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RELATIONSHIPS AMONG WOOD VARIABLES IN TWO SPECIES OF RING-POROUS TREES

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ABSTRACT

One way of assessing the functional significance of wood-anatomical variables is by examining the relationships among these variables. This paper presents results of factor analysis of wood variables in two species of ring-porous trees (*Quercus rubra* and *Fraxinus americana*). Factor analysis of vessel diameter and density, conductive area, and conductivity in the early- and latewood plus width of the early- and latewood increment reveals from three to four independent sources of variance. Generally, these can be characterized as diameter-related factors in the early- and latewood, tentatively related to water conduction, and a factor identified with width of the latewood increment and density of the latewood vessels, which may be a generalized representation of growth. Individual correlations among the variables show that variation in ring width is almost entirely variation in width of the latewood portion of the ring and that ring width (or latewood width) varies with the latewood characteristics (being positively correlated with vessel diameter and inversely correlated with vessel density). Vessel diameter and density are inversely correlated, but only in the latewood.

Key words: Wood-anatomical variables, temporal variance, ring-porous wood, factor analysis.

INTRODUCTION

The way in which wood structure should be characterized functionally is far from clear. Among the aspects of the wood that have been cited as significant in water conduction or response to water stress are vessel diameter and density (Carlquist 1975), percent of area taken up by vessels (conductive area; Carlquist 1984), and sum of the vessel diameters to the fourth power (proportional to conductivity; Zimmermann 1983). The latter measure is a representation of flow through a series of pipes in parallel; because of the dependence on the fourth power of the diameter, the larger conduits contribute disproportionately to the flow. Whether flow through vessels can be approximated in this way has been questioned since vessels are known to twist around the trunk, anastomose, and have constrictions along their length. One way of evaluating the functional significance of these variables in determining flow rates is by measuring flow and comparing measured rates to rates calculated based on the wood anatomy. Such measurements have yielded values both considerably less than and approximating calculated values of conductivity (Zimmermann 1983; Salleo 1984; Ellmore and Ewers 1986).

Other approaches to this problem are possible. Baas (1986) mentions that spatial variance can be studied a) within species, b) among species, and c) within local floras. Identifiable patterns of spatial variance (such as that for vessel diameter and density; Carlquist 1975) can be related to broad climatic controls and in this way give information about wood function. Another type of variance that is relatively easy to study in woody plants is temporal variance, and yearly variations in wood structure do appear to be affected by climatic factors (Eckstein and Frisse 1982; Woodcock 1989a).

The focus of the present study is the relationships among wood-anatomical variables of possible functional significance, viewed from the standpoint of their temporal variance. Limiting the study to 20-year sequences from two trees made it possible to obtain values for all the anatomical variables cited above, many of which are quite tedious to measure or calculate. Objectives are evaluation of the various anatomical variables in terms of their interrelationships and identification of the number of sources of variance present within the wood. Of additional interest is the way in which wood characteristics vary with width of the growth increment.

The trees investigated, *Quercus rubra* L. and *Fraxinus americana* L., have wood of the ring-porous type. These species were chosen because they are native to the study area (southeastern Nebraska) and are in addition wide-ranging. Because these trees produce two types of wood during the year, all of the variables cited above can be measured in both the early- and latewood. Diagrams of a typical transverse section through these two woods are presented in Figure 1. The distribution by size of the vessels, also presented in Figure 1, shows the two distinct populations of vessels that are present within one annual ring in these two species.

MATERIALS AND METHODS

Breast-height tree cores were obtained from two species of ring-porous trees (*Quercus rubra* and *Fraxinus americana*) growing near Lincoln, Nebraska. The individuals cored were both canopy trees approximately 40 years old. The cores were thin-sectioned and mounted for light microscopy. Measurements were obtained by means of a microscope equipped with an ocular micrometer within an area of uniform width (approximately 5 mm) extending across the rings. All the cells within this area were measured; the number of cells thus varied from ring to ring but was in all cases greater than 30. A 20-year sequence (1966–1985) from each individual (one core) is analyzed in each case. The variables measured (or calculated) (see Appendix) are average vessel diameter, vessel density, conductive area, and conductivity in both the early- and latewood. Since yearly variation in conductivity is equivalent to the yearly variation in sum of the diameters to the fourth power calculated with respect to area, the term is used in this sense here (strictly speaking, conductivity is only proportional to the sum of the diameters⁴ since several other quantities figure in the equation). Difficulties in distinguishing early- and latewood in ring-porous trees have been discussed elsewhere (Woodcock 1989b); presence of an abrupt shift in vessel size across the ring or greater contiguity of vessels within the earlywood increment was used to delineate the two different parts of the ring. Where vessels deviated from circular in cross section, the long and short axes were averaged. The other anatomical variables (as, for example, density or conductivity) are calculated with respect to a transsectional area (with the large rays of *Q. rubra* not included in total area). Width of the entire growth increment and of the early- and latewood is also included in the analysis. Average values of the variables, together with their coefficients of variation, are presented in Table 1.

