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CHEMICAL RELATIONSHIPS IN TROPICAL FORESTS

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All ecological systems have a chemical structure. This structure may be expressed in several ways. One of these is as a formula or table showing the abundance or concentration of each chemical element comprising the system. It is well known that carbon, hydrogen, and oxygen are present in greatest concentrations in such ecosystems, while nitrogen, calcium, potassium, silicon, magnesium, and sulfur usually occur in moderate quantities, and many other elements are present in trace amounts. Presumably each ecosystem has a unique chemical composition, but would share common characteristics with systems of similar species composition, similar functions, and growing on similar chemical substrates. Unfortunately there are no analyses of ecosystem elemental structure available to support these suppositions ; indeed most studies of elemental abundance focus on only a few of the tens of elements that occur in these systems.

In the present study data on 16 elements were collected from nine forests in eastern Panama. Each forest was divided into five compartments (leaves, stems, fruits and flowers, litter, and roots). These forests represented various degrees of similarity in species composition, life form and ecological characteristics. Two stands were mature Tropical Moist forest characteristic of undulating upland (Figure 1). Four stands represented young second growth of Tropical Moist forest.

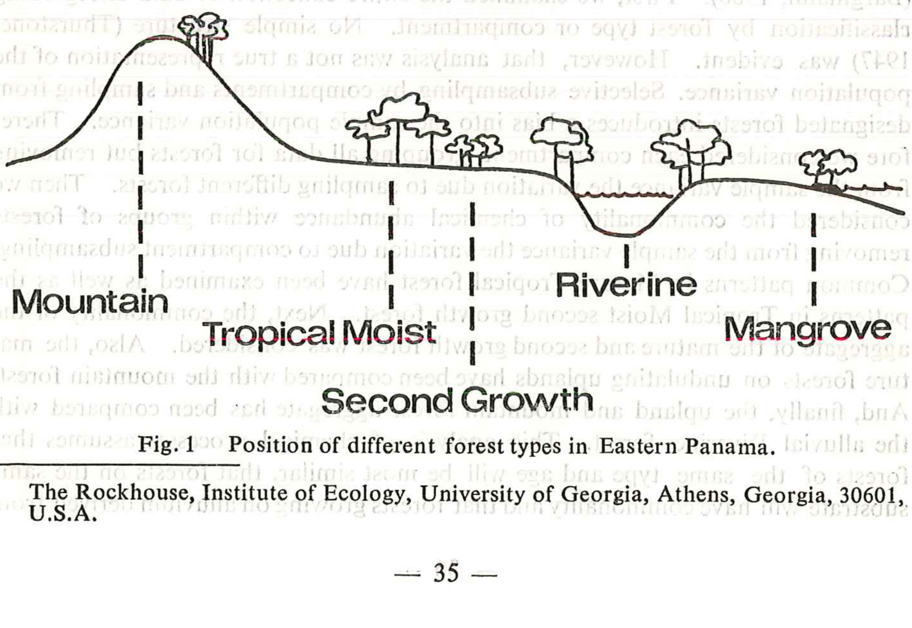

Fig. 1 Position of different forest types in Eastern Panama.

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One stand was mature Moutain forest. Another, was Riverine forest growing on alluvium adjacent to a river traversing Tropical Moist forest. And the last was a Mangrove forest on the coastline. Thus six stands representing vegetation of different ages were from the same geological region and four stands represented different geological regions.

The object of the study was to examine the degree of commonality in chemical elemental abundance between the nine stands and the five compartments. An initial analysis of the chemical data showed that there were statistical differences between the chemical concentrations of almost all elements in all forests (Golley et al., 1975). Generally Tropical Moist forests growing on shale had higher concentrations of calcium, magnesium and strontium, while mountain and alluvial forests had higher concentrations of iron, sodium, titanium and zinc. Second growth also had higher elemental concentrations than mature forest. An analysis of within forest chemistry showed that there were generally numerous but irregular differences in elemental concentration between compartments within forests. Our conclusion from this initial detailed examination of the forest chemistry was that the chemical abundances appeared to be distributed in very complex patterns. The present study carries the analysis of forest chemistry further to determine if there are common patterns of element abundance present within forests and compartments which would not be revealed by the comparisons of central tendency. As suggested above, we anticipate that commonality might be explained by similarity of geological substrate, by age of forest, by physiological function of the compartment, or by the physical-chemical characteristics of the elements.

