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Multi-trait Mixed Smoothing Spline Models for Wood Properties - FFR Mathematical Modelling Framework Progress Report to 31/3/2010

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EXECUTIVE SUMMARY

Multi-trait mixed smoothing spline models were developed and tested for the FFR mathematical modelling framework, in order to predict and simulate wood properties within and between stems. The models were fitted to the WQI benchmarking data (Cown *et al.* 2005). The data consisted of ring mean observations of wood properties on SilviScan strips taken at four heights (0, 1, 5, 20m), from 133 trees sampled from 17 sites (mostly 6 –10 trees per site).

Models were fitted using the `lme` function from the `R/nlme` package (Pinheiro and Bates 2000; Pinheiro *et al.* 2009) with smoothing spline terms generated by the `R/lmeSplines` package (Ball 2003), based on Verbyla *et al.* 1999.

- The models had random terms at various levels including linear and smoothing spline terms in ring number and height at the overall, site, tree, disc levels.
- A 3-trait model for ring width, ring density and microfibril angle has been fitted across all sites.
- The models fit the general trends well, and demonstrate proof of concept.

Examination of residual variance from predictions at various levels showed substantial between-site and between-tree variability, showing that a one model fits all approach would not be accurate, and suggesting that sampling a number of trees from a site, and/or sampling a core from a tree would significantly improve predictions for individual trees.

The models are large and take a long time to fit, but once fitted, future predictions, including predicted values suitable for input into the mechanical modelling system t `pqsim`, can be made relatively easily.

Some discrepancies between various observed inter-trait correlations and the same correlations in data simulated from the model were observed. Variograms from data simulated from the model appeared larger than the raw data, although this was only borderline-significant.

Further work is required for:

- investigating and remedying the discrepancies in correlations, and improving the models; more data and/or Bayesian models may be needed to overcome the limitations of maximum likelihood with this type and size of dataset; and
- adapting the core `lme` model fitting algorithms to better handle the large datasets, to reduce time to fit and restrictions on models that can be fitted.

INTRODUCTION

The goal of the `pqsim` project is to predict wood mechanical properties as a function of position within a stem. To do this it needs to be able to simulate values of wood properties (*e.g.* wood density, microfibril angle) in three dimensions within stems, for input into deterministic (*e.g.* finite elements) mechanical models. For these simulations to be representative of real populations, models are needed which capture the structure of variation within and between trees for the relevant traits. Mixed smoothing spline models have been developed for this purpose, and also for general empirical modelling of wood properties.

Previously, we have fitted mixed smoothing spline models to individual traits separately. However, there is a high degree of correlation between different wood properties, especially within stems due to the well-known pattern of variation, *e.g.* pith-to-bark trends in wood density, and microfibril angle. Simulation of each trait from its respective separate model assumes independence of the traits and would not be realistic. For example, a high density ring (hence likely to be further from the pith) would tend to be a low microfibril angle ring. This would induce a negative correlation between density and microfibril angle. Hence the need for a multi-trait model. However, the same correlation may not apply at the site, tree, or genotype (if applicable) level. Hence the need to model inter-trait correlations at different levels in the multi-level mixed model.

This work extends the mixed smoothing spline models to multi-level multi-trait models allowing for inter-trait correlations. Multi-trait mixed smoothing spline models have been fitted to subsets of the WQI benchmarking data.

Smoothing Spline Models

Deterministic or fixed effects models fit a function (*e.g.* straight line or Chapman-Richards growth curve) to a dataset, assuming that all trees follow the same curve and errors are independent. Neither of these assumptions is true, in general. These models could be generalised by allowing the parameters of the curve to vary randomly, *i.e.* using non-linear mixed models. Non-linear mixed models still require that each tree follows the same functional form, which is often not the case. With non-linear models, even if individual trees follow the specified functional form, their mean may not, and vice versa. Moreover, non-linear models are difficult to fit, *e.g.* with the fitting process often not converging, limiting the covariance structure and parameters that can be fitted.

Smoothing splines are an alternative. Rather than specifying a formula, a curve is represented by a set of random effects with a certain variance structure, within a *linear model*. The smoothness of the curve could be selected by choosing the smoothing parameter manually, but with many spline terms at different levels this is too cumbersome for our purposes. In mixed models with smoothing splines, the maximum likelihood fitting process automatically estimates the smoothness, giving a tradeoff between accuracy of fit to the data, and smoothness of the resulting curve.

Mixed Models

In an ideal world we would have perfect knowledge of the processes determining growth, and exact knowledge of environmental conditions, and parameters of the process. A deterministic formula would give exact predictions. In the real world we have imperfect knowledge. Departures from the deterministic formulae are represented by random effects in mixed models. We don't observe these effects but can estimate them or their distributions from samples. The distributions of random effects are represented by variance structures in mixed models. Estimating the variance parameters by fitting the model to a sample allows us to estimate the structure of variation of the trait in the population.

Mixed models enable estimation of components of variance which determine the structure of variation. Use of smoothing splines (rather than parametric formulae) means we don't require individual trees to follow any pre-determined functional form. Nor do we require all trees to follow the same functional form, or assume independent increments, as is commonly done in tree growth modelling. The models fitted elucidate the structure of variation. Variation occurs at different levels: overall, site, tree, disc, and ring; and is represented by random effects at each level and inter-trait correlations are estimated. Smoothing splines in height and ring number are fitted at these various levels.

Smoothing Splines in Mixed Models

For a single spline in ring number, the model fitted has the following form:

$$y = X_l b_l + Z_s b_s + e, \quad b_s \sim N(0,V_s), \qquad e \sim N(0,\sigma^2) \qquad (1)$$

where X_l is the model matrix for a linear term representing *e.g.* $b_0 + b_1 \cdot r + b2 \cdot h$, where r is ring number, h is height, and b_s is a vector of random effects for the spline, Z_s is the (transformed) model matrix created by `lmeSplines`, and V_s is the variance matrix. With the transformation used by `lmeSplines` , V_s is a multiple of the identity:

$$V_s = I_s \ \sigma_s^2$$
(2)

In the full model with nested classification *e.g.* `overall/site/tree/disc` the b_l linear terms will be random effects with their own variance structure

$$b_l \sim N(0,V_l) \qquad (3)$$

and there will be separate vectors b_l, and b_s for each level of the classifying factor *e.g.* for each tree within each site (*cf.* Pinheiro and Bates 2000).

The spline at the site level represents departures from the overall spline, while the spline at the tree level within a site represents departures from the spline for the site. If all trees within a site are very similar, the variance component for the tree-level spline and linear terms will be small compared to the overall and site-level components. On the other hand if trees within a site are not at all similar the tree-level component will be relatively large.

In our models, there are in addition splines in height at the overall, site, and tree levels. In addition to the linear and smooth terms, there may also be ‘rough' terms, *e.g.* where we fit ring number as a factor. The rough terms particularly at the overall level are important, representing calendar year fluctuations in wood density (if ring number is measured from the bark). A further practical consideration for fitting the models is the fact that different numbers of rings are available at different heights. This may necessitate choosing different sets of knot points at each height.

Note: Unlike regression splines, the number of knot points does not affect the smoothness of a smoothing spline curve provided there are sufficient knot points to represent the functional form of the underlying curve.

Three traits (ring width (`rw`), density (ring mean density, `rd`), microfibril angle (`mfa`) have been fitted simultaneously across multiple sites. R code for model specification and output of fitted models is shown in Appendix 1.

Data

The data used consisted of ring mean observations of wood properties on SilviScan strips taken at four heights (0, 1, 5, 20m), from 133 trees sampled from 17 sites (~ 6–10 trees per site) from the WQI benchmarking study (Cown *et al.* 2005). The data included a single strip sampled at each disc. For testing the three-dimensional model incorporating circumferential variation, additional strips were simulated within each disc.

Fitting Smoothing Spline Models

Mixed smoothing spline models were fitted using the `R/lmeSplines` package (Ball 2003). The `lmeSplines` package enables fitting smoothing spline terms within mixed models in the `R/nlme` package. A previously developed `pdMat` class enabled fitting tensor product terms that are commonly used in the ASReml mixed model package used in plant and animal breeding (Gilmour *et al.* 2008). This enabled allowing for inter-trait correlations between various terms.

Terms in the 3-trait multi-site model are shown in Table 1. Terms are labelled as used in R, as shown in the model summary output (Appendix 1), and symbolically, *e.g.* `spl(h)` for a spline in height, `lin(r|h=5)` for a linear term in ring number within height 5. There are five 'levels' (`overall, site, tree, disc, unit`).

Within each of the main 'levels' (`overall, site, tree, unit`) there are 'groups' corresponding to the different terms in Table 1. Each group contains a set of random effects with a covariance matrix summarised in the model summary output (Appendix 1).

Note: The `disc` level is not represented explicitly because the relevant terms occur within each height. The `unit` level refers to *experimental units*, *i.e.* individual ring mean values for the traits. In the 3-trait model there are three points, one per trait, for each unit.

Note: All terms have their covariance matrix tensored with full symmetric covariance matrix for trait, except spline terms at site and tree levels which are tensored with diagonal variance for trait. No terms are fitted at disc level in this model due to the use of ring linear and spline terms within heights at the site and tree levels. Linear terms `lin(1+r+h)` are fitted with a full symmetric covariance matrix, while spline terms are represented by a set of independent random effects.

Note: When referring to variation at a certain level, *e.g.* 'tree level', this refers to random effects at that level (*e.g.* a single random effect per tree), while 'between-tree' variation refers to all variation between trees, *i.e.* variation at the overall, site and tree levels combined, and 'within-tree' variation refers to variation at the disc or unit (*i.e.* individual ring within disc) levels.

Correlations

Correlations at different levels reflect contributions to variability from causal factors acting at that level or higher levels; for example, the tree level correlations reflect variability between sites, perhaps due to different climate or soil, and variability and differences between trees within sites possibly due to genotypes, micro-climates, aspect etc. The mixed models treat each level separately, however raw correlations from the observed data can be calculated directly and can be a useful diagnostic tool.

Predictions

The mixed modelling framework enables prediction of values for future samples from the population. Predictions and residuals from the model can be obtained at any level Using, for example

```
> predict(fit,level=l).
```

Predictions at the *l*th level correspond to predictions using estimated effects for all terms up to the given level. For example site-level predictions would use estimated effects from the fixed effects, all overall-level effects and all site-level effects. More generally, predictions for new data can be made with

```
> predict(fit,level,newdata)
```

where `newdata` is a dataframe similar to the dataframe used when fitting the model.

These predictions can give the best prediction for a new random site (from the same 'population') or a new random tree from within one of the sites. However the results below show considerable between-site variability and between-tree within-site variability. Hence it is often desirable to base predictions on a sample, separate from the database used in constructing the model. This could be for a random future site, or for further random trees from a site where a sample of trees has been measured, or for future growth for a given set of trees. Data for such samples may include SilviScan strips from a sample of trees and/or non-destructively sampled outer-wood cores.

From the predicted values within each disc it is then possible to predict trait values at any position within stem by interpolation. As with any model, predictions are valid for the population sampled. For other populations, *e.g.* with a radical new silviculture, or when extrapolating beyond the range of the data, predictions are not strictly valid and are at the risk of the user. With smoothing splines, predictions beyond the range of the data tend to be extrapolated by straight lines. This behaviour could be modified, for example by using a transformation based on a non-linear curve fit. It is however possible to make predictions for future rings of a given tree from the population, provided the age range for predictions is covered within the sample.

Simulations

We have simulated 100 replicate datasets for the 3-trait model, and a simplified 3-trait model. Simulations used predictions from the overall level plus simulations of random effects from their distributions, estimated from the variance structures in the model. Correlations for the raw data have been calculated and compared to correlations for the simulated data. Variograms (within height) for the raw data and residuals have been plotted. Variograms for the raw data have been compared to variograms for the simulated data.