The statistical treatment consisted of factor analysis (Biomedical Data Program 4M) of the included wood variables in these two species. This is the appropriate type of procedure when the proportioning of the shared variance is of interest, although it should be recognized that the results are only one representation of

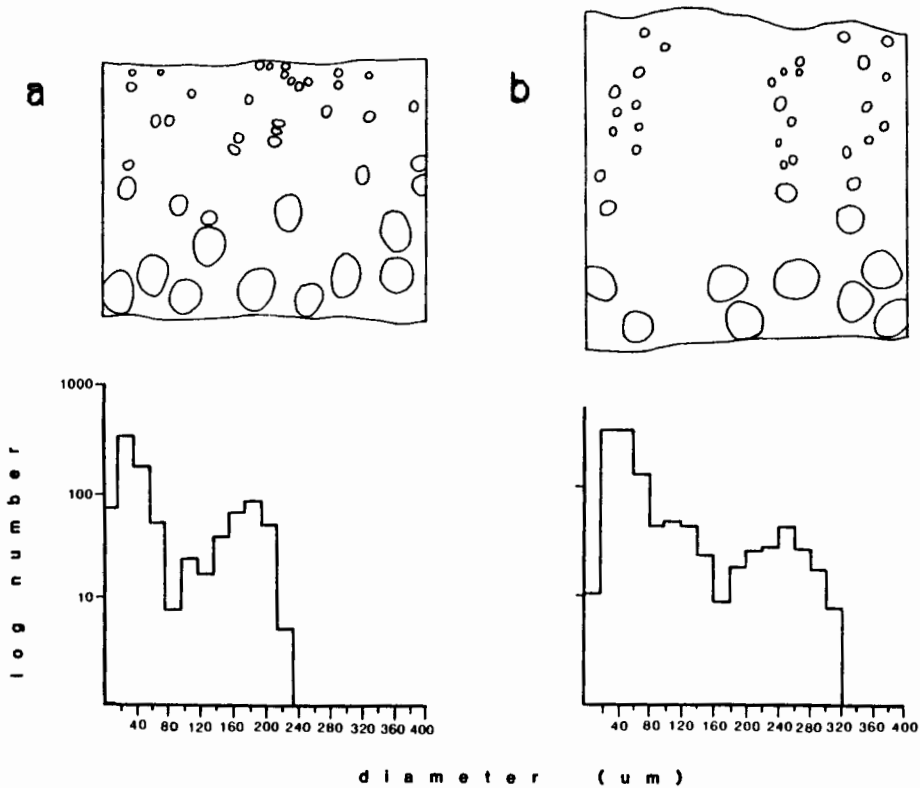


Fig. 1. Transverse section through the wood of a) *Fraxinus americana* and b) *Quercus rubra*. Also shown is the distribution of vessels by size over a 20-year sequence within the wood.

the data rather than a unique solution. From the set of 10 variables in each tree, a correlation matrix is produced representing the common sources of variance among the variables. Linear transformation of the correlation matrix yields the factors, which represent the independent sources of variance among the variables. All the variables but total ring width are included in the analysis; high correlations between total width and latewood width did not permit transformation of the correlation matrix with this variable included. Orthogonal rotation of the factors emphasizes the high-loading variables and helps in interpretation. This type of analysis permits identification of those variables most closely associated with the different factors. It is also possible in many cases to interpret the factors in terms of function. Other statistical results presented here are correlations among selected variables.

RESULTS AND DISCUSSION

Factor Analysis

Factor analysis of wood variables in *Quercus rubra* reveals that four independent axes of variance can be recognized among the variables (Table 2). Two of these factors relate to the earlywood and two to the latewood. Factor 1 is identified most closely with diameter-related characteristics of the earlywood (average vessel

Table 1. The wood variables.

