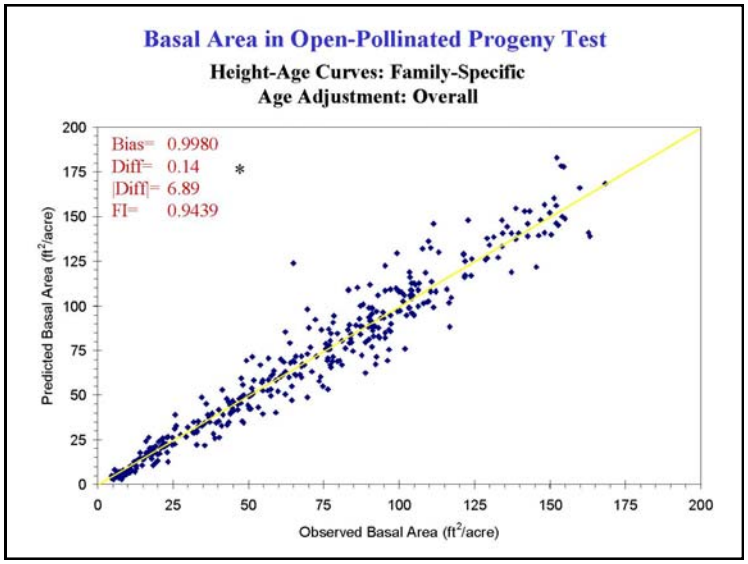
Age Adjustment: None



Basal Area in Open-Pollinated Progeny Test

Height-Age Curves: Base (Unimproved Check)

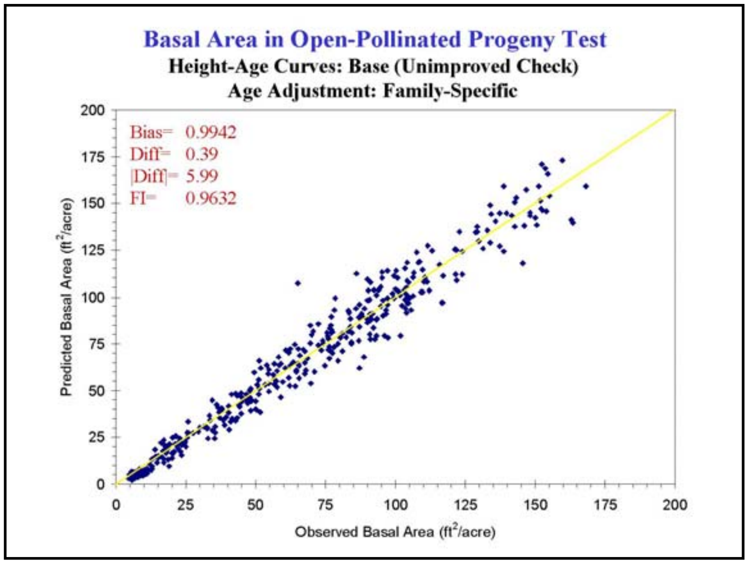
Age Adjustment: Overall

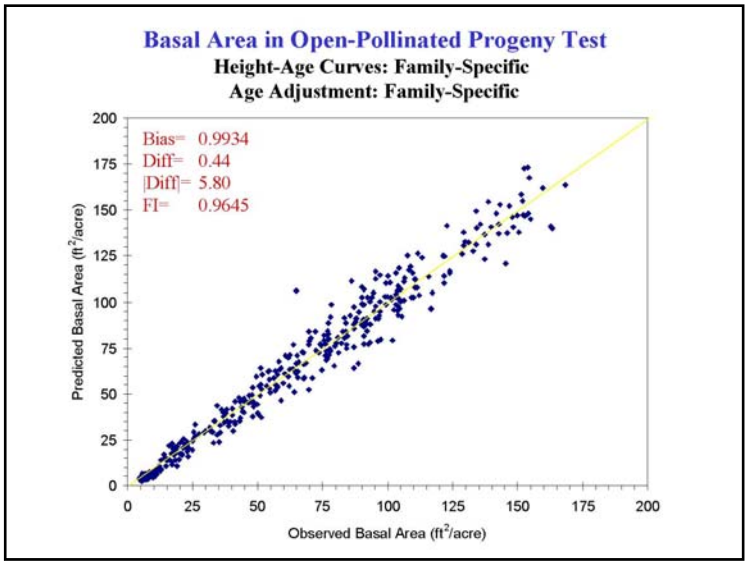


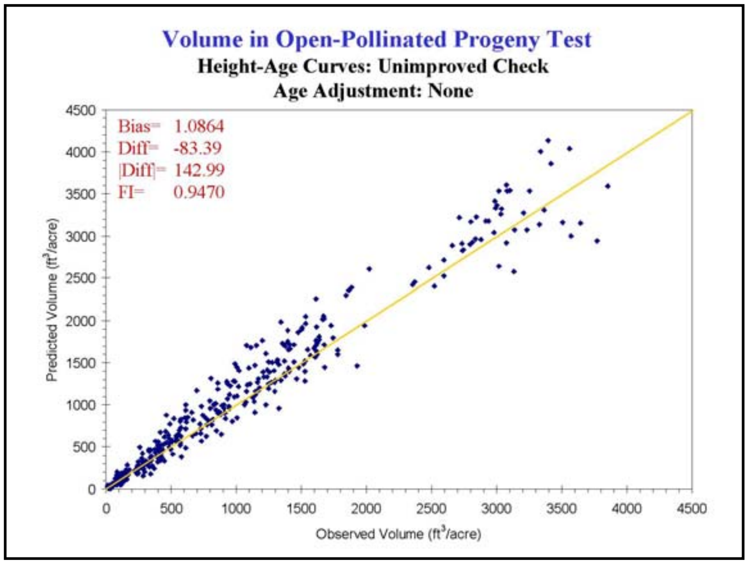
Basal Area in Open-Pollinated Progeny Test

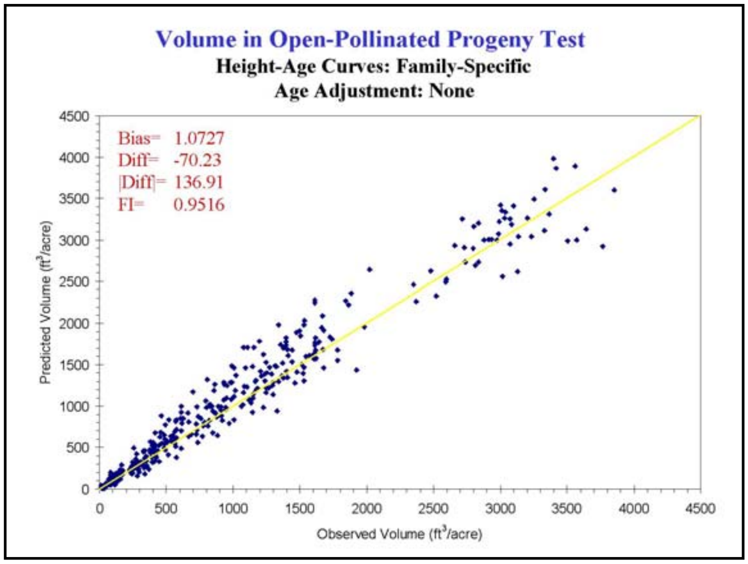
Height-Age Curves: Family-Specific

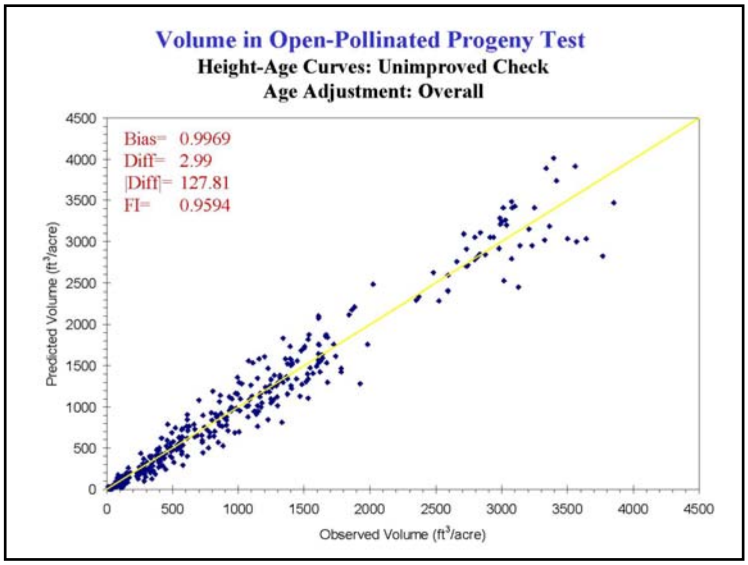
Age Adjustment: Overall

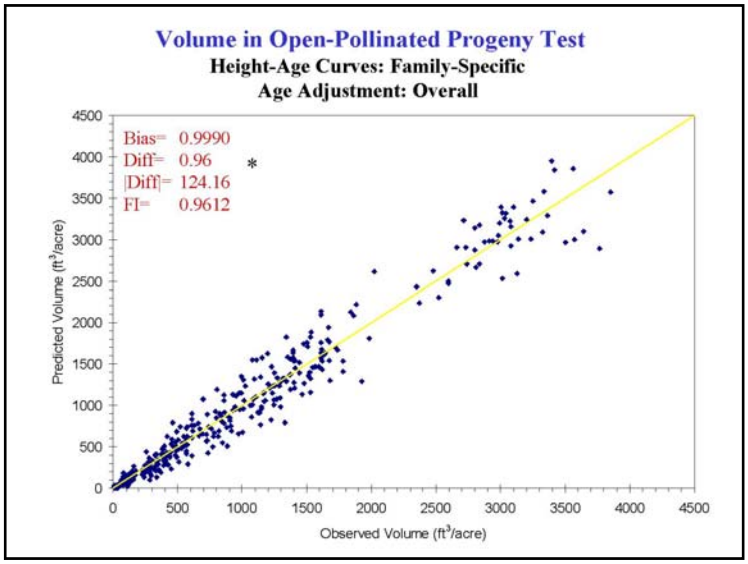

Basal Area in Open-Pollinated Progeny Test
Height-Age Curves: Base (Unimproved Check)
Age Adjustment: Family-Specific
Bias= 0.9942
Diff= 0.39
|Diff|= 5.99
FI= 0.9632
Predicted Basal Area (ft^2/acre)
Observed Basal Area (ft^2/acre)
0
25
50
75
100
125
150
175
200

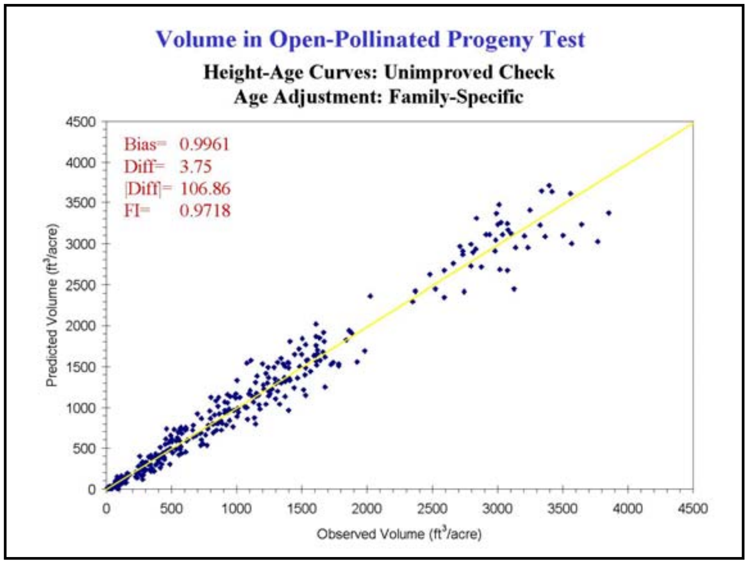

Basal Area in Open-Pollinated Progeny Test
Height-Age Curves: Family-Specific
Age Adjustment: Family-Specific
Bias= 0.9934
Diff= 0.44
|Diff|= 5.80
FI= 0.9645
Predicted Basal Area (ft^2/acre)
Observed Basal Area (ft^2/acre)
0
25
50
75
100
125
150
175
200


Volume in Open-Pollinated Progeny Test
Height-Age Curves: Unimproved Check
Age Adjustment: None
Bias= 1.0864
Diff= -83.39
|Diff|= 142.99
FI= 0.9470
Predicted Volume (ft^3/acre)
Observed Volume (ft^3/acre)
0
500
1000
1500
2000
2500
3000
3500
4000
4500


Volume in Open-Pollinated Progeny Test
Height-Age Curves: Family-Specific
Age Adjustment: None


Volume in Open-Pollinated Progeny Test
Height-Age Curves: Unimproved Check
Age Adjustment: Overall