RESULTS

Correlations

Selected inter-trait correlations from the raw data are shown in Tables 2,3,4.

Note: in the standardisation of the traits, the sign of density was reversed so as to give positive correlations between all traits.

Note fairly high correlations at the site level (Tables 2,3,4), particularly when controlling for disc height and ring number (Table 4). This suggests that the same differences between sites are driving all three variables. This was confirmed by examination of principal components.

Principal components for site means, for disc 1, ring 10, showed the first principal component explained 82% of the variation compared to 12% and 5% for the 2nd and 3rd components, *i.e.* at the site level the three traits are behaving largely as one (Figure 1).

In contrast, in the model fit, *i.e.* after allowing for site and tree effects and within tree trends, the correlations between ring density and ring width or microfibril angle at the units level was low (Table 5, *cf.* Appendix 1, `units-level covariance between traits`), and the correlation between ring width and microfibril angle was high, suggesting that ring-to-ring (or year-to-year) fluctuations in density within a tree are nearly independent of those for ring width and microfibril angle. This could partly be due to the fact that we haven't allowed for calendar year climatic effects. This needs to be tested by an additional non-smooth (*i.e.* factor) term for ring number from the bark at the overall or site levels.

For the within-site tree level correlations, 100 replicates were simulated from the model (Table 7), or a simplified model (Table 8). In the simulations, the overall-level random effects were set to their estimates (conditional modes), and other level random effects sampled from their distributions according to the fitted model. Standard errors are based on the standard deviation of correlation estimates from the simulations. Correlations are correlations of tree means within site, averaged over sites.

Note: the standard deviation of correlations from individual simulations was quite high (around 0.34, or 10 times the standard errors based on the mean of 100 simulations in Table 7. This explains the seemingly un-related correlations for the simulated data in Table 7 compared with those for the raw data in Table 6, since the raw data is in effect a single replicate. One hundred times more data would give quite accurate estimates of correlations.

Based on 133 trees, we would expect a lower standard error comparable to the standard errors of correlations for the raw data, *i.e.* around 0.1. With this standard error the correlations for simulated data would not be consistent with those for the raw data. Possible sources of the problem include: too few trees on some sites, especially site 17 with only two trees; lack of 'rough' terms in ring number; correlation estimates converging to plus or minus 1 in REML likelihood optimisation.

Graphs of Model Fits

Residual sums of squares versus model terms for 3-trait multi-site model are shown in Figure 2. Each trait is shown in a separate ‘panel'. Each point represents the residual sum of squares based on predictions using estimated random effects for the term, and previous terms. Points are coded `f,o,s,t,u` for fixed effects, and overall, site, tree and units, respectively. The model consists of 27 terms, starting with fixed effects (one term), followed by overall random effects (five terms), site-level random effects (ten terms), tree-level random effects (ten terms), and units (one term).

The panel for ring width (`rw`) shows the fixed effects explaining approximately 35% of the variation, and no improvement until the last four site terms, representing splines in ring number within each height. Approximately 63% of the variation is explained by fixed, overall and site terms. Note the quantum drop to the first ‘`t`' point. This drop indicates that the tree linear term is explaining approximately 10% of the variation, and the subsequent tree terms explaining progressively more up to approximately 83% of the variation. The quantum jump to the ‘`u`' point represents variation that is not readily fitted by a smooth curve. Examining Figure 5 (below) shows that this is largely due to fluctuations in the first few rings from the pith, which are not readily accommodated by a smoothing spline, but which could be accomodated with some ring-specific terms.

The panel for ring density (rd) shows the fixed effects explaining approximately 20% of the variation, with no improvement until the 4^{th} site level effect (linear trend in ring number at height 1). Fixed, overall, and site effects explained around 37% of the variation. Again, there was a quantum drop of around 40% to the first ‘`t`' point , showing substantial differences in linear trends between trees within sites. In these data, trees within sites are accounting for much more (around 60% compared to around 17%) of the variation in density than site differences.

The panel for microfibril angle (`mfa`) shows the fixed effects explaining approximately 58% of the variation. An additional 10% is explained by the site-level splines within height, and 20% by the tree-level linear terms, and the remainder approximately equally by the other tree-level terms. Tree-level differences are explaining nearly four times more variation than site-level differences.

Figure 3 shows *stratum correlations* (our terminology). These are correlations between means at the given level, but include components of correlations present at higher levels.

Figure 4 shows *level correlations* (our terminology). These are averages of correlations between means taken at the given level for each value of the higher levels. Level correlations attempt to isolate correlation to the given level. For example at the tree level, correlations are taken for each site and averaged over sites.

Recall that in the standardisation of the traits, the sign of density was reversed so as to give positive correlations between traits. In Figure 4, the level correlations between traits are approximately similar, except for `cor(rd,mfa)` at the disc level. Although there is no reason to expect correlations between different pairs of traits to be similar, or physical significance of such similarity, it does make some simplification of the model possible which may help when fitting the model to limited datasets – the full positive symmetric variance for traits can be replaced by a simpler ‘compound symmetry' structure, to a first approximation.

Both stratum and level correlations decrease with level except for the ring (unit) level where they increase. Note that the level correlations for `cor(rd,mfa)` are even negative at the disc level. This is not unexpected, because microfibril angle decreases while density increases when moving pith-to-bark, while both microfibril angle and density both decrease with height on a disc average basis (noting that the average density for a higher disc occurs closer to the pith). Hence the reverse sign of correlation at the disc level.

Variograms for raw data and residuals at height 1 are shown in Figure 6.

The semi-variance, defined as

$$V(x_1,x_2) = ½ (\text{cov} (Z(x_1),Z(x_1)) + \text{cov} (Z(x_2),Z(x_2)) - 2 \text{cov} (Z(x_1),Z(x_2))) \quad (4)$$

for points x_1,x_2 is averaged over pairs of rings for each given distance ('lag') and plotted against lag. Lags correspond to differences in ring number. For the raw data, note the steadily increasing upward trends. These indicate a long range dependency, for example due to a trend, which is not surprising. The corresponding variograms for the residuals show an adequate fit to the model. The variogram for the residuals jumps to an approximately constant variance level immediately from lag 1 and remains at that level, except for a possibly slightly lower value at lag 1 for density and microfibril angle, and a possible increase at high lags. At high lags however the estimated variances have higher sampling error due to fewer pairs of points existing at the lag, *e.g.* with 23 rings there are only 3 pairs of points at lag 20.

Variograms for first differences of the raw data and residuals at height 1 are shown in Figure 7. First differences are of interest because a smoothing spline is equivalent to an ARIMA (2,1,0) model, hence first differences would be auto-regressive of order 2. Additionally, growth modellers often assume first differences in ring width (growth increments) are independent. If this were the case, the first differenced raw data variograms would immediately jump to an approximately constant variance level. This does not seem to be the case – *e.g.* for ring width the semi-variance increases linearly from lag 5.

For ring width, the variogram for the residuals is approximately constant from lag 1, with a possible smaller linear increase (not exceeding the lag 1 level until lag 10) than for the raw data. For ring width the increasing trend in the first differenced raw data variogram suggests a significant non-linear trend while the residual variogram suggests that the smoothing splines have accommodated this but not perfectly.

For ring density, the variogram for first-differenced raw data jumps to an approximately constant level immediately, followed by an increasing linear trend from lag 15. The same pattern applies for the residuals, also with a possible but less pronounced increasing linear trend from lag 15. (Note: different scales on the graphs). Hence for ring density, the raw data variogram is consistent with an approximately linear trend with independent errors, while the residual variogram suggests that the smoothing splines have accommodated this but not perfectly.

For microfibril angle, the variogram for first-difference raw data jumps to an approximately constant level followed by an increasing linear trend from lag 10. For the residuals, a less pronounced possible trend is visible increasing slightly from lag 10 and more strongly from lag 15. Again the variograms suggest a non-linear trend which is reasonably well accommodated by the smoothing splines.

Variograms for raw and simulated data are shown in Figure 8. The solid line is the mean variogram for 100 datasets simulated from the fitted model. The dashed lines are 10, and 90% confidence intervals based on the simulated data. The raw data variogram is plotted with the symbol '○'. The raw data variogram lies near the lower end of the distribution, near the 10% quantile.

DISCUSSION AND CONCLUSIONS

For a given disc and ring, site level correlations between traits, ring width, ring density, and microfibril angle were quite high.

Some of the models are large with 26 or more random terms, each with tensor product of variance structures, and can be slow to fit using gigabytes of RAM, pushing the limits of the modelling system, and not all terms could be fitted that may be desirable to include. Further developments to the modelling methodology and algorithms would be needed to fit more complex models more rapidly. These include specialised modifications to the `lme` algorithm, specialised variance structures, effective use of sparse matrices, block-update or parallel computing. Unfortunately no package with these features exists that can fit these models. The `R/lme4` system runs faster and incorporates sparse matrices, as does the proprietary ASReml system, but these programmes lack the facilities to fit the required models, *e.g.* to fit a given variance structure to a given set of random effects, not necessarily corresponding to a factor in the data. The new ASReml '`grp`' and '`str`' facilities come close but require special columns to be added to the dataframe which is impractical for the large number of nested terms required.

It was possible to fit these larger models due to the 'unconstrained parameterisation' used by the `lme` system and the ability to choose the slower but more robust Nelder-Mead optimiser.

There are some differences between correlations between the raw data and data simulated from the full splines model. Investigation of the causes of these differences and adapting the models is a topic for future work.

Nevertheless, we have established proof-of-concept that general models can be fitted to model multiple traits in three dimensions within and between stems. Further work is needed to adapt the modelling system to handle these models more efficiently, and robustly. Possible approaches include Bayesian methods or adaptations of `lme` to use block updates that don't require the full set of equations to be solved simultaneously. Although the sample size was large (~ 28000 experimental units) there was still a limited number of sites and trees per site particularly site 17 which had only two trees. Increased sample size and/or Bayesian methods may help overcome the limitations of maximum likelihood or REML in these situations.

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Tables and Figures

Table 1. Terms in the 3-trait model.

```
Terms fitted:

fixed
 bark.ring*height*trait

random
 overall level
            term
        -----------------
group    R         symbolic
  all    Zh        spl(h)
  all.1  Zr3h0     lin(r|h=0)
  all.2  Zr3h1     lin(r|h=1)
  all.3  Zr3h5     lin(r|h=5)
  all.4  Zr3h20    lin(r|h=20)

 site level
            term
        -----------------
group    R         symbolic
 site    1+bark.ring+height         lin(1+r+h)
 site.1  Zh        spl(h)
 site.2  Zbrlh0    lin(r|h=0)
 site.3  Zbrlh1    lin(r|h=1)
 site.4  Zbrlh5    lin(r|h=5)
 site.5  Zbrlh20   lin(r|h=20)
 site.6  Zr3h0     spl(r|h=0)
 site.7  Zr3h1     spl(r|h=1)
 site.8  Zr3h5     spl(r|h=5)
 site.9  Zr3h20    spl(r|h=20)

 tree level
           term
       -----------------
group    R         symbolic
 tree    1+bark.ring+height         lin(1+r+h)
 tree.1  Zh
 tree.2  Zbrlh0    lin(r|h=0)
 tree.3  Zbrlh1    lin(r|h=1)
 tree.4  Zbrlh5    lin(r|h=5)
 tree.5  Zbrlh20   lin(r|h=20)
 tree.6  Zr3h0     spl(r|h=0)
 tree.7  Zr3h1     spl(r|h=1)
 tree.8  Zr3h5     spl(r|h=5)
 tree.9  Zr3h20    spl(r|h=20)

 unit level
           term
       -----------------
group    R         symbolic
 unit    1         lin(1)
```

Table 2. Site-, tree-, disc-, and ring-level correlations between ring width (`rw`), ring density (`rd`), and microfibril angle (`mfa`) from the raw data.

