

Genetic Evaluation Using the TREEPLAN® System

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ABSTRACT

The TREEPLAN® genetic evaluation system is designed for the efficient and accurate prediction of genetic values in trees for breeding and deployment purposes. TREEPLAN® fits a reduced individual tree model BLUP, and can model multiple genetic groups, handle clonal data, fit multi-trait models, accommodate heterogeneous variances, and fit site specific models. TREEPLAN® is fully integrated with a web based data management system that efficiently handles data and pedigree information. The Southern Tree Breeding Association (STBA) is using TREEPLAN® for genetic evaluation in the Australian tree improvement programs for *Pinus radiata*, *Eucalyptus globulus* and *E. nitens*. TREEPLAN® enables data across generations to be combined in a multi-trait analysis to produce single lists of genetic values for each trait for given production environments. TREEPLAN® is easy to use and has the 'industrial strength' to handle large amounts of unbalanced data with complex pedigree structures. The systematic approach adopted by the STBA for genetic evaluation makes full use of all related pedigree and performance data. This has led to cost savings and other operational efficiencies in the programs, while increasing genetic gain. It can be difficult to predict the commercial performance of genotypes in plantations using data from trees measured at an early age in small plot experiments. Despite this, genetic values should be expressed in terms of breeding objective traits, which are those influencing profit and/or other community issues. Economic weights are applied in multi-trait indices to derive profit equations for purposes of ranking genotypes on economic worth. These profit indices are then used by STBA for selection of trees for breeding purposes and by member companies for decision making in commercial deployment programs.

INTRODUCTION

The Southern Tree Breeding Association (STBA) was formed in 1983, and runs national tree improvement programs for *Pinus radiata* and *Eucalyptus globulus* in Australia. These two species comprise about seventy percent of the national plantation estate of 1.6 million hectares, with *P. radiata* primarily used for solid wood products and *E. globulus* for pulp and paper production. The establishment of cooperative breeding programs for *P. radiata* (1983) and *E. globulus* (1994) resulted in the consolidation of genetic resources and amalgamation of existing breeding programs of a number of member companies. As a consequence, large amounts of performance data for both species that had been collected over time on trees from hundreds of research experiments and genetic trials were made available to the Association. The STBA is continuing breeding of advanced generations, with testing and selection activities resulting in the accumulation of more data and traits for genetic analysis. The TREEPLAN® genetic evaluation system (Kerr *et al.* 2001, 2002; McRae *et al.* 2003) was developed for the purpose of analysing this performance data on a program wide basis, as existing software was inadequate for the task.

It is generally accepted that best linear unbiased prediction (BLUP) is the optimal and preferred statistical method for breeding value prediction. Although BLUP is not new technology, its industry wide application in trees had been limited in the past by a lack of computer power and software capability. Genetic analysis was usually done on subsets of data from single generations with limited sites and the fitting of single trait models. As a result, genetic evaluation was done inefficiently, breeding values were often biased, and it was also difficult to compare genetic values for trees included in different analyses. Although the STBA adopted the individual tree additive genetic model BLUP in its tree improvement programs during the 1990s (Jarvis *et al.* 1995), its application was limited to relatively small and uncomplicated data sets until the recent development of the TREEPLAN® system. The STBA with assistance from the livestock industry (Animal Genetics and Breeding Unit) and its other research members developed a working version of TREEPLAN® in 2001, which had the capability to process performance data on a national and/or international scale. The TREEPLAN® system was specifically designed to apply best practice analytical technologies to large scale commercial tree improvement programs like those managed by the STBA.

TREEPLAN® has allowed data with genetic linkage across generations, sites, years and age classes to be combined into a single multi-trait analysis to produce, for all genotypes, a complete list of genetic (breeding) values for each trait and environment combination. TREEPLAN® is relatively easy to use and has the 'industrial strength' to handle large amounts of unbalanced data with complex pedigree structures. TREEPLAN® fits a reduced individual tree model for purposes of efficiency. TREEPLAN® can model

multiple genetic groups, handle individual and clonal data, fit multi-trait models with more than 50 traits, accommodate heterogeneous variances (allows for differing heritability), fit site specific statistical and genetic mixed models, and also weights information across environments to account for genotype by environment interaction (GxE), and time to allow for age:age correlations.