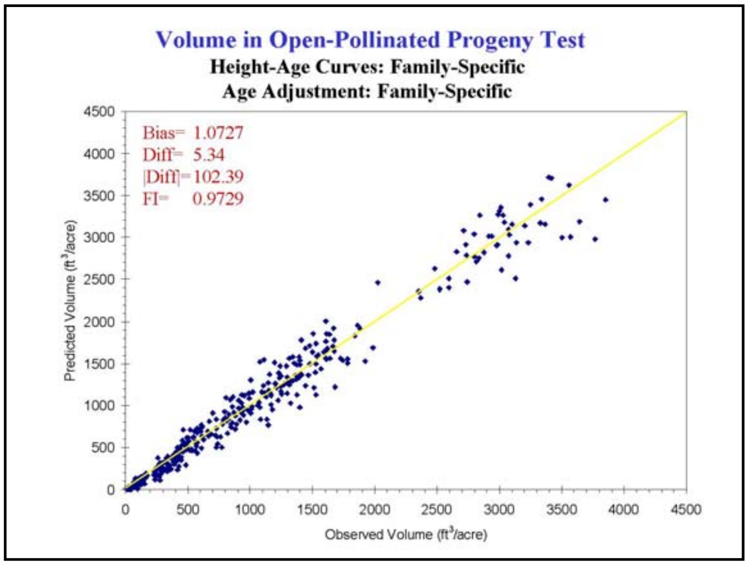

Volume in Open-Pollinated Progeny Test
Height-Age Curves: Family-Specific
Age Adjustment: Overall



Volume in Open-Pollinated Progeny Test

Height-Age Curves: Unimproved Check
Age Adjustment: Family-Specific

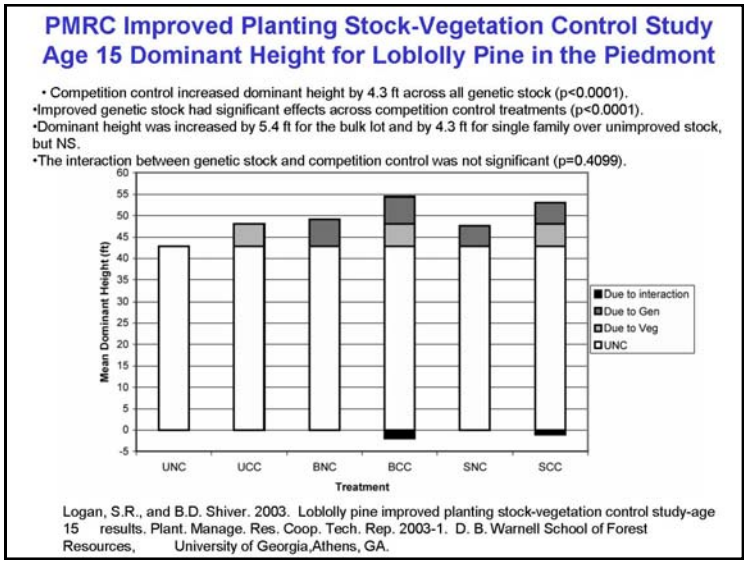
Bias= 0.9961
Diff= 3.75
|Diff|= 106.86
FI= 0.9718



Volume in Open-Pollinated Progeny Test

Height-Age Curves: Family-Specific
Age Adjustment: Family-Specific

Bias= 1.0727
Diff= 5.34
|Diff|=102.39
FI= 0.9729

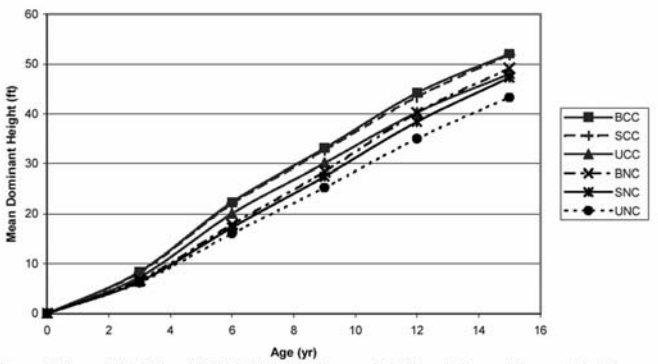


PMRC Improved Planting Stock-Vegetation Control Study Age 15 Dominant Height for Loblolly Pine in the Piedmont

- Competition control increased dominant height by 4.3 ft across all genetic stock ($p<0.0001$).
- Improved genetic stock had significant effects across competition control treatments ($p<0.0001$).
- Dominant height was increased by 5.4 ft for the bulk lot and by 4.3 ft for single family over unimproved stock, but NS.
- The interaction between genetic stock and competition control was not significant ($p=0.4099$).

Logan, S.R., and B.D. Shiver. 2003. Loblolly pine improved planting stock-vegetation control study-age 15 results. Plant. Manage. Res. Coop. Tech. Rep. 2003-1. D. B. Warnell School of Forest Resources, University of Georgia,Athens, GA.

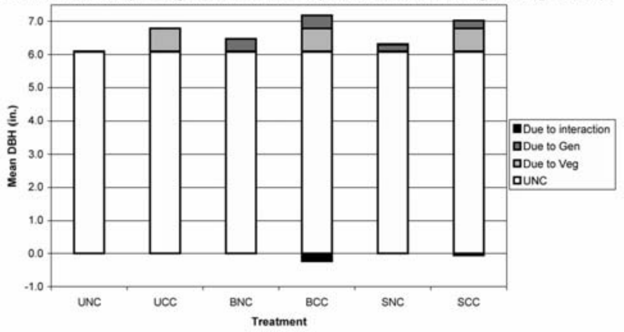
PMRC Improved Planting Stock-Vegetation Control Study
Dominant Height of Loblolly Pine in the Piedmont



Logan, S.R., and B.D. Shiver. 2003. Loblolly pine improved planting stock-vegetation control study-age 15 results. Plant. Manage. Res. Coop. Tech. Rep. 2003-1. D. B. Warnell School of Forest Resources, University of Georgia,Athens, GA.

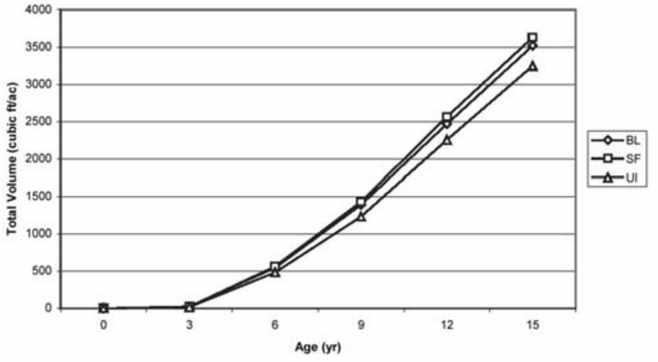
PMRC Improved Planting Stock-Vegetation Control Study
Age 15 DBH for Loblolly Pine in the Piedmont

- Competition control significantly increased average dbh by 0.7 in. across all genetic stock. ($p<0.0001$).
- Genetic effects were significant ($p=0.0126$), but no significant difference detected between bulk lot and single fa
- Bulk lot increased average dbh by 0.28 in. and single family increased average dbh by 0.19 in over unimproved
- The interaction between improved genetic stock and competition control was not significant ($p=0.4207$).



Logan, S.R., and B.D. Shiver. 2003. Loblolly pine improved planting stock-vegetation control study-age 15 results. Plant. Manage. Res. Coop. Tech. Rep. 2003-1. D. B. Warnell School of Forest Resources, University of Georgia,Athens, GA.

PMRC Improved Planting Stock-Vegetation Control Study
Total Volume of Loblolly Pine in the Piedmont



Logan, S.R., and B.D. Shiver. 2003. Loblolly pine improved planting stock-vegetation control study-age 15 results. Plant. Manage. Res. Coop. Tech. Rep. 2003-1. D. B. Warnell School of Forest Resources, University of Georgia,Athens, GA.

PMRC Improved Planting Stock-Vegetation Control Study
Stem Quality of Loblolly Pine in the Piedmont

Source	Fusifor mRust	Forked trees	Sweep
Genetics	<.0001 (-)	0.2532	0.0035 (-)
Competition Control	0.5554	0.0009 (+)	0.1517
Genetics* Competition	0.4057	0.2202	0.5005

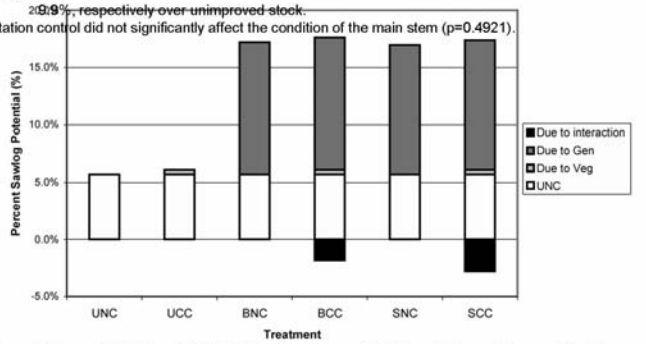
Logan, S.R., and B.D. Shiver. 2003. Loblolly pine improved planting stock-vegetation control study-age 15 results. Plant. Manage. Res. Coop. Tech. Rep. 2003-1. D. B. Warnell School of Forest Resources, University of Georgia,Athens, GA.

PMRC Improved Planting Stock-Vegetation Control Study
Sawlog Potential of Loblolly Pine in the Piedmont

Genetic improvement increased the percentage of trees that were free from defects on the main bole (p<0.0001).

There were no significant differences between bulk lot and single family, but defects were decreased by 10.6% and 9.9%, respectively over unimproved stock.

Vegetation control did not significantly affect the condition of the main stem (p=0.4921).



Logan, S.R., and B.D. Shiver. 2003. Loblolly pine improved planting stock-vegetation control study-age 15 results. Plant. Manage. Res. Coop. Tech. Rep. 2003-1. D. B. Warnell School of Forest Resources, University of Georgia,Athens, GA.

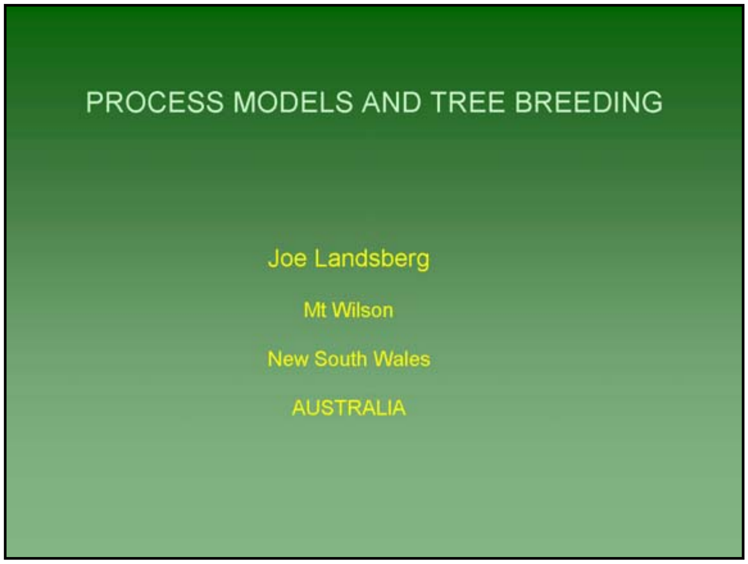
Process models and tree breeding

Joe Landsberg
Mt Wilson, NSW, Australia

Process-based simulation models describe the essential features of systems such as forest stands in terms of the (physiological) processes that determine the way the systems behave and respond to change. These processes include the absorption of solar energy (light) by plants, the conversion of this energy into carbohydrate by the process of photosynthesis and the allocation of the carbohydrate (biomass) to the component parts of the plants. Models have to account for losses by respiration and the way these processes are modified by environmental conditions. Breeders have relatively limited opportunities to improve productivity: light interception can be changed by changing canopy structure (this can also be done by stand management); photosynthesis is conservative and not amenable to modification except (possibly) through stomata; it is possible to modify frost and drought tolerance, but these relate more to ecological location and climatic probabilities than growth and yield improvement in a particular location. The best candidate for genetic modification appears to be biomass distribution to roots and stems.

Process-based models (PBMs) can be used to explore the feasible limits of possible modifications and 'genetic gain', provided the genetic gain can be described in terms of processes amenable to quantitative description. (If it cannot, we have to ask: through what process are the genes modifying growth?). PBMs can also be used to explore the effects of environment on the growth of trees/stands, and hence should be able to contribute to evaluation of genotype x environment interaction. In this presentation the 3-PG model (Landsberg and Waring, 1997) is used to illustrate some likely results of genetic modification and to provide a basis for more detailed discussion.

Hybrid models – which combine PBMs and conventional mensuration-based models – appear to offer the most promising tool for assisting tree breeders to analyze the options for change and its possible consequences. Progress is likely to be most rapid if physiologists and process modelers work with tree breeders and statisticians.