Site level correlations (correlations between site means):

	rw	rd	mfa
rw	1.000	0.565	0.575
rd	0.565	1.000	0.802
mfa	0.575	0.802	1.000

Tree level correlations (correlations between tree means):

	rw	rd	mfa
rw	1.000	0.483	0.454
rd	0.483	1.000	0.537
mfa	0.454	0.537	1.000

Disc level correlations (correlations between disc means):

	rw	rd	mfa
rw	1.000	0.392	0.330
rd	0.392	1.000	0.179
mfa	0.330	0.179	1.000

Ring level correlations:

	rw	rd	mfa
rw	1.000	0.486	0.644
rd	0.486	1.000	0.457
mfa	0.644	0.457	1.000

Table 3. Site-, tree-, and disc-level correlations between ring width (`rw`), ring density (`rd`), and microfibril angle (`mfa`) using data from ring 10 only.

Site level correlations for ring 10:

	rw	rd	mfa
rw	1.000	0.641	0.767
rd	0.641	1.000	0.825
mfa	0.767	0.824	1.000

Tree level correlations for ring 10:

	rw	rd	mfa
rw	1.000	0.457	0.670
rd	0.457	1.000	0.592
mfa	0.670	0.592	1.000

Disc level correlations for ring 10:

	rw	rd	mfa
rw	1.000	0.357	0.634
rd	0.357	1.000	0.352
mfa	0.634	0.352	1.000

Table 4. Site- and tree-level correlations between ring width (`rw`), ring density (`rd`), and microfibril angle (`mfa`) using data from ring 10 and disc 1 only.

Site level correlations for disc 1, ring 10:

	rw	rd	mfa
rw	1.000	0.712	0.824
rd	0.712	1.000	0.889
mfa	0.824	0.889	1.000

Tree level correlations for disc 1, ring 10:

	rw	rd	mfa
rw	1.000	0.468	0.644
rd	0.468	1.000	0.626
mfa	0.644	0.626	1.000

Table 5. Estimated correlations between random effects for traits ring-width (`rw`), ring density (`rd`) and microfibril angle (`mfa`) at the unit- (*i.e.* experimental unit, or ring) level, from the 3-trait model.

	correlations		
	rw	rd	mfa
rw	1.000	0.155	0.813
rd	0.155	1.000	0.082
mfa	0.813	0.082	1.000

Table 6. Average within-site tree-level correlations. Correlations are averages over sites of correlations between tree means for each site for the raw data. Standard errors are based on sites as replicates.

	correlations			standard errors		
	rw	rd	mfa	rw	rd	mfa
rw	1.000	0.393	0.311	0.000	0.101	0.092
rd	0.393	1.000	0.374	0.101	0.000	0.064
mfa	0.311	0.374	1.000	0.092	0.063	0.000

Table 7. Average within-site tree-level correlations. One hundred replicate datasets were simulated from the 3-trait model. Correlations are averages over sites of correlations between tree means for each site and replicate simulation. Standard errors are based on sites and repeated simulations as replicates.

	correlations			standard errors		
	rw	rd	mfa	rw	rd	mfa
rw	1.000	-0.178	0.297	0.000	0.034	0.024
rd	-0.178	1.000	-0.012	0.034	0.000	0.031
mfa	0.297	-0.012	1.000	0.024	0.031	0.000

Table 8. Average within-site tree-level correlations. One hundred replicate datasets were simulated from a simpler 3-trait model, with smoothing splines and a non-smooth (factor) term fitted at the overall level, and just random trait effects fitted at lower levels. Correlations are averages over sites of correlations between tree means for each site and replicate simulation. Standard errors are based on sites and repeated simulations as replicates.

	correlations			standard errors		
	rw	rd	mfa	rw	rd	mfa
rw	1.000	0.447	0.333	0.000	0.080	0.096
rd	0.447	1.000	0.142	0.080	0.000	0.068
mfa	0.333	0.142	1.000	0.096	0.068	0.000

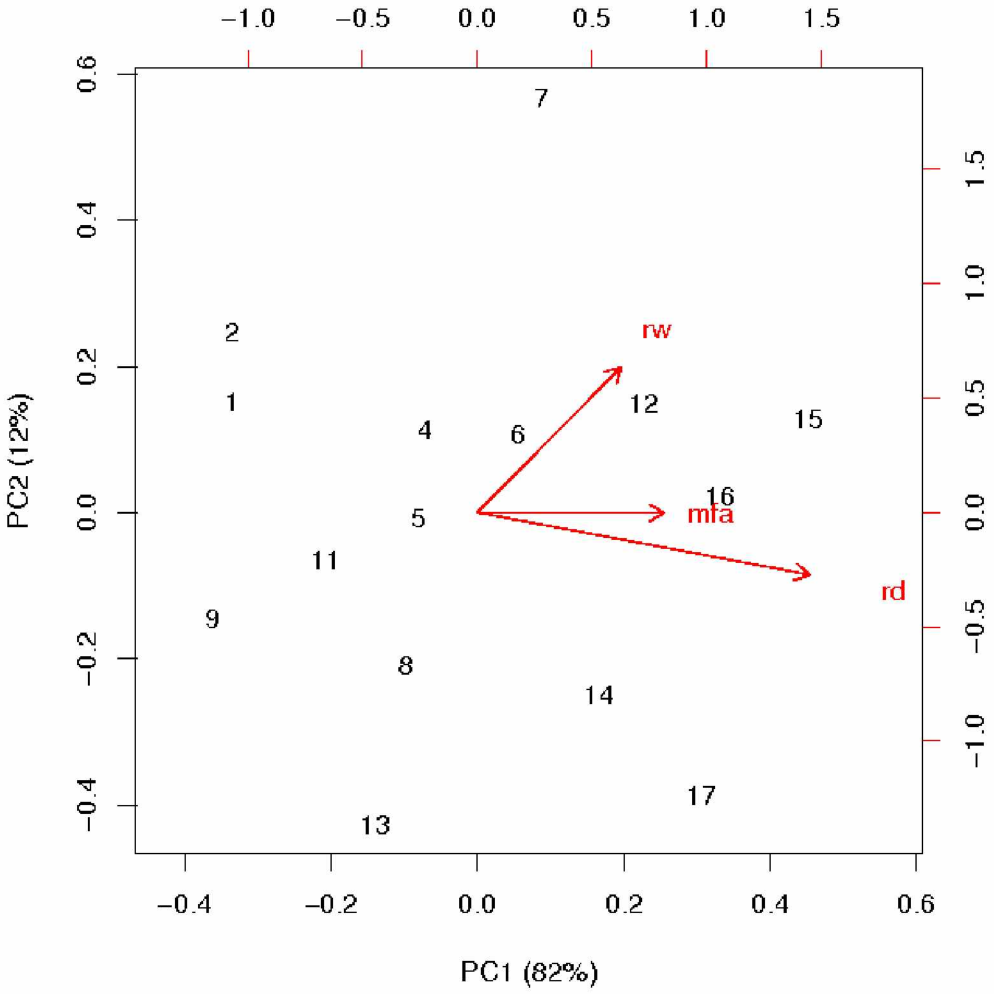

Figure 1: Biplots for principal components of site means.

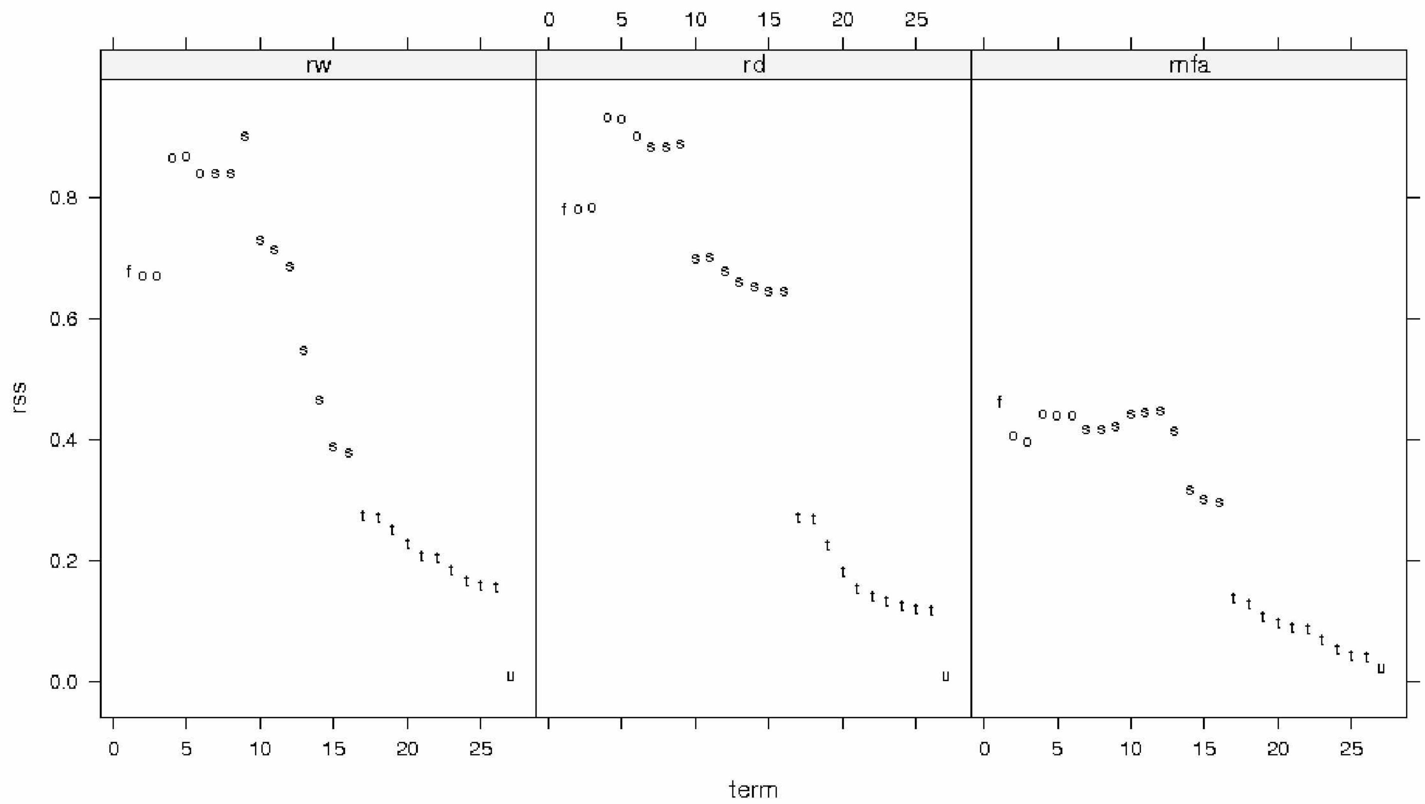

Figure 2: Residual sums of squares by model term. The model consists of 27 terms, starting with fixed effects('f') with 1 term, followed by overall effects('o') with 5 terms, site-level effects('s') with 10 terms, tree-level effects('t') with 10 terms, and units('u') with 1 term. The values plotted for the ith term are the residual sums of squares that apply when predictions are made based on the estimated effects for the all terms up to the given term for the given trait.

