CONDITION AND CAUSE IN ECOLOGICAL INTERPRETATION

by

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My colleague Lam, in whose honour this volume is composed, has made it very easy for contributors to find a subject in a field in which he has worked himself. His versatile interest nearly covered the whole of the taxonomy and phylogeny of vascular plants, subjects in theoretical biology, plant morphology, plant geography, and plant ecology. In the latter section his "Fragmenta papuana" contains an inspiring picture of tropical vegetation in correlation with environment.

I have pleasure on this occasion in offering some considerations in the field of plant ecology. The subject which I have chosen deals with the way of reasoning when interpreting a correlation found to exist between vegetation and environment. I have not infrequently traced a deficiency in such interpretation and I feel a need of discussing this point which is, in my opinion, a matter of vital importance.

The finding of a correlation is naturally the first step for understanding vegetation. But the next step is as essential as the first and consists of verifying the nature of this correlation by putting the crucial question: is the correlation direct or indirect, in other words what is cause and what is condition.

In many cases correlations have been rashly declared to be direct, but I have reason to believe that they are of that kind only in a surprisingly small number of cases. In the majority of instances correlations are far more complicated and require a chain of reasoning instead of a simple link.

In textbooks on plant ecology this matter is generally treated very lightly.

Tansley (1) illustrated the point clearly by "the explanation for the puzzling distribution of two plant communities, found side by side, with no difference in soils save that the one is on drier and the latter on damper soil, though the communities inhabiting, on the whole, the drier and damper areas respectively are apparently quite capable of growing on either. This suggests a difference in the incidence of competition between the plants of the two soils, and the difference in competition may finally turn out to be determined by the attacks of animals which avoid, for instance, very wet ground."

The problem confronting us with the discrimination of condition and
cause deserves, in my opinion, great emphasis and is a basic principle in vegetatiology ("Vegetationskunde").

I have formerly pointed out the great importance of this discrimination with regard to the correlation of grasslands and savannahs with dry climates, a correlation which, through the logarithmically increasing influence of man and beast with increasing dryness of climate, can never be regarded as direct (2, 3). With respect to the origin of deserts and semi-deserts many ecologists are still blind and accept unwarranted direct correlation.

The discrimination of cause and condition naturally concerns all correlations between environment and vegetation. The following examples derived from the Malaysian flora may illustrate this.

**East Java savannahs.** — In East Java the climate is distinctly seasonal, due to the SE. trade wind which manifests itself in the occurrence of a long dry period (May to Oct. or Nov.). On the S. slopes of the mountains there is rain-forest, due to the rain given off throughout the year by the ascending winds. On the N. side of the mountains and ranges it is, therefore, extra dry (rain-shadow). On certain N. slopes there is more grassland. The conclusion is that there is a distinct correlation between the occurrence of drought and occurrence of grassland, but it must not rashly be concluded that the grassland is caused by the dry climate.

The grassland is really caused by anthropogenous action (fire) during a very long period in the past but the conversion into grassland has only been possible under seasonally very dry climatic conditions, which make the vegetation extremely inflammable during part of the year. The climax on the N. slopes is a poor, dry type of mixed forest, sometimes being replaced by a volcanicolous or fire-climax forest of *Casuarina junghuhniana*. On the northern slopes we find this mixed climax forest still present in pockets which have escaped the destructive action of man. In other places which were protected from fire by the Forest Service we observe the slow, gradual receding of the grass in favour of mixed-forest pioneers, corroborating our conclusion that the dry climate on the north slopes is the condition under which anthropogeneous deforestation has resulted into grassland.

**Padangs.** — In Borneo there are various places, called 'padangs', where amidst a rather luxuriant rain-forest there are low sand plateaus which bear a most remarkable resemblance to a European heath, with low shrubs, much open sand, partly covered by mosses and lichens, and some herbs. It is clear that the climate, distinctly everwet here, cannot be held responsible for this heath vegetation, but that there is a distinct correlation with the soil. This conclusion appears to contain on closer study only half the truth, however, as in digging pits in the neighbouring forest exactly the same podsolic soil profile is found of pure white quartz sand with a black hardpan at 1—2 m depth. Obviously something has happened on the sites of the padangs to destroy the forest climax on this kind of soil which is so poor that, once the vegetation has been removed, regeneration is well-nigh impossible. This suspicion is strengthened by the observation that the padang heath is surrounded by a sharp forest border which almost always points to an unnatural condition. What has happened is irrelative for the reasoning. The main conclusion is that the poor
soil is the condition under which the origin of the padang heath can take place, but the real cause of their origin is to be ascribed to some other agent.

Mangrove. — It is a matter of fact that in Malaysia the mangrove is, in the seasonally dry regions, generally poorly developed. This is not accidental, and it has already been concluded elsewhere in the world that mangrove is not resistant against drought, and that it would directly respond to climatic conditions.

Really this correlation is indirect. For the explanation it must be realized that the majority of the mangrove plants grow on accrescent coasts where silt is deposited or at least not removed. Very few species can grow on old coral reefs covered with a thin veneer of sand (Sonneratia) and an occasional one is bound to pure sand (Rhizophora stylosa). The conditions for silt accumulation are fulfilled where in bays and estuaries or along more or less sheltered coasts the surf is not too heavy and the fore-shore currents are not too strong. The other factor is the transport of the silt; this is derived from the debris of the rivers and the larger the river and the higher and more constant the amount of silt it transports to the sea, the larger the delta and the more opportunity will be afforded to the settling of mangrove along the adjacent coastal parts. If the fore-shore falls off abruptly the silt is lost for the purpose, but if the fore-shore is shallow conditions will be favourable.

As the amount of silt in dry or seasonally dry areas is generally — though not always — low, as rivers in seasonal areas are dry or nearly so during a large part of the year, and moreover the sea and its currents are more turbulent than under everwet conditions, large coastal silt deposits are rare or scarcer in seasonal regions. As the amount of silt bringing water in the rivers is naturally bound to rainfall — eventually only in the headwaters in the mountains — the development of the mangrove is indirectly correlated with the climate which represents a condition for silt depositing. The silt is finally decisive for the occurrence of the mangrove. And that is what is actually found: in the driest areas of Malaysia, before the coasts of Timor, there are some small bays and lagoons with mangrove, but for the rest the coast is very poorly provided with mangrove, except for some reefs with low Sonneratia.

Nypa. — Preference of Nypa to water current velocity can easily be observed along coastal creeks subject to daily recurrence of the tides. These mangrove creeks are often fringed with Nypa fruticans, the massive and dense root system of which is better fitted to resist erosive forces of swift running water than that of most other mangroves. From this it derives its dominance in these places, but it must not be rashly inferred that Nypa is bound to such localities, or that such localities are optimal for its growth; this is by no means the case.