ON THE OSMOTIC CONCENTRATION OF THE TISSUE FLUIDS OF PHANEROGAMIC EPIPHYTES

J. Arthur Harris

INTRODUCTORY REMARKS

The purpose of this paper, which is one of a series dealing with the problem of the physico-chemical properties of vegetable saps in relation to environmental factors and to geographical distribution, is to present the results of three series of determinations of the osmotic concentration of the tissue fluids of phanerogamic epiphytes, and to compare them briefly and in a preliminary way with available data for the osmotic concentrations found in the sap of terrestrial vegetation.

Notwithstanding the enthusiastic interest aroused in the mind of the botanical traveler by the remarkable range of form and the obvious physiological peculiarities of the Orchidaceae, Bromeliaceae, and other epiphytic forms so characteristic of tropical vegetation, our knowledge, in quantitative terms, of the physiology of these organisms is exceedingly meager.

Since I hope on another occasion to discuss epiphytism in greater detail, I shall not in this place review the general literature.

MATERIALS AND METHODS

In this paper I have meant to include only those species which may unquestionably be considered typical epiphytes. It was for this reason that a few determinations made on plants which may be either terrestrial or epiphytic were included by Mr. Lawrence and myself in our paper on the Jamaican montane rain forest vegetation (1917a). In some instances it is extremely difficult to determine just which species shall be regarded as epiphytes. Our data are given in detail, and any botanist who chooses may arrange them differently.

The methods employed in the present study are those sufficiently described in our earlier discussion of the parasitic and the terrestrial vegetation of the Blue Mountains (Harris and Lawrence, 1916, 1917a).

1 This study was made possible by the Department of Botanical Research and the Department of Experimental Evolution of the Carnegie Institution of Washington.
The determinations here recorded were secured in three periods of field work, the first in Jamaica in 1915, the second and third in southern Florida in 1916 and 1917. In the first period I had the advantage of the co-operation of Mr. John V. Lawrence, who remained on the island for some time longer than I was able to do, and to whom I am indebted for a large part of the work on Jamaican forms. In the third period Mr. Charles W. Crane rendered most efficient service in several phases of the work.

The determinations were carried out in the Tropical Laboratory at Cinchona, Jamaica, and in the Subtropical Laboratory of the United States Department of Agriculture at Miami, Florida. I have to thank Mr. William Harris, F.L.S., and the members of the British Association Committee for the use of the Laboratory at Cinchona, and am much indebted to Dr. David Fairchild, Agricultural Explorer, and to Mr. Edward Simmonds, in charge of the Plant Introduction Garden at Miami, for the use of the laboratory and other favors. All the species were determined in the herbarium of the New York Botanical Garden. In addition, I am indebted to Dr. Small for various courtesies in the field work.

PRESENTATION OF DATA

The following protocol gives the individual determinations for the several species in terms of freezing point lowering, $\Delta$, corrected for undercooling, and osmotic concentration in atmospheres as determined from a published table (Harris and Gortner, 1914). The averages, designated by bars for each species, are given at the extreme right. When only a single determination is available it has of necessity served to represent the species in place of the average.

In the Bromeliaceae an attempt has been made to arrange the forms in a rough series from the most typical tank forms to those departing most widely from the type in which water storage in the bases of the leaves is possible. Ultimately I hope our determinations will cover a range of forms sufficiently wide and be numerous enough to justify consideration of the problem of the relationship between sap properties and morphological structure in this fascinating family of plants. It has not seemed feasible to attempt any logical classification of the Orchidaceae, and they are merely alphabetically arranged for each of the regions.

All the Jamaican montane rain forest determinations were made in 1915. Hence the year is omitted when dates are cited. In the case of
the Florida determinations, the year as well as the day of the month has been given.

**Bromeliaceae**

_Guzmania Sintensis_ (Baker) Mez

Montane Rain Forest, Leeward Slopes, Feb. 24, $\Delta = 0.31$, $P = 3.7$; Ridges, Feb. 9, $\Delta = 0.34$, $P = 4.1$; Mar. 9, $\Delta = 0.45$, $P = 5.5$; Jim Crow Peak, Feb. 17, $\Delta = 0.25$, $P = 3.0$; Feb. 17, $\Delta = 0.28$, $P = 3.4$; Windward Slopes and Ravines, Feb. 13, $\Delta = 0.25$, $P = 3.0$; Feb. 13, $\Delta = 0.23$, $P = 2.8$; Feb. 20, $\Delta = 0.28$, $P = 3.3$; Mar. 13, $\Delta = 0.44$, $P = 5.3$.

_Guzmania capituligera_ (Griseb.) Mez (?)

Montane Rain Forest, Leeward Slopes, Feb. 18, $\Delta = 0.46$, $P = 5.5$; Windward Slopes and Ravines, Feb. 22, $\Delta = 0.41$, $P = 4.9$.

_Guzmania monostachya_ (L.) Rusby

Subtropical Florida. Sykes Hammock, Jan. 27, 1916, $\Delta = 0.42$, $P = 5.1$; Mar. 16, 1917, $\Delta = 0.50$, $P = 6.0$.

_Catopsis Berteroniana_ (Schult.) Mez

Subtropical Florida. Hattie Bauer Hammock, Mar. 19, 1917, $\Delta = 0.46$, $P = 5.5$; Mar. 19, 1917, $\Delta = 0.42$, $P = 5.0$; Royal Palm Hammock, Mar. 3, 1916, $\Delta = 0.50$, $P = 6.0$; Feb. 21, 1917, $\Delta = 0.48$, $P = 5.7$; Small Hammock between Florida City and Biscayne Bay, Feb. 17, 1917, $\Delta = 0.46$, $P = 5.6$.