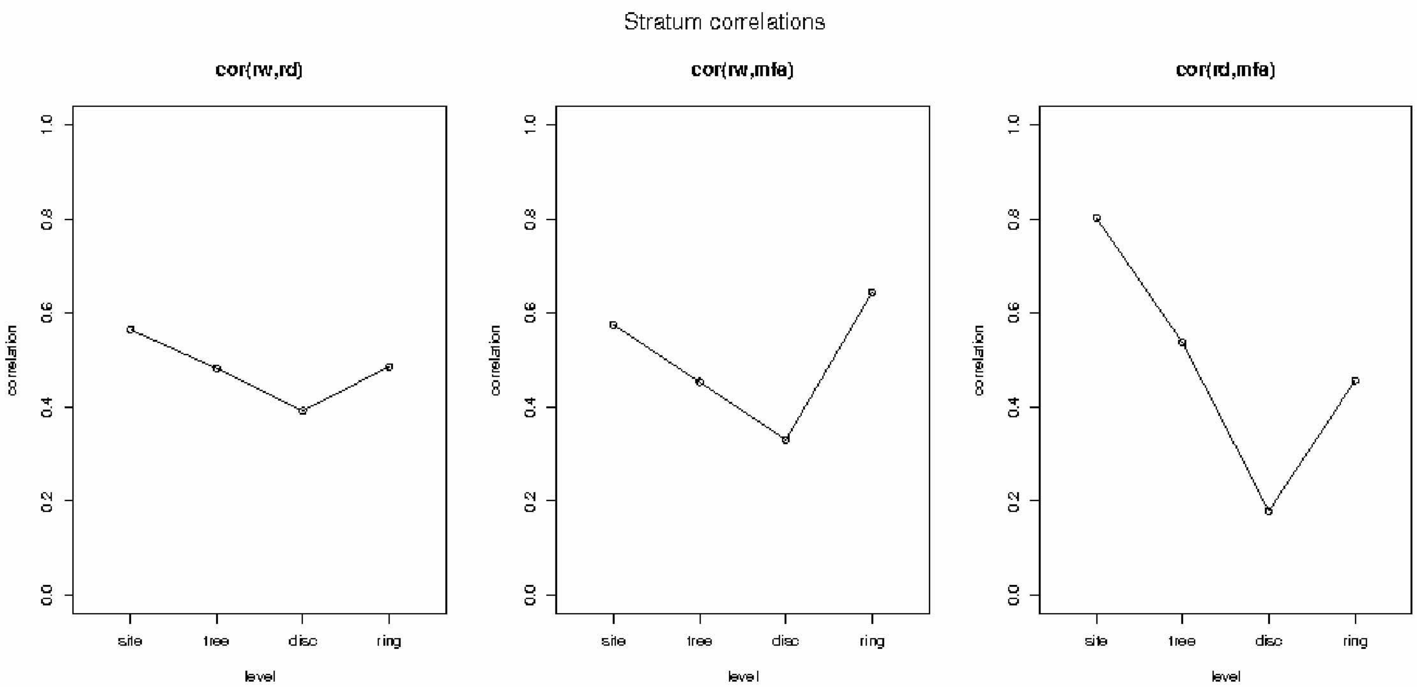

Figure 3: Stratum correlations. These are correlations between means taken at the given level, *e.g.* site means, tree means, disc means, or ring means.

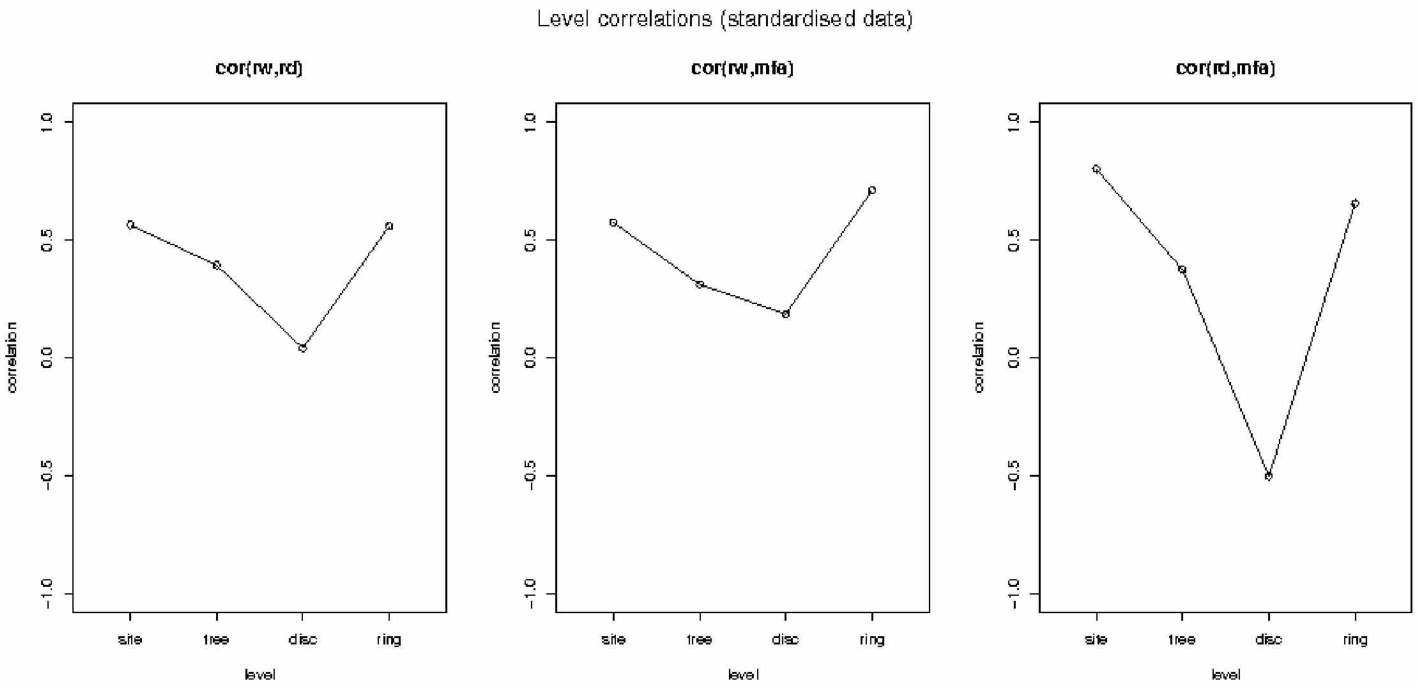

Figure 4: Level correlations. These are averages of correlations between means taken at the given level for each value of the higher levels. For example at the tree level correlations are taken for each site and averaged over sites.

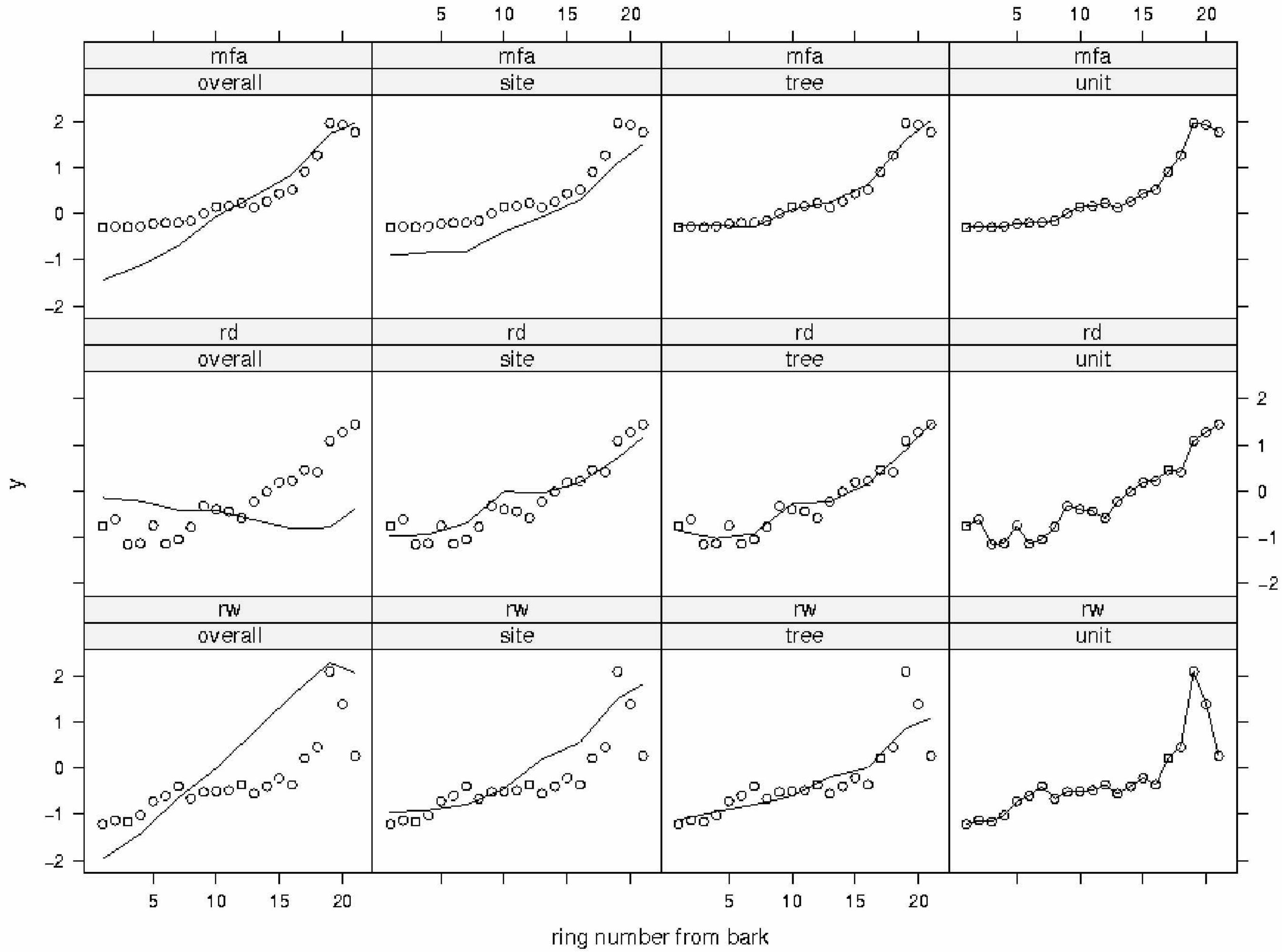

Figure 5: Observed and predicted values for tree A10 at height 1. Observed and predicted values are plotted for each trait (`rw,rd,mfa`) at each level (overall, site, tree, unit) in separate panels. Within each panel the observed values for the standardised trait are plotted as points (symbol '`o`') against ring number from the bark. The lines plotted represent the model predictions at the given level.

