COMPARISON OF GENETIC PARAMETERS FOR WOOD PROPERTIES EXPRESSED ON VOLUMETRIC AND GRAVIMETRIC BASES

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Abstract.--Estimates of genetic parameters for wood properties and their interpretations can vary substantially depending on the units in which the wood properties are expressed. Of particular concern in this respect are estimates of genetic variances for moisture content, extractives yield and pulp yield when these traits are expressed on a gravimetric (dry weight) rather than volumetric basis. Corresponding estimates of genetic correlations of these variables with density depend strongly on the unit basis used. Arguments favoring the use of the volumetric basis for expression of certain wood properties are strengthened by comparing results of genetic analyses of traits expressed on the gravimetric versus volumetric bases.

Additional keywords: Density, moisture content, extractives yield, pulp yield, heritability, phenotypic correlations, genetic correlations.

Many studies have been conducted in recent years to achieve a clearer understanding of the relationships between wood density, moisture content, extractives yield and pulp yield. For reasons of tradition, ease of measurement, and consistency with industrial standards, most researchers have expressed moisture content, extractives yields and pulp yields on the gravimetric basis (i.e., per unit dry weight of wood) rather than the volumetric basis (i.e., per unit volume of wood). It has been recently shown that estimates of statistical correlations can be substantially biased if analyses are done between density and moisture content, extractives yield and pulp yield when the latter three variables are expressed on the gravimetric basis (Franklin and Squillace, In press). Similar biases are introduced into estimates of genetic parameters which are based on analyses of the relationships between density and other traits expressed on the gravimetric basis.

An introduction to the problem might be best accomplished by use of a contrived, though realistic example (table 1). Note that a wide array of densities has been listed in the first column. For purpose of illustration, moisture content and extractives yields were held constant on the volumetric basis and pulp yield was varied on the volumetric basis in direct proportion to density. This situation agrees closely with observed data. The key to understanding the problem lies in the simple mathematical conversion of volumetric to gravimetric bases, which is accomplished by dividing the volumetric array by density and multiplying by 100.

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Table 1.--A contrived example for comparisons of unit volume and unit dry weight expressions of moisture content, extractives yield, and pulp yield.[a]

Density	Moisture content		Extractives yield		Pulp yield	
$\frac{W}{V}$	$\frac{M}{V}$	$\frac{M}{W} \times 100$	$\frac{E}{V}$	$\frac{E}{W} \times 100$	$\frac{P}{V}$	$\frac{P}{W} \times 100$
(g/cc)	(g/cc)	(g/g)	(g/cc)	(g/g)	(g/cc)	(g/g)
.16	.45	281	.014	8.8	.08	50
.24	.45	188	.014	5.8	.12	50
.32	.45	141	.014	4.4	.16	50
.4o	.45	112	.014	3.5	.20	50
.48	.45	94	.014	2.9	.24	50
.56	.45	8o	.014	2.5	.28	50
.64	.45	7o	.014	2.2	.32	50
.72	.45	62	.014	1.9	.36	50

W = weight of wood substance (cellulose, lignin, sugars, etc.)
M = weightof moisture
E = weightof extractives
P = weightof pulp
V = volumeof sample of green wood

Using the symbols in Table 1, the formula for converting moisture content on the volumetric basis to the gravimetric basis is as follows:

$$\frac{M}{W} \times 100 = \frac{M}{V} \div \frac{W}{V} \times 100$$
$$= \frac{M}{\not{V}} \times \frac{\not{V}}{W} \times 100$$
$$= \frac{M}{W} \times 100$$

Two important facts should be noted in comparing the volumetric and gravimetric arrays in Table 1. First, gravimetric arrays for moisture content and extractives yields are non-linear with respect to density (i.e., unit changes in the volumetric arrays do not correspond with unit changes in the gravimetric arrays). Second, constancy on one basis is accompanied by large amounts of variation on the other basis and the variation depends directly on density.