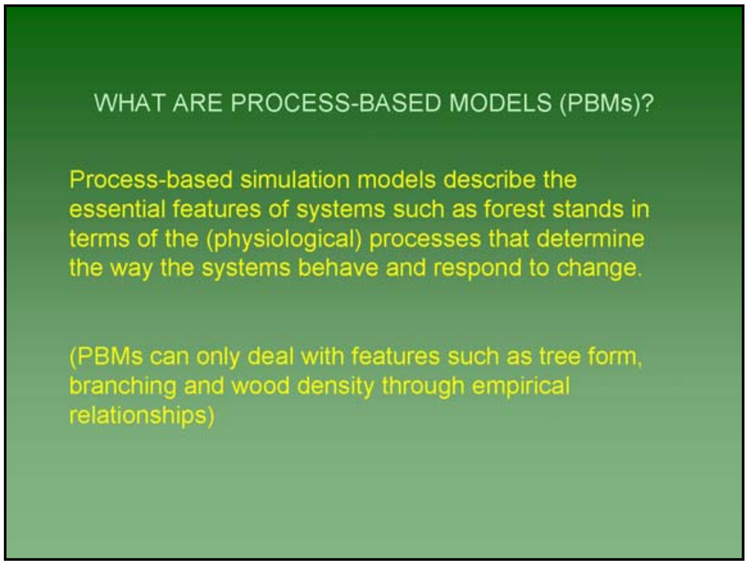
PROCESS MODELS AND TREE BREEDING

Joe Landsberg

Mt Wilson

New South Wales

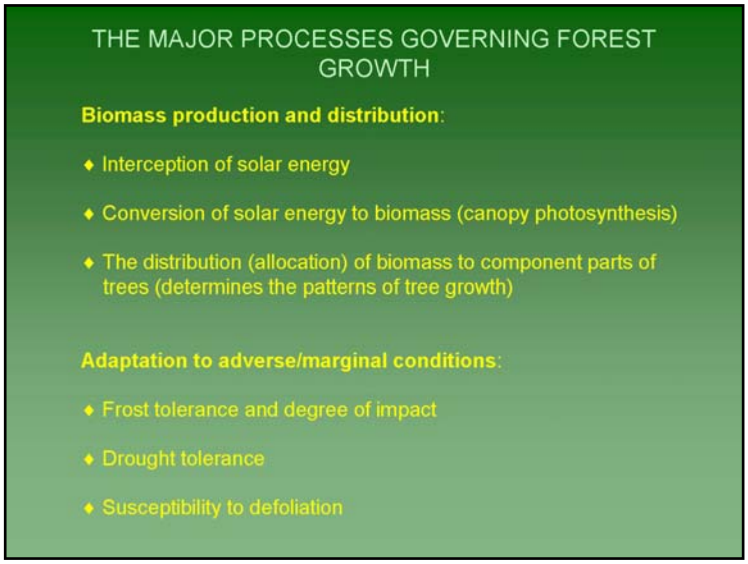
AUSTRALIA



WHAT ARE PROCESS-BASED MODELS (PBMs)?

Process-based simulation models describe the essential features of systems such as forest stands in terms of the (physiological) processes that determine the way the systems behave and respond to change.

(PBMs can only deal with features such as tree form, branching and wood density through empirical relationships)



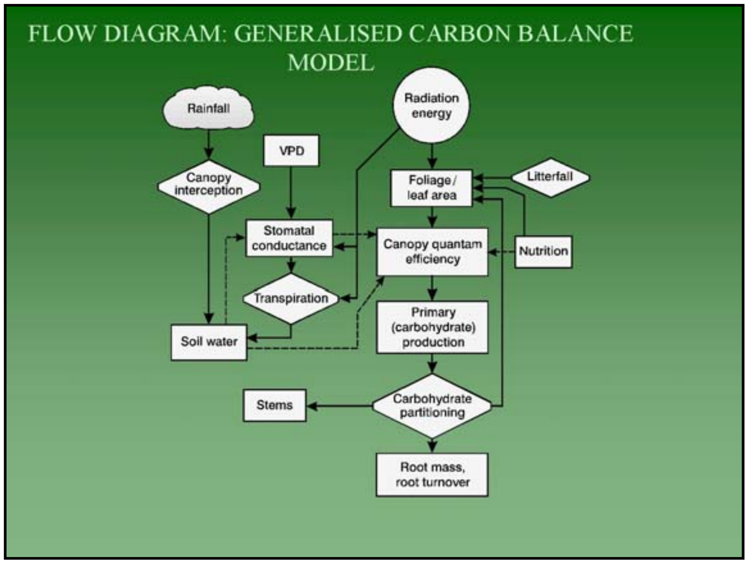
THE MAJOR PROCESSES GOVERNING FOREST GROWTH

Biomass production and distribution:

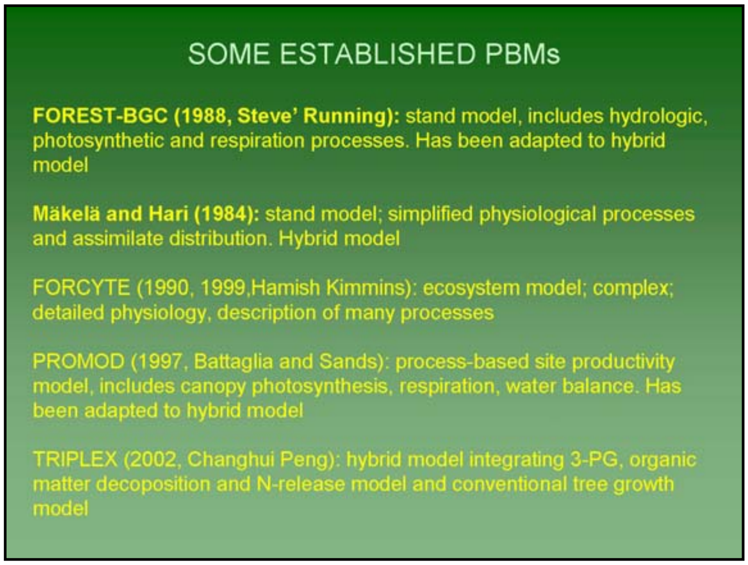
- Interception of solar energy
- Conversion of solar energy to biomass (canopy photosynthesis)
- The distribution (allocation) of biomass to component parts of trees (determines the patterns of tree growth)

Adaptation to adverse/marginal conditions:

- Frost tolerance and degree of impact
- Drought tolerance
- Susceptibility to defoliation



FLOW DIAGRAM: GENERALISED CARBON BALANCE MODEL



SOME ESTABLISHED PBMs

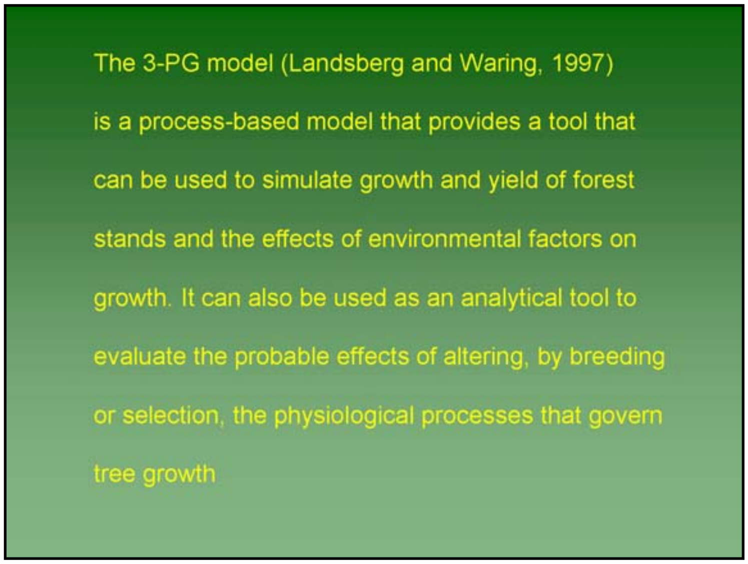
FOREST-BGC (1988, Steve' Running): stand model, includes hydrologic, photosynthetic and respiration processes. Has been adapted to hybrid model

Mäkelä and Hari (1984): stand model; simplified physiological processes and assimilate distribution. Hybrid model

FORCYTE (1990, 1999,Hamish Kimmins): ecosystem model; complex; detailed physiology, description of many processes

PROMOD (1997, Battaglia and Sands): process-based site productivity model, includes canopy photosynthesis, respiration, water balance. Has been adapted to hybrid model

TRIPLEX (2002, Changhui Peng): hybrid model integrating 3-PG, organic matter decoposition and N-release model and conventional tree growth model



The 3-PG model (Landsberg and Waring, 1997) is a process-based model that provides a tool that can be used to simulate growth and yield of forest stands and the effects of environmental factors on growth. It can also be used as an analytical tool to evaluate the probable effects of altering, by breeding or selection, the physiological processes that govern tree growth

MAIN COMPONENTS OF 3-PG

Production of biomass – Based on environmental modification of light use efficiency and constant ratio of NPP to GPP.

Biomass partitioning – Affected by growing conditions and tree size.

Stem mortality – Based on self-thinning rule.

Soil water balance – A single soil layer model with evapo-transpiration determined from Penman-Monteith equation.

Stand properties – Determined from biomass pools and assumptions about specific leaf area, branch+bark fraction, and wood density.

To establish confidence in the performance of the model, and its use as an analytical tool, the following slides illustrate its performance

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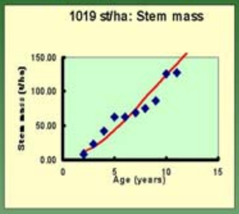
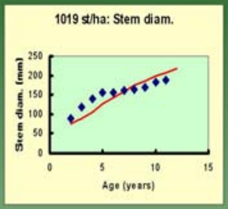
THE 3-PG MODEL: CALIBRATION

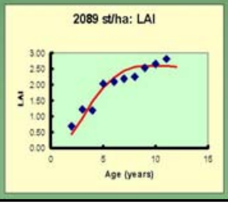
Stem mass, stem diameter and LAI
calculated with single set of best-fit parameters.
Eucalyptus grandis spacing trial, Swaziland, southern Africa



1019 st/ha: Stem mass



1019 st/ha: Stem diam.



2089 st/ha: LAI

Data courtesy of Dr Peter Dye, Environmentek, CSIR, Natal, South Africa

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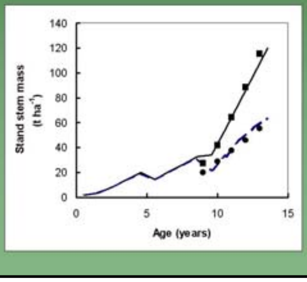
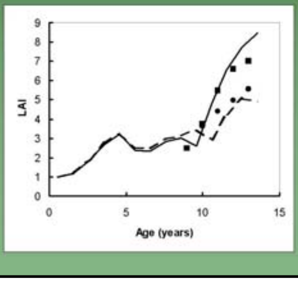
THE 3-PG MODEL: VALIDATION

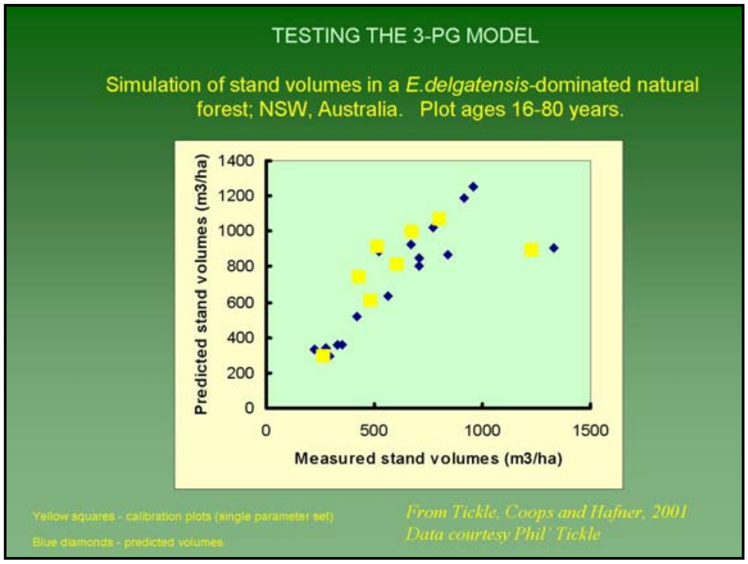
Stand stem mass and LAI,
Pinus radiata, Australian Capital Territory

Control - lower lines
Irrigated+fertilized - upper lines

Simulations, lines.
Points are measured values







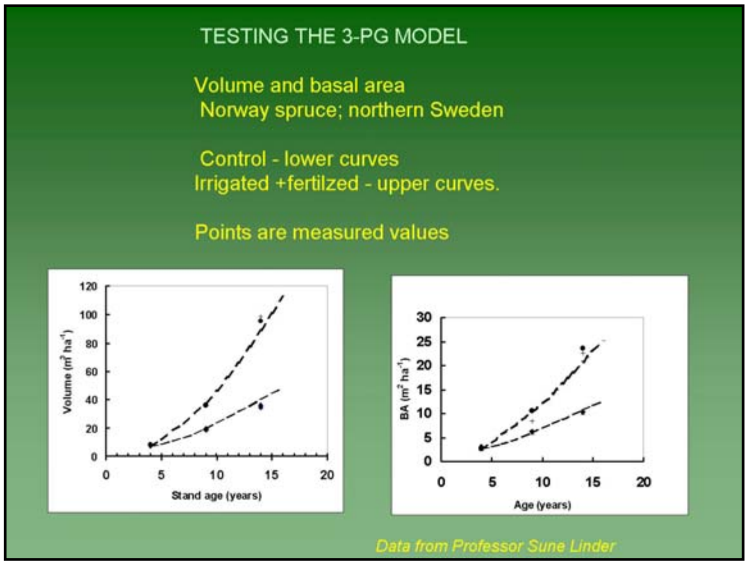
TESTING THE 3-PG MODEL

Simulation of stand volumes in a *E.delgatensis*-dominated natural forest; NSW, Australia.   Plot ages 16-80 years.