A strength of the TREEPLAN® system is that it is fully integrated with a modern web based data management system that efficiently handles large databases with full pedigree information. The data management system acts as a dynamic repository for data and pedigree information and has the capability to handle multiple species. The system not only facilitates efficient storage and retrieval of data for genetic evaluation, but also the delivery of genetic values and other information to STBA member companies and nominated parties through the Internet. As new trials and traits are assessed the data are validated and entered into a database, and preliminary analyses are done on a single site basis using ASREML (Gilmour *et al.* 2001) or similar software to estimate variance and covariance components which are used to allow for differences in productivity and heritability between sites. When TREEPLAN® is run on the full data set, breeding values for all trees (genotypes) in a specified population are updated using all information available on the individual genotype itself, any correlated traits, and information from all relatives in the pedigree. Prediction of genetic values is now a more dynamic and relatively straightforward process, such that TREEPLAN® breeding values are updated regularly as traits are measured, data compiled and validated. TREEPLAN® is now being used to routinely update genetic values in *E. globulus*, *P. radiata* and *E. nitens* on a program wide basis, and is easily adapted for other species.

This systems approach that has been adopted by STBA in TREEPLAN® genetic evaluation makes much more effective use of all pedigree and performance data, but also has led to other operational efficiencies, including cost savings in the programs.

The Genetic and Statistical Models

The statistical approach used in TREEPLAN® is designed for maximal efficiency as it includes all the design effects used in simpler analyses, but can incorporate in a combined analysis all of the data that has been collected for different traits and across all pedigrees. It fits a linear mixed model of the form:

$$y = Wf + Xr + Yu + Zs + e$$

where: y is the vector of observations on one or more traits; f is the vector of fixed site and design effects, with its incidence matrix W ; r is the vector of random design effects, with its incidence matrix X ; u is the vector of random additive genetic effects (breeding values) with its incidence matrix Y ; s is the vector of random specific combining ability effects (SCA) with its incidence matrix Z ; and e is the vector of residuals.

The estimates of the fixed and random design and genetic effects are obtained by solving the mixed model equations (MME's) (Henderson 1984) using the Gauss-Seidel iteration:

$$\begin{bmatrix} W'R^{-1}W & W'R^{-1}X & W'R^{-1}Y & W'R^{-1}Z \\ X'R^{-1}W & X'R^{-1}X + [I \otimes G_r]^{-1} & X'R^{-1}Y & X'R^{-1}Z \\ Y'R^{-1}W & Y'R^{-1}X & Y'R^{-1}Y + [A \otimes G_a]^{-1} & Y'R^{-1}Z \\ Z'R^{-1}W & Z'R^{-1}X & Z'R^{-1}Y & Z'R^{-1}Z + [I \otimes G_s]^{-1} \end{bmatrix} \begin{bmatrix} \hat{f} \\ \hat{r} \\ \hat{u} \\ \hat{s} \end{bmatrix} = \begin{bmatrix} W'R^{-1}y \\ X'R^{-1}y \\ Y'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where, the new terms represent variance-covariance matrices of the error (R), random design effects (G_r), additive genetic effects (G_a), and specific combining effects (G_s) and the relationships between the additive genetic effects (A , the additive (or numerator) relationship matrix) and independent random effects (I), and \otimes is the Kronecker product. The R and G_r matrices are specific to each site to allow site specific design and error (co-)variances.

This model offers substantial advantages over the models usually used in forest genetic trial analysis. Breeding values (and other genetic effects) are estimated for all traits, for all trees in the pedigree – both parents and offspring, in a single analysis. Where a trait has not been measured on a tree then the best prediction is made of its breeding value using information from relatives and from traits correlated at the genetic, design or error levels. If there is no such information, then the estimate is at the population mean, but the variance of the estimates grow as the amount of information, and thus its reliability, increases. The use of correlated traits allows correction for the effect of selection in measurement, as long as the data used for selection is included. The solutions to the mixed model equations give the highest correlation between true and estimated values, provided that the variances and covariances are known. This is a substantial improvement over best linear prediction (BLP), where the fixed effects are assumed to be known. The STBA has previously used BLP for breeding value estimation in *P. radiata* (White *et al.* 1992 ab). The mixed model equations are extremely robust, and can be readily extended to more complex models.

