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Causes and Ecological Significance of Stomatal Frequency[1]

Because the contact between the aerial portions of plants and the environment is so largely influenced by the stomata, the study of these pores has long been recognized as yielding data of importance to ecology. But, while the comparison of the structural modifications of the stomata of plants from habitats of various degrees of humidity has received considerable attention, the relation between the frequency of stomata, or their number per unit of

[1] Salisbury, E. J. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. Philosophical Transactions of the Royal Society of London. Series B, Vol. 216, pp. 1–65. 1927.

leaf area, and the environment of the leaf has not been given the study it deserves, probably because it involves the laborious accumulation of large amounts of data. The recent investigations by Salisbury form a welcome contribution to this neglected field of ecological inquiry.

The author begins with a consideration of the relation between leaf area and stomatal frequency, and shows that of the two leaves at a single node of *Mercurialis perennis,* the smaller leaf has generally the greater frequency of stomata. This negative correlation between area and stomatal frequency holds good for the other species studied. When investigated in relation to position on the plant, it is found that the higher the insertion of the leaf, the greater the frequency of stomata. This frequency gradient is independent of the decrease in the size of leaves with increasing height of insertion so often true of herbaceous plants. Similarly, cauline leaves have relatively more stomata than radical leaves. The frequency of stomata is not constant over the entire area of even a single leaf, but certain well-marked tendencies of distribution are evident. Thus in dicotyledonous leaves the frequency increases from the base of the leaf upward, and from the midrib toward the margins, the base and the midrib being the regions poorest in stomata. In monocotyledonous leaves with intercalary growth, the central portion of the leaf, which is the latest formed and often develops under conditions of greater exposure, exhibits a greater frequency than the earlier formed basal and apical portions. In general, however, the frequency gradient both of the individual leaf and of the plant as a whole corresponds to the gradient of suction force demonstrated by Molz [2]; both increase with increasing distance from the source of the water supply.

Much may be learned about the probable relationship between the stomatal frequency of a species and the community in which it is found by a study of the factors responsible for the observed gradients in individual leaves and plants. Plants which developed under glass in a uniformly moist atmosphere did not show the frequency gradient from the base to the apex of the stem, which indicated that the greater frequency on the upper leaves is related to the decreased humidity at the greater distance from the ground. There was no important difference in frequency between plants grown in moist air in the light, and those grown in darkness under the same conditions of humidity. These and other experiments and observations furnish satisfactory evidence that stomatal frequency is not altered by light or by the rate of photosynthesis, but that among external factors aridity is the important one in increasing its value.

These studies of the individual plant paved the way for a consideration of the plant community. The author selected for investigation the British woodland flora. The conclusions he draws are based upon several thousand

[2] Molz, Francis John. A study of suction force by the simplified method. Am. Jour. Bot., 13: 433–501. 1926.

determinations made on over two hundred species. The counts were made for the most part by the author himself, but in some cases the results of other workers are drawn upon. The plants of the woodland flora were divided into the tree layer, the shrub layer and the herbaceous plants, and the stomatal frequency was found to decrease in the order named. When the trees and shrubs are grouped together, they show a markedly greater average frequency than the herbs. Among the herbaceous plants, the marginal flora shows a considerably greater stomatal frequency than the shade flora. Thus the more exposed the plant, the greater the frequency of stomata on its leaves, a condition which the study of the individual plant would lead one to expect, but just the opposite of the conclusions derived from some of the teleological reasoning of the past.

The generalizations drawn in this study are based upon a wealth of data which is adequately presented in the form of tables and graphs. The experimental work, which consisted in the determination of the effect of various artificial environments upon the distribution of the stomata, is of particular value in giving an insight to the conditions which affect stomatal frequency. The concept of " Stomatal Index," which the author introduces to express the percentage of the entire number of epidermal cells which are modified as stomata, helps us to understand the way in which these external conditions operate in altering the stomatal frequency. The stomatal index tends to be constant for a given species, at least far more so than the stomatal frequency. Thus in both the sun and the shade leaves of a given tree approximately the same proportion of epidermal cells are specialized as stomata; there are more stomata per unit of area in the sun leaf because all of the epidermal cells are smaller than in the shade leaf, and the stomata are accordingly more crowded. Since the stomatal index is more constant for the species than the stomatal frequency, the former may prove to be of more value in ecological work, and more characteristic of the association. It is greatly to be desired that studies of this character be extended to other formations, and that similar data be secured for more xerophytic communities for purposes of comparison with the present work.

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