_Tillandsia uliculata_ L.

Subtropical Florida. Hattie Bauer Hammock, Mar. 16, 1917, $\Delta = 0.43$, $P = 5.2$; Mar. 19, 1917, $\Delta = 0.45$, $P = 5.4$; Royal Palm Hammock, Mar. 4, 1916, $\Delta = 0.42$, $P = 5.1$; Mar. 3, 1916, $\Delta = 0.33$, $P = 4.0$; Small Hammock near Royal Palm Hammock, Feb. 23, 1917, $\Delta = 0.43$, $P = 5.2$; Bryan Hammock, Feb. 13, 1917, $\Delta = 0.37$, $P = 4.5$; Palm and Live Oak Hammock, Peninsula, near the Narrows, Indian River, Apr. 1, 1917, $\Delta = 0.44$, $P = 5.3$; on dwarfed _Rhizophora Mangle_, near Biscayne Bay, Feb. 17, 1917, $\Delta = 0.40$, $P = 4.8$; Feb. 17, 1917, $\Delta = 0.57$, $P = 6.9$; Feb. 17, 1917, $\Delta = 0.39$, $P = 4.7$; Feb. 17, 1917, $\Delta = 0.34$, $P = 4.1$; Orange Grove, Miami, Feb. 10, 1917, $\Delta = 0.58$, $P = 6.9$.

These determinations are for the older, outer leaves. Sap from the younger leaves gave $\Delta = 0.35$, $P = 4.2$. 

\[ \bar{\Delta} = 0.31, \bar{P} = 3.8 \]

\[ \bar{\Delta} = 0.44, \bar{P} = 5.2 \]

\[ \bar{\Delta} = 0.46, \bar{P} = 5.6 \]

\[ \bar{\Delta} = 0.43, \bar{P} = 5.2 \]
Tillandsia Valenzuelana A. Rich.  
Subtropical Florida. Royal Palm Hammock, Jan. 29, 1916, \( \Delta = 0.35, P = 4.2 \); Jan. 29, 1916, \( \Delta = 0.36, P = 4.3 \); Feb. 23, 1917, \( \Delta = 0.34, P = 4.0 \); Small Hammock near Royal Palm Hammock, Feb. 23, 1917, \( \Delta = 0.41, P = 4.9 \); Bryan Hammock, Feb. 13, 1917, \( \Delta = 0.32, P = 3.9 \); Brickell Hammock, Mar. 9, 1917, \( \Delta = 0.38, P = 4.5 \).

Tillandsia incurva Griseb. (?)  
Montane Rain Forest, Ridges, Feb. 18, \( \Delta = 0.28, P = 3.3 \); Windward Slopes and Ravines, Mar. 2, \( \Delta = 0.22, P = 2.7 \).

Tillandsia fasciculata Swartz  
Subtropical Florida. Hattie Bauer Hammock, Mar. 16, 1917, \( \Delta = 0.36, P = 4.3 \); Mar. 19, 1917, \( \Delta = 0.33, P = 3.9 \); Royal Palm Hammock, Mar. 4, 1916, \( \Delta = 0.40, P = 4.8 \); Feb. 27, 1917, \( \Delta = 0.41, P = 5.0 \); Small Pineland Hammock, near Royal Palm Hammock, Mar. 4, 1916, \( \Delta = 0.44, P = 5.3 \); Sykes Hammock, Jan. 27, 1916, \( \Delta = 0.40, P = 4.8 \); Bryan Hammock, Feb. 13, 1917, \( \Delta = 0.31, P = 3.7 \); Small Hammock near Royal Palm Hammock, Feb. 23, 1917, \( \Delta = 0.43, P = 5.2 \); Murden Hammock, Jan. 28, 1916, \( \Delta = 0.45, P = 5.4 \); Small Hammock between Biscayne Bay and Florida City, Feb. 17, 1917, \( \Delta = 0.32, P = 3.9 \).

Tillandsia aloifolia Hook.  
Subtropical Florida. On dwarfed Rhizophora Mangle near Biscayne Bay, Feb. 17, 1917, \( \Delta = 0.43, P = 5.1 \).

Tillandsia Balbisiana Schult.  
Subtropical Florida. Hattie Bauer Hammock, Mar. 19, 1917, \( \Delta = 0.53, P = 6.4 \); Royal Palm Hammock, Jan. 29, 1916, \( \Delta = 0.40, P = 4.8 \); Mar. 3, 1916, \( \Delta = 0.39, P = 4.7 \); Feb. 23, 1917, \( \Delta = 0.47, P = 5.7 \); Small Hammock near Royal Palm Hammock, Feb. 23, 1917, \( \Delta = 0.49, P = 6.0 \); Bryan Hammock, Feb. 13, 1917, \( \Delta = 0.38, P = 4.6 \); on dwarfed Rhizophora Mangle near Biscayne Bay, Feb. 29, 1916, \( \Delta = 0.50, P = 6.0 \); Feb. 17, 1917, \( \Delta = 0.51, P = 6.1 \).