The model uses the numerator relationship matrix (**A**) to track the proportion of genes in common between trees in the pedigree and gives solutions for all of them without any secondary processing of the data in what has been called an individual tree model (ITM). It easily handles half-sib and full-sib pedigrees, and simple rules have been worked out (Henderson 1976) to create the inverse that is used in the MME's. The matrix can be modified for the types of pedigrees that are common in forest genetic trials: fixed provenance or selected parentage (such as seed orchard) effects (Quaas 1988), partial selfing (Dutkowski and Gilmour 2001), and even pollen mixes (Perez-Enciso and Fernando 1992).

In forestry, parents of first-generation progeny are typically trees from native stands (or plantations) sampled from many different geographical regions that represent different provenances or races. Because provenances are quite genetically distinct it is important to assume that $E(\mathbf{g}) \neq 0$, where \mathbf{g} is the vector of genetic values. Male parents are usually unknown and female parents are assumed to be unrelated. Seeds from the female parents (founders) are collected from various localities spread across a wide geographical area. Thus, it is reasonable to consider that progeny are from more than one genetically divergent sub-population. TREEPLAN® relates all foundation parents on the basis of their original provenance to genetic groups. In practice, data sets are likely to be far more complex, for example, a male parent (pollen) might be identified as belonging to a particular population, such as a routine or an improved population. Founders introduced from another unrelated breeding program might also constitute a different genetic group. The modified mixed model equations of Quaas (1988) are used to derive solutions to \mathbf{g} .

Trees can be partially self-fertile, generating pedigrees where two progeny may be selfed sibs (both progeny result from selfing), a selfed sib and an outcrossed sib, full-sibs or half-sibs. In the *E. globulus* breeding program, most progeny tested in the first-generation are derived from open-pollinated seed collected from founder trees in native forest stands. Until many more second-generation progeny (from controlled pollination crosses) are included in the analysis, the accuracy of breeding value prediction is dependent on how well the relationship coefficients between sibs of open-pollinated trees can be defined. Dutkowski and Gilmour (2001) have outlined simple rules to modify the NRM when a selfing rate in native stands is assumed. These rules can be further extended to account for the equilibrium level of inbreeding in the stand and the level of coancestry in trees local to the female parent from which seed was collected. Sparse and isolated stands of trees are expected to have a higher level of inbreeding among the progeny than dense stands. This functionality is currently being implemented in TREEPLAN®.

The software uses an equivalent gametic model for computational efficiency in the prediction of breeding values for trees without offspring (the majority).

$$y_i = \mu_i + \frac{u_f + u_m}{2} + s_j + \phi_i + e_i$$

where: μ_i is the mean, y_i , s_j and e_i are as defined above, u_f and u_m represent the breeding values for the tree's female and male parents respectively, and ϕ_i represents Mendelian sampling in the formation of the tree's genotype. That is, $0.5u_f + 0.5u_m$ represent 'average' gametes from each parent, and ϕ_i represents the deviation from the average of the gametes received by the progeny. The genotypic and gametic models are equivalent models, in that the solutions to the unknowns will be exactly the same for both models. Their combined use is called a 'reduced' individual tree model (Quaas and Pollak 1980).

Details of key features of the TREEPLAN® system and its routine application of BLUP in forestry have been previously reported by Kerr *et al.* (2001, 2002) and McRae *et al.* (2003), and are only briefly discussed in this paper.

Trait Mapping to Selection Criteria

The mapping of multiple measured traits to a smaller number of meaningful selection criteria (SC) traits is a desirable feature of TREEPLAN®. In theory, each trait measured on each site could be treated as a unique trait, as long as all the variances and correlations are known. In practice, however, such an approach is computationally infeasible, not all variances and correlations are known, and dealing with output would be very confusing to the breeder, because of the many traits involved. The mapping of measured traits to SC traits, results in a reduction (consolidation) in the number of traits for which breeding values are predicted in a multi-trait analysis. This mapping gives TREEPLAN® its flexibility and ease of use as the breeder can easily define the SC of interest in a given analysis. The mapping allows the breeder to consolidate data with different forms and scales of measurement, different ages and sites, as long as it can be realistically assumed that all the measured traits are highly genetically correlated and can be treated as the same trait.

