Atoll Vegetation and Salinity

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Coral atolls are flat rings of reef-rock and calcareous debris usually forming islets with an elevation of only a few feet above sea level. They are distributed throughout the tropical Pacific and Indian Oceans, except the eastern Pacific, with somewhat similar formations in the Atlantic, principally in the Bahama Islands.

The great Pacific groups of atolls are such archipelagoes as the Tuamotus, Carolines, Marshalls, Gilberts, the Phoenix-Ellice group, and those scattered clusters and individual islands collectively termed the Pacific Equatorial or Line Islands. The observations forming the basis of this paper were made on visits to all these groups, except the Phoenix-Ellice and Gilberts, as well as to the Austral Islands and to the essentially similar barrier reef islets around various high islands.

Atolls are characterized by small floras with few endemic species and a preponderance of widely dispersed strand plants. The plant cover is a strand vegetation which is generally regarded as very uniform and uninteresting. Actually, however, this uniformity exists only in the minds of those who have visited very few atolls or who have observed them only superficially.

The major differences in vegetation are those between islands in dry and wet climatic belts. The driest atolls, such as Malden, Jarvis, Howland, and Baker, have a sparse desert-like vegetation of a few grasses, herbs, and dwarf shrubs that contrasts strikingly with the luxuriant jungles on atolls in the central and eastern Carolines and southern Marshalls.

Another important difference occurs between the vegetation of small or narrow islets and that of large land areas. The smaller the area of an islet the more extreme is the strand character of its vegetation, and the larger the area the more divergence is shown from this type. This divergence may be of different sorts, as in the

![Fig. 1. Northwest corner of Mili Atoll, Marshall Islands, showing a number of small islets. PHOTOGRAPH BY LEONARD E. MASON.](image1)

![Fig. 2. Outer beach on Nomwin Islet, Hall Island, Caroline Islands, showing scrub vegetation, principally Scavola frutescens. PHOTOGRAPH BY F. R. FOSBERG.](image2)
extensive *Lepturus-Messerschmidia* savannah on dry Christmas Island, the dense moist forest of Nomwin, the tangled swamp on Ailinglapalap, or the solid forest of a single species on isolated Vostok Island (*Bishop Mus. Spec. Publ. 30: 19, 1936*).

On most atolls may be seen a very definite vegetational zonation. This varies on different atolls, but a certain order is usual, oriented concentrically from the outer beach to the inner, or lagoon, beach.

The outermost zone is a scrub, principally of *Scaevola frutescens*, reaching a height of 2–5 meters and often mixed on its inner edges with *Cordia subcordata* and *Souiname amara*. On very narrow islets and spits between islets this may extend the full width of the islet. In sandy soil *Suriana maritima* may be an important component.

Next inward there is usually a halophytic forest zone of the tree heliotrope (*Messerschmidia argentea*) and *Pandanus*. In some regions, as in the Marshalls and Carolines, *Terminalia littoralis* is commonly found in this forest. This is ordinarily a rather narrow belt.

The greater part of the interior of an islet is usually occupied by a more mesophytic type of forest. At the present time on most atolls this is largely made up of coconut plantations, which, contrary to popular opinion, are not the natural vegetation of atolls but are planted by man. In places on the wetter atolls the coconuts are partly replaced by breadfruit trees which occasionally reach enormous size, towering above the coconuts and making a dense shade. *Pandanus* is also common among the coconuts.

Where scraps of the original vegetation of this zone remain they are found to be composed of such trees as *Pisonia grandis*, *Pandanus* spp., *Ochrosia parviflora*, *Pipturus argenteus*, *Hibiscus vilicaceus*, *Messerschmidia argentea*, *Calophyllum inophyllum*, *Barringtonia asiatica*, *Eugenia* sp., and others. On the drier islands the buka (*Pisonia grandis*) tends to be dominant.

In the interior of this zone there are frequently swales, marshes, ponds termed "man-
In general the indigenous flora of atolls is more meager to the eastward in the Pacific, richer in the west, as would be expected from the isolation of those in the east and the proximity of the western ones to large islands with their complex floras.