	<i>Q. rubra</i>		<i>F. americana</i>	
	Mean	Coefficient of variation	Mean	Coefficient of variation
Earlywood vessel diameter (mm)	0.238	0.084	0.168	0.054
Earlywood conductive area (%)	0.320	0.166	0.250	0.203
Earlywood conductivity (mm ⁻²) ¹	0.030	0.215	0.011	0.226
Earlywood vessel density (mm ⁻²)	7.03	0.140	10.61	0.164
Latewood vessel diameter (mm)	0.0584	0.265	0.0329	0.118
Latewood conductive area (%)	0.042	0.388	0.031	0.276
Latewood conductivity (mm ⁻²)	0.0011	0.547	0.00009	0.369
Latewood vessel density (mm ⁻²)	12.00	0.306	33.11	0.522
Earlywood ring width (mm)	0.87	0.216	0.748	0.142
Latewood ring width (mm)	3.82	0.399	0.614	0.514
Total ring width (mm)	4.66	0.471	1.362	0.279

¹ mm⁴ per unit area.

diameter, conductive area, and conductivity). Factor 2 is identified primarily with latewood vessel density and secondarily with other characteristics of the latewood (width and vessel diameter). Factor 3 is identified with diameter-related characteristics of the latewood (conductive area, primarily). Factor 4 can be identified with earlywood vessel density. Other points are that latewood width varies closely with latewood anatomical characteristics, whereas this is not so clearly the case with earlywood width.

In *Fraxinus americana*, three independent axes of variance can be recognized (Table 3), one relating to the latewood and two to the earlywood. Factor 1 is related most closely to latewood vessel density and is also related to other latewood characteristics (conductive area, vessel diameter, and width). Factor 2 is related most closely to earlywood vessel density and other earlywood characteristics (conductive area and conductivity). Factor 3 is identified mainly with earlywood vessel diameter. Factor 1, which represents latewood characteristics, explains

Table 2. Factor analysis of wood variables in *Quercus rubra*: sorted, rotated factor loadings.¹

	Factor 1	Factor 2	Factor 3	Factor 4
Earlywood vessel diameter	0.858	0.000	0.000	-0.276
Earlywood conductive area	0.840	0.000	0.000	0.528
Earlywood conductivity	0.744	0.000	0.330	0.000
Latewood vessel density	0.000	-0.945	0.000	0.000
Latewood ring width	0.000	0.794	0.000	0.000
Latewood vessel diameter	0.000	0.696	0.680	0.000
Latewood conductive area	0.269	0.000	0.961	0.000
Latewood conductivity	0.000	0.000	0.782	0.000
Earlywood vessel density	0.000	0.000	0.000	0.995
Earlywood ring width	0.458	0.456	0.000	-0.298
VP	2.327	2.248	2.142	1.526
% of explained variance	28%	27%	26%	19%

¹ A varimax rotation was performed on the factors. Factor loadings less than 0.250 have been replaced by 0.000.

Table 3. Factor analysis of wood variables in *Fraxinus americana*: sorted, rotated factor loadings.¹

	Factor 1	Factor 2	Factor 3
Latewood vessel density	0.951	0.000	0.000
Latewood conductive area	0.936	0.000	0.000
Latewood vessel diameter	-0.797	0.000	0.000
Latewood ring width	-0.772	0.000	0.000
Latewood conductivity	0.505	0.000	0.272
Earlywood vessel density	0.000	0.961	0.000
Earlywood conductive area	0.269	0.925	0.344
Earlywood conductivity	0.000	0.794	0.499
Earlywood vessel diameter	0.000	0.000	0.972
Earlywood ring width	0.489	-0.404	0.295
VP	3.558	2.732	1.524
% of explained variance	46%	35%	20%

¹ As in Table 2.

approximately half of the total variance in the data set. As is the case in *Q. rubra*, latewood width is related to latewood anatomical characteristics.