As an example, diameter at breast height (DBH) in *E. globulus* is measured at different ages and the SC traits defined are: DBH ≤ 4 yrs, DBH 5–8 yrs, DBH 9–12 yrs and DBH ≥ 12 years. As well as age differences, geographical location and site type are other possible criteria for proposing new SC traits out of the one generic trait such as growth. For example, it may be necessary to partition the SC trait, DBH ≤ 4

years, further in a multi-site run, according to province, state or soil type, in order to account for GxE. Although GxE due to scale effects is effectively removed by data transformation (standardisation), we must properly account for GxE where it results in a change of ranking of genotypes across environments. In practice, the best method to handle GxE is to consider the same character measured in two different environments as two different but correlated traits (Falconer and Mackay 1994). A trait measured at different locations can be considered biologically the same SC trait when the genetic correlation is high (for example, ≥ 0.8). Studies with more extensive data sets are currently being done in Australia to estimate across site correlations and better define the target production environments for *P. radiata* and *E. globulus*. Previous studies designed to quantify the magnitude and nature of GxE for these species have been based on too limited data sets.

Only traits displaying significant genetic variance in preliminary single-site analyses are included in genetic evaluation. The definitions of selection criteria, development of rules for the trait mapping, and estimation of correlations between criteria are based on periodic analyses of data in the database and meta-analyses of other estimates.

Heterogeneous Variances

Breeding programs collect data from trials spread across a diverse range of site types and age classes. Some traits are or have been assessed using different protocols and scales. For example, growth may have been measured as tree height, stem diameter or tree volume; and stem form assessed using several scales with different levels of precision. The variance of performance traits such as growth usually increases with size, growth rate and age of trees. A linear transformation of the data such that the phenotypic variance is unity and a simple model with standard genetic design and error variances is an approach often used in plant and animal breeding. This approach is probably sub-optimal as recent work (Dutkowski *pers. comm.*) has shown that this assumption is unrealistic in many instances. A disadvantage of this approach for tree breeding is that a constant heritability would need to be assumed across all sites, despite some sites being more homogeneous. Tree breeders usually have the benefit of large designed trials that usually provide good estimates of genetic, error and design feature (co-) variances for each site. TREEPLAN® takes advantage of the availability of these estimates to transform the data for each trait to unit additive variance on a site by site basis and uses a model with site specific error and design feature variances to produce the genetic estimates. The recent analysis has also shown that this approach is very close to the ideal multivariate approach.

Clonal Data

Individual trees can be replicated using various forms of vegetative propagation. Clonal tests are common in *P. radiata* and are also used in some eucalypt breeding programs. TREEPLAN® currently treats clones as the same individual and matches unique clone identities to a single genotype. Clonal replication is important for accurately predicting clonal deployment values, but also for improving the precision of an individual's breeding value. An enhanced version of TREEPLAN® is currently being developed that will be capable of predicting genetic values, including additive and non-additive genetic effects, for individual clones, recognising the potential for somaclonal variation and propagation effects.

Running the TREEPLAN® system

An efficient data management system is critical for accessing data and pedigree information to produce breeding values quickly. The TREEPLAN® analytical system is fully integrated with a data management system (STBA-DMS™) which operates via a web based interface. TREEPLAN® could be run independently of the STBA-DMS™, but its interactive nature makes the process of genetic evaluation far more straightforward and efficient. It also facilitates data entry and analysis from various locations. The STBA-DMS™ is mainly designed for storage and retrieval of tree data for the purposes of genetic evaluation. It is flexible and accommodates different species of trees. User access is restricted and data is password protected to the level of traits within trials. This allows us to easily complete multiple TREEPLAN® runs for the membership, firstly using only generic data, but then also including confidential data for traits belonging to a restricted group of members. This provides the flexibility needed in large cooperative tree improvement programs to satisfy individual client needs by producing customised genetic values.

TREEPLAN® extracts genetic parameters, data and run specifications from the STBA-DMS™, and making changes to specifications for a new TREEPLAN® run is straightforward. That is, it is a simple process to include (exclude) new trials and/or more traits in a multi-trait BLUP analysis. As new trials are assessed, the data is validated and entered. Multi-variate analyses are first done on a trial by trial basis using ASREML and the variances and correlations for all significant design and random genetic components estimated are stored in the STBA-DMS™. TREEPLAN® is then run with the complete database updating all genetic values for all genotypes, including individuals, founders and families.