Tillandsia tenuifolia L.  
Subtropical Florida. Royal Palm Hammock, Jan. 29, 1916, \( \Delta = 0.38, P = 4.6 \); Feb. 21, 1917, \( \Delta = 0.45, P = 5.4 \); Sykes Hammock, Jan. 27, 1916, \( \Delta = 0.46, P = 5.5 \); Mar. 15, 1917, \( \Delta = 0.45, P = 5.5 \); Bryan Hammock, Feb. 13, 1917, \( \Delta = 0.37, P = 4.4 \).
CONCENTRATION OF TISSUE FLUIDS OF EPIPHYTES

Anacheilium cochleatum (L.) Hoffmannsegg

Subtropical Florida. Royal Palm Hammock, Mar. 3, 1916, $\Delta = 0.52$, $P = 6.2$; Feb. 23, 1917, $\Delta = 0.45$, $P = 5.4$. $\bar{\Delta} = 0.43$, $\bar{P} = 5.2$

Dendropogon usneoides (L.) Raf.

Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916, $\Delta = 0.44$, $P = 5.3$; Royal Palm Hammock, Jan. 29, 1916, $\Delta = 0.41$, $P = 5.0$. $\bar{\Delta} = 0.75$, $\bar{P} = 9.0$

Auliza nocturna (L.) Small

Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916, $\Delta = 0.46$, $P = 5.5$; Mar. 16, 1917, $\Delta = 0.47$, $P = 5.7$; Mar. 19, 1917, $\Delta = 0.52$, $P = 6.3$; Royal Palm Hammock, Jan. 29, 1916, $\Delta = 0.38$, $P = 4.5$; Feb. 21, 1917, $\Delta = 0.29$, $P = 3.5$; Small Pineland Hammock, near Royal Palm Hammock, Mar. 3, 1916, $\Delta = 0.41$, $P = 4.9$; Bryan Hammock, Feb. 13, 1917, $\Delta = 0.40$, $P = 4.8$; Feb. 13, 1917, $\Delta = 0.39$, $P = 4.6$.

Encyclia tampense (Lindl.) Small

Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916, $\Delta = 0.48$, $P = 5.8$; Mar. 16, 1917, $\Delta = 0.50$, $P = 6.1$; Mar. 19, 1917, $\Delta = 0.51$, $P = 6.2$; Royal Palm Hammock, Jan. 29, 1916, $\Delta = 0.44$, $P = 5.3$; Brickell Hammock, Mar. 22, 1917, $\Delta = 0.49$, $P = 5.9$; Mar. 24, 1917, $\Delta = 0.40$, $P = 4.8$; Bryan Hammock, Feb. 13, 1917, $\Delta = 0.45$, $P = 5.4$; Palm and Live Oak Hammock, Peninsula, near the Narrows, Indian River, Apr. 1, 1917, $\Delta = 1.32$, $P = 15.8$; Sykes Hammock, Mar. 15, 1917, $\Delta = 0.57$, $P = 6.8$; Orange Grove, Miami, Mar. 6, 1916, $\Delta = 0.70$, $P = 8.4$; Feb. 9, 1917, $\Delta = 0.65$, $P = 7.9$.

Macradenia lutescens R.Br.

Subtropical Florida. Royal Palm Hammock, Jan. 29, 1916, $\Delta = 0.53$, $P = 6.4$; Feb. 21, 1917, $\Delta = 0.48$, $P = 5.7$.

Polystachya minuta (Aubl.) Britton


Spathiger rigidus (Jacq.) Small

Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916, $\Delta = 0.47$, $P = 5.7$; Mar. 16, 1917, $\Delta = 0.36$, $P = 4.4$; Mar. 19, 1917, $\Delta = 0.42$, $P = 5.0$; Royal Palm Hammock, Jan. 29, 1916, $\Delta = 0.35$.

Sample from Hattie Bauer Hammock obtained January 28, 1916, and one from the Brickell Hammock, March 22, 1917, were so mucilaginous that no determination could be made. The juice of the sample from the Bryan Hammock was also highly mucilaginous and could not be filtered. Until verification this determination must be taken as only approximate.

Orchidaceae

Epidendrum imbricatum Lindl.

Montane Rain Forest, Windward Slopes and Ravines, Feb. 13, $\Delta = 0.30$, $P = 3.6$.

Lepanthes ovalis (Swartz) Fawc. & Rendle

Montane Rain Forest, Leeward Ravines, Mar. 18, $\Delta = 0.35$, $P = 4.2$.

Lepanthes divaricata Fawc. & Rendle

Montane Rain Forest, Ridges, Feb. 9, $\Delta = 0.19$, $P = 2.3$; Mar. 9, $\Delta = 0.27$, $P = 3.3$; Jim Crow Peak, Feb. 17, $\Delta = 0.16$, $P = 1.9$; Windward Slopes and Ravines, Feb. 20, $\Delta = 0.19$, $P = 2.3$; Feb. 24, $\Delta = 0.18$, $P = 2.2$; Mar. 4, $\Delta = 0.20$, $P = 2.4$.

Octadesmia montana (Swartz) Benth.

Montane Rain Forest, Jim Crow Peak, Feb. 17, $\Delta = 0.41$, $P = 5.0$; Windward Slopes and Ravines, Feb. 20, $\Delta = 0.46$, $P = 5.5$.

Pleurothallis racemiflora (Swartz) Lindl.

Montane Rain Forest, Leeward Ravines, Mar. 11, $\Delta = 0.21$, $P = 2.6$.

Stelis micrantha Swartz

Montane Rain Forest, Ridges, Feb. 9, $\Delta = 0.23$, $P = 2.7$; Windward Slopes and Ravines, Feb. 4, $\Delta = 0.24$, $P = 2.9$; Feb. 13, $\Delta = 0.20$, $P = 2.4$; Feb. 20, $\Delta = 0.21$, $P = 2.5$.