Clearly, many of the variables investigated in these two species are closely related. Among the 10 variables, only three to four independent axes of variance are represented. In both species, two independent axes of variance are represented among the earlywood characteristics. The latewood contains essentially one source of variance in *F. americana* and two sources in *Q. rubra*. A tentative functional interpretation is as follows. The diameter-related factors probably relate to flow characteristics. In this sense, then, separate flow-related factors can be recognized within the early- and latewood. A third factor that can be recognized in both species relates to latewood characteristics (anatomical variables and latewood width). This factor may be considered as a generalized representation of growth (yield), as influenced by total photosynthate produced, although mechanical considerations relating to support may also be a consideration in determining the amount of wood produced.

Correlations between Selected Variables

Earlywood width, latewood width, and total width.—In these ring-porous woods, width of the entire ring and width of the latewood are very highly correlated, and in fact statistically would be considered the same variable (Table 4). Thus in both species, variation in width of the ring from year to year is almost entirely variation in the amount of latewood produced.

Table 4. Correlations between growth ring measurement.¹

	Width vs. earlywood width	Width vs. latewood width	Earlywood width vs. latewood width
<i>Q. rubra</i>	0.479 (0.016)	0.996 (<0.001)	0.410 (0.036)
<i>F. americana</i>	0.783 (<0.001)	0.978 (<0.001)	0.637 (0.001)

¹ Significance levels shown in parentheses.

Table 5. Correlations between ring width and the anatomical variables.¹

	Width vs. vessel diameter	Width vs. vessel density
<i>Q. rubra</i>		
Earlywood	0.347 (0.067)	0.028 (0.453)
Latewood	0.600 (0.003)	-0.746 (<0.001)
<i>F. americana</i>		
Earlywood	0.140 (0.278)	-0.445 (0.025)
Latewood	0.752 (<0.001)	-0.735 (<0.001)

¹ Significance levels shown in parentheses.

In *F. americana*, width of the earlywood increment varies with latewood width, so that both parts of the increment are positively related to total width. In *Q. rubra*, on the other hand, amount of earlywood produced is independent of width and latewood width. This latter finding is consistent with the observation that, in some ring-porous oaks, the amount of earlywood produced is not significantly affected by precipitation amounts, with very dry years being marked by production of earlywood only (Phipps 1967; Woodcock 1989a). If the interpretation of earlywood as an advanced adaptation is correct (Chalk 1937), then these trees have developed a high degree of reliance on this adaptive characteristic. The large vessels of the earlywood are generally thought to ensure adequate flow during the early part of the year when the leaves are expanding, and ring-porosity is coupled to a growth pattern in which the leaves emerge during a relatively short period and the need for water may be particularly high (Lechowicz 1984).

Width and the anatomical variables.—Since width is the most widely used measure of growth in trees, the relationships between ring width and wood characteristics are of special interest. In both species examined here, ring width shows significant relationships to latewood characteristics but is nonsignificantly related to earlywood characteristics (Table 5). In both cases, width is positively correlated with vessel diameter and inversely correlated with vessel density in the latewood.

These variables are, however, all interrelated (appear on the same factor in the factor analysis). That is, latewood vessel diameter and density also exhibit significant correlations. One way of assessing these relationships is by means of partial correlations analysis. When this is done (Table 6), it can be seen that the significant relationships between variables, with the effects of the other variables controlled for, are between width and latewood density in *Q. rubra* and latewood vessel diameter and density in *F. americana*.

The diameter measures.—Table 7 presents correlations between vessel diameter and three other variables, vessel density, conductive area (percent of cross-sectional area taken up by vessels), and conductivity (sum of the vessel diameters to the fourth power). Vessel diameter is negatively correlated with density in the latewood only. The absence of significant correlations between diameter and density in the earlywood of these two species is somewhat counter to expectation; it

Table 6. Partial correlations between ring width and latewood characters.¹

	Zero-order correlation	Partial correlation, controlling for:		
		Vessel diameter	Vessel density	Width
<i>Q. rubra</i>				
Width vs. vessel diameter	0.600 (0.003)		0.265 (0.136)	
Width vs. vessel density	-0.746 (0.001)	-0.598 (0.003)		
Vessel diameter vs. density	-0.617 (0.002)			-0.318 (0.092)
<i>F. americana</i>				
Width vs. vessel diameter	0.752 (<0.001)		0.388 (0.050)	
Width vs. vessel density	-0.735 (<0.001)	-0.348 (0.043)		
Vessel diameter vs. density	-0.817 (0.001)			-0.591 (0.004)

¹ Significance levels in parentheses.