The conclusion to be drawn from Table 1 is that correlations based on relationships between density and the other three variables will be quite different depending on which basis of expression is used. The question then is, "Which basis accurately reflects the biological relationships which are being studied?" The answer is the volumetric basis because the gravimetric basis has a negative correlation with density because it is derived from the volumetric basis by dividing by density. The correlation between a variable and its reciprocal is non-linear and negative; therefore, the relationships between density and the other three variables on the gravimetric basis is a combination of the induced reciprocal relationships plus any biological relationship which may also exist. This can be shown very neatly by a mathematical analysis of the expected correlation coefficients.[2/]

Estimates of genetic parameters for wood properties and their interpretation can vary substantially depending on the basis of expression, (volumetric or gravimetric). This will be illustrated by an example based on data from slash pine (*Pinus elliottii* Engelm.) and one based on data previously published by van Buijtenen et al. (1968) from loblolly pine (P. *taeda* L.).

The slash pine study consisted of single-tree plots from 31 nominal half-sib families replicated 5 times. Measurements of green weight, dry weight of ethanol-benzene extractives were obtained by standard laboratory procedures. Estimates of density, moisture content and extractives yields were then obtained. Moisture content and extractives yield were expressed both on volumetric and gravimetric bases. Components of phenotypic and genotypic variances were derived by analysis of variance procedures. The coefficient of relationship for siblings was assumed to be 1/3 rather than 1/4; therefore, a multiplier of 3 rather than 4 was appropriate.[3/]

The loblolly study has been described in detail previously (van Buijtenen et al. 1968). It consisted of 4 ramets from each of 6 clones. The same measurements as those in the slash pine study were obtained in addition to pulp yield. Density, yield of ethanol-benzene extractives, and pulp yield were analyzed by analysis of variance to derive phenotypic and genotypic variance components.

Values in Tables 2 and 3 indicate that both the direction and magnitude of changes in heritability estimates are rather erratic. Heritability estimates for moisture content and extractives yield are higher on the gravimetric than on the volumetric bases. This is because the heritability for density is usually higher than that for moisture content or extractives yield, thus dividing by density increases the heritability estimate for the gravimetric basis by increasing the family intraclass correlation. In the case of a trait such as pulp yield (table 3) where the heritability on the volumetric basis is approximately equal to that of density, the change in the estimate of heritability for pulp yield on the gravimetric basis becomes much less predictable.

The situation with reference to phenotypic and genotypic correlations was much more consistent. In every case, correlation estimates based on the gravimetric basis were consistently larger negative values or smaller-positive values than comparable estimates based on the volumetric basis. Differences in all cases were large enough to lead to serious errors of interpretation unless the researcher realized that the differences were simply the result of an algebraic manipulation. This does not mean that the gravimetric basis has

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Table 2.--Heritabilities, phenotypic and genetic correlations for three wood properties estimated by sibling intraclass correlations with 31 families of slash pine (*Pinus eliottii* Engelm.) and expressed on gravimetric versus volumetric bases.

	Gravimetric basis	Volumetric basis
HERITABILITIES[a/]		
Density of Extracted Wood		0.59
Moisture Content of Green Wood	.26	.22
Extractives Yield of Wood	.48	.41
PHENOTYPIC CORRELATIONS		
Density with Moisture Content	-0.33	- .08
Density with Extractives Yield	-0.35	.00
GENETIC CORRELATION[a/]		
Density with Moisture Content	- .37	+ .27
Density with Extractives Yield	- .49	- .13

[a/] Narrow-sense heritabilities and genetic correlations (Hanson 1963)

Table 3.--Heritabilities, phenotypic and genotypic correlations for three wood properties estimated by ramet intraclass correlations with 6 clones of loblolly pine (*Pinus taeda*. L.) and expressed on gravimetric versus volumetric bases portions of original data from van Buijtenen 1968).

	Gravimetric basis	Volumetric basis
HERITABILITIES		
Density of Extracted Wood		0.88
Extractives Yield of Wood	0.66	0.51
Pulp Yield	.52	.85
PHENOTYPIC CORRELATIONS		
Density with Extractives Yield	- .34	0.16
Density with Pulp Yield	.43	.98
GENETIC CORRELATIONS[a/]		
Density with Extractives Yield	-0.50	0.04
Density with Pulp Yield	0.57	0.97

[a/] Broad-sense heritabilities and genetic correlations (Hanson 1963) no valid uses; it does mean that the volumetric basis is better than the gravimetric basis for expression of wood properties if those properties are to be compared with density, and those comparisons used for estimation of genetic parameters.

LITERATURE CITED

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