The introduced flora, both wild and cultivated, is extremely limited. The wild introduced species are mainly shallow-rooted herbs. It was the cultivated flora that offered the original clue to the distribution of atoll vegetation. It was noticed that, though numerous species have been tried out, both by the plant-loving natives and by residents of foreign origin, relatively few of them have survived. Still fewer can be considered successful even under the protection and cultivation of man. Those that survive, but are not especially successful, show, without exception, signs of a severe localized chlorosis (yellow coloring) of the type usually associated with excessive sodium, with resultant deficiency of assimilated potassium and a more general chlorosis possibly associated with deficiencies of other ions due, perhaps, to high pH. *Lantana camara*, ordinarily a most aggressive weed, is yellow and sterile where planted in the Marshall Islands. Even some of the species, such as the papaya, which survive and reproduce themselves, are often chlorotic. Also these species are much more successful toward the center of an islet where the salinity is naturally lower. Very few of the introduced plants, excepting those which are themselves strand plants with a tolerance toward high salinity, or those which are shallow-rooted, thus living in the upper layers where the salt is to some extent leached out by rains, have succeeded in becoming naturalized.

That there is a high water table in this type of island is shown by the numerous wells only a few feet deep, dug by the natives. The water is ordinarily more or less brackish. Hence it is not reasonable to suppose that the sparseness of woody vegetation of the drier islands is due to actual physical lack of water, since the tree roots can undoubtedly go down to the water table. Physiological dryness resulting from high...
salinity is doubtless the limiting factor. This
would be mitigated in direct relation to the
amount of rain that falls on the island and to
the distance that salt water has to diffuse
through the porous limestone and debris making
up the island. Mesophytic conditions would
exist in direct proportion to the predominance
of outward flow of fresh water over the inward
diffusion of salt. The pattern of the distribu-
tion of vegetation in relation to the general
rainfall and to the land area of an islet is exactly
what would be expected on this basis; the more
mesophytic types of vegetation exist in the
interiors of larger islands in relatively rainy
regions. Native agriculture is a reflection of
this also. Coconut and breadfruit culture is
more or less coincidental with the inner, more
mesophytic, forest, and the excavated taro
patches are found in the interior, least brackish
locations and are absent on the driest islands.
On very dry islands there is no agriculture.

The distribution of herbaceous seed plants,
general wherever there is sufficient sunlight, is
a reflection of the leaching of the salt from the
upper layers. Ferns are found only in the shade
of the mesophytic forests.

The few mangroves found on atolls, again,
reflect the same pattern. Bruguiera conjugata
and Lumnitzera coccinea, which are found on
high islands toward the inner edges of the
mangrove swamps where the salinity is less,
are on atolls in the brackish mangrove depres-
sions, while the Rhizophora and Sonneratia,
which grow on the seaward sides of the swamps,
are found on atolls on the highly saline shores
of lagoons and in swamps with direct tidal
channels.

Further support for this principle is found
in the flora and vegetation of elevated atolls
and reefs. Here, even with a small degree of
elevation, the flora shows a marked increase in
number of species and vegetation becomes more
mesophytic. This is demonstrated in the slightly
raised portion of Anaa Atoll, the more strongly
raised Henderson Island, the high platform of
Makatea Island, as well as in the jungle-covered
limestone plateaus and cliffs of the Marianas
and the southern Palaus. The salt would nat-
urally be largely leached out in these situations.

Summary: The atoll flora, both native and
introduced, is restricted to such species as can
tolerate considerable salinity. The vegetation
is controlled by the salinity of the ground water.
The fresh water of an atoll islet exists in the
form of a very shallow Ghyben-Herzberg lens,
with its freshness directly proportional to the
product of the rainfall and the distance from
the beaches. The vegetation, as a result, is meso-
phytic in relation to the same factors, tending
to be most luxuriant and arborescent toward the
center of large islets in wet regions, and more
sparse, desert-like, and predominantly herba-
ceous or dwarf-shrubby on beaches, spits, and
small islets in climatically dry areas of the
ocean.