Yellow squares - calibration plots (single parameter set)

Blue diamonds - predicted volumes

From Tickle, Coops and Hafner, 2001
Data courtesy Phil' Tickle



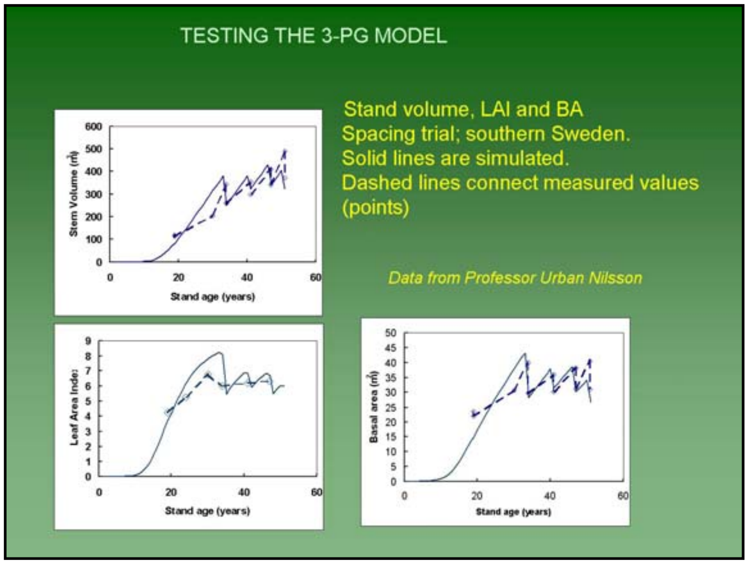
TESTING THE 3-PG MODEL

Volume and basal area
Norway spruce; northern Sweden

Control - lower curves
Irrigated +fertilzed - upper curves.

Points are measured values

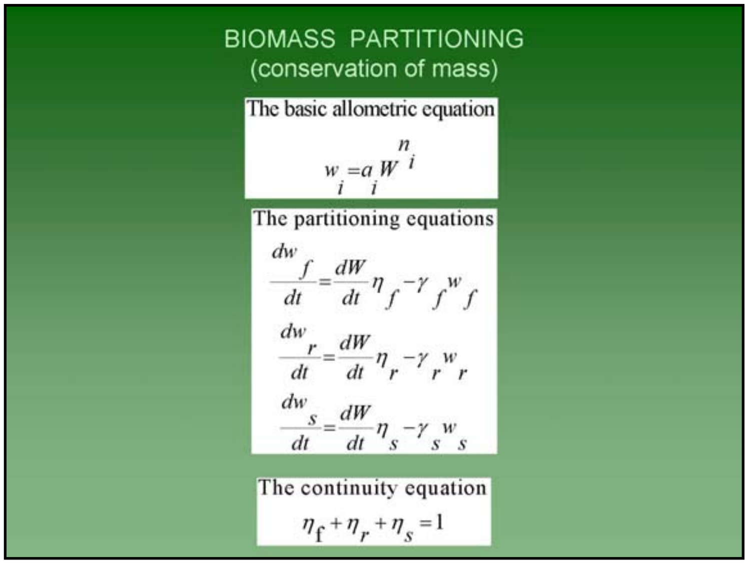
Data from Professor Sune Linder



TESTING THE 3-PG MODEL

Stand volume, LAI and BA
Spacing trial; southern Sweden.
Solid lines are simulated.
Dashed lines connect measured values (points)

Data from Professor Urban Nilsson



BIOMASS PARTITIONING
(conservation of mass)

The basic allometric equation

$$w_i = a_i W^{n_i}$$

The partitioning equations

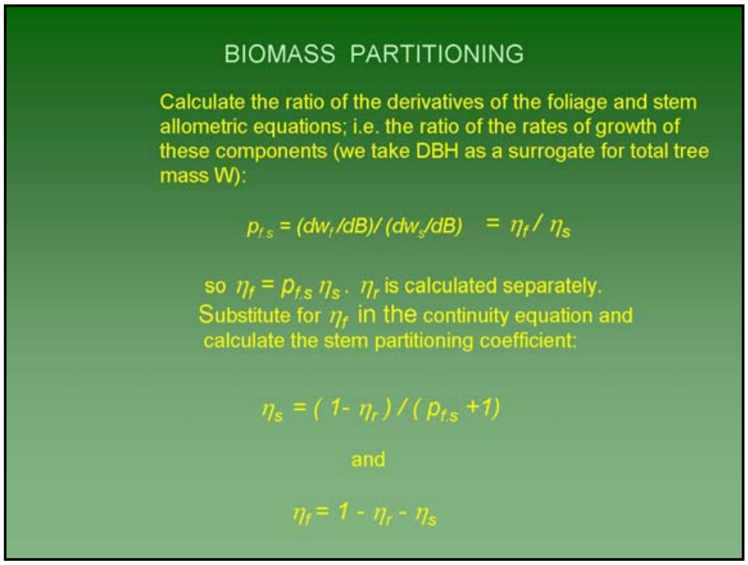
$$\frac{dw_f}{dt} = \frac{dW}{dt}\eta_f - \gamma_f w_f$$

$$\frac{dw_r}{dt} = \frac{dW}{dt}\eta_r - \gamma_r w_r$$

$$\frac{dw_s}{dt} = \frac{dW}{dt}\eta_s - \gamma_s w_s$$

The continuity equation

$$\eta_f + \eta_r + \eta_s = 1$$



BIOMASS PARTITIONING

Calculate the ratio of the derivatives of the foliage and stem allometric equations; i.e. the ratio of the rates of growth of these components (we take DBH as a surrogate for total tree mass W):

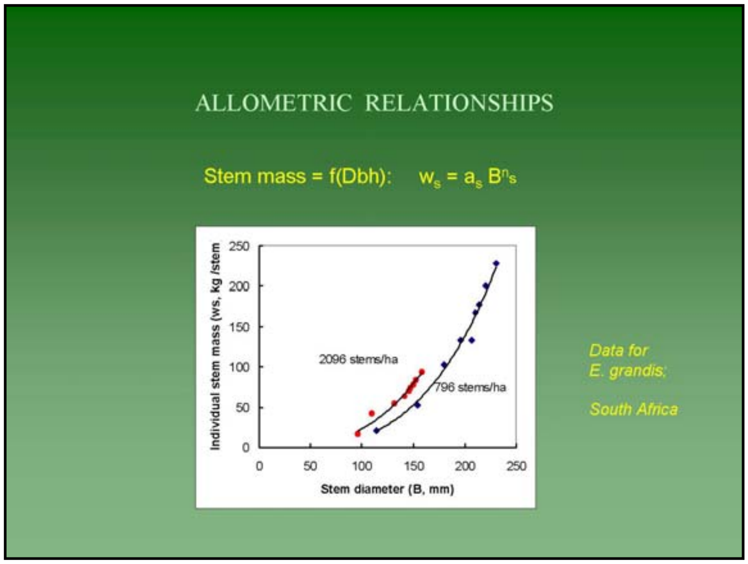
$$p_{f.s} = (dw_f/dB)/(dw_s/dB) = \eta_f / \eta_s$$

so $\eta_f = p_{f.s}\,\eta_s$. η_r is calculated separately. Substitute for η_f in the continuity equation and calculate the stem partitioning coefficient:

$$\eta_s = (1 - \eta_r) / (p_{f.s} + 1)$$

and

$$\eta_f = 1 - \eta_r - \eta_s$$

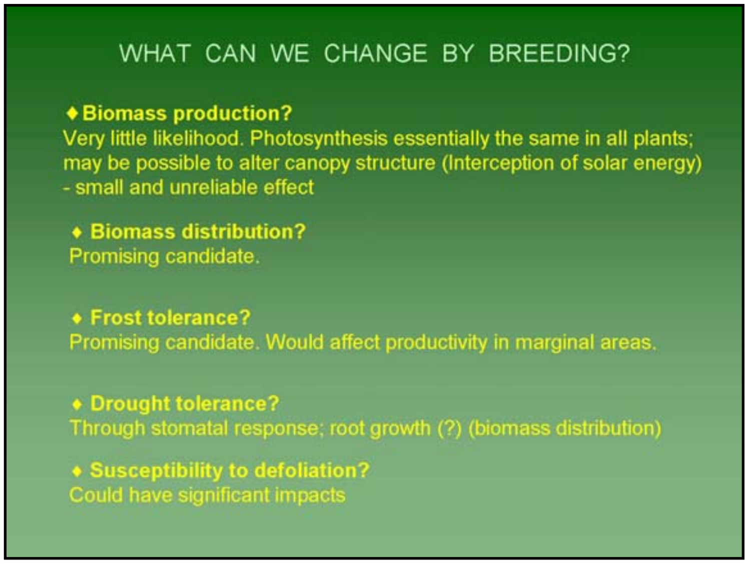


ALLOMETRIC RELATIONSHIPS

Stem mass = f(Dbh): $w_s = a_s B^{n_s}$

Data for *E. grandis*;

South Africa



WHAT CAN WE CHANGE BY BREEDING?

- **Biomass production?**

Very little likelihood. Photosynthesis essentially the same in all plants; may be possible to alter canopy structure (Interception of solar energy) - small and unreliable effect

- **Biomass distribution?**

Promising candidate.

- **Frost tolerance?**

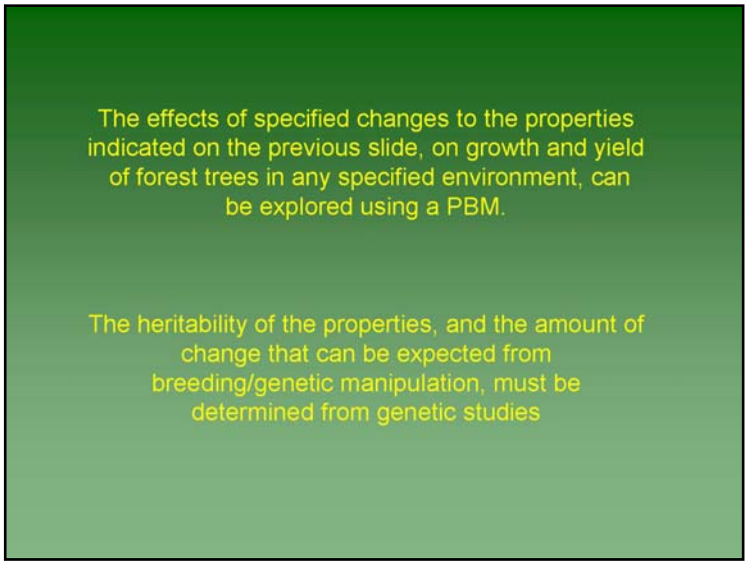
Promising candidate. Would affect productivity in marginal areas.

- **Drought tolerance?**

Through stomatal response; root growth (?) (biomass distribution)

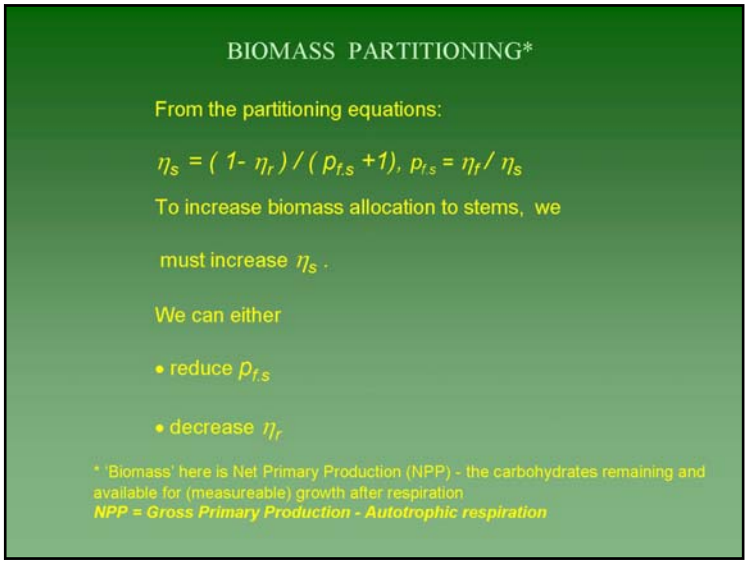
- **Susceptibility to defoliation?**

Could have significant impacts



The effects of specified changes to the properties indicated on the previous slide, on growth and yield of forest trees in any specified environment, can be explored using a PBM.