Methods

In this study we have employed the statistical technique of factor analysis (Bargmann, 1968). First, we examined the entire collection of data disregarding classification by forest type or compartment. No simple structure (Thurstone, 1947) was evident. However, that analysis was not a true representation of the population variance. Selective subsampling by compartments and sampling from designated forests introduces a bias into the sample population variance. Therefore we considered each compartment, grouping all data for forests but removing from the sample variance the variation due to sampling different forests. Then we considered the commonality of chemical abundance within groups of forests removing from the sample variance the variation due to compartment subsampling. Common patterns in Mature Tropical forest have been examined as well as the patterns in Tropical Moist second growth forest. Next, the commonality of the aggregate of the mature and second growth forest was considered. Also, the mature forests on undulating uplands have been compared with the mountain forest. And, finally, the upland and mountain forest aggregate has been compared with the alluvial Riverine forest. This analysis of chemical processes assumes that forests of the same type and age will be most similar, that forests on the same substrate will have commonality and that forests growing on alluvium derived from a geological region will have common chemistry with that forest growing on the uplands of that region.

The methods of sampling vegetation and of analyzing for chemical abundance is discussed in Golley et al. (1975). In general, there are ten samples of plant tissue for each of five vegetation compartments in each of nine forests. The data are in concentrations of parts per million.

The analytical method used in the study is factor analysis. Common artificial factors are extracted from the sample variance/covariance matrix adjusted for sampling bias and the relationship of each element to these factors is examined. The common factors are then varied (rotated) to form a simple structure. Common factors which overlap are removed from the simple structure leaving independent factors to explain the relationships of commonality within the sample. It is hypothesized that elements which relate or correlate highly with the common factor have something in common with each other. It is for the investigator to hypothesize a meaningful process to represent the commonality of the factors and then substantiate his hypothesis with further study such as regression analysis. An element's degree of relationship with an extracted factor can be determined from the factor loadings (> 0.3). The square of the loadings are commonalities which represent the amount of variation an element has is common with other elements present in the sample. The technique assumes that every element has three types of variation present : 1) variation which it shares with other elements ; 2) variation which is unique to the element itself ; 3) variation which is due to random sampling or error. In some cases, an element has been fully determined. This implies that the element's variation can be fully explained by that part of its variation which it shares with the other elements. No variation remains to be explained by the uniqueness of the element or by random chance. The procedure then suggests removal of that element from the battery of elements and reanalyzing to obtain the simple structure to describe the chemical patterns in the data.

Results

1. Comparison of Mature Tropical Moist Forest

The structure of Tropical Moist forest at site 1, during the dry season (Table 1) showed an extremely complex pattern. Sr, Cu, Ti, Ni, and Fe were fully determined and showed commonality with all elements except P, Mg, and Zn. When the fully determined elements were removed, there was no observable simple structure at this site.

In contrast, site 2, collected in the wet season, showed a much less complex chemical structure. The initial analysis with the fixed effect of compartment removed showed Ca and Sr were highly correlated (above 0.8) and that Fe was fully determined. Removing Sr indicated a one factor structure and no fully determined elements. However, removing Ca did not generate a duplicate factor as expected. Instead, Fe was again fully determined and now three factors resulted (Table 1).

Table 1 : Chemical structure of mature Tropical Moist forest in Darien, Panama. Elements listed together represent those with commonality, the numerical scores are factor loadings.