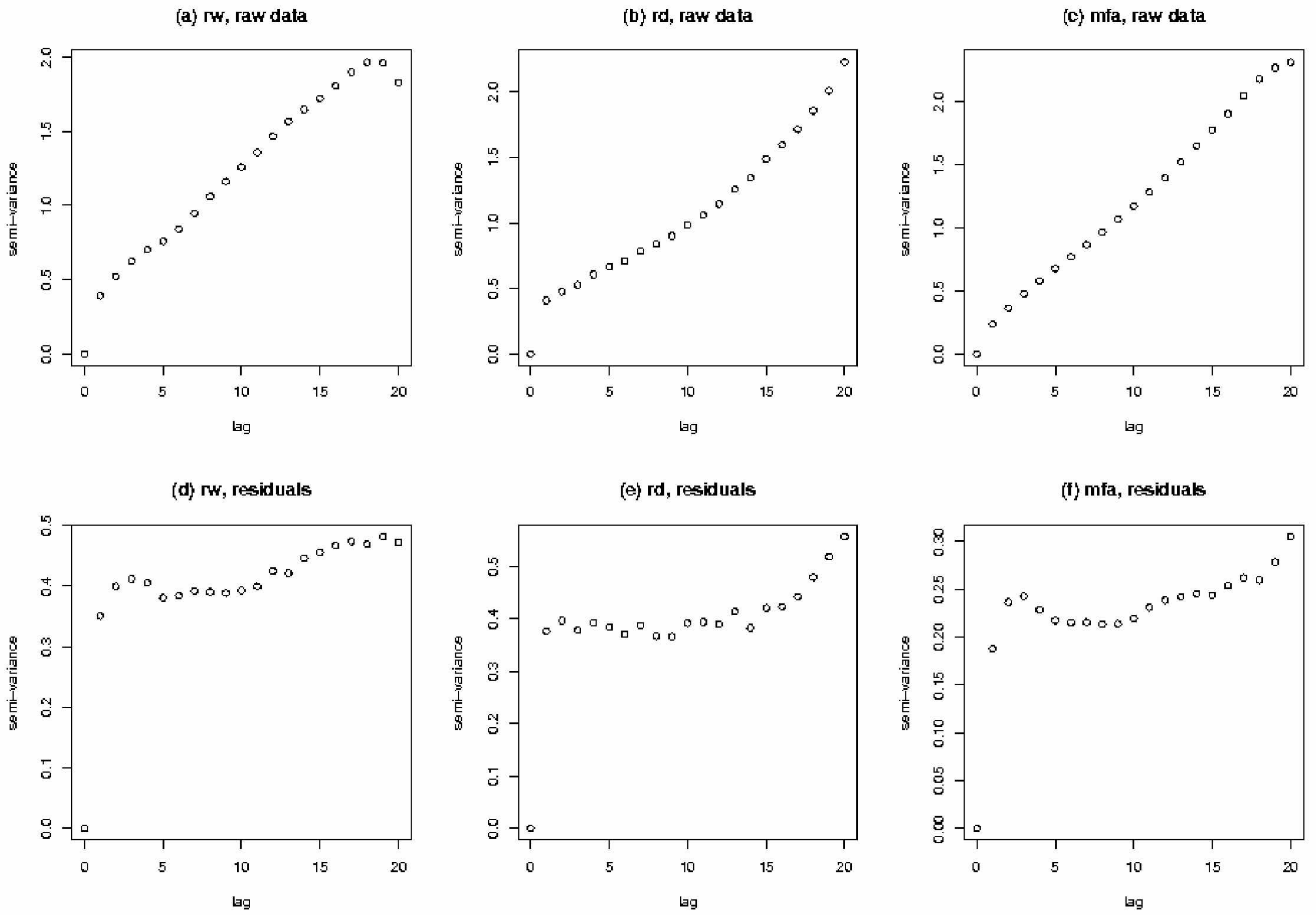

Figure 6: Variograms for raw data and residuals at height 1. Variograms for ring width (`rw`), ring density (`rd`), and microfibril angle (`mfa`) are plotted for the raw data (panels (a)–(c)) and residuals from the 3-trait model (panels (d)–(f)). The plotted points are semi-variances, for each lag, or difference in ring number.

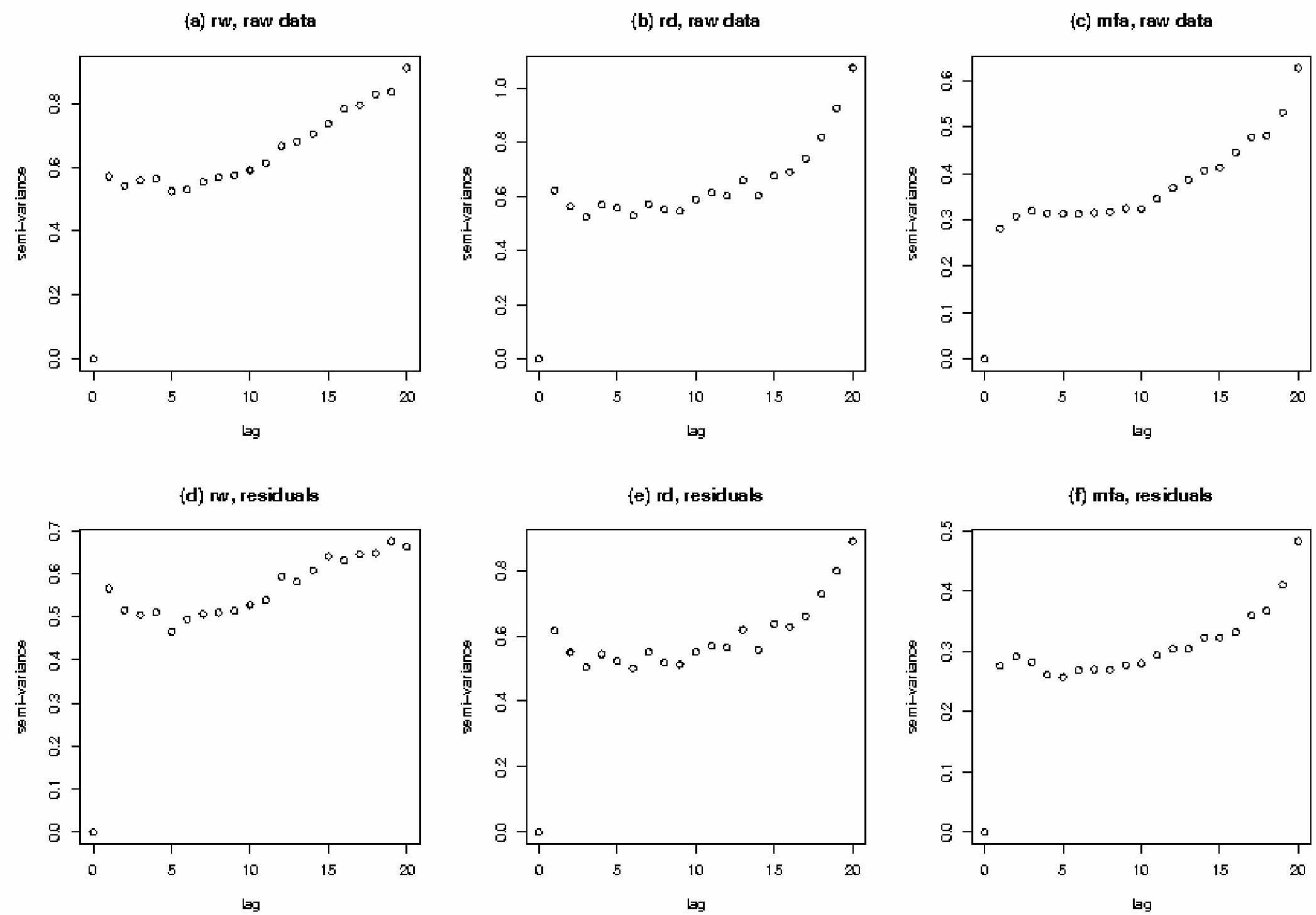

Figure 7: Variograms for first differences of raw data and residuals at height 1. Variograms for ring width (rw), ring density (rd), and microfibril angle (mfa) are plotted for the first differences (differences in values between successive rings within a disc) from the raw data (panels (a)–(c)) and residuals from the 3-trait model (panels (d)–(f)). The plotted points are semi-variances, for each lag, or difference in ring number.

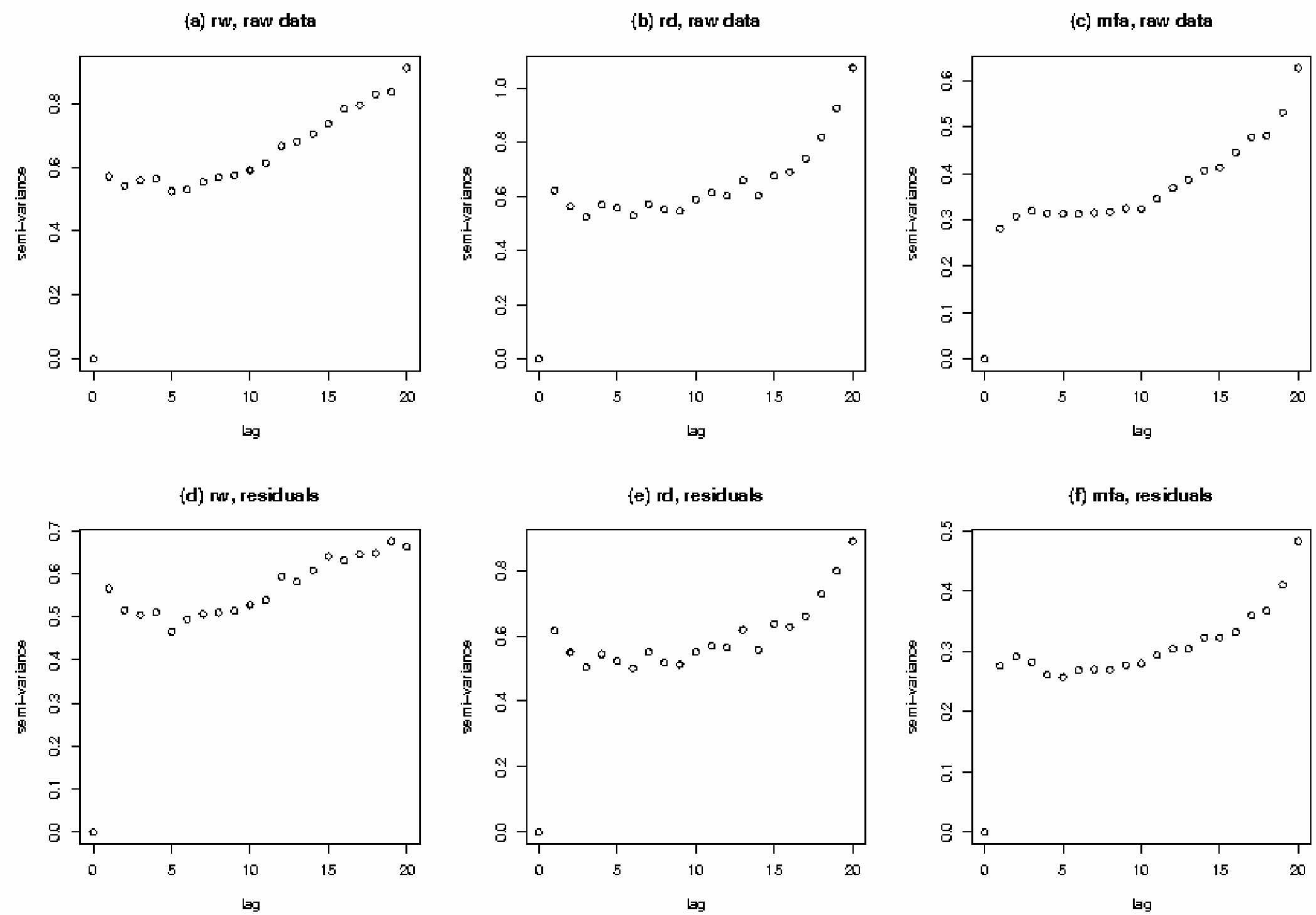

Figure 7: Variograms for first differences of raw data and residuals at height 1. Variograms for ring width (`rw`), ring density (`rd`), and microfibril angle (`mfa`) are plotted for the first differences (differences in values between successive rings within a disc) from the raw data (panels (a)–(c)) and residuals from the 3-trait model (panels (d)–(f)). The plotted points are semi-variances, for each lag, or difference in ring number.

APPENDICES

Appendix 1. R code and output for the 3 trait, multi-site model.