Stelis ophioglossoides Swartz

Montane Rain Forest, Jim Crow Peak, Feb. 17, $\Delta = 0.22$, $P = 2.7$. 
Anacheilium cochleatum (L.) Hoffmannsegg  
Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916,  
\[ \Delta = 0.44, \bar{P} = 5.3; \] Royal Palm Hammock, Jan. 29, 1916,  
\[ \Delta = 0.41, \bar{P} = 5.0. \]

Auliza nocturna (L.) Small  
Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916,  
\[ \Delta = 0.46, \bar{P} = 5.5; \] Mar. 16, 1917,  
\[ \Delta = 0.47, \bar{P} = 5.7; \] Mar. 19, 1917,  
\[ \Delta = 0.52, \bar{P} = 6.3; \] Royal Palm Hammock, Jan. 29, 1916,  
\[ \Delta = 0.38, \bar{P} = 4.5; \] Feb. 21, 1917,  
\[ \Delta = 0.29, \bar{P} = 3.5; \] Small Pineland Hammock,  
near Royal Palm Hammock, Mar. 3, 1916,  
\[ \Delta = 0.41, \bar{P} = 4.9; \] Bryan Hammock, Feb. 13, 1917,  
\[ \Delta = 0.40, \bar{P} = 4.8; \] Feb. 13, 1917,  
\[ \Delta = 0.39, \bar{P} = 4.6. \]

Encylica tampense (Lindl.) Small  
Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916,  
\[ \Delta = 0.48, \bar{P} = 5.8; \] Mar. 16, 1917,  
\[ \Delta = 0.50, \bar{P} = 6.1; \] Mar. 19, 1917,  
\[ \Delta = 0.51, \bar{P} = 6.2; \] Royal Palm Hammock, Jan. 29, 1916,  
\[ \Delta = 0.44, \bar{P} = 5.3; \] Brickell Hammock, Mar. 22, 1917,  
\[ \Delta = 0.49, \bar{P} = 5.9; \] Mar. 24, 1917,  
\[ \Delta = 0.40, \bar{P} = 4.8; \] Bryan Hammock, Feb. 13, 1917,  
\[ \Delta = 0.45, \bar{P} = 5.4; \] Palm and Live Oak Hammock, Peninsula, near the  
Narrows, Indian River, Apr. 1, 1917,  
\[ \Delta = 0.62, \bar{P} = 7.4; \] Small Hammock near Royal Palm Hammock, Feb. 23, 1917,  
\[ \Delta = 0.47, \bar{P} = 5.6. \]

Macradenia lutescens R. Br.  
Subtropical Florida. Royal Palm Hammock, Jan. 29, 1916,  
\[ \Delta = 0.53, \bar{P} = 6.4; \] Feb. 21, 1917,  
\[ \Delta = 0.48, \bar{P} = 5.7. \]

Polystachya minuta (Aubl.) Britton  
Subtropical Florida. Bryan Hammock, Feb. 13, 1917,  
\[ \Delta = 0.50, \bar{P} = 5.0.\]

Spathiger rigidos (Jacq.) Small  
Subtropical Florida. Hattie Bauer Hammock, Jan. 28, 1916,  
\[ \Delta = 0.47, \bar{P} = 5.7; \] Mar. 16, 1917,  
\[ \Delta = 0.36, \bar{P} = 4.4; \] Mar. 19, 1917,  
\[ \Delta = 0.42, \bar{P} = 5.0; \] Royal Palm Hammock, Jan. 29, 1916,  
\[ \Delta = 0.35. \]

*Sample from Hattie Bauer Hammock obtained January 28, 1916, and one  
from the Brickell Hammock, March 22, 1917, were so mucilaginous that no deter-
mination could be made. The juice of the sample from the Bryan Hammock was  
also highly mucilaginous and could not be filtered. Until verification this deter-
mination must be taken as only approximate.*
$P = 4.2$; Jan. 29, 1916, $\Delta = 0.31, P = 3.7$; Mar. 3, 1916, $\Delta = 0.40, P = 4.8$; Feb. 21, 1917, $\Delta = 0.32, P = 3.9$.

Vanilla Eggersii Rolfe

Subtropical Florida. Brickell Hammock, Feb. 14, 1916, $\Delta = 0.24, P = 2.9$. This determination is of course based on sap from the stems.

**Piperaceae**

*Peperomia basellifolia* H.B.K. $\bar{\Delta} = 0.35, \overline{P} = 4.2$

Montane Rain Forest, Windward Slopes and Ravines, Feb. 20, $\Delta = 0.40, P = 4.8$; Feb. 24, $\Delta = 0.35, P = 4.2$; Mar. 4, $\Delta = 0.33, P = 3.9$; Mar. 13, $\Delta = 0.31, P = 3.7$.

*Peperomia crassicaulis* Fawc. & Rendle $\bar{\Delta} = 0.40, \overline{P} = 4.9$

Montane Rain Forest, Ridges, Feb. 18, $\Delta = 0.40, P = 4.8$; Mar. 9, $\Delta = 0.44, P = 5.2$; Mar. 13, $\Delta = 0.42, P = 5.1$; Mar. 16, $\Delta = 0.46, P = 5.6$; Windward Slopes and Ravines, Mar. 4, $\Delta = 0.30, P = 3.6$.