Sites	*Dry Season, Santa Fe*	*Wet Season, Rio Lara*			
N	65	65			
Correlated above 0.8	None	Ca/Sr			
Fully determined	Sr, Cu, Ti, Ni, Fe	Fe			
Structure	None	Removal Sr		Removal	Ca
		Mg	.64	K	.55
		Zn	.52	P	.51
		Cu	.48	Mn	.48
		Ba	.45	Ti	.38
		Mn	—.31		
				Mg	.59
				Zn	.47
				Cu	.46
				Na	.32
				Ti	—.31
				Mg	.58
				K	.52
				Na	.44
				Cu	.43
				P	.38
				Zn	.37

These analyses do not show any obvious common factors present in both forests. The lack of commonality is interesting especially since statistical analysis of concentrations in the vegetation showed that statistical differences existed for Ca, B, Ba, Ni, and Sr. On the other hand, analysis of soil concentrations showed that for all elements except Cu, Fe, and Mn the two sites were different at the $\alpha =$ .05 level of significance. Thus while there was similarity in the mean concentration of specific elements in the vegetation of these two forest, there is little commonality in their abundances. Possibly the differences in substrate are important in regulating these patterns.

2. Comparison of Tropical Moist Forest Second Growth

Four second growth stands of 2, 2, 4, and 6 years of age were harvested very near the second mature Tropical Moist forest site. Comparisons of these four stands also show surprisingly little commonality (Table 2). Six elements were fully determined in one or more stands and there was no simple structure determined for one of the two year-old sites or for the six year-old stand. A Mo, Ti factor with either Na or Ba included was obtained for a two year-old site and also for the four year-old site. The analysis of mean concentrations (Golley et al., 1975) showed that there was about equal similarity between the vegetation concentrations in the stands as there was in the soil concentrations. So, apparently age of the vegetation or species composition may have an effect on elemental abundance in these systems.

3. Comparison of Mature and Second Growth Tropical Moist Forest

For this comparison the wet and dry forest have been combined as have the

Table 2 : Chemical structure of second growth tropical moist forest in Darien, Panama. Elements listed together represent those with commonality, the numerical scores are factor loadings.

Years of age	2	2	4	6
N	46	68	65	68
Correlated above 0.8	Ca/Sr	None	Sr/Ca Ti/A1, Fe Fe/A1, Ti A1/Fe, Ti	None
Fully determined	A1, Ti	Ba, Mn, Ca	Mn	A1, Ba, Fe
Structure	None	Ti .55 Mo .43 Na .33	Removing Sr, A1, Ti Mo .95 Fe .69 Ba .30 or Removing Sr, Fe, Ti Mo .98 A1 .68 Ba .30 or Removing Sr, Fe, A1 Mo .92 Ti .70 Ba .30	None

four second growth forests representing stands 2, 2, 4, and 6 years of age. All sitel were located within five to ten miles from each other. Three common factors (Table 3) were identified in mature forests. One of these may represent structuras

Table 3 : Chemical structure of combined mature Tropical Moist forests and Second Growth forests. Elements listed together represent those with commonality, numerical scores are the factor loadings.

Sites	*Mature Forest*	*Second Growth*
N	130	247
Correlated above 0.8	None	None
Fully determined	None	None
Structure	Ca .67 Sr .63 Ti .41 B .38 Fe .78 Ti .62 A1 .37 B .44 A1 —.41 Ni .40 Ba —.40	Sr .60 B .54 Ca .50 Mn —.43 Ba .36 Mg .31 A1 .73 Fe .72 Mo .58 Mn .78 K .63 Zn .41 Cu .34 Sr .69 B .67 Ca .63 Ba .43

tissue and consists of calcium and strontium with highest factor loadings and includes boron and titanium. The other two factors appear to be related to the soil and consist of Fe, Ti and Al in one case and B, Al, Ni and Ba in the other.

In the combined second growth forests four factors were identified. Two of these were similar to the structural factor of mature forests and consisted of Sr, B, Ca, Mn, Ba, Mg and Sr, B, Ca and Ba. A third factor has commonality to the soil factor Al, Fe, Mo ; and a fourth factor (Mn, K, Zn, Cu) is unexplainable at present, but is similar to the factors obtained in the wet season sample of the mature forest. This comparison shows that the mature and second growth forests share common structural factors and soil factors when the stands are combined. Aggregation of data may lead to more visible general patterns because of the larger data set available for comparison and/or to the deemphasis in local microsite or species effects on the one-quarter hectare plots.

4. Comparison of Mature Tropical Moist and Mature Mountain Forest

The factor analysis of the Mountain forest showed that Sr and Ca were correlated above 0.8. Removal of Sr generated two factors which may be related to the soil substrate (Table 4). Interchanging Sr and Ca did not generate the

Table 4 : Chemical structure of combined mature Tropical Moist forests and Mountain forest. Elements listed together represent those with commonality, numerical scores are the factor loadings.

Sites	*Tropical Moist*	*Mountain*	
N	130	60	
Correlated above 0.8	None		
Fully determined	None		
		Sr removed	Ca removed
Structure	Ca .67	Na .78	Na .61
	Sr .63	Al .62	Al .58
	Ti .41	Ba .53	Mo .54
	B .38	Mo .48	Ba .49
		K .30	Sr .33
	Fe .75		
	Ti .62	Al .74	
	Al .37	Na .58	
		Mo .47	
	B .44	Ba .39	
	Al —.41		
	Ni .40		
	B —.40		

second factor but did extract the first factor substituting Sr for K. This factor was not extracted in Tropical Moist forest, nor was the Tropical Moist forest structural factor identified in the Mountain forest. In the uplands, the soil factor consisted of Fe, Al and Ti, while in the mountains it consisted of Na, Al, Mo, Ba and other elements. These differences may be related to differences in geological substrate. The Tropical Moist forest grows on a calcareous shale, while the Mountain forest occurs on basalt.

5. Comparison of Riverine and Mangrove Forests

There is little reason to expect that the two inundated forests, the Riverine and Mangrove, would show commonality due to the differences in substrates and salinity of the water. Riverine forest had Sr correlated with Ca and Fe correlated with Al and Mo. Magnesium and Sr were fully determined and no simple structure was apparent. Mangrove forest had a complex set of correlated elements, but indicated several factors dominated by Na, Ca, and Ni (Table 5).

Table 5 : Chemical structure of Riverine and Mangrove forest. Elements listed together represent those with commonality, numerical scores are the factor loadings

Sites	*Riverine*	*Mangrove*	
N	45	53	
Correlated above 0.8	Sr/Ca Fe/Al, Mo	P/K Fe/Mn, Al, Mo, Ti Fi/Mn, Fe, Mo	
Fully determined	Mg, Sr	None	
Structure	None	K, Fe, Ti Removed	P, Fe, Ti Removed
		P .65 Na .89 An .64	Na .81 Zn .71 K .67 Mn .32
		Ca .97 Sr .74 Ba .51 Mg .32	Ca .97 Sr .74 Ba .51 Mg .32
		Ni .83 Sr .48 Mn .35	Ni .83 Sr .46 Mn .39 Al .31
			Na —.67 K —.54 Zn —.49 Mn —.43 Ca .37 Ni —.35 B .32

6. Comparison of Combined Upland and Mountain Forests with Riverine Forest

In the comparison between combined upland forests and the Riverine forest we might expect commonality due to substrate effects. The alluvium on which Riverine forest grows is derived ultimately from both the mountain and the undulating uplands. Even though the two upland forests did not exhibit much commonality, possibly the combined substrate effect might be important in influencing the chemical structure of the Riverine forest.

The combined upland forests exhibited two factors (Table 6). One factor grouped P, K, Ca, Mn, and Cu and the other grouped B, Al, Ni, and Ba. The first factor may be related to the vegetation and the second to soils although the

Table 6 : Chemical structure of Upland forests and Riverine forests in Darien, Panama. Elements listed together represent those with commonality, numerical scores are the factor locadings.

Sites	*Upland*	*Riverine*
N	190	45
Correlated above 0.8	None	Sr/Ca, Fe/Al, Mo
Fully determined	Na	Mg, Sr
Structure	P .53 K .45 Ca .39 Mn —.37 Cu .35 B .56 Al —.36 Ni .46 Ba —.31	None

interpretation of the structure is unclear. On the other hand, Riverine forest exhibited no simple structure. At this site Ca/Sr and Fe/Al, Mo were correlated, while Mg and Sr were fully determined. There appears to be no commonality between upland and Riverine forests.

7. Comparison of Compartments

The forests were each divided into five compartments ; leaves, stems, fruits, litter and roots. These five compartments in all forests have been examined, removing the fixed effect of forest (Table 7). Leaves have two interpretable

Table 7 : Chemical structure of Tropical forest compartments, with fixed effects of forests removed. Elements listed together are those with commonality, numerical scores are the factor loadings.

Compartment	*Leaves*	*Litter*	*Fruits & Flowers*	*Stems*	*Roots*
N	168	69	87	152	59
Correlated above 0.8	Fe/Ti	None	Al/Mo	B/Fe	None
Fully determined	None	Na, Ti None	Ca, Ti, P, Na, B	Al	None
Structure	Removing Fe P .62 K .60 Cu .45 Zn .41 Mg .33 Ca .77 Sr .68 Ba .46 B .43 K .36 Na —.33 Na .90 Zn .47 Mn .44	Mo .94 Mg .59 Fe .53 Mn .50 Cu .44 Al .41 Ca .73 Sr .71 Ba .33	No simple structure	K— —.83 Mn —.81 Zn —.35 P —.34	Sr .93 Ca .63 Na —.47 Mn —.39

factors. The first (P, K, Cu, Zn, Mg) is apparently related to photosynthesis and other metabolic activity since all the elements are involved in this type of dynamic process. The second (Ca, Sr, Ba, B) may be the structural factor which was identified earlier. The remaining two factors in leaves can not be interpreted at this time.

In litter the structural factor persists, as would be expected since litter undergoing decomposition almost entirely consists of structural material (Table 7). In addition, a factor made up of Mo, Mg, Fe, Mn, Cu and Al is observed, which may be related to soil, representing contamination of the litter through the activity of burrowing soil organisms.

Fruits and flowers exhibit no simple structure (Table 7). The analysis of this component was quite complicated. The first analysis showed that Ca was fully determined and that Al and Mo were highly correlated. Removal of Ca and Al showed a structure with Sr and P fully determined, while removal of Ca and Mo showed that Na was fully determined. Removal of Ca, Na, Al and Ti showed that B was fully determined. Thus, in fruits and flowers we conclude that there is very little commonality of the elements sampled in elemental abundance. Rather it appears that requirements for specific elements in specific fruits and flowers among the plant species results in each element being concentrated at different rates.

Stems analysis showed that Al was fully determined and that B was highly correlated. Removal of Al and B resulted in identification of one factor which corresponds to the photosynthesis factor of leaves (Table 7).

Roots had one factor which is similar to the structural factor in leaves (Table 7)

The analysis of vegetation components revealed three groups of common factors ; a structural, physiological, and a soil factor. We conclude that the biochemical, and ecological requirements mainly overlay the geochemical substrate effects as far as the vegetation components are concerned. This conclusion supports the suggestion of Kline (1975) that vegetation is decoupled from its substrate.

Conclusions

This analysis of the elemental structure of tropical forests shows that there is relatively little commonality between types of forest, and that there is much more between forest components. The conclusion suggests that the biological constraints override the geochemical factors governing elemental distribution. That is, a vegetation component (leaves, stems, etc.) is more chemically similar to a like component in another forest, then there are two forests which are classed as representatives of the same type. In one sense, this conclusion supports the strategy of separating forests into functional components, but it also leads to the conclusion that the species mix may regulate the forest chemical structure. In this study we did not study effects of individual species so it was not possible to test the conclusion that species mix may regulate the chemical structure. Finally, it may also be necessary to have samples representing sufficiently large areas to observe common structure within a type otherwise microsite effects may obscure the commonality.

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