This model uses the nested stratification

`all/site/tree/disc/unit`

Splines in height and ring number are fitted at each level, except that disc does not appear explicitly because separate linear and spline terms are fitted within each height

Linear terms `Zbrlh0, Zbrlh1, Zbrlh5, Zbrlh20` have terms for intercept and ring number from the bark, zeroed out except for data at the respective heights (0,1,5,20) and centred within each height, for minimum correlation between intercept and slope.

```
> summary(mtrait.fit7a)

Linear mixed-effects model fit by REML
 Data: wqirings.mtrait.df
       AIC      BIC    logLik
  31069.17 32480.85 -15363.59

Random effects:

**********  overall-level spline in height ************

 Structure: pdTE2
   StdDev     Corr
V1 0.08645710 V1     V2     V3     V4     V5
V2 0.08645710  0.000
V3 0.05339115 -0.998  0.000
V4 0.05339115  0.000 -0.998  0.000
V5 0.18173458 -1.000  0.000  0.999  0.000
V6 0.18173458  0.000 -1.000  0.000  0.999  0.000
attr(.,"tensor.blocks")
 Formula: ~Zh - 1
 Structure: Multiple of an Identity
               Zh1        Zh2
StdDev: 0.04107018 0.04107018
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev   Corr
traitrw  2.105107 tratrw tratrd
traitrd  1.299998 -0.998
traitmfa 4.424977 -1.000  0.999


**********  overall-level spline in ring number, height 0 ************

 Structure: pdTE2
    StdDev      Corr
V1  0.009563195 V1    V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17
V2  0.009563195  0
V3  0.009563195  0     0
V4  0.009563195  0     0  0
V5  0.009563195  0     0  0  0
V6  0.009563195  0     0  0  0  0
V7  0.009563195  0     0  0  0  0  0
V8  0.017744650 -1     0  0  0  0  0  0
V9  0.017744650  0    -1  0  0  0  0  0  0
```

```
V10 0.017744650  0     0 -1  0  0  0  0  0  0
V11 0.017744650  0     0  0 -1  0  0  0  0  0  0
V12 0.017744650  0     0  0  0 -1  0  0  0  0  0    0
V13 0.017744650  0     0  0  0  0 -1  0  0  0  0    0    0
V14 0.017744650  0     0  0  0  0  0 -1  0  0  0    0    0    0
V15 0.032641281  1     0  0  0  0  0  0 -1  0  0    0    0    0    0
V16 0.032641281  0     1  0  0  0  0  0  0 -1  0    0    0    0    0    0
V17 0.032641281  0     0  1  0  0  0  0  0  0 -1    0    0    0    0    0    0
V18 0.032641281  0     0  0  1  0  0  0  0  0  0   -1    0    0    0    0    0    0
V19 0.032641281  0     0  0  0  1  0  0  0  0  0    0   -1    0    0    0    0    0
V20 0.032641281  0     0  0  0  0  1  0  0  0  0    0    0   -1    0    0    0    0
V21 0.032641281  0     0  0  0  0  0  1  0  0  0    0    0    0   -1    0    0    0

V1  V18 V19 V20
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19  0
V20  0   0
V21  0   0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h0 - 1
 Structure: Multiple of an Identity
             Zr3h01      Zr3h02      Zr3h03      Zr3h04      Zr3h05      Zr3h06
StdDev: 0.001970099 0.001970099 0.001970099 0.001970099 0.001970099 0.001970099
             Zr3h07
StdDev: 0.001970099
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw   4.854170 tratrw tratrd
traitrd   9.006983 -1
traitmfa 16.568344  1     -1

**********  overall-level spline in ring number, height 1 ************

 Structure: pdTE2
    StdDev    Corr
V1  0.3450238 V1     V2     V3     V4     V5     V6     V7     V8     V9
V2  0.3450238  0.000
V3  0.3450238  0.000  0.000
V4  0.3450238  0.000  0.000  0.000
V5  0.3450238  0.000  0.000  0.000  0.000
V6  0.3450238  0.000  0.000  0.000  0.000  0.000
V7  0.3450238  0.000  0.000  0.000  0.000  0.000  0.000
V8  0.1795142 -0.988  0.000  0.000  0.000  0.000  0.000  0.000
V9  0.1795142  0.000 -0.988  0.000  0.000  0.000  0.000  0.000  0.000
V10 0.1795142  0.000  0.000 -0.988  0.000  0.000  0.000  0.000  0.000  0.000
V11 0.1795142  0.000  0.000  0.000 -0.988  0.000  0.000  0.000  0.000  0.000
V12 0.1795142  0.000  0.000  0.000  0.000 -0.988  0.000  0.000  0.000  0.000
```

```
V13 0.1795142  0.000  0.000  0.000  0.000  0.000 -0.988  0.000  0.000  0.000
V14 0.1795142  0.000  0.000  0.000  0.000  0.000  0.000 -0.988  0.000  0.000
V15 0.2156604  0.943  0.000  0.000  0.000  0.000  0.000  0.000 -0.880  0.000
V16 0.2156604  0.000  0.943  0.000  0.000  0.000  0.000  0.000  0.000 -0.880
V17 0.2156604  0.000  0.000  0.943  0.000  0.000  0.000  0.000  0.000  0.000
V18 0.2156604  0.000  0.000  0.000  0.943  0.000  0.000  0.000  0.000  0.000
V19 0.2156604  0.000  0.000  0.000  0.000  0.943  0.000  0.000  0.000  0.000
V20 0.2156604  0.000  0.000  0.000  0.000  0.000  0.943  0.000  0.000  0.000
V21 0.2156604  0.000  0.000  0.000  0.000  0.000  0.000  0.943  0.000  0.000

V1  V10    V11    V12    V13    V14    V15    V16    V17    V18    V19
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11  0.000
V12  0.000  0.000
V13  0.000  0.000  0.000
V14  0.000  0.000  0.000  0.000
V15  0.000  0.000  0.000  0.000  0.000
V16  0.000  0.000  0.000  0.000  0.000  0.000
V17 -0.880  0.000  0.000  0.000  0.000  0.000  0.000
V18  0.000 -0.880  0.000  0.000  0.000  0.000  0.000  0.000
V19  0.000  0.000 -0.880  0.000  0.000  0.000  0.000  0.000  0.000
V20  0.000  0.000  0.000 -0.880  0.000  0.000  0.000  0.000  0.000  0.000
V21  0.000  0.000  0.000  0.000 -0.880  0.000  0.000  0.000  0.000  0.000

V1  V20
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21  0.000
attr(.,"tensor.blocks")
 Formula: ~Zr3h1 - 1
 Structure: Multiple of an Identity
           Zr3h11    Zr3h12    Zr3h13    Zr3h14    Zr3h15    Zr3h16    Zr3h17
StdDev: 0.1392939 0.1392939 0.1392939 0.1392939 0.1392939 0.1392939 0.1392939
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev   Corr
traitrw  2.476949 tratrw tratrd
traitrd  1.288745 -0.988
traitmfa 1.548240  0.943 -0.880
```

```
**********  overall-level spline in ring number, height 5 ************

 Structure: pdTE2
    StdDev     Corr
V1  0.04674432 V1    V2    V3    V4    V5    V6    V7    V8    V9    V10
V2  0.04674432 0.000
V3  0.04674432 0.000 0.000
V4  0.04674432 0.000 0.000 0.000
V5  0.04674432 0.000 0.000 0.000 0.000
V6  0.04674432 0.000 0.000 0.000 0.000 0.000
V7  0.05870113 0.620 0.000 0.000 0.000 0.000 0.000
V8  0.05870113 0.000 0.620 0.000 0.000 0.000 0.000 0.000
V9  0.05870113 0.000 0.000 0.620 0.000 0.000 0.000 0.000 0.000
V10 0.05870113 0.000 0.000 0.000 0.620 0.000 0.000 0.000 0.000 0.000
V11 0.05870113 0.000 0.000 0.000 0.000 0.620 0.000 0.000 0.000 0.000 0.000
V12 0.05870113 0.000 0.000 0.000 0.000 0.000 0.620 0.000 0.000 0.000 0.000
V13 0.05923724 0.903 0.000 0.000 0.000 0.000 0.000 0.897 0.000 0.000 0.000
V14 0.05923724 0.000 0.903 0.000 0.000 0.000 0.000 0.000 0.897 0.000 0.000
V15 0.05923724 0.000 0.000 0.903 0.000 0.000 0.000 0.000 0.000 0.897 0.000
V16 0.05923724 0.000 0.000 0.000 0.903 0.000 0.000 0.000 0.000 0.000 0.897
V17 0.05923724 0.000 0.000 0.000 0.000 0.903 0.000 0.000 0.000 0.000 0.000
V18 0.05923724 0.000 0.000 0.000 0.000 0.000 0.903 0.000 0.000 0.000 0.000

V1  V11   V12   V13   V14   V15   V16   V17
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11
V12 0.000
V13 0.000 0.000
V14 0.000 0.000 0.000
V15 0.000 0.000 0.000 0.000
V16 0.000 0.000 0.000 0.000 0.000
V17 0.897 0.000 0.000 0.000 0.000 0.000
V18 0.000 0.897 0.000 0.000 0.000 0.000 0.000
attr(.,"tensor.blocks")
 Formula: ~Zr3h5 - 1
 Structure: Multiple of an Identity
           Zr3h51    Zr3h52    Zr3h53    Zr3h54    Zr3h55    Zr3h56
StdDev: 0.0718094 0.0718094 0.0718094 0.0718094 0.0718094 0.0718094
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.6509499 tratrw tratrd
traitrd  0.8174575 0.620
traitmfa 0.8249233 0.903  0.897

**********  overall-level spline in ring number, height 20 ************

 Structure: pdTE2
    StdDev      Corr
V1  0.084918129 V1     V2     V3     V4     V5     V6     V7     V8     V9
V2  0.084918129  0.000
V3  0.084918129  0.000  0.000
V4  0.084918129  0.000  0.000  0.000
V5  0.090717961 -0.999  0.000  0.000  0.000
```

```
V6  0.090717961  0.000 -0.999  0.000  0.000  0.000
V7  0.090717961  0.000  0.000 -0.999  0.000  0.000  0.000
V8  0.090717961  0.000  0.000  0.000 -0.999  0.000  0.000  0.000
V9  0.005003256  0.000  0.000  0.000  0.000  0.039  0.000  0.000  0.000
V10 0.005003256  0.000  0.000  0.000  0.000  0.000  0.039  0.000  0.000  0.000
V11 0.005003256  0.000  0.000  0.000  0.000  0.000  0.000  0.039  0.000  0.000
V12 0.005003256  0.000  0.000  0.000  0.000  0.000  0.000  0.000  0.039  0.000

V1  V10    V11
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11  0.000
V12  0.000  0.000
attr(.,"tensor.blocks")
 Formula: ~Zr3h20 - 1
 Structure: Multiple of an Identity
           Zr3h201    Zr3h202    Zr3h203    Zr3h204
StdDev: 0.06221453 0.06221453 0.06221453 0.06221453
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev     Corr
traitrw  1.36492443 tratrw tratrd
traitrd  1.45814754 -0.999
traitmfa 0.08041942  0.000  0.039

**********  site-level linear in ring number and height ************

 Structure: pdTE2
   StdDev      Corr
V1 0.027061875 V1     V2     V3     V4     V5     V6     V7     V8
V2 0.017856333 -0.991
V3 0.005256657 -0.728  0.627
V4 0.018446139 -0.896  0.888  0.652
V5 0.012171381  0.888 -0.896 -0.562 -0.991
V6 0.003583086  0.652 -0.562 -0.896 -0.728  0.627
V7 0.015095250 -0.373  0.370  0.272 -0.076  0.076  0.056
V8 0.009960352  0.370 -0.373 -0.234  0.076 -0.076 -0.048 -0.991
V9 0.002932190  0.272 -0.234 -0.373  0.056 -0.048 -0.076 -0.728  0.627
attr(.,"tensor.blocks")
 Formula: ~bark.ring + height
 Structure: General positive-definite
            StdDev     Corr
(Intercept) 0.18173501 (Intr) brk.rn
bark.ring   0.11991486 -0.991
height      0.03530127 -0.728  0.627
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev     Corr
traitrw  0.14890843 tratrw tratrd
traitrd  0.10150019 -0.896
traitmfa 0.08306187 -0.373 -0.076

**********  site-level spline in  height ************

 Structure: pdTE2
   StdDev      Corr
V1 0.004633176 V1    V2    V3    V4    V5
```

```
V2 0.004633176 0.000
V3 0.002722509 0.499 0.000
V4 0.002722509 0.000 0.499 0.000
V5 0.005736206 0.816 0.000 0.841 0.000
V6 0.005736206 0.000 0.816 0.000 0.841 0.000
attr(.,"tensor.blocks")
 Formula: ~Zh - 1
 Structure: Multiple of an Identity
                Zh1        Zh2
StdDev: 0.04931613 0.04931613
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev     Corr