Genetic Values for Breeding Objective Traits and Economic Indices

TREEPLAN® predicts breeding and genetic values for Selection Criteria which are the traits that are measured in trials and genetics experiments. These traits are usually used as surrogates for the Breeding Objective traits, which are those that directly affect profitability. For instance, currently the STBA uses three breeding objective traits for *E. globulus*: Harvest Volume, Basic Density, and Kraft Pulp Yield. Genetic values for the breeding objective traits can be readily estimated from the selection criteria using the method of Schneeberger *et al.* (1992), as long as the correlations between the selection criteria and the breeding objective traits are known, or can be estimated, and the variance of these traits is similarly known. Breeding objective traits for each genotype are then combined into a single economic index with different economic weights applied to each trait, reflecting its commercial importance. Economic breeding objective functions have been developed for kraft pulp markets in *E. globulus*, and are being developed for alternative products in *E. globulus*, and for various products and markets in *P. radiata*.

Genetic Evaluation in *E. globulus* and *P. radiata*

TREEPLAN® is being used routinely by the STBA to predict genetic (breeding) values for trees included in its databases for *E. globulus* and *P. radiata*. Table 1 lists details of example data sets used in some recent runs of TREEPLAN®.

Table 1 — Example data sets used in recent runs of TREEPLAN® for *P. radiata* and *E. globulus*.

	Species	
	<i>Pinus radiata</i>	<i>Eucalyptus globulus</i>
Generations	3	2
Trials included in Analysis	78	90
Number of Selection Criteria Traits Analysed	21	11
Genetic (founder) Groups fitted	11	25
Families	3,110	1,610
Genotypes included in Analysis	134,767	152,170

Pinus radiata. Breeding values for 21 selection criteria for 132,700 genotypes were updated recently (Powell *et al.* 2004). This included data from 78 first-, second and third-generation trials spread across southern Australia. At this stage, growth selection criteria reflect six different production regions defined in the National Plantation Inventory for Australia (Wood *et al.* 2001) by four age classes (0-5 yrs, 6-12 yrs, 13-24 yrs and >24 years). Branch angle, branch quality, branch size, and stem straightness comprise the form traits. Basic density (0-12 yrs and ≥13 years) and spiral grain (0-6 yrs and ≥6 years) constitute wood quality traits. Data for disease and pest resistance/tolerance traits (*Phytophthora cinnamomi*, *Dothistroma septospora*, pine pitch canker (*Fusarium circinatum*), *Cyclaneusma* spring needle cast and *Essigella* pine aphid) are currently being incorporated. Some hundreds of historical first- and second-generation trials will be included as resources permit, with links to first-generation trials of all major lineages already included.

Current breeding objective traits are, harvest volume, whole tree basic density, branching and stem straightness (Powell *et al.* 2004). The current breeding objective function and coefficients in the selection indices for *P. radiata* have not been derived formally using economic data. However, the increased emphasis on density and other wood quality traits reflects the perceived economic importance of these traits as profit drivers in industry. The undesirable characteristics of juvenile wood that affect quality of timber, including grade recovery, strength, distortion, surface checks, and finishing properties for structural timber are also increasingly more of an issue at harvest as rotation length reduces.

The STBA and CSIRO-FFP in partnership with the Forest and Wood Products Research and Development Corporation (FWPRDC) are currently undertaking research to clearly define economic breeding objectives for *P. radiata* which are more commercially relevant to STBA members and industry, including the impacts of juvenile wood properties. A study by Wu *et al.* (2004) has included estimation of genetic parameters among key breeding objective (harvest age) and SC traits measured at younger ages. Preliminary results by Ivkovich *et al.* (2004) using bio-economic models suggest mean annual increment, sweep, branch size and modulus of elasticity (MOE) will be important breeding objective traits for *P. radiata*. These traits and associated economic weights are likely to be adopted in selection indices by STBA in its breeding program and by industry in deployment systems in the near future.