The heritability of the properties, and the amount of change that can be expected from breeding/genetic manipulation, must be determined from genetic studies



BIOMASS PARTITIONING*

From the partitioning equations:

$\eta_s = (1-\eta_r)/(p_{f.s}+1)$, $p_{f.s} = \eta_f/\eta_s$

To increase biomass allocation to stems, we

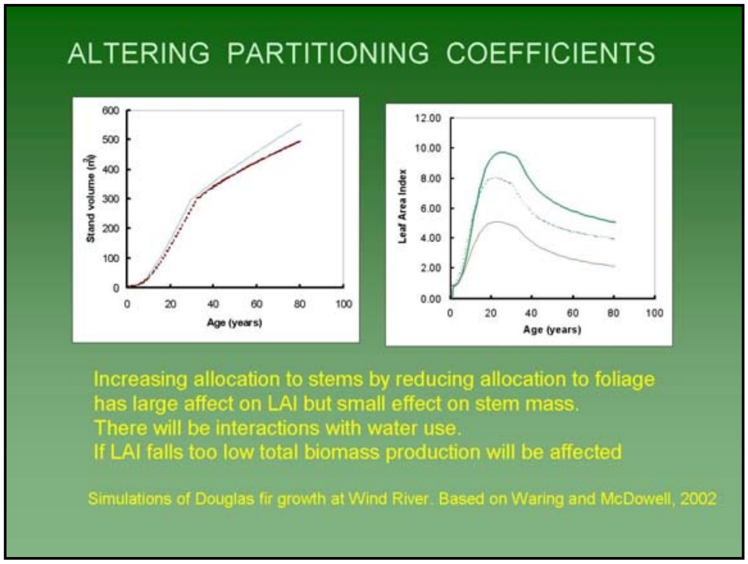
must increase η_s .

We can either

- reduce $p_{f.s}$
- decrease η_r

* 'Biomass' here is Net Primary Production (NPP) - the carbohydrates remaining and available for (measureable) growth after respiration

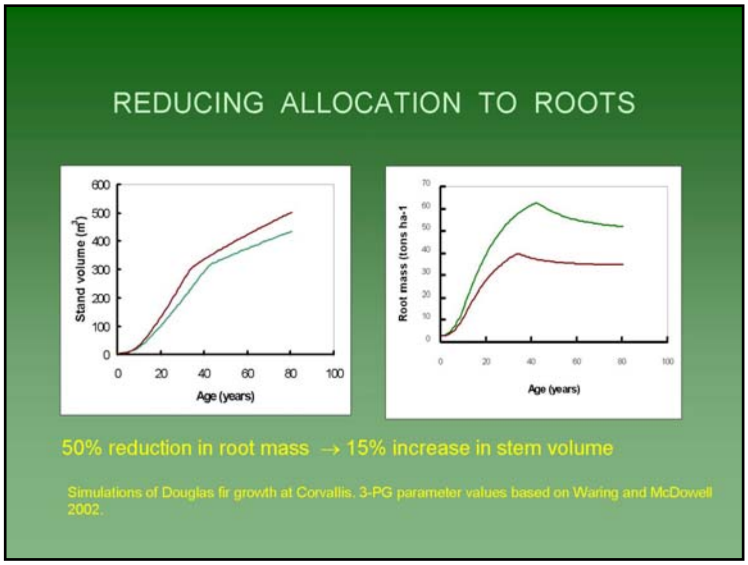
NPP = Gross Primary Production - Autotrophic respiration



ALTERING PARTITIONING COEFFICIENTS

Increasing allocation to stems by reducing allocation to foliage has large affect on LAI but small effect on stem mass.
There will be interactions with water use.
If LAI falls too low total biomass production will be affected

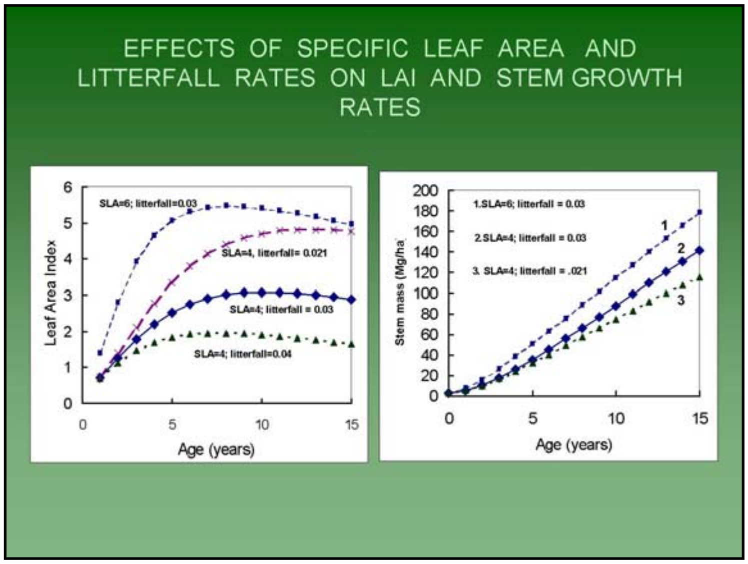
Simulations of Douglas fir growth at Wind River. Based on Waring and McDowell, 2002



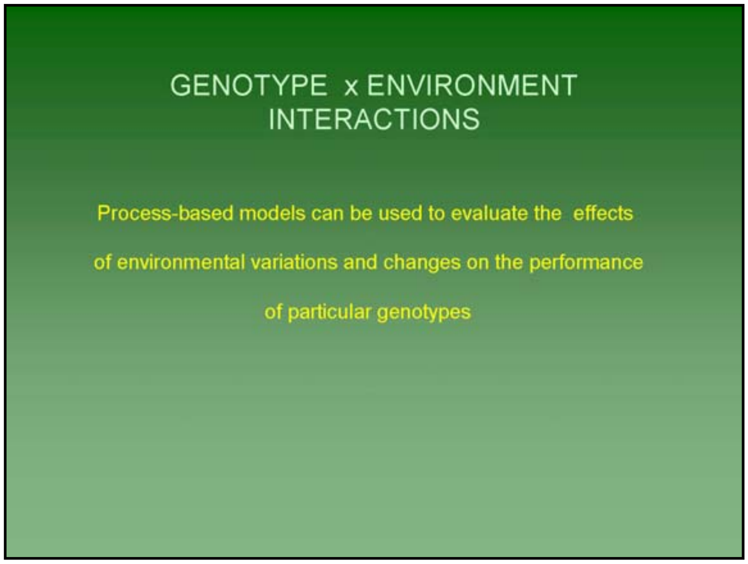
REDUCING ALLOCATION TO ROOTS

50% reduction in root mass → 15% increase in stem volume

Simulations of Douglas fir growth at Corvallis. 3-PG parameter values based on Waring and McDowell 2002.

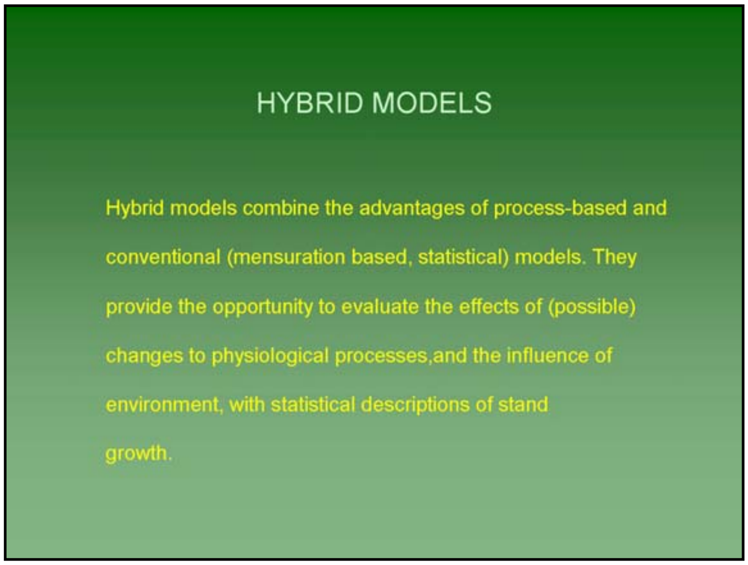


EFFECTS OF SPECIFIC LEAF AREA AND LITTERFALL RATES ON LAI AND STEM GROWTH RATES



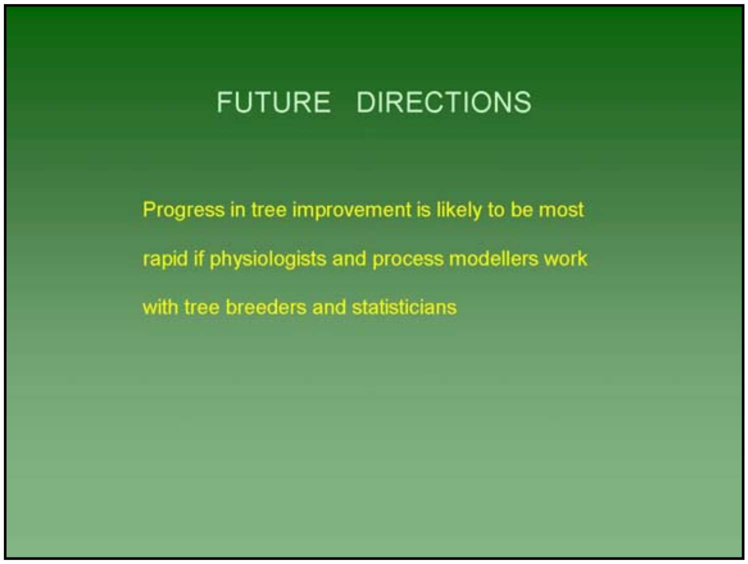
GENOTYPE x ENVIRONMENT INTERACTIONS

Process-based models can be used to evaluate the effects of environmental variations and changes on the performance of particular genotypes



HYBRID MODELS

Hybrid models combine the advantages of process-based and conventional (mensuration based, statistical) models. They provide the opportunity to evaluate the effects of (possible) changes to physiological processes,and the influence of environment, with statistical descriptions of stand growth.

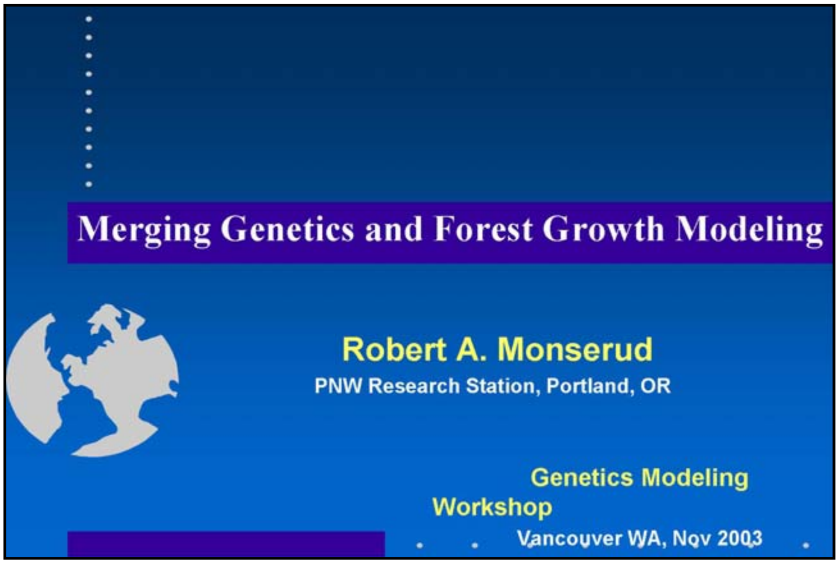


FUTURE DIRECTIONS

Progress in tree improvement is likely to be most rapid if physiologists and process modellers work with tree breeders and statisticians

Merging genetics and forest growth modeling

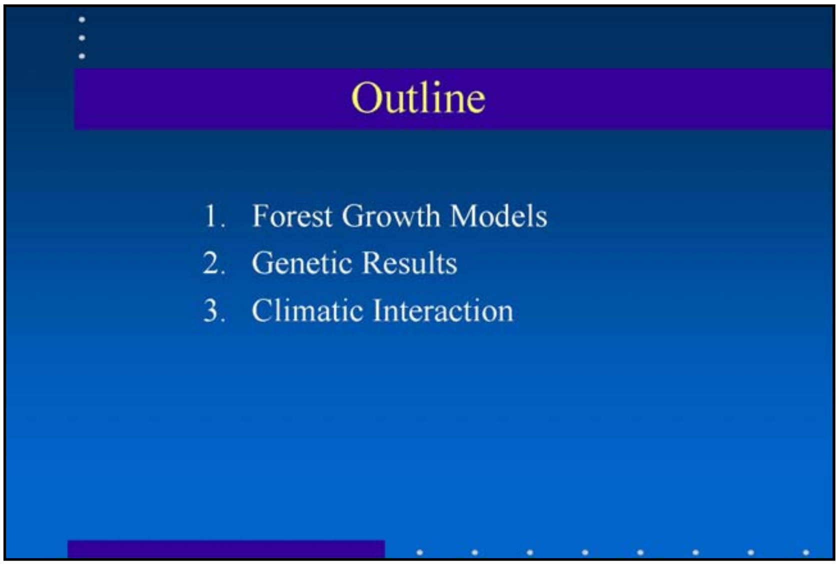
Robert A. Monserud
USFS Pacific Northwest Research Station
Portland, Oregon



Merging Genetics and Forest Growth Modeling

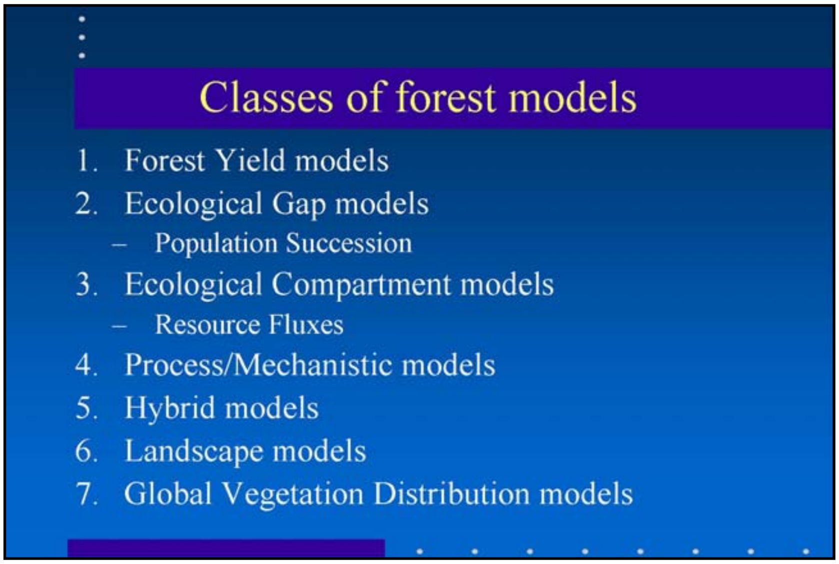
Robert A. Monserud
PNW Research Station, Portland, OR

Genetics Modeling Workshop
Vancouver WA, Nov 2003



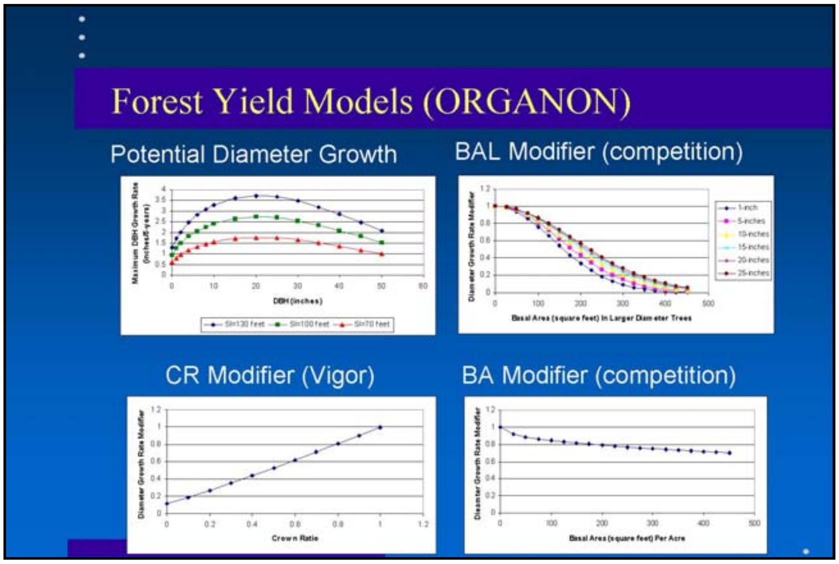
Outline

1. Forest Growth Models
2. Genetic Results
3. Climatic Interaction



Classes of forest models

1. Forest Yield models
2. Ecological Gap models
   - Population Succession
3. Ecological Compartment models
   - Resource Fluxes
4. Process/Mechanistic models
5. Hybrid models
6. Landscape models
7. Global Vegetation Distribution models



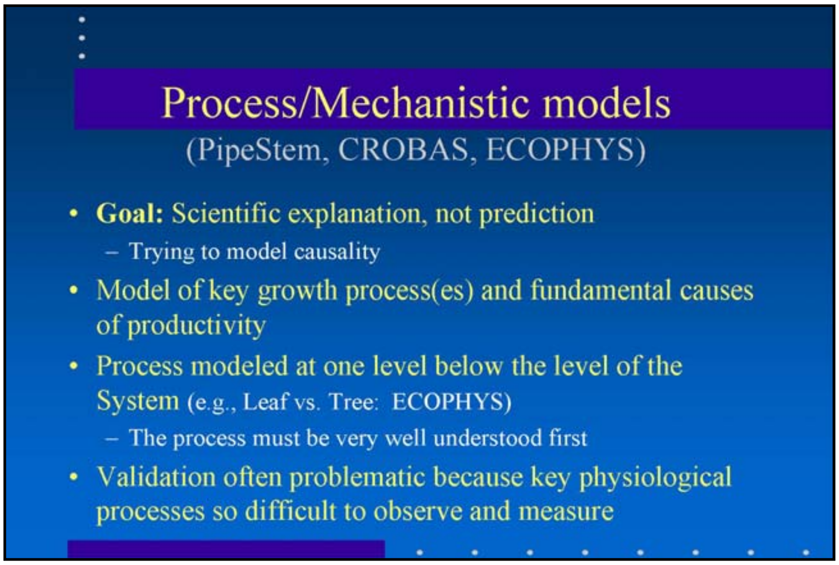
Forest Yield Models (ORGANON)

Potential Diameter Growth

BAL Modifier (competition)

CR Modifier (Vigor)

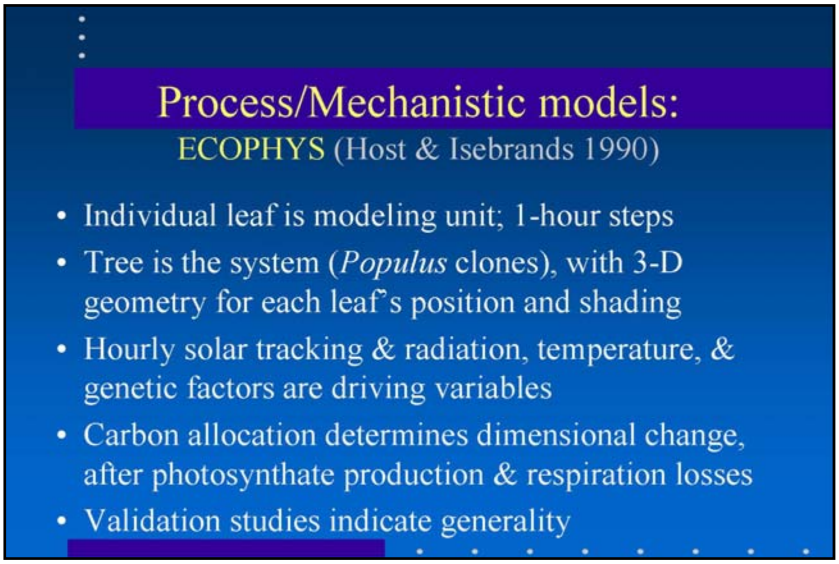
BA Modifier (competition)



Process/Mechanistic models

(PipeStem, CROBAS, ECOPHYS)

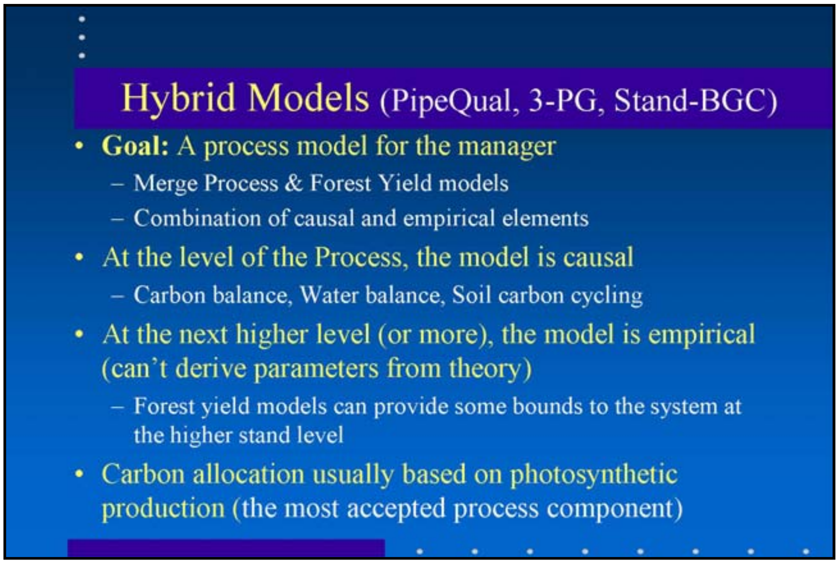
- **Goal:** Scientific explanation, not prediction
  - Trying to model causality
- Model of key growth process(es) and fundamental causes of productivity
- Process modeled at one level below the level of the System (e.g., Leaf vs. Tree: ECOPHYS)
  - The process must be very well understood first
- Validation often problematic because key physiological processes so difficult to observe and measure



Process/Mechanistic models:

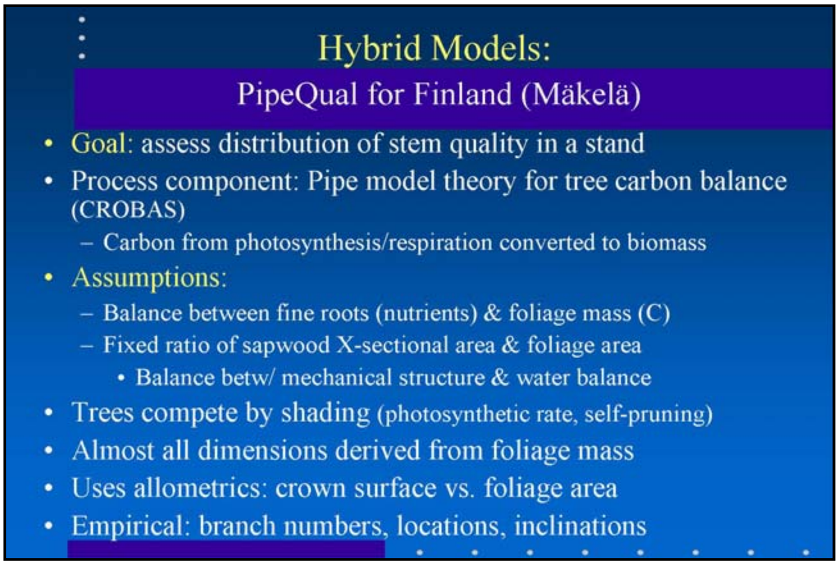
ECOPHYS (Host & Isebrands 1990)

- Individual leaf is modeling unit; 1-hour steps
- Tree is the system (*Populus* clones), with 3-D geometry for each leaf's position and shading
- Hourly solar tracking & radiation, temperature, & genetic factors are driving variables
- Carbon allocation determines dimensional change, after photosynthate production & respiration losses
- Validation studies indicate generality



Hybrid Models (PipeQual, 3-PG, Stand-BGC)

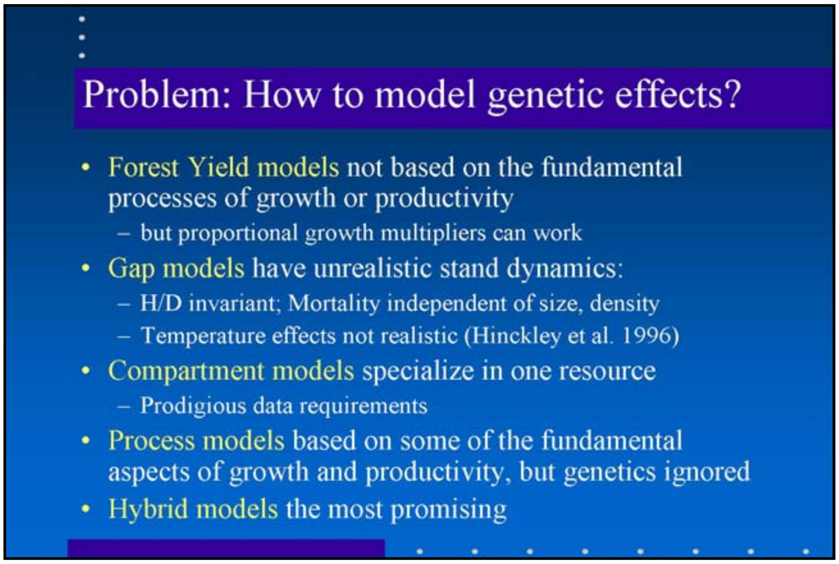
- **Goal:** A process model for the manager
  - Merge Process & Forest Yield models
  - Combination of causal and empirical elements
- At the level of the Process, the model is causal
  - Carbon balance, Water balance, Soil carbon cycling
- At the next higher level (or more), the model is empirical (can't derive parameters from theory)
  - Forest yield models can provide some bounds to the system at the higher stand level
- Carbon allocation usually based on photosynthetic production (the most accepted process component)



Hybrid Models:

PipeQual for Finland (Mäkelä)

- Goal: assess distribution of stem quality in a stand
- Process component: Pipe model theory for tree carbon balance (CROBAS)
  - Carbon from photosynthesis/respiration converted to biomass
- Assumptions:
  - Balance between fine roots (nutrients) & foliage mass (C)
  - Fixed ratio of sapwood X-sectional area & foliage area
    - Balance betw/ mechanical structure & water balance
- Trees compete by shading (photosynthetic rate, self-pruning)
- Almost all dimensions derived from foliage mass
- Uses allometrics: crown surface vs. foliage area
- Empirical: branch numbers, locations, inclinations



Problem: How to model genetic effects?

- Forest Yield models not based on the fundamental processes of growth or productivity
  - but proportional growth multipliers can work
- Gap models have unrealistic stand dynamics:
  - H/D invariant; Mortality independent of size, density
  - Temperature effects not realistic (Hinckley et al. 1996)
- Compartment models specialize in one resource
  - Prodigious data requirements
- Process models based on some of the fundamental aspects of growth and productivity, but genetics ignored
- Hybrid models the most promising

Hybrid Models: A promising approach

- Complementary merging of well-understood processes & reliable tree/stand empiricism
  - Carbon allocation merged with Crown allometry and geometry
  - Genetics could enter via climatic drivers
    - Temperature and water stress on photosynthesis
  - Genetics could enter via physical (branch inclination) or physiological characteristics (greater WUE or altered Carbon allocation)

Outline

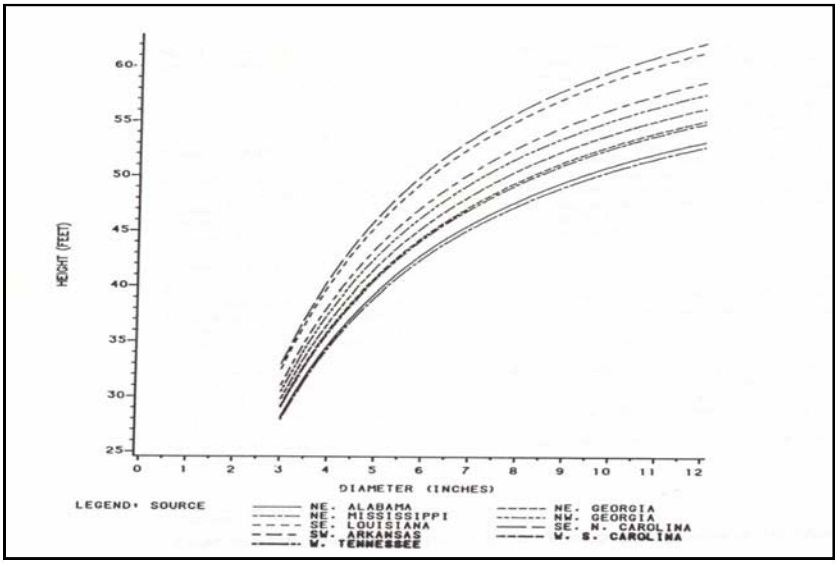
1. Forest Growth Models
2. Genetic Results
3. Climatic Interaction

Buford 1986 *Forest Science*

- Compared 9 So. Pine seed sources at age 15:

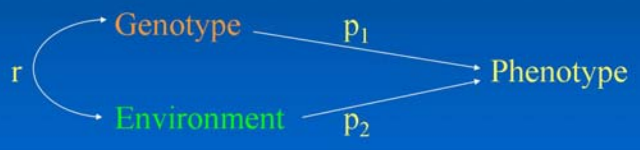
  $\ln H = a + b/D$

- Found common shape (b) for all
- Level (intercept a) differed by seed source
- Directly related to Site Index level
- Genetic differences can be modeled by a multiplier on the SI curve



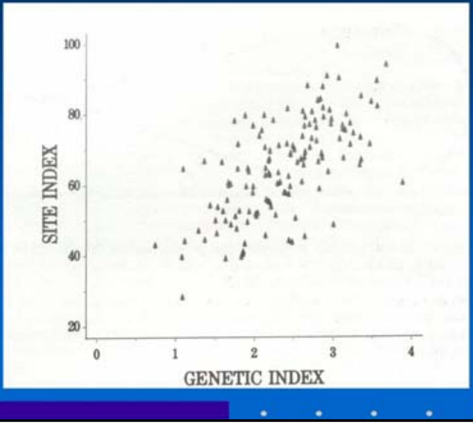
Monserud & Rehfeldt 1990 *Forest Science*

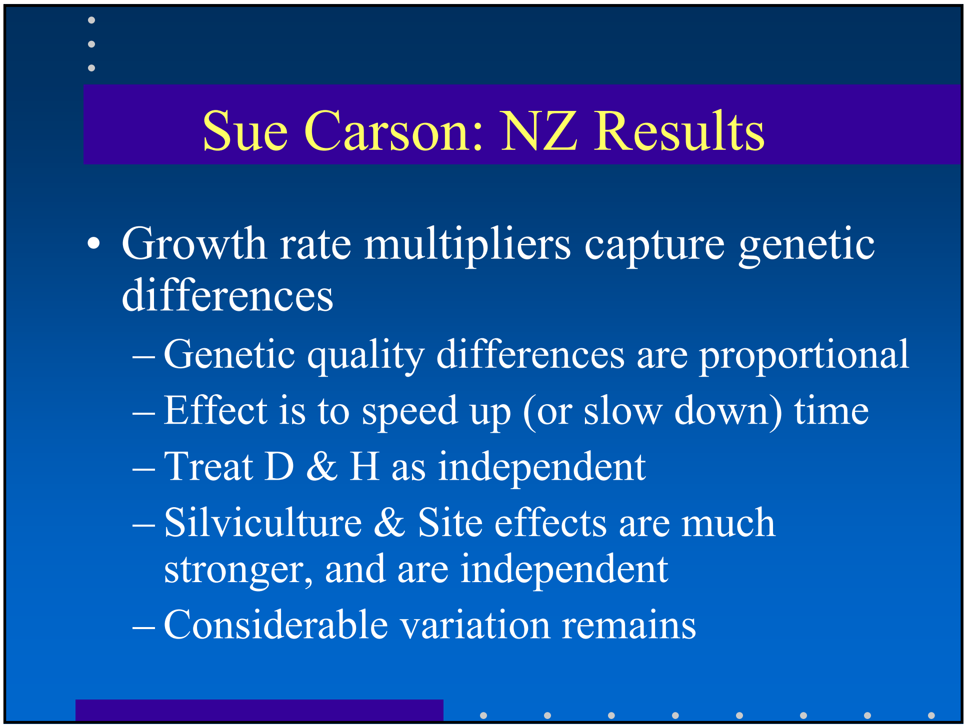
- Used Path Analysis to estimate separate G & E effects (p_1, p_2), and their correlation r:



- Found that $p_1 = 0.41$, $p_2 = 0.30$, $r = 0.76$ for D-fir SI

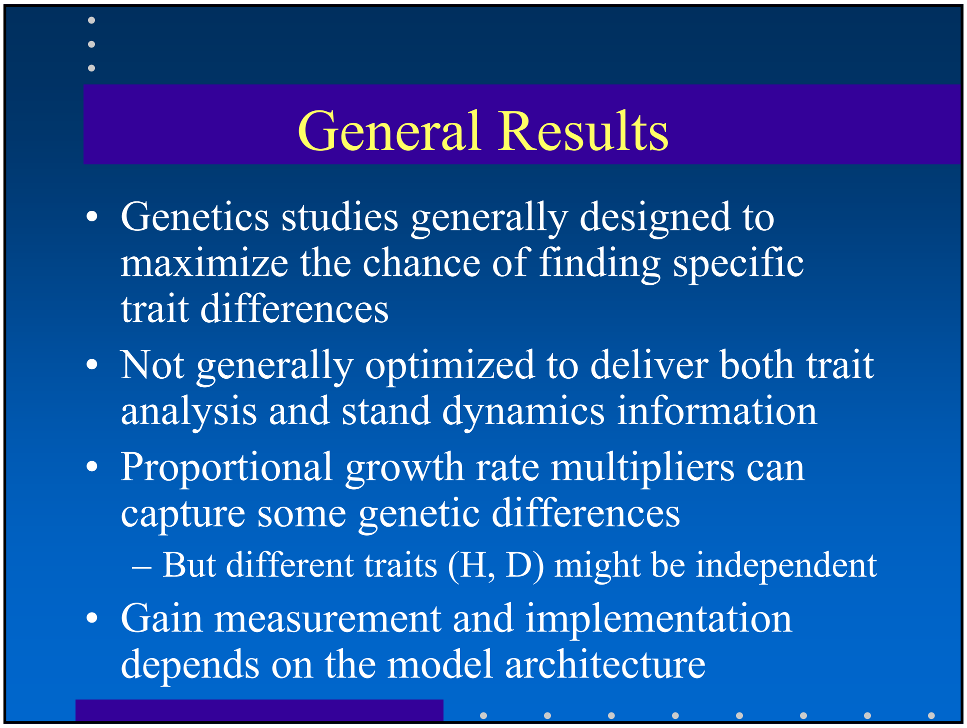
Douglas-fir in N. Rockies





Sue Carson: NZ Results

- Growth rate multipliers capture genetic differences
  - Genetic quality differences are proportional
  - Effect is to speed up (or slow down) time
  - Treat D & H as independent
  - Silviculture & Site effects are much stronger, and are independent
  - Considerable variation remains



General Results

- Genetics studies generally designed to maximize the chance of finding specific trait differences
- Not generally optimized to deliver both trait analysis and stand dynamics information
- Proportional growth rate multipliers can capture some genetic differences
  - But different traits (H, D) might be independent
- Gain measurement and implementation depends on the model architecture

General Results

- Revisit the Lambeth study
- Model genetic gain as a process
  - How this is done depends on model architecture
  - How does genetic gain change the fundamental operation of the growth model?
  - Always need to accurately model silviculture and site productivity accurately

Outline

1. Forest Growth Models
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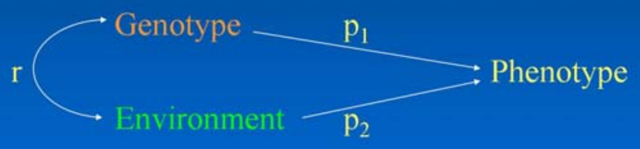
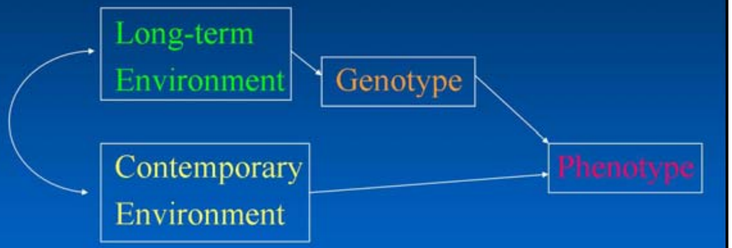
Monserud & Rehfeldt 1990 *Forest Science*

- Used Path Analysis to estimate separate G & E effects (p_1, p_2), and their correlation r:



- Found that $p_1 = 0.41$, $p_2 = 0.30$, $r = 0.76$ for D-fir SI

Climate & Weather



Long-term Environment

Genotype

Contemporary Environment

Phenotype

Mayr (1983): All biological phenomena have an evolutionary cause and a proximate cause

Rehfeldt *et al.* 1999 *Ecol. Monogr.*

- *Pinus contorta* in BC
  - 118 populations on 60 common garden sites
- Estimated climatic transfer functions to predict 20-yr height
  - 513 weather stations for climatic surfaces
  - Mean Annual Temp worked well

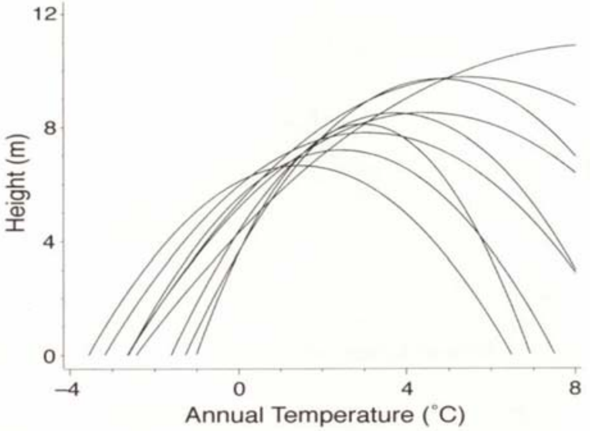


FIG. 8. Response functions using mean annual temperature as a predictor of height for nine populations that represent a variety of responses for ssp. *latifolia*.

Rehfeldt *et al.*: Results

- Density-dependent selection to a narrow ecological (realized) niche
  - Fundamental niche is very broad, though
- Almost all populations in suboptimal environments now
- Small changes in climate will greatly affect growth and survival (steep clines)
  - N populations are 6°C below optimum

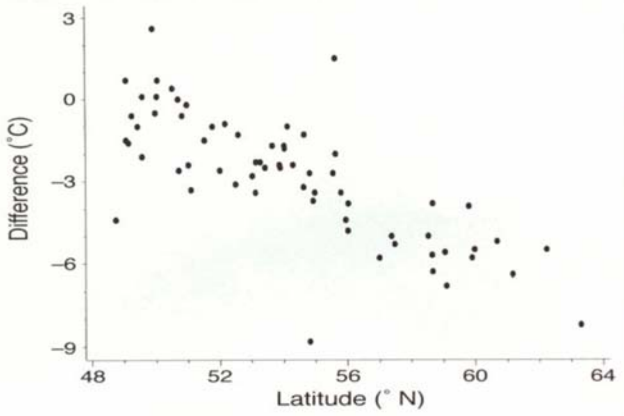
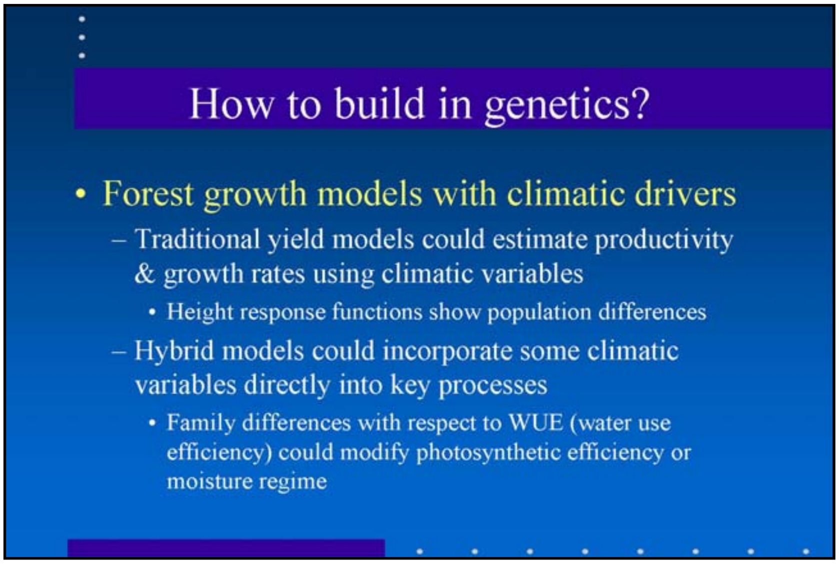


FIG. 10. Discrepancy between the mean annual temperature of the inhabited environment and that of the optimal environment plotted by population latitude. Discrepancies are based on response functions that describe 20-yr height of ssp. *latifolia*. Negative values denote an optimum that is warmer than the inhabited environment.

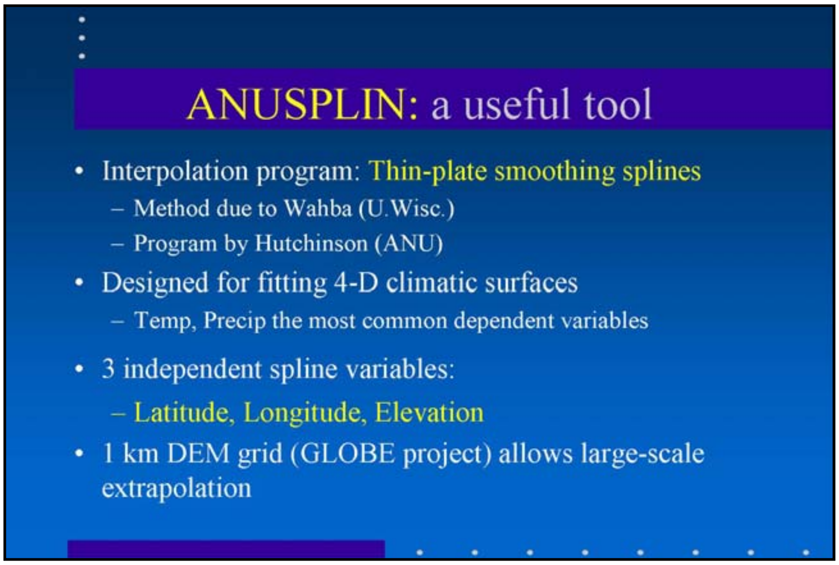
How to build in genetics?

- Consider forest growth models with climatic drivers
  - All of Rehfeldt's results are in terms of climatic variables:
    - Ave. Annual Temp; GDD_5; Min Temp; frost-free period; Annual heat/moisture index
  - Forest productivity can also be mapped with climate variables, supplemented with edaphic factors
    - Coops, Waring, Landsberg (2001); Ung et al. (2001)
  - Climate change questions can be addressed directly



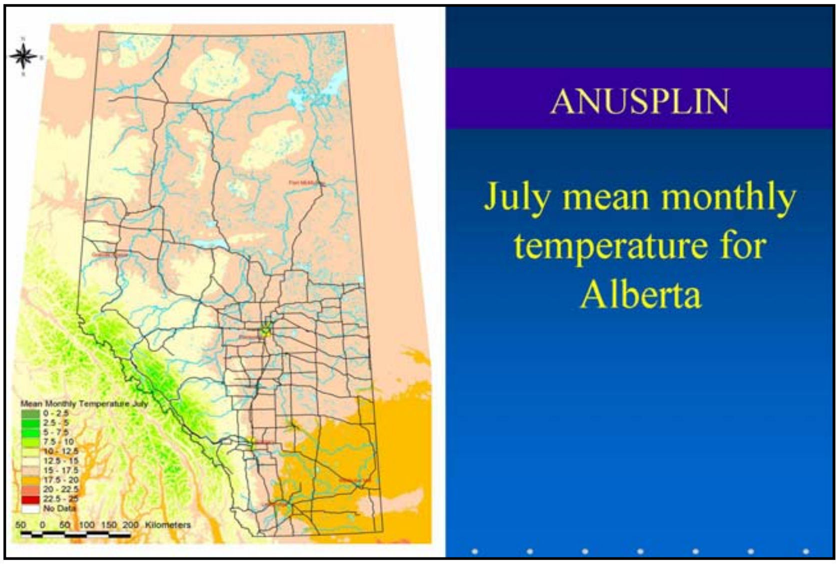
How to build in genetics?

- Forest growth models with climatic drivers
  - Traditional yield models could estimate productivity & growth rates using climatic variables
    - Height response functions show population differences
  - Hybrid models could incorporate some climatic variables directly into key processes
    - Family differences with respect to WUE (water use efficiency) could modify photosynthetic efficiency or moisture regime



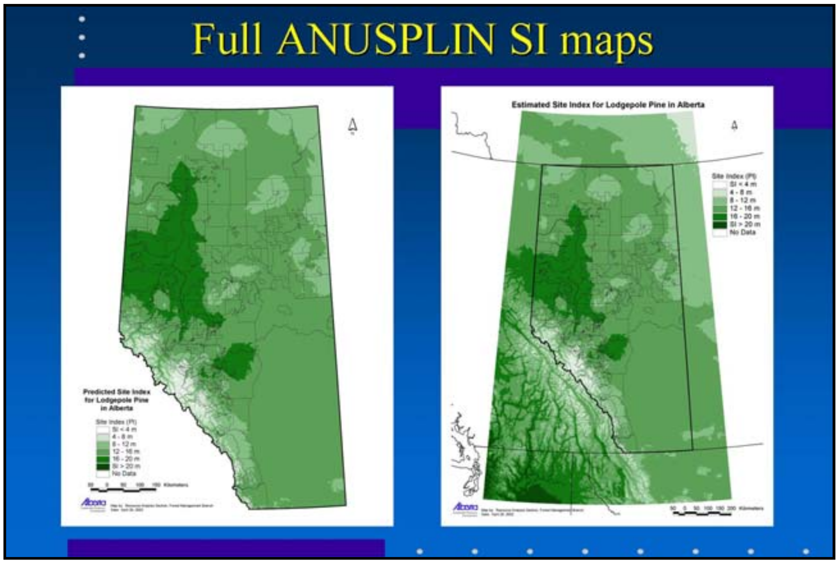
ANUSPLIN: a useful tool

- Interpolation program: Thin-plate smoothing splines
  - Method due to Wahba (U.Wisc.)
  - Program by Hutchinson (ANU)
- Designed for fitting 4-D climatic surfaces
  - Temp, Precip the most common dependent variables
- 3 independent spline variables:
  - Latitude, Longitude, Elevation
- 1 km DEM grid (GLOBE project) allows large-scale extrapolation

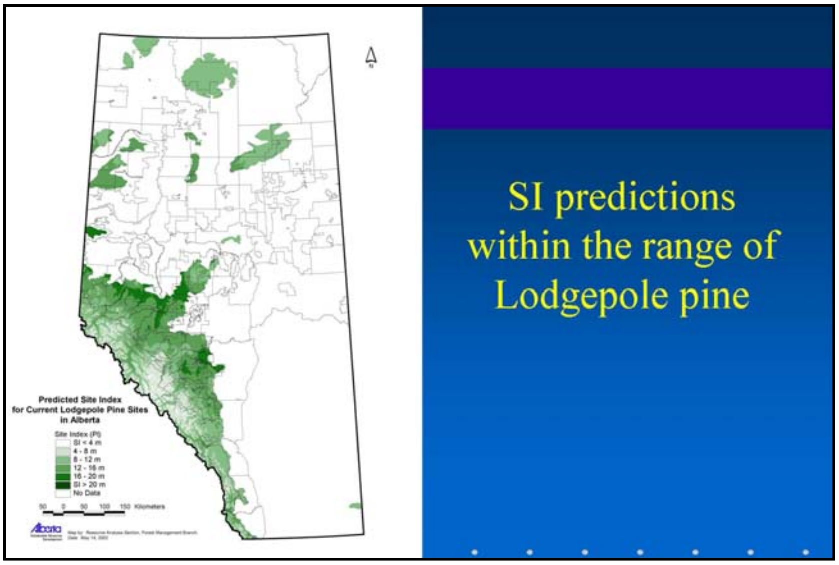


ANUSPLIN

July mean monthly temperature for Alberta



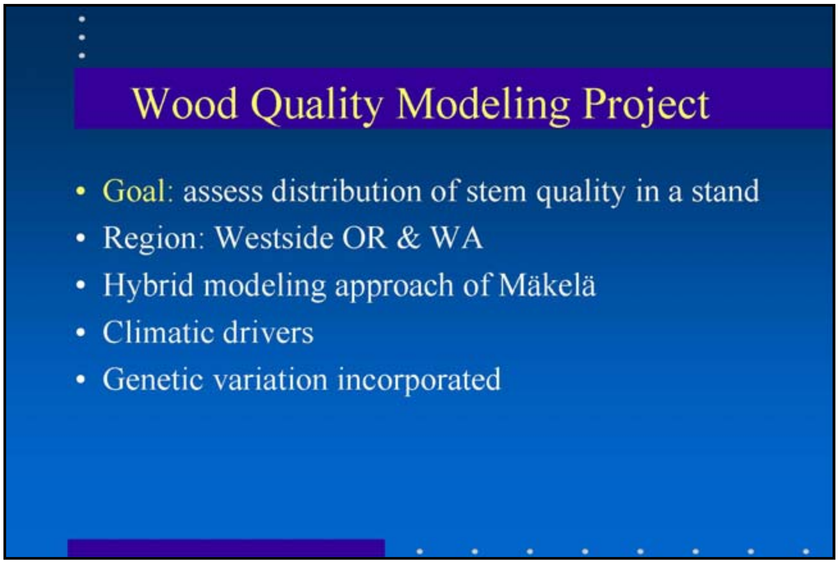
Full ANUSPLIN SI maps



SI predictions within the range of Lodgepole pine

Alberta Project: Next Steps

- Co-author: Shongming Huang
- Predict and map m^3/ha/yr (~ NPP)
- Predict productivity from climatic variables
- Climate Change Scenarios then possible
- Incorporate genetic effects (Rehfeldt) with climate change & productivity



Wood Quality Modeling Project

- Goal: assess distribution of stem quality in a stand
- Region: Westside OR & WA
- Hybrid modeling approach of Mäkelä
- Climatic drivers
- Genetic variation incorporated

Citation

Cherry, M.L., and Howe, G.T. (eds.) 2004. Proceedings, Genetics and Growth Modeling Workshop. November 4 - 6, 2003, Vancouver, Washington. Pacific Northwest Research Cooperative Report #21, Oregon State University. 171 pp.