traitrw  0.09394850 tratrw tratrd
traitrd  0.05520526 0.499
traitmfa 0.11631502 0.816  0.841

**********  site-level linear in ring number at  height 0 ************

 Structure: pdTE2
   StdDev     Corr
V1 0.15619979 V1     V2     V3     V4     V5
V2 0.10085221  0.995
V3 0.06930997 -0.045 -0.045
V4 0.04475079 -0.045 -0.045  0.995
V5 0.05995806 -0.259 -0.257  0.727  0.723
V6 0.03871262 -0.257 -0.259  0.723  0.727  0.995
attr(.,"tensor.blocks")
 Formula: ~Zbrlh0 - 1
 Structure: General positive-definite
                  StdDev    Corr
Zbrlh0(Intercept) 0.5653612 Zb0(I)
Zbrlh0br.c        0.3650320 0.995
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.2762832 tratrw tratrd
traitrd  0.1225941 -0.045
traitmfa 0.1060527 -0.259  0.727

**********  site-level linear in ring number at  height 1 ************

 Structure: pdTE2
   StdDev    Corr
V1 0.3306805 V1     V2     V3     V4     V5
V2 0.1073183  0.954
V3 0.3930870 -0.915 -0.873
V4 0.1275716 -0.873 -0.915  0.954
V5 0.3499340  0.892  0.851 -0.649 -0.620
V6 0.1135669  0.851  0.892 -0.620 -0.649  0.954
attr(.,"tensor.blocks")
 Formula: ~Zbrlh1 - 1
 Structure: General positive-definite
                  StdDev     Corr
Zbrlh1(Intercept) 0.29094928 Zb1(I)
Zbrlh1br.c        0.09442408 0.954
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev   Corr
traitrw  1.136557 tratrw tratrd
traitrd  1.351050 -0.915
traitmfa 1.202732  0.892 -0.649

**********  site-level linear in ring number at  height 5 ************
```

```
 Structure: pdTE2
   StdDev     Corr
V1 0.05841186 V1    V2    V3    V4    V5
V2 0.04145644 0.990
V3 0.07171549 0.315 0.312
V4 0.05089837 0.312 0.315 0.990
V5 0.01865596 0.476 0.472 0.660 0.653
V6 0.01324062 0.472 0.476 0.653 0.660 0.990
attr(.,"tensor.blocks")
 Formula: ~Zbrlh5 - 1
 Structure: General positive-definite
                   StdDev    Corr
Zbrlh5(Intercept) 0.3355484 Zb5(I)
Zbrlh5br.c        0.2381475 0.99
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev     Corr
traitrw  0.17407882 tratrw tratrd
traitrd  0.21372623 0.315
traitmfa 0.05559841 0.476  0.660

**********  site-level linear in ring number at  height 20 ************

 Structure: pdTE2
   StdDev     Corr
V1 0.60894583 V1     V2     V3     V4     V5
V2 0.16303742  0.813
V3 0.38647386 -0.987 -0.802
V4 0.10347341 -0.802 -0.987  0.813
V5 0.31579721  0.739  0.601 -0.703 -0.571
V6 0.08455064  0.601  0.739 -0.571 -0.703  0.813
attr(.,"tensor.blocks")
 Formula: ~Zbrlh20 - 1
 Structure: General positive-definite
                    StdDev    Corr
Zbrlh20(Intercept) 0.5738403 Z20(I)
Zbrlh20br.c        0.1536384 0.813
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  1.0611765 tratrw tratrd
traitrd  0.6734868 -0.987
traitmfa 0.5503225  0.739 -0.703

**********  site-level spline in ring number at  height 0 ************

 Structure: pdTE2
    StdDev     Corr
V1  0.26816933 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17 V18
V2  0.26816933 0
V3  0.26816933 0    0
V4  0.26816933 0    0  0
V5  0.26816933 0    0  0  0
V6  0.26816933 0    0  0  0  0
V7  0.26816933 0    0  0  0  0  0
V8  0.07141035 0    0  0  0  0  0  0
V9  0.07141035 0    0  0  0  0  0  0  0
V10 0.07141035 0    0  0  0  0  0  0  0  0
V11 0.07141035 0    0  0  0  0  0  0  0  0  0
V12 0.07141035 0    0  0  0  0  0  0  0  0  0   0
V13 0.07141035 0    0  0  0  0  0  0  0  0  0   0   0
V14 0.07141035 0    0  0  0  0  0  0  0  0  0   0   0   0
V15 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0
```

```
V16 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0
V17 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0
V18 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0
V19 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V20 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V21 0.10181876 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0

V1  V19 V20
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20 0
V21 0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h0 - 1
 Structure: Multiple of an Identity
           Zr3h01    Zr3h02    Zr3h03    Zr3h04    Zr3h05    Zr3h06    Zr3h07
StdDev: 0.4956184 0.4956184 0.4956184 0.4956184 0.4956184 0.4956184 0.4956184
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw   traitrd  traitmfa
StdDev: 0.5410802 0.1440833 0.2054378

**********  site-level spline in ring number at  height 1 ************

 Structure: pdTE2
    StdDev    Corr
V1  0.2008941 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17 V18
V2  0.2008941 0
V3  0.2008941 0    0
V4  0.2008941 0    0  0
V5  0.2008941 0    0  0  0
V6  0.2008941 0    0  0  0  0
V7  0.2008941 0    0  0  0  0  0
V8  0.1079359 0    0  0  0  0  0  0
V9  0.1079359 0    0  0  0  0  0  0  0
V10 0.1079359 0    0  0  0  0  0  0  0  0
V11 0.1079359 0    0  0  0  0  0  0  0  0  0
V12 0.1079359 0    0  0  0  0  0  0  0  0  0   0
V13 0.1079359 0    0  0  0  0  0  0  0  0  0   0   0
V14 0.1079359 0    0  0  0  0  0  0  0  0  0   0   0   0
V15 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0
V16 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0
V17 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0
V18 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0
V19 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V20 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V21 0.1568209 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
```

```
V1  V19 V20
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20 0
V21 0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h1 - 1
 Structure: Multiple of an Identity
           Zr3h11    Zr3h12    Zr3h13    Zr3h14    Zr3h15    Zr3h16    Zr3h17
StdDev: 0.4833865 0.4833865 0.4833865 0.4833865 0.4833865 0.4833865 0.4833865
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw   traitrd  traitmfa
StdDev: 0.4155972 0.2232912 0.3244214

**********  site-level spline in ring number at  height 5 ************

 Structure: pdTE2
    StdDev     Corr
V1  0.19480219 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17
V2  0.19480219 0
V3  0.19480219 0    0
V4  0.19480219 0    0  0
V5  0.19480219 0    0  0  0
V6  0.19480219 0    0  0  0  0
V7  0.03601027 0    0  0  0  0  0
V8  0.03601027 0    0  0  0  0  0  0
V9  0.03601027 0    0  0  0  0  0  0  0
V10 0.03601027 0    0  0  0  0  0  0  0  0
V11 0.03601027 0    0  0  0  0  0  0  0  0  0
V12 0.03601027 0    0  0  0  0  0  0  0  0  0   0
V13 0.08952606 0    0  0  0  0  0  0  0  0  0   0   0
V14 0.08952606 0    0  0  0  0  0  0  0  0  0   0   0   0
V15 0.08952606 0    0  0  0  0  0  0  0  0  0   0   0   0   0
V16 0.08952606 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0
V17 0.08952606 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0
V18 0.08952606 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h5 - 1
 Structure: Multiple of an Identity
           Zr3h51    Zr3h52    Zr3h53    Zr3h54    Zr3h55    Zr3h56
StdDev: 0.4705658 0.4705658 0.4705658 0.4705658 0.4705658 0.4705658
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw    traitrd  traitmfa
StdDev: 0.4139744 0.07652549 0.1902520

**********  site-level spline in ring number at  height 20 ************
```

```
 Structure: pdTE2
    StdDev     Corr
V1  0.12293930 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11
V2  0.12293930 0
V3  0.12293930 0    0
V4  0.12293930 0    0  0
V5  0.11346522 0    0  0  0
V6  0.11346522 0    0  0  0  0
V7  0.11346522 0    0  0  0  0  0
V8  0.11346522 0    0  0  0  0  0  0
V9  0.09565703 0    0  0  0  0  0  0  0
V10 0.09565703 0    0  0  0  0  0  0  0  0
V11 0.09565703 0    0  0  0  0  0  0  0  0  0
V12 0.09565703 0    0  0  0  0  0  0  0  0  0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h20 - 1
 Structure: Multiple of an Identity
        Zr3h201  Zr3h202  Zr3h203  Zr3h204
StdDev: 0.399778 0.399778 0.399778 0.399778
 Formula: ~trait - 1
 Structure: Diagonal
         traitrw   traitrd  traitmfa
StdDev: 0.3075189 0.2838206 0.2392754


**********  tree-level linear in ring number and  height  ************

 Structure: pdTE2
   StdDev     Corr
V1 0.09069015 V1    V2    V3    V4    V5    V6    V7    V8
V2 0.01580338 0.913
V3 0.01177364 0.153 0.450
V4 0.16427594 0.624 0.569 0.095
V5 0.02862621 0.569 0.624 0.281 0.913
V6 0.02132675 0.095 0.281 0.624 0.153 0.450
V7 0.11398096 0.561 0.512 0.086 0.778 0.710 0.119
V8 0.01986196 0.512 0.561 0.253 0.710 0.778 0.350 0.913
V9 0.01479732 0.086 0.253 0.561 0.119 0.350 0.778 0.153 0.450
attr(.,"tensor.blocks")
 Formula: ~bark.ring + height
 Structure: General positive-definite
            StdDev     Corr
(Intercept) 0.28196479 (Intr) brk.rn
bark.ring   0.04913429 0.913
height      0.03660544 0.153  0.450
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.3216364 tratrw tratrd
traitrd  0.5826115 0.624
traitmfa 0.4042383 0.561  0.778

**********  tree-level spline in height  ************

 Structure: pdTE2
   StdDev      Corr
V1 0.010428368 V1     V2     V3     V4     V5
V2 0.010428368  0.000
V3 0.008560219 -0.790  0.000
V4 0.008560219  0.000 -0.790  0.000
V5 0.020941014  0.785  0.000 -0.540  0.000
V6 0.020941014  0.000  0.785  0.000 -0.540  0.000
attr(.,"tensor.blocks")
```

```
 Formula: ~Zh - 1
 Structure: Multiple of an Identity
              Zh1        Zh2
StdDev: 0.07057279 0.07057279
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.1477676 tratrw tratrd
traitrd  0.1212963 -0.790
traitmfa 0.2967293  0.785 -0.540

**********  tree-level linear in ring number at height 0 ************

 Structure: pdTE2
   StdDev     Corr
V1 0.15729418 V1     V2     V3     V4     V5
V2 0.03303537 -0.373
V3 0.21198452  0.193 -0.072
V4 0.04452160 -0.072  0.193 -0.373
V5 0.17833270  0.175 -0.065 -0.019  0.007
V6 0.03745395 -0.065  0.175  0.007 -0.019 -0.373
attr(.,"tensor.blocks")
 Formula: ~Zbrlh0 - 1
 Structure: General positive-definite
                  StdDev     Corr
Zbrlh0(Intercept) 0.39408076 Zb0(I)
Zbrlh0br.c        0.08276597 -0.373
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.3991420 tratrw tratrd
traitrd  0.5379215  0.193
traitmfa 0.4525283  0.175 -0.019

**********  tree-level linear in ring number at height 1 ************

 Structure: pdTE2
   StdDev     Corr
V1 0.20907302 V1     V2     V3     V4     V5
V2 0.03662893 -0.241
V3 0.25404986  0.146 -0.035