Eucalyptus globulus. Breeding values for 152,170 genotypes in the national *E. globulus* database were recently updated in a multi-trait analysis with 11 SC traits using TREEPLAN® (Pilbeam *et al.* 2004). This included genetic values for native provenances (sub-races), native stand (founder) trees, first- and second-

generation progeny. Data was from 90 trials, including 16 second-generation progeny trials, spread across Tasmania, Victoria, South Australia and Western Australia (Pilbeam *et al.* 2004), and includes all trials for which measurements are available. Breeding values for growth are predicted in four production regions by three age classes (0-4 yrs, 5-8 yrs and 9-12 years). Basic density, by two age classes, pilodyn penetration and NIRA predicted pulp yield comprise wood quality traits. Data for pest and disease resistances (defoliation), kraft pulp yield, NIRA cellulose content, collapse, shrinkage and tree form traits will be incorporated with time. Trees in the CSIRO collections (Gardner and Crawford 1987, 1988) are used to establish a baseline for monitoring genetic improvement over time.

The primary economic breeding objective for the national *E. globulus* tree improvement program is to maximise the net present value per hectare (\$NPV) from forests grown for kraft pulp production. The breeding objective traits are harvest volume (VOL), whole tree basic density (DEN) and kraft pulp yield (KPY). Table 2 gives summary statistics for trees included in a recent TREEPLAN® run for *E. globulus*. The economic weights currently used by STBA were derived after the method of Borralho *et al.* (1993), and adapted by Greaves *et al.* (1997) and Dutkowski *et al.* (2000). Although the primary objective of most STBA member companies is to produce wood chips for kraft pulp markets, there is an increasing interest in sawlog regimes and other alternative products (Volker 2002). Research studies (Greaves *et al.* 2004; Whittock *et al.* 2004) are investigating alternative breeding objective functions for other products and markets including carbon revenues.

Table 2 — TREEPLAN® breeding values for volume (VOL), wood density (DEN) and pulp yield (KPY) for *E. globulus*. Averages for baseline, founder parents, and first- and second-generation trees are given for comparative purposes with selected groups of genotypes. Gains as a percentage of base productivity are given in brackets (%).

	VOL		DEN		KPY		\$Index
Base Productivity*	313 m ³ /ha		542 kg/m ³		55.7 %		
CSIRO collection (616 trees)	0		0		0		0
Base Generation (all native stand founder trees)	0.42	(0%)	0.88	(0%)	0.01	(0%)	\$27.69
First Generation	3.10	(1%)	0.47	(0%)	-0.02	(0%)	\$45.06
Second Generation	51.41	(16%)	3.11	(1%)	-0.90	(-2%)	\$466.93
Top 20 trees \$Index	34.49	(11%)	72.88	(13%)	-0.72	(-1%)	\$1,964.95
Top 20 trees VOL	132.69	(42%)	-19.10	(-4%)	-1.42	(-3%)	\$814.55
Top 20 trees DEN	-8.09	(-3%)	87.47	(16%)	-0.74	(-1%)	\$1,770.27
Best Provenance \$Index	-0.61	(0%)	20.96	(4%)	-0.02	(0%)	\$486.30
Worst Provenance \$Index	-125.65	(-40%)	23.20	(4%)	1.18	(2%)	-\$697.11

Future Enhancements

In partnership with AGBU and FWPRDC, STBA is developing an enhanced version of TREEPLAN® with additional features including: (1) Better modelling of intra-site environmental variation using spatial and competition models, (2) Incorporation of information at the DNA level (markers and candidate genes), (3) Modelling of dominance and epistatic effects to allow for the full exploitation of these non-additive genetic effects in family and clonal deployment populations, and (4) Development of a clearer understanding of GxE to better target different production environments.

CONCLUSIONS

The TREEPLAN® genetic evaluation system has facilitated the routine application of individual tree model BLUP in the Australian tree improvement programs for *P. radiata*, *E. globulus* and *E. nitens*. The system was developed for processing performance data from efficient rolling front breeding programs with overlapping generations, and has resulted in significant cost savings in genetic evaluation. TREEPLAN® has allowed data with genetic linkage across generations, sites, years and age classes to be combined into a single multi-trait analysis to produce for all genotypes a complete list of genetic (breeding) values for each trait and environment combination. TREEPLAN® is easy to use and has the 'industrial strength' to handle large amounts of unbalanced data with complex pedigree structures. TREEPLAN® is fully integrated with a web based data management system that efficiently handles data and pedigree information, and delivery of genetic information to customers. TREEPLAN® generates accurate breeding and genetic values for measured traits using objective performance data collected in genetics trials. For commercial relevance, these values are converted into breeding objective traits in selection indices that are used for making breeding and deployment decisions.

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