*Peperomia magnoliifolia* (Jacq.) A. Dietr. $\bar{\Delta} = 0.38, \overline{P} = 4.6$

Subtropical Florida, Royal Palm Hammock, Jan. 29, 1916, $\Delta = 0.38, P = 4.6$; Small Hammock near Royal Palm Hammock, Feb. 23, 1917, $\Delta = 0.39, P = 4.7$; Bryan Hammock, Feb. 13, 1917, $\Delta = 0.37, P = 4.5$; Feb. 13, 1917, $\Delta = 0.35, P = 4.2$; Sykes Hammock, Jan. 27, 1916, $\Delta = 0.41, P = 4.9$.

*Peperomia Myrtillus* Miquel $\bar{\Delta} = 0.36, \overline{P} = 4.3$

Montane Rain Forest, Leeward Ravines, Mar. 11, $\Delta = 0.35, P = 4.2$; Windward Slopes and Ravines, Mar. 13, $\Delta = 0.36, P = 4.4$.

*Peperomia quadrifolia* (L.) H.B.K.$\bar{\Delta} = 0.36, \overline{P} = 4.3$.

Montane Rain Forest, Leeward Ravines, Mar. 11, $\Delta = 0.39, P = 4.6$.

*Peperomia septemnervis* Ruiz & Pav. $\bar{\Delta} = 0.31, \overline{P} = 3.7$

Montane Rain Forest, Leeward Ravines, Mar. 11, $\Delta = 0.33, P = 3.9$; Windward Slopes and Ravines, Feb. 13, $\Delta = 0.31, P = 3.7$; Feb. 13, $\Delta = 0.30, P = 3.6$.

**Gesneraceae**

*Columnnea hirsuta* Swartz $\bar{\Delta} = 0.36, \overline{P} = 4.3$

Montane Rain Forest, Leeward Ravines, Feb. 26, $\Delta = 0.40, P = 4.8$; Windward Slopes and Ravines, Feb. 13, $\Delta = 0.33, P = 4.0$; Feb. 20, $\Delta = 0.34, P = 4.1$; Feb. 22, $\Delta = 0.33, P = 4.0$; Feb. 22,
The table brings out clearly two facts:
1. That in all four families and in both Jamaica and Florida, the osmotic concentration of epiphytic forms is extremely low.
2. That for the three groups represented in both regions the osmotic concentration of the epiphytes (chiefly from the hammocks) of subtropical Florida is higher than that demonstrated in the Jamaican rain forest. The average difference is 1.57 atmospheres higher for the Bromeliaceae, 1.74 atmospheres higher for the Orchidaceae, and 0.24 atmospheres higher for the single species of Peperomia.

The comparison may be made somewhat more analytically on the basis of the means for the genera. The constants in table 2 are averages of the species means of each of the genera.

<table>
<thead>
<tr>
<th>Table 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genera of Jamaican and Floridian Epiphytes Arranged in the Order of the Average Osmotic Concentration of Their Species</td>
</tr>
<tr>
<td>Jamaica</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td>Bromeliaceae...</td>
</tr>
<tr>
<td>2 genera, 3 species</td>
</tr>
<tr>
<td>Orchidaceae...</td>
</tr>
<tr>
<td>5 genera, 7 species</td>
</tr>
<tr>
<td>Piperaceae...</td>
</tr>
<tr>
<td>Peperomia only, 5 species</td>
</tr>
<tr>
<td>Gesneraceae...</td>
</tr>
<tr>
<td>Columnnea hirsuta only</td>
</tr>
</tbody>
</table>
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<table>
<thead>
<tr>
<th>Genus</th>
<th>( \bar{P} )</th>
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<th>( \bar{P} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jamaica</td>
<td></td>
<td>Florida</td>
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</tr>
<tr>
<td>Pleurothallis</td>
<td>2.57</td>
<td>2.90</td>
<td>Vanilla</td>
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<td>Stelis</td>
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<tr>
<td>Tillandsia</td>
<td>3.00</td>
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<tr>
<td>Lepanthes</td>
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<td>Epidendrum</td>
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<td>Columnnea</td>
<td>4.33</td>
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<tr>
<td>Peperomia</td>
<td>4.34</td>
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<tr>
<td>Guzmannia</td>
<td>4.49</td>
<td>4.52</td>
<td>Spathiger</td>
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<td>4.58</td>
<td>Peperomia</td>
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<td>4.97</td>
<td>Auliza</td>
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<td>5.09</td>
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<td>Anacheilium</td>
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<td></td>
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<td>8.97</td>
<td>Dendropogon</td>
</tr>
</tbody>
</table>

4 That the higher value for Floridian Bromeliaceae is not primarily due to the inclusion of *Dendropogon usneoides* (= *Tillandsia usneoides*) is shown by the fact that if this species be omitted from the Florida series, the remaining 9 species average \( \bar{\Delta} = 0.433, \bar{P} = 5.19 \), which are respectively 0.100 and 1.19 greater than the Jamaican average.
It is clear at a glance that with the exception of the stem-succulent Vanilla in the Floridian and of Octadesmia montana in the Jamaican constants, the two series do not overlap in the average (generic) magnitude of their constants. With the exceptions noted, the Jamaican (rain forest) genera range from 2.57 to 4.49 atmospheres, whereas the Floridian genera range from 4.52 to 8.97 atmospheres.

Instead of limiting our comparisons between the two regions to means, the individual determinations may be seriated according to their magnitude and the frequency distributions compared. This has the advantage of giving a general view of the range of variation in the individual constants, but the disadvantage from the standpoint of exact comparison that certain species are far more extensively represented than others. The frequency distributions are given in table 3.

<table>
<thead>
<tr>
<th>Osmotic Concentration in Atmospheres</th>
<th>Orchidaceae</th>
<th>Bromeliaceae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jamaica</td>
<td>Florida</td>
<td>Jamaica</td>
</tr>
<tr>
<td>1.5-1.9</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td>2.0-2.4</td>
<td>5</td>
<td>—</td>
</tr>
<tr>
<td>2.5-2.9</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>3.0-3.4</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>3.5-3.9</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>4.0-4.4</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>4.5-4.9</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>5.0-5.4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>5.5-5.9</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>6.0-6.4</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>6.5-6.9</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>7.0-7.4</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>13</td>
</tr>
</tbody>
</table>

Because of the unusually high values found in the Spanish moss (*Dendropogon usneoides*) it has been omitted from this table. Notwithstanding this fact, the Floridian Bromeliaceae as well as the Orchidaceae show distinctly higher minima and maxima than the Jamaican forms. The distinction between the two regions is not as clearly shown by the distribution of the individual determinations as by the generic means, since individual determinations must be expected to show much wider variation than averages.
I now turn to the relative magnitude of the osmotic concentration of terrestrial and epiphytic plants.

Since in a number of series of determinations we have found a differentiation in the sap properties of ligneous and herbaceous plants, I shall compare epiphytic Orchidaceae, Bromeliaceae, and Piperaceae primarily with terrestrial herbaceous plants.

Unfortunately the several hundreds of determinations from the various coastal, pineland, hammock, and Everglade habitats of Subtropical Florida are as yet unclassified, and it will probably require some time before the results from this highly interesting region are discussed in detail.

The averages for the various groups of epiphytes from Jamaica and from Subtropical Florida have been given in table 1.

The average freezing-point lowering of the saps ranges from 0.276° to 0.464°, less than two tenths of one degree. In terms of osmotic concentration the values lie between 3.3 and 5.6 atmospheres, a range of less than two and one third atmospheres.

The only extensive series of averages for herbaceous terrestrial vegetation are those for the Arizona deserts made by Harris, Lawrence, and Gortner (1916), and the first Long Island series, by Harris, Lawrence, and Gortner, as yet unpublished, and the Jamaican montane rain forest series which will be treated in greater detail below.

For the Long Island habitats the preliminary average values are:

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Average Concentration, P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beaches, coastal sand dunes, and marshes</td>
<td>13.62</td>
</tr>
<tr>
<td>Dryer woods and open fields</td>
<td>10.04</td>
</tr>
<tr>
<td>Permanently moist localities</td>
<td>9.27</td>
</tr>
<tr>
<td>All habitats</td>
<td>10.41</td>
</tr>
</tbody>
</table>

Note that the epiphytic forms show a sap concentration about one third to one half as great.

For the Arizona desert (vernal) flora the averages for herbaceous plants are:

---

6 For averages for divergent growth forms from the Arizona deserts see Harris, Lawrence, and Gortner (1916). Averages for Long Island and Jamaican habitats are given by Harris and Lawrence (1917a). Some general comparisons are made by Harris (1917).
Habitat ................................................. Average Concentration, $\bar{P}$
Rocky slopes ......................................... 15.94
Canyons .............................................. 13.33
Arroyos ............................................... 12.99
Bajada slopes ........................................ 20.53
Salt spots ........................................... 23.57
All habitats ........................................... 15.15

These values are (roughly speaking) from 4 to 7 times as large as those for the epiphytic families.

For the Jamaican series, and unfortunately only for the Jamaican series, it is possible at this time to compare the averages for epiphytic and terrestrial forms from the same habitat.

Table 4 gives the averages of the species means for each habitat for the Orchidaceae and Bromeliaceae and for the genus Peperomia of

<table>
<thead>
<tr>
<th>Table 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Comparison of Osmotic Concentration of Epiphytic Plants with that of Terrestrial Herbaceous Plants in the Montane Rain Forest</strong></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Habitats</th>
<th>Average for Terrestrial Herbs</th>
<th>Average for Epiphytic Orchidaceae</th>
<th>Difference and Relative Value</th>
<th>Average for Epiphytic Bromeliaceae</th>
<th>Difference and Relative Value</th>
<th>Average for Epiphytic Piperaceae</th>
<th>Difference and Relative Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruinate of the leeward slopes</td>
<td>$\bar{P}=9.77$ (n=17)</td>
<td>$\Delta=0.812$</td>
<td>---</td>
<td>$\Delta=0.385$</td>
<td>$-0.427$</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Leeward ravines</td>
<td>$\bar{P}=7.59$ (n=13)</td>
<td>$\Delta=0.628$</td>
<td>---</td>
<td>$\Delta=0.305$</td>
<td>$-0.413$</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Ridges and peaks</td>
<td>$\bar{P}=8.63$ (n=8)</td>
<td>$\Delta=0.718$</td>
<td>---</td>
<td>$\Delta=0.305$</td>
<td>$-0.413$</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Windward slopes and ravines</td>
<td>$\bar{P}=7.52$ (n=15)</td>
<td>$\Delta=0.627$</td>
<td>---</td>
<td>$\Delta=0.310$</td>
<td>$-0.317$</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>All habitats</td>
<td>$\bar{P}=8.43$ (n=53)</td>
<td>$\Delta=0.700$</td>
<td>---</td>
<td>$\Delta=0.330$</td>
<td>$-0.370$</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

This method of computing the average has both advantages and disadvantages. For present purposes it is quite adequate.

Practically the same percentages are secured by using the average values of freezing-point lowering, but since the relationship between $A$ and $P$ is not strictly linear the results are not exactly identical.

Comparisons with the herbaceous plants of the regions as a whole show a concentration 5.1 atmospheres lower for Orchidaceae, 4.5 atmospheres lower for Bromeliaceae, and 4.2 atmospheres lower for Peperomia of the Piperaceae. The averages for the whole region is obtained by weighting those of the individual habitats with the number of species examined.
the Piperaceae. The number under each of the averages is the number of species, not the number of determinations, upon which it is based.

The averages for terrestrial herbaceous species are those already published (Harris and Lawrence, 1917a).

The general mean for the region has been computed by averaging the species means for the individual habitats. Thus if a species occurs in both the Leeward Ravines and the Ridge Forest it is counted twice, whereas the species which occur in one of these habitats only will be counted but once. Thus the numbers of the species given for all habitats is the number of species weighted with the number of the sub-habitats in which they occur.6

The comparison between the epiphytic and the terrestrial herbaceous forms has been made in two ways. First, the actual differences in the average depression of the freezing point and in the average calculated osmotic concentration have been determined and are given with their signs. Second, the average values of $P$ of the epiphytes have been expressed as a percentage of the value for terrestrial herbs.7

An examination of the nine comparisons between the epiphytic and terrestrial herbs of the four individual habitats shows that the concentration is in every instance lower for the epiphytic forms. The averages are roughly 4.0 to 5.4 atmospheres lower in the Orchidaceae, 3.8 to 5.2 atmospheres lower in the Bromeliaceae, and 3.4 to 3.6 atmospheres lower in Peperomia of the Piperaceae.8

There now remains for consideration only the half shrubby gesneraceous epiphyte *Columnnea hirsuta*. One determination from the Leeward Ravines gives $\Delta = 0.395$, $P = 4.76$. Eight constants from the Windward Slopes and Ravine average $\bar{\Delta} = 0.354$, $\bar{P} = 4.28$. If these be compared with the averages for herbaceous vegetation from the same habitats, differences in $P$ of $-2.83$ for the Leeward Ravine determination and of $-3.24$ for the Windward habitats are secured.

6 This method of computing the average has both advantages and disadvantages. For present purposes it is quite adequate.

7 Practically the same percentages are secured by using the average values of freezing-point lowering, but since the relationship between $\Delta$ and $P$ is not strictly linear the results are not exactly identical.

8 Comparisons with the herbaceous plants of the regions as a whole show a concentration 5.1 atmospheres lower for Orchidaceae, 4.5 atmospheres lower for Bromeliaceae, and 4.2 atmospheres lower for Peperomia of the Piperaceae. The averages for the whole region is obtained by weighting those of the individual habitats with the number of species examined.
If the comparison be made with the ligneous terrestrial vegetation, the differences are -6.07 for the Leeward and -5.45 for the Windward habitats.

In relative terms, the osmotic concentrations of the sap of the epiphytic Orchidaceae is only 37.3 to 46.5 percent as high as that of the terrestrial herbs of the same habitat, the constants for the Bromeliaceae range from 42.3 to 49.6 percent of the comparable values for terrestrial herbs, while the determinations based on Peperomia range from 52.9 to 60.1 percent of those for the non-epiphytic herbs of the same habitats. Columnnea shows a concentration of 56.9 percent of that of herbaceous plants in the Windward habitats and 62.7 percent of that of herbaceous plants in the Leeward habitats. If compared with ligneous terrestrial vegetation it shows a concentration of 44.0 percent in the Windward and of 44.0 percent in the Leeward habits.

Summarizing the results of this comparison: the osmotic concentration of the fluids of the epiphytic Orchidaceae, Bromeliaceae, Piperaceae, and Gesneraceae of the montane rain forest of Jamaica is roughly speaking only 37.3 to 62.7 percent as high as that of the terrestrial plants of the same region.

The averages for herbaceous forms include, as already explained, a few determinations based on species which may occur on the ground or as epiphytes. They also include those based on a few ferns and fern allies. The removal of these constants might change slightly the actual values of the difference in the table. Since the forms which have been classified as terrestrial but may occur as epiphytes are characterized by lower osmotic concentration than the vegetation as a whole, the removal of these species from the list of herbaceous plants would make the differences demonstrated between terrestrial and epiphytic vegetation even larger. The exclusion of the few determinations for terrestrial ferns and fern allies could be justified only on the assumption that they are sensibly differentiated in their sap properties from flowering plants. There is, at present, no basis for such an assumption.

The low concentration of the sap of epiphytic Phanerogams may perhaps be most clearly brought out by comparing it with that of the ligneous species upon which they may occur. Table 5 gives the differences and relative concentrations for the Jamaican materials.

Epiphytic Orchidaceae show from 28 to 36 percent, the epiphytic Bromeliaceae from 32 to 38 percent, the epiphytic Piperaceae from 39 to 45 percent, and the epiphytic Gesneraceae about 44 percent
of the osmotic concentration exhibited by the foliage of the ligneous forms upon which they find lodgment. Of course these figures are only approximations, which will be somewhat modified by further work, but they are based on sufficient data to justify the conclusion that the epiphytic species of the rain forest are characterized by a concentration of about one third to one half that of the ligneous terrestrial species.

**Table 5**

Comparison of Osmotic Concentration of Epiphytic Forms with that of Ligneous Terrestrial Species in the Montane Rain Forest

<table>
<thead>
<tr>
<th>Habitats</th>
<th>Average for Ligneous Plants</th>
<th>Difference and Relative Value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Orchidaceae</td>
<td>Bromeliaceae</td>
</tr>
<tr>
<td>Ruinate of the leeward slopes...</td>
<td>13.05 (n = 40)</td>
<td>-8.45</td>
</tr>
<tr>
<td>Leeward ravines</td>
<td>10.83 (n = 32)</td>
<td>-7.43</td>
</tr>
<tr>
<td></td>
<td>31.4%</td>
<td></td>
</tr>
<tr>
<td>Ridges and peaks</td>
<td>11.54 (n = 36)</td>
<td>-8.32</td>
</tr>
<tr>
<td></td>
<td>27.9%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>31.6%</td>
<td></td>
</tr>
<tr>
<td>Windward slopes and ravines...</td>
<td>9.73 (n = 28)</td>
<td>-6.23</td>
</tr>
<tr>
<td></td>
<td>36.0%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>34.3%</td>
<td></td>
</tr>
<tr>
<td>All habitats</td>
<td>11.44 (n = 136)</td>
<td>-8.07</td>
</tr>
<tr>
<td></td>
<td>29.5%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>29.5%</td>
<td></td>
</tr>
</tbody>
</table>

In passing it may be worth while to point out that these results have an important bearing upon theories of the origin of parasitism. The suggestion has been made that epiphytism is the first stage in the evolution of parasitism in the flowering plants. But all of these most typical epiphytes are characterized by very low osmotic concentration in comparison with the ligneous species of the same region, whereas the Loranthaceae of these forests have been shown (Harris and Lawrence, 1916) to have generally higher concentration of their tissue fluids than their hosts. Similar relationships have been found to exist in desert Loranthaceae (Harris, 1918).

Theoretically one of the best methods of comparison would be to lay side by side constants for terrestrial and epiphytic members of the same family. Unfortunately I have not been able to secure terrestrial Orchidaceae from subtropical Florida. Determinations have been published (Harris and Lawrence, 1917a) for Jamaican species. *Epidendrum verrucosum*, which we included in our first paper because we always found it growing on the ground, although Fawcett and Rendle
record it as occurring "on trees, rocks, and dry banks," gives on the 
average $\Delta = 0.51$, $P = 6.1$ in the Leeward ravines and $\Delta = 0.55$, $P = 6.6$ in the ruinate. *Prescottia stachyoides* from the windward ravines and slopes gave an average depression of $\Delta = 0.52$, or an 
average concentration in atmospheres of $P = 6.3$.

All of these values are distinctly, and in many cases very much, 
greater than those obtained from the individual species of epiphytic Orchidaceae.

For comparison with the epiphytic Peperomia we have only *Peperomia stellata*, which we collected in Jamaica only as a terrestrial 
herb. It gave the following values:

- Leeward ravines, $\Delta = 0.43$, $P = 5.2$
- Ridge Forest, $\Delta = 0.45$, $P = 5.4$
- Leeward habitats, $\Delta = 0.42$, $P = 5.1$

These values are slightly higher than the averages for any of the 
epiphytic species from the rain forest.

As far as I am aware, the only determination of osmotic concen-
tration of the tissue fluids of any bromeliad hitherto made is that for
*Bromelia Pinguim*, which Mr. Lawrence and I (1917b) found growing 
as a terrestrial plant in the Jamaican coastal deserts. This gave
$\Delta = 0.63$, $P = 7.6$. This is a value higher than any of those recorded
in this paper with the exception of those for *Dendropogon usnecoides*. 
It is, however, extremely low for such a habitat as the Jamaican Coastal Deserts.

With regard to two species which Mr. Lawrence and I treated with
the terrestrial vegetation but which others have observed growing as 
air plants, the following points may be noted.

The woody-stemmed *Blakea trinervia*, which may be rooted in the 
soil or, according to Shreve, grown as an epiphyte, has a concentration 
measured by $\Delta = 0.58$, $P = 6.9$, as compared with the general average 
of $\Delta = 0.81$, $P = 9.7$ for the ligneous species of the windward habitats 
in which it occurs.

*Tradescantia multiflora*, which we included with terrestrial vege-
tation in our earlier paper, but which may also occur as an epiphyte, 
gave in a single determination $\Delta = 0.39$, $P = 4.7$. This is far lower 
than the general averages of $\Delta = 6.3$, $P = 7.6$ for the herbs of the 
Leeward ravines.
CONCLUSIONS

The osmotic concentration of the tissue fluids of epiphytic Bromeliaceae, Orchidaceae, Piperaceae, and Gesneraceae is far lower than that of terrestrial vegetation.

In the Jamaican montane rain forest where direct comparisons for individual habitats are possible, the epiphytes show from 37 to 60 percent of the concentration characteristic of herbaceous terrestrial vegetation, and from 28 to 45 percent of the concentration of ligneous terrestrial vegetation.

In the Bromeliaceae, Orchidaceae, and Peperomia of the Piperaceae, the osmotic concentration of the species of the Jamaican montane rain forest is lower than that of the species of the hammocks of subtropical Florida.

At some future time I hope to deal with the problem of the osmotic concentration of cryptogamic epiphytes and to obtain data on the inorganic and organic constituents of the fluids of epiphytes which will justify further discussion of the physiology of these ecologically remarkable forms.

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