V4 0.04450873 -0.035  0.146 -0.241
V5 0.16784924  0.405 -0.098 -0.132  0.032
V6 0.02940666 -0.098  0.405  0.032 -0.132 -0.241
attr(.,"tensor.blocks")
 Formula: ~Zbrlh1 - 1
 Structure: General positive-definite
                  StdDev     Corr
Zbrlh1(Intercept) 0.44670572 Zb1(I)
Zbrlh1br.c        0.07826143 -0.241
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.4680330 tratrw tratrd
traitrd  0.5687186  0.146
traitmfa 0.3757490  0.405 -0.132

**********  tree-level linear in ring number at height 5 ************

 Structure: pdTE2
   StdDev     Corr
V1 0.14135114 V1     V2     V3     V4     V5
V2 0.04311355 -0.652
V3 0.15929198  0.274 -0.179
```

```
V4 0.04858568 -0.179  0.274 -0.652
V5 0.09307793  0.555 -0.362  0.253 -0.165
V6 0.02838972 -0.362  0.555 -0.165  0.253 -0.652
attr(.,"tensor.blocks")
 Formula: ~Zbrlh5 - 1
 Structure: General positive-definite
                  StdDev    Corr
Zbrlh5(Intercept) 0.3688960 Zb5(I)
Zbrlh5br.c        0.1125171 -0.652
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.3831734 tratrw tratrd
traitrd  0.4318072 0.274
traitmfa 0.2523148 0.555  0.253

**********  tree-level linear in ring number at height 20 ************

 Structure: pdTE2
   StdDev     Corr
V1 0.11673559 V1     V2     V3     V4     V5
V2 0.05079675  0.532
V3 0.21047171 -0.414 -0.220
V4 0.09158542 -0.220 -0.414  0.532
V5 0.13769966  0.425  0.226 -0.556 -0.296
V6 0.05991912  0.226  0.425 -0.296 -0.556  0.532
attr(.,"tensor.blocks")
 Formula: ~Zbrlh20 - 1
 Structure: General positive-definite
                   StdDev    Corr
Zbrlh20(Intercept) 0.3333565 Z20(I)
Zbrlh20br.c        0.1450579 0.532
 Formula: ~trait - 1
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.3501825 tratrw tratrd
traitrd  0.6313713 -0.414
traitmfa 0.4130703  0.425 -0.556

**********  tree-level spline in ring number at height 0 ************


 Structure: pdTE2
    StdDev     Corr
V1  0.04952985 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17 V18
V2  0.04952985 0
V3  0.04952985 0    0
V4  0.04952985 0    0  0
V5  0.04952985 0    0  0  0
V6  0.04952985 0    0  0  0  0
V7  0.04952985 0    0  0  0  0  0
V8  0.02764964 0    0  0  0  0  0  0
V9  0.02764964 0    0  0  0  0  0  0  0
V10 0.02764964 0    0  0  0  0  0  0  0  0
V11 0.02764964 0    0  0  0  0  0  0  0  0  0
V12 0.02764964 0    0  0  0  0  0  0  0  0  0   0
V13 0.02764964 0    0  0  0  0  0  0  0  0  0   0   0
V14 0.02764964 0    0  0  0  0  0  0  0  0  0   0   0   0
V15 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0
V16 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0
V17 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0
V18 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0
V19 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V20 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
```

```
V21 0.06360492 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0

V1  V19 V20
V2
V3
V4
V5
V6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20 0
V21 0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h0 - 1
 Structure: Multiple of an Identity
           Zr3h01    Zr3h02    Zr3h03    Zr3h04    Zr3h05    Zr3h06    Zr3h07
StdDev: 0.2263163 0.2263163 0.2263163 0.2263163 0.2263163 0.2263163 0.2263163
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw   traitrd  traitmfa
StdDev: 0.2188523 0.1221725 0.2810443

**********  tree-level spline in ring number at height 1 ************

 Structure: pdTE2
    StdDev     Corr
V1  0.04464623 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17 V18
V2  0.04464623 0
V3  0.04464623 0    0
V4  0.04464623 0    0  0
V5  0.04464623 0    0  0  0
V6  0.04464623 0    0  0  0  0
V7  0.04464623 0    0  0  0  0  0
V8  0.02737526 0    0  0  0  0  0  0
V9  0.02737526 0    0  0  0  0  0  0  0
V10 0.02737526 0    0  0  0  0  0  0  0  0
V11 0.02737526 0    0  0  0  0  0  0  0  0  0
V12 0.02737526 0    0  0  0  0  0  0  0  0  0   0
V13 0.02737526 0    0  0  0  0  0  0  0  0  0   0   0
V14 0.02737526 0    0  0  0  0  0  0  0  0  0   0   0   0
V15 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0
V16 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0
V17 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0
V18 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0
V19 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V20 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0
V21 0.06154615 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0   0

V1  V19 V20
V2
V3
V4
V5
```

```
V6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20 0
V21 0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h1 - 1
 Structure: Multiple of an Identity
           Zr3h11    Zr3h12    Zr3h13    Zr3h14    Zr3h15    Zr3h16    Zr3h17
StdDev: 0.2204542 0.2204542 0.2204542 0.2204542 0.2204542 0.2204542 0.2204542
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw   traitrd  traitmfa
StdDev: 0.2025193 0.1241766 0.2791789

**********  tree-level spline in ring number at height 5 ************

 Structure: pdTE2
    StdDev     Corr
V1  0.03183229 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11 V12 V13 V14 V15 V16 V17
V2  0.03183229 0
V3  0.03183229 0    0
V4  0.03183229 0    0  0
V5  0.03183229 0    0  0  0
V6  0.03183229 0    0  0  0  0
V7  0.03027072 0    0  0  0  0  0
V8  0.03027072 0    0  0  0  0  0  0
V9  0.03027072 0    0  0  0  0  0  0  0
V10 0.03027072 0    0  0  0  0  0  0  0  0
V11 0.03027072 0    0  0  0  0  0  0  0  0  0
V12 0.03027072 0    0  0  0  0  0  0  0  0  0   0
V13 0.05146565 0    0  0  0  0  0  0  0  0  0   0   0
V14 0.05146565 0    0  0  0  0  0  0  0  0  0   0   0   0
V15 0.05146565 0    0  0  0  0  0  0  0  0  0   0   0   0   0
V16 0.05146565 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0
V17 0.05146565 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0
V18 0.05146565 0    0  0  0  0  0  0  0  0  0   0   0   0   0   0   0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h5 - 1
 Structure: Multiple of an Identity
           Zr3h51    Zr3h52    Zr3h53    Zr3h54    Zr3h55    Zr3h56
StdDev: 0.1800039 0.1800039 0.1800039 0.1800039 0.1800039 0.1800039
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw   traitrd  traitmfa
StdDev: 0.1768423 0.1681671 0.2859141

**********  tree-level spline in ring number at height 20 ************

 Structure: pdTE2
    StdDev     Corr
V1  0.04109602 V1   V2 V3 V4 V5 V6 V7 V8 V9 V10 V11
V2  0.04109602 0
```

```
V3  0.04109602 0    0
V4  0.04109602 0    0  0
V5  0.05236284 0    0  0  0
V6  0.05236284 0    0  0  0  0
V7  0.05236284 0    0  0  0  0  0
V8  0.05236284 0    0  0  0  0  0  0
V9  0.08393852 0    0  0  0  0  0  0  0
V10 0.08393852 0    0  0  0  0  0  0  0  0
V11 0.08393852 0    0  0  0  0  0  0  0  0  0
V12 0.08393852 0    0  0  0  0  0  0  0  0  0   0
attr(.,"tensor.blocks")
 Formula: ~Zr3h20 - 1
 Structure: Multiple of an Identity
          Zr3h201   Zr3h202   Zr3h203   Zr3h204
StdDev: 0.2220244 0.2220244 0.2220244 0.2220244
 Formula: ~trait - 1
 Structure: Diagonal
          traitrw   traitrd  traitmfa
StdDev: 0.1850969 0.2358427 0.3780599

**********  units-level covariance between traits ************

 Formula: ~trait - 1 | unit %in% tree %in% tree %in% tree %in% tree %in% tree
%in% tree
    %in% tree %in% tree %in% tree %in% tree %in% site %in% site %in% site %in%
site
    %in% site %in% site %in% site %in% site %in% site %in% site %in% all %in%
all
    %in% all %in% all %in% all
 Structure: General positive-definite
         StdDev    Corr
traitrw  0.3867379 tratrw tratrd
traitrd  0.3224742 0.155
traitmfa 0.1285441 0.813  0.082
Residual 0.1892592

Fixed effects: y.std ~ bark.ring * height * trait
                               Value  Std.Error    DF    t-value p-value
(Intercept)                -1.1956312 0.06865459 18958 -17.415168  0.0000
bark.ring                   0.0971412 0.00819109  9347  11.859370  0.0000
height                      0.0667844 0.00898243  9347   7.434999  0.0000
traitrd                     0.3877367 0.11991108 18958   3.233536  0.0012
traitmfa                   -0.0777244 0.07988414 18958  -0.972964  0.3306
bark.ring:height           -0.0090366 0.00118709  9347  -7.612440  0.0000
bark.ring:traitrd          -0.0568861 0.01401931 18958  -4.057695  0.0000
bark.ring:traitmfa          0.0212198 0.01049603 18958   2.021696  0.0432
height:traitrd             -0.0619839 0.01467330 18958  -4.224267  0.0000
height:traitmfa            -0.0478995 0.00906978 18958  -5.281215  0.0000
bark.ring:height:traitrd    0.0203799 0.00186619 18958  10.920612  0.0000
bark.ring:height:traitmfa   0.0075610 0.00152686 18958   4.951980  0.0000
 Correlation:
                           (Intr) brk.rn height tratrd tratmf brk.rng:h
bark.ring                  -0.807
height                     -0.566  0.526
traitrd                    -0.722  0.620  0.451
traitmfa                   -0.686  0.604  0.380  0.725
bark.ring:height            0.359 -0.378 -0.827 -0.275 -0.286
bark.ring:traitrd           0.633 -0.791 -0.424 -0.836 -0.652  0.300
bark.ring:traitmfa          0.551 -0.749 -0.355 -0.599 -0.817  0.288
height:traitrd              0.482 -0.443 -0.904 -0.575 -0.405  0.725
height:traitmfa             0.433 -0.440 -0.740 -0.490 -0.673  0.692
bark.ring:height:traitrd   -0.313  0.326  0.769  0.369  0.321 -0.889
bark.ring:height:traitmfa  -0.235  0.268  0.548  0.325  0.525 -0.744
                           brk.rng:trtr brk.rng:trtm hght:trtr hght:trtm
```

```
bark.ring
height
traitrd
traitmfa
bark.ring:height
bark.ring:traitrd
bark.ring:traitmfa          0.776
height:traitrd              0.536        0.379
height:traitmfa             0.495        0.639        0.737
bark.ring:height:traitrd  -0.387       -0.315       -0.832    -0.692
bark.ring:height:traitmfa -0.346       -0.515       -0.543    -0.849
                          brk.rng:hght:trtr
bark.ring
height
traitrd
traitmfa
bark.ring:height
bark.ring:traitrd
bark.ring:traitmfa
height:traitrd
height:traitmfa
bark.ring:height:traitrd
bark.ring:height:traitmfa  0.732

Standardized Within-Group Residuals:
         Min           Q1          Med            Q3          Max
-7.913549771 -0.277583870 -0.004640318  0.268382166  6.179970020

Number of Observations: 28449
Number of Groups:
```