is in the earlywood with its large, relatively closely spaced vessels that packing constraints would be expected to come into play. Evidently, the earlywood vessels are not sufficiently tightly packed for this to be the case. Carlquist (1977) associates vessel diameter and density with vulnerability to water stress since vessel size influences susceptibility to embolism and vessel density determines availability of backup conduits should some conductive elements become nonfunctional. The trade-off between conductive efficiency and safety thus leads to some degree of covariance between these two variables. The general pattern of covariance that can be recognized on a spatial basis (along a gradient from mesic to xeric; Carlquist 1975) between these two variables is seen here only in the latewood, a result that suggests that the earlywood is adapted for efficiency alone.

Vessel diameter exhibits a significant positive correlation with conductive area

Table 7. Correlations between selected anatomical variables.¹

	Vessel diameter vs. vessel density	Vessel diameter vs. conductive area	Vessel diameter vs. conductivity
<i>Q. rubra</i>			
Earlywood	-0.289 (0.108)	0.584 (0.003)	0.594 (0.003)
Latewood	-0.617 (0.002)	0.689 (0.001)	0.322 (0.083)
<i>F. americana</i>			
Earlywood	-0.023 (0.461)	0.528 (0.008)	0.654 (0.001)
Latewood	-0.817 (0.001)	-0.650 (0.001)	-0.072 (0.381)

¹ Significance levels in parentheses.

in the early- and latewood of *Q. rubra*. In *F. americana*, on the other hand, the relationship is positive in the earlywood and negative in the latewood. Vessel diameter is significantly correlated with sum of the vessel diameters to the fourth power (conductivity) in the earlywood of both species.

Both conductive area and conductivity are calculated from diameter measurements. Although not expressed in the same terms (since conductive area is a percentage measure and conductivity is represented in mm^4 per unit area), they are similar in the sense that conductivity is the sum of the diameters to the fourth power and the *variance* in conductive area is variance in the sum of the diameters squared. That is, both variables are dependent on a summed representation of vessel diameter. Both conductive area (expressed in absolute terms as vessel lumina cross-sectional area of Salleo, Lo Gullo, and Oliveri 1985) and conductivity (theoretical relative conductance of Ellmore and Ewers 1986) have been investigated in studies of hydraulic properties of wood. Results presented here suggest that although these variables, and average vessel diameter, may be related in some cases, they are in general not closely related and should be considered distinct. Since conductive area and conductivity are more difficult to measure than average vessel diameter, it would be appealing to approximate these measures—to represent conductive area, for instance, as average vessel diameter times vessel density (Carlquist 1988). The validity of these approximations will depend on the degree of variability in vessel size. The data collected here permit comparison of actual and approximated values (average conductive area and average conductivity, calculated from average vessel diameter) of these variables. In the case of the two species studied here, conductive area and average conductive area are highly correlated (>0.9) in both the early- and latewood. Conductivity and average conductivity show correspondences ranging from 0.94 ($P < 0.001$) to 0.59 ($P = 0.003$). (A better approximation to conductivity may be diameter of the largest vessel; in bur oak, diameter of the largest earlywood vessel and conductivity have a correlation coefficient of 0.84 ($P = 0.001$); Woodcock 1987.)

SUMMARY AND CONCLUSIONS

Several findings are significant with respect to interpretation of ring-porosity as an adaptation: 1) independence of early- and latewood variables in terms of their temporal variance; 2) presence of a significant inverse relationship between vessel diameter and density in the latewood only; and 3) variance of latewood anatomical characteristics with total ring width. Latewood characteristics are thus affected by the same conditions that influence total growth while at the same time displaying a trade-off between efficiency and safety (covariance of vessel diameter and density). Earlywood characteristics, on the other hand, do not display these relationships and may have a different response to the environment, consistent with the idea that this wood may be functionally important during a relatively short period of the year.

Of the several sources of variance that are present, one (identified with latewood variables and width) can be related to yield and others (identified with diameter measures) probably relate to water conduction. The diameter measures, within either the early- or latewood, are largely interrelated, so no clear-cut answer as to the functional significance of average diameter vs. conductive area vs. conductivity is possible on the basis of these results. The patterns of temporal covariance

identified here in some cases parallel those seen on the spatial scale and in some cases do not.

The sources of variance present within the wood can be represented by the three or four variables most closely identified with the factors. Choice of variables for further analysis may, however, also be influenced by ease and nonambiguity of measurement. In the trees studied here, earlywood vessel diameter and either latewood vessel diameter or ring width are representative of more than half of the total variance. Although conductivity may be the significant factor in representing volumetric flow through a tree and be important in experimental work, difficulties in measuring or approximating this quantity may mean that studies of spatial variance should focus on vessel diameter and range of vessel sizes present, perhaps in conjunction with features such as grouping of vessels and occurrence of the ring-porous vs. diffuse-porous condition.

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APPENDIX

Variables

1. Earlywood vessel diameter (mm)
2. Earlywood vessel density (mm^{-2})
3. Earlywood conductive area (%)
4. Earlywood conductivity (mm^{-2})
5. Latewood vessel diameter (mm)
6. Latewood vessel density (mm^{-2})
7. Latewood conductive area (%)
8. Latewood conductivity (mm^{-2})
9. Latewood ring width (mm)
10. Earlywood ring width (mm)

Quercus rubra

Yr	1	2	3	4	5	6	7	8	9	10
85	0.246	7.3	0.361	0.029	63.5	11.9	0.044	0.000521	4.31	0.81
84	0.224	6.6	0.267	0.026	82.8	9.0	0.067	0.002030	3.75	0.81
83	0.256	7.0	0.371	0.035	91.4	9.2	0.074	0.001870	5.19	1.00
82	0.244	8.5	0.401	0.032	79.4	8.2	0.053	0.001780	5.19	0.94
81	0.240	7.4	0.271	0.026	65.7	12.7	0.065	0.002110	4.75	0.63
80	0.239	6.8	0.332	0.034	56.3	11.1	0.035	0.000500	6.75	1.00
79	0.243	6.8	0.321	0.025	65.6	8.3	0.040	0.001010	6.38	1.13
78	0.230	5.9	0.249	0.018	84.2	5.5	0.040	0.001260	6.25	1.25
77	0.280	7.1	0.406	0.027	57.0	10.1	0.033	0.000610	6.13	0.88
76	0.256	6.3	0.342	0.034	52.6	11.8	0.042	0.001400	3.63	1.13
75	0.220	8.8	0.335	0.022	47.6	9.8	0.020	0.000120	4.19	0.69
74	0.238	5.7	0.270	0.025	55.7	16.7	0.061	0.001270	1.63	0.88
73	0.237	7.5	0.334	0.018	48.0	12.5	0.032	0.000513	3.94	0.69
72	0.246	5.5	0.268	0.023	50.4	10.0	0.032	0.001290	1.69	0.94
71	0.200	8.2	0.300	0.023	42.5	13.0	0.024	0.000268	2.63	0.75
70	0.269	5.9	0.334	0.031	43.5	15.0	0.041	0.001770	1.94	0.88
69	0.238	8.8	0.390	0.030	49.8	21.7	0.061	0.001260	1.38	0.94
68	0.232	6.2	0.249	0.020	39.3	12.8	0.018	0.000637	3.31	0.75
67	0.195	7.1	0.233	0.016	41.3	17.1	0.026	0.001470	1.38	0.44
66	0.231	7.1	0.321	0.027	50.4	13.3	0.034	0.000650	1.94	0.94

APPENDIX
Continued

68	0.161	8.2	0.180	0.008	27.8	42.9	0.031	0.000073	0.31	0.69
67	0.180	12.3	0.323	0.015	38.4	22.0	0.030	0.000110	0.63	0.81
66	0.153	13.7	0.265	0.010	31.8	39.0	0.034	0.000079	0.44	0.69
Correlation matrix										
1	1.000									
2	0.023	1.000								
3	0.528	0.846	1.000							
4	0.654	0.685	0.912	1.000						
5	0.167	-0.152	-0.027	-0.066	1.000					
6	-0.086	0.342	0.242	0.172	-0.817	1.000				
7	-0.045	0.333	0.249	0.152	-0.650	0.922	1.000			
8	0.210	0.003	0.061	0.069	-0.072	0.388	0.643	1.000		
9	0.091	-0.369	-0.244	-0.227	0.780	-0.745	-0.763	-0.295	1.000	
10	0.238	-0.539	-0.312	-0.149	0.463	-0.509	-0.541	-0.158	0.636	1.000