BIOTROPICA 24(4): 488–502 1992

# Ecological Site Classification of Florida Keys Terrestrial Habitats[1]

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## ABSTRACT

Site and vegetation characteristics were examined in 113 Florida Keys locations that had been undisturbed for at least 50 years. Detrended correspondence analysis (DECORANA) indicated that Keys vegetation was arranged along two major environmental gradients: an elevational gradient within islands, and a geographic gradient associated with position along the NE-SW trending island chain. Both were complex gradients, with soil depth and type, periodicity of tidal inundation, ground water depth and salinity, climate, and geological substrate as potential contributing factors. Two-way indicator species analysis (TWINSPAN) was used to divide the samples into 14 major groups on the basis of plant species composition. Finally, the TWINSPAN classification was modified to recognize 13 Ecological Site Units which were homogeneous in important site factors as well as vegetation characteristics. Plant species diversity increased from intertidal to upland site units, while canopy height, basal area, and fine litter production increased both upslope and downslope of the supratidal units.

*Key words: dry tropical forest; ecological site classification; Florida Keys; limestone islands; TWINSPAN; vegetation analysis.*

Ecological site classifications which express the interrelationships between vegetation, physiography, and soils (Barnes *et al.* 1982) have been developed in Europe and applied in Canada (Jurdant *et al.* 1975, Hills & Pierpoint 1960) and the United States (Spies & Barnes 1985a, b). A classification based on one factor alone (*e.g.*, vegetation, topography, soil) may ignore important ecological characteristics that are not expressed by that factor. For instance, subsoil characteristics can affect deep-rooted trees without affecting shallow rooted herbs, and different topographic settings can support similar vegetation. In low islands like the Florida Keys, the ecosystem effects of physical changes such as sea level rise or anthropogenic impacts on ground water are best projected on a habitat classification which includes physical as well as vegetation features.

Previous authors identified and described broad vegetation units in the Florida Keys (Small 1917, Davis 1943, Snyder *et al.* 1990), but none used the multifactor approach discussed above, or were specific enough to express the ecosystem diversity apparent in field observations. Elsewhere in the West Indies, there have been a number of descriptive studies of floristically and ecologically similar vegetation complexes. Beard's (1944, 1955) classification of tropical American vegetation included a number of units applicable to the Florida Keys. Studies in Jamaica (Asprey & Robbins 1953, Asprey & Loveless 1958, Kapos 1986), the Bahamas (Howard 1950), Cuba (Seifreiz 1943), and Venezuela (Medina *et al.* 1989) describe several vegetation types that were similar in species composition and site characteristics to those found in the Keys. Nevertheless, none included the full assemblage of sites found in our study area, nor expressed interrelationships between adjacent units important in the Florida Keys.

Our overall objective was therefore to develop a site classification which was organized in an ecologically meaningful way, and which subdivided the natural areas of the Florida Keys into units that were physically and compositionally homogeneous. Our approach was to use an ordination technique to assess the association of important compositional gradients with measurable site variables; to apply a classification procedure to point out natural divisions among species assemblages; and, to adjust the units resulting from Step 2 to create field-recognizable Ecological Site Units which were as homogeneous as possible in important site and structural characteristics, while retaining compositional homogeneity.

[1] Received 26 April 1991, revision accepted 20 April 1992.

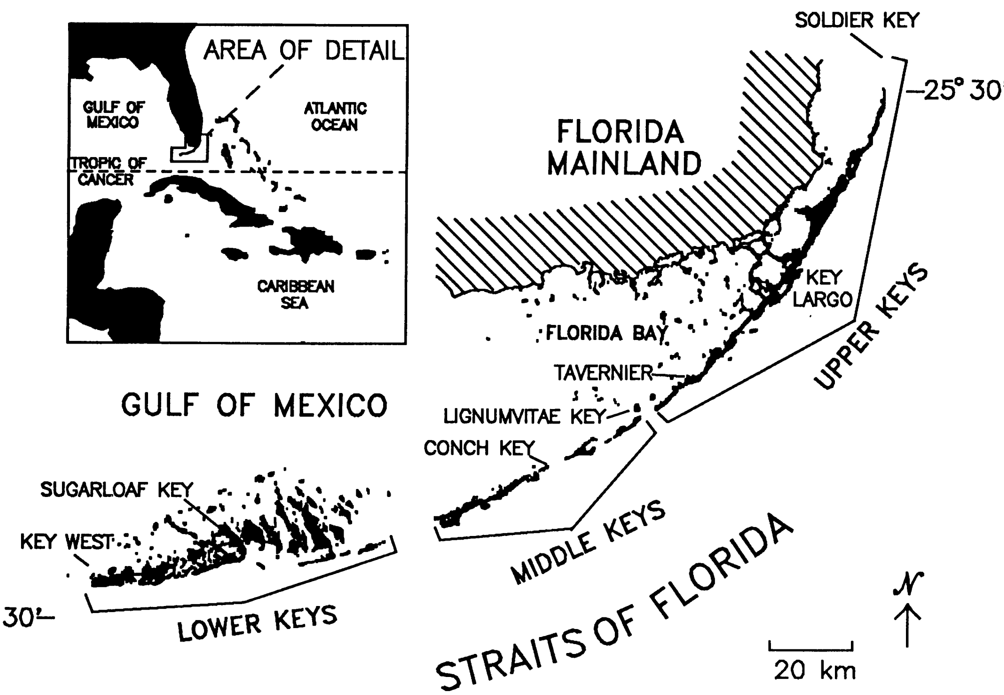


FIGURE 1. South Florida and the Florida Keys.

## STUDY SITE AND METHODS

The Florida Keys are a 210 km island arc sweeping southwest from Soldier Key (25°36′N, 80°10′W) to Key West (24°33′N, 81°49′W). The islands have traditionally been grouped into Upper, Middle, and Lower Keys (Fig. 1), a division based on contrasting climatic, geological, and geographical features. Although the Keys lie a few degrees north of the Tropic of Cancer, the climate can be considered tropical. The Keys had a mean annual temperature of 25.2°C for the period of 1951–1980 (U.S. National Climatic Data Center 1989). Brief periods of freezing temperatures have occurred in the northernmost Keys closest to the Florida mainland, while temperatures below 5°C have never been recorded in the Lower Keys (pers. comm., U.S. Weather Service). Rainfall is seasonal, two-thirds occurring during the months of June through October, with conditions becoming drier and slightly warmer from Upper to Lower Keys (Fig. 2). The effect of climate on upland vegetation in the Florida Keys is apparent in the drought-deciduous nature of many of the dominant plants. The March–April period of water deficit illustrated in Figure 2 is an interval when much of the forest canopy is leafless (Carrington & Ross 1991). The Keys are included in Holdridge's (1967) Tropical Dry Forest Life Zone and Walter's (1985) Zonobiome II (tropical with summer rain). Homoclines of the Keys occur in Cuba, Bahamas, Yucatan Peninsula, and the north coast of Jamaica (Walter 1975, Kapos 1986).

The highest elevation in the Keys is 5.5 m above sea level, but most of the land area is below 2 m. The islands are comprised of two types of Pleistocene-aged limestone of marine origin: Miami and Key Largo Limestones (Hoffmeister & Multer 1968). The Keys were part of the Florida peninsula until approximately 4000 years BP, when rising sea level began to inundate low lying areas between the present islands (Lidz & Shinn 1991). Key Largo Limestone, a rock comprised of fossil coral reef materials, forms the surface rock substrate in the Upper, Middle, and southeasternmost Lower Keys. The Miami Limestone which covers the remainder of the Lower Keys is formed of poorly cemented carbonate grains (ooids), and is underlain by Key Largo Limestone (Hoffmeister *et al.* 1967). Both rock types are highly porous, but the Miami Limestone has low permeability; whereas, Key Largo Limestone is considered very permeable (Hanson 1980).

The contrasting geology of the Keys is also expressed in their geography. The ancient reefs that formed the Upper and Middle Keys were oriented end-to-end along a southwest-trending arc, while the depositional environment of Miami Limestone resulted in the Lower Keys being oriented parallel to each other and perpendicular to the Upper Keys (Hoffmeister *et al.* 1967). Furthermore, the wide tidal passes that separate the Middle Keys contrast with the narrow Upper and Lower Keys channels.

Most of the Keys have ground water fresher than the surrounding sea water. Ground water salinity is determined by the island's permeability, size, shape, and ground water recharge rate (Vacher 1978). These factors result in brackish ground water in most islands, with only the largest of the Lower Keys having nearly fresh ground water. The elevation of the water table is affected by the semidiurnal tide cycle (amplitude usually less than 1.25 m) that occurs in most nearshore waters, with an increasing attenuation in the tidal signal toward the center of the island. In general, mean ground water level is slightly higher than mean sea level, but because this difference is usually 30 cm or less, the elevation of the ground is a useful approximation of the distance to the water table.

A soil survey conducted in 1987 by the U.S. Department of Agriculture and Soil Conservation Service categorized Florida Keys soils into 17 series (USDA 1988). Soils generally lack strong horizonation and are most simply combined into four categories on the basis of their dominant constituent: rocky soils, organic soils, fine mineral soils (calcareous muds), and coarse mineral soils (carbonate sands). Upland organic soils and muds are generally thin (<20 cm), but sands and wetland peats are often quite deep. Sand deposits are most extensive along shorelines facing the Straits of Florida.

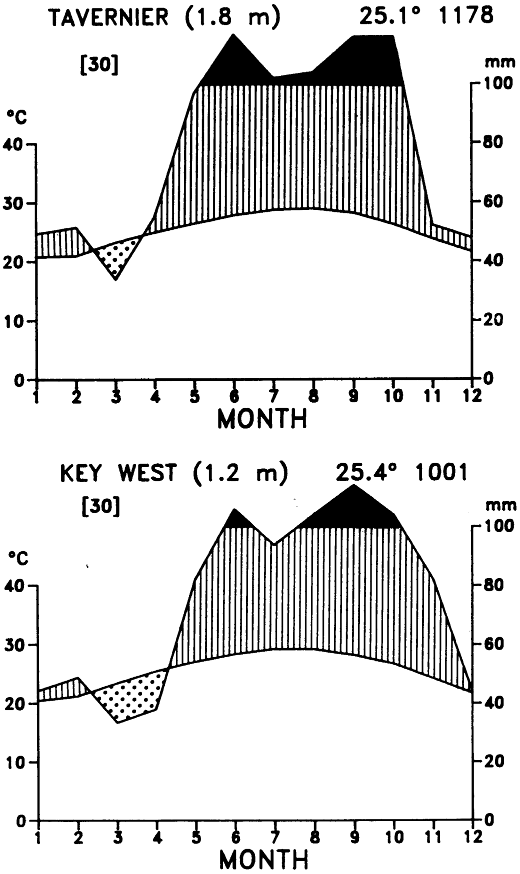


FIGURE 2. Climate diagram (after Walter 1985) for Tavernier (Upper Keys) and Key West (Lower Keys), based on monthly means for period 1951–1980. The stippled areas represent dry conditions, the vertical bars represent humid conditions, and the black areas represent perhumid conditions.

VEGETATIVE CHARACTERISTICS.—25 islands were chosen for study, covering a 177 km stretch from North Key Largo, 35 km southwest of Soldier Key, to Sugarloaf Key, 24 km east of Key West (Fig. 1). Within each island, sites were selected to represent the variation in plant community structure apparent on 1:24,000 aerial photographs. Vegetation surveys were conducted in 113 locations during the periods of December 1988–June 1989, and December 1989–February 1990. Field observations and older aerial photos indicated that these sites had undergone no stand-replacing disturbance during the last 50 years, though many had been affected by noncatastrophic storms, surface fires, or removal of individual trees.

In each of the sampled communities, a plotless technique was used to assess tree abundance, while fixed quadrats were used for smaller individuals. Four sampling locations were randomly chosen at least 30 m apart. From these points, sample trees were determined using a 10-factor prism (English units) for trees greater than 7.6 cm DBH and a 5-factor prism for trees 2.5–7.6 cm in diameter. Species, bole diameter, crown diameter, and height were determined for each sample tree. These data were used to estimate tree density, basal area, and crown cover on a species basis (Dilworth 1975). Cover estimates for smaller stems were made in 5 × 5 m quadrats centered on each prism sampling point. Species canopy cover was estimated separately in four height strata: 0–30 cm, 30–100 cm, 1–2 m, and >2 m. Total species cover was the sum of understory and overstory estimates. Taxonomic nomenclature followed Long and Lakela (1978).

The annual production of fine litter was estimated in 21 forested sites among the 113 sample locations. Production estimates were based on the accumulation of leaves, small twigs (<1 cm diameter), and reproductive parts in three 1 × 1 meter litter traps set 0.5 meters above the ground. A stratified random process was used to select trap locations within the area circumscribed by the vegetation subplots. Accumulated material was collected at two month intervals over the period December 1989–November 1991, dried at 65°C for 48 hr, and weighed.

PHYSICAL CHARACTERISTICS OF THE SITES.—In order to examine the physical setting underlying Florida Keys vegetation patterns, we made observations on edaphic, topographic, and hydrologic characteristics of a number of the sample locations.

Soil depth and type were examined in each of the 113 sites. In each plot, we sampled 4 points 1 m from the plot center, and at cardinal directions from it. A 1 cm diameter probe was used to measure the thickness of organic, coarse-textured mineral, and fine-textured mineral soil layers, if present.

We estimated surface elevation in 62 of the sample sites. Of these 62 estimates, 48 were based on topographic surveys that were initiated from a National Ocean Survey (NOS) vertical control benchmark. In 14 locations with no nearby benchmark, we surveyed from the landward edge of the red mangrove fringe. The datum used was 47 cm above sea level, the average for this zone in surveys from NOS benchmarks.

Hydrologic information was gathered in 27 locations which covered a wide range of site conditions on two Upper and two Lower Keys islands. Between April and October 1989, 5 cm diameter wells were drilled into the limestone bedrock at each of these locations. The wells extended to at least 30 cm below mean sea level. The wells were cased belowground with well screening, and sealed from surface water by solid PVC casing cemented to the rock. Beginning in mid-October 1989 and continuing through early October of the following year, the salinity of water at the surface of the water table, as well as the location of the water table relative to the ground surface were monitored at approximately two-week intervals. The salinity data were used to calculate an annual mean for each site. The water table observations gave us a good idea of the depth and frequency of inundation of various sites over the study period. These observations were supplemented by continuous water level recordings in eight wells and four nearby tidal stations.

We also determined a geographic parameter (GEO) for each sampling site, which was equal to the distance in km along the main axis of the Florida Keys from their northeastern terminus on Soldier Key. Our northeasternmost sample location in North Key Largo therefore had a GEO of 35, while our southwesternmost location on Lower Sugarloaf Key had a GEO of 186.

DATA INTERPRETATION.—Detrended correspondence analysis (DECORANA) (Hill 1979a) was applied to the species cover estimates. Species present in fewer than 3 sites were excluded from the analysis. In order to equalize the effect on the analyses of stands with different total cover, the remaining species values were relativized within each stand. Finally, an octave transformation was applied as a means of reducing the influence of dominant species. We then examined the distribution of site variables among stands arranged according to their ordination scores, and calculated linear correlations between ordination scores and structural parameters.

Two-way indicator species analysis (TWINSPAN), a hierarchical divisive classification method (Hill 1979b), was applied to the same data set as that described above. Pseudospecies cut levels of 0, 1, 3, 5, and 7 were chosen. Six levels of division were possible. However, we did not recognize divisions with eigenvalues less than 0.25, as well as subsequent divisions within the same branch. Furthermore, the procedure was truncated within a branch when group size reached five sites or less. Because the TWINSPAN analysis was intended to categorize common vegetation units in the Keys, subgroups representing fewer than three sites were ultimately reintegrated into the most similar larger compositional group.

The vegetation classification indicated by the TWINSPAN procedure was used as a guide in identifying Ecological Site Units which were relatively homogeneous on the basis of physical as well as vegetative characteristics. We examined the hydrologic, physiographic, and structural attributes of the sample sites assigned to each TWINSPAN unit for commonalities which would sharpen its description as an Ecological Site Unit, and express important functional relationships which distinguished it. The refining of unit definitions to include site factors sometimes required that sample plots with atypical site characteristics be reassigned to a group other than that indicated by the TWINSPAN procedure.

## RESULTS

VEGETATION/SITE RELATIONSHIPS.—Axes 1, 2, and 3 of the DECORANA ordination had eigenvalues

TABLE 1. *Coefficients of correlation (r) of 5 site factors with site scores on first three DECORANA axes. Significance levels: *, α = .01; **, α = .001.*

| Site factor | *N* | DECORANA | | |
|---|---|---|---|---|
| | | Axis 1 | Axis 2 | Axis 3 |
| Ground water salinity | 27 | .66** | −.33 | −.25 |
| Surface elevation | 62 | −.70** | −.28 | −.40** |
| GEO[a] | 113 | .07 | −.43** | .06 |
| Organic soil depth | 113 | .24* | −.06 | .33** |
| Mineral soil depth | 113 | .07 | .03 | −.24* |

[a] Km from northeastern terminus of Florida Keys at Soldier Key, along main axis of islands.

of 0.79, 0.40, and 0.29, respectively. Axis 1 scores were negatively correlated with elevation, but positively correlated with salinity and organic soil depth (Table 1). Axis 1 therefore separated plant communities along a topographic gradient extending from island interior to island edge. Because ground water in interior locations tended to be fresher and soils shallower than near the shoreline, Axis 1 also represented a secondary gradient in ground water salinity and soil depth. Finally, the frequency distribution of Axis 1 scores was characterized by peaks at high and low scores, separated by a relative absence of intermediate values. This pattern is illustrative of a sharp contrast in vegetation composition between high interior and lower coastal locations.

Axis 2 exhibited a negative association with GEO, but was uncorrelated with other site factors (Table 1). Thus, Axis 2 scores were generally higher in the Lower Keys than in the Upper Keys. The relationship between GEO and Axis 2 was slightly stronger when sites with Axis 1 scores less than 300 (*i.e.*, upland locations) were considered separately ($r = -0.47$; $P < .001$). Elevation and salinity, which changed in opposite directions within individual islands and along Axis 1, changed in the same direction along Axis 2. This pattern resulted from the contrasting geology and geomorphology of Upper and Lower Keys islands. Because of the more permeable nature of their geologic substrate, high Upper Keys islands tended to have higher salinities than less elevated Lower Keys islands. The covariance among site factors such as elevation, salinity, and various climatic variables along Axis 2 prevented us from ascribing to any single factor the "geographic" effect encompassed in Axis 2.

Site scores for Axis 3 exhibited a strong positive association with organic soil thickness, but were negatively correlated with elevation and mineral soil thickness (Table 1). However, Axis 3 did not appear to represent a strong or general environmental gradient. Instead, it was rather specific in separating relatively restricted marsh assemblages, *i.e.*, those occupying depressions in island interiors and those inhabiting slightly raised muds near the edge of some islands and peninsulas.

Vegetation classification.—The initial TWINSPAN division separated the 113 sample sites into a group of tidal wetlands and a second group including upland forests and interior wetlands (Fig. 3). At Level 2, the classification program separated a small group of marshes dominated by *Spartina spartinae* from other tidal wetlands. It also distinguished a group of broad-leaved forests of relatively large stature from a structurally heterogeneous array of pine forests, low broad-leaved forests, and interior wetlands. Differentiation among groups distinguished at these upper levels of the classification was quite strong, as indicated by high eigenvalues (Level 1 division = 0.74; mean of Level 2 divisions = 0.46).

Representation in the group of *Spartina* marshes was too small for further division, but the other three Level 2 assemblages were divided at the next two levels, yielding five major groups of upland forests, two types of interior wetlands, and four intratidal and supratidal compositional units after Level 4 (Fig. 3). Groupings identified at Levels 3 and 4 were still relatively distinct, with eigenvalues ranging from 0.27 to 0.50.

Beyond Level 4, TWINSPAN divisions of upland forest and interior wetland assemblages re-

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FIGURE 3. TWINSPAN vegetation classification, from species abundances in 113 Florida Keys locations. Ecological Site Units derived from TWINSPAN categories are indicated at bottom.

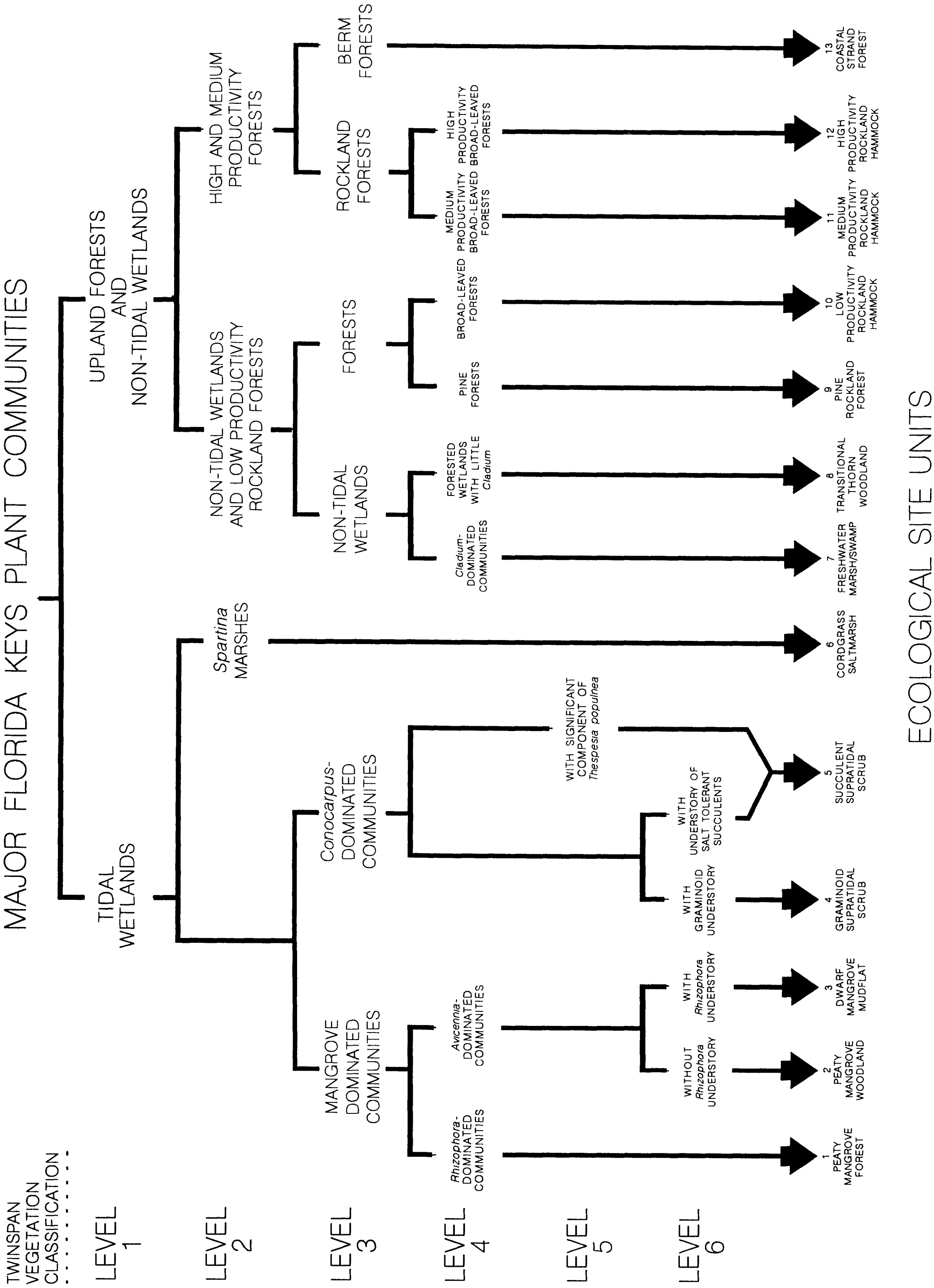
MAJOR FLORIDA KEYS PLANT COMMUNITIES
TWINSPAN VEGETATION CLASSIFICATION
LEVEL 1
LEVEL 2
LEVEL 3
LEVEL 4
LEVEL 5
LEVEL 6
TIDAL WETLANDS
UPLAND FORESTS AND NON-TIDAL WETLANDS
MANGROVE DOMINATED COMMUNITIES
*Conocarpus*-DOMINATED COMMUNITIES
*Spartina* MARSHES
NON-TIDAL WETLANDS AND LOW PRODUCTIVITY ROCKLAND FORESTS
HIGH AND MEDIUM PRODUCTIVITY FORESTS
NON-TIDAL WETLANDS
FORESTS
ROCKLAND FORESTS
BERM FORESTS
*Rhizophora*-DOMINATED COMMUNITIES
*Avicennia*-DOMINATED COMMUNITIES
WITH SIGNIFICANT COMPONENT OF *Thespesia populnea*
*Cladium*-DOMINATED COMMUNITIES
FORESTED WETLANDS WITH LITTLE *Cladium*
PINE FORESTS
BROAD-LEAVED FORESTS
MEDIUM PRODUCTIVITY BROAD-LEAVED FORESTS
HIGH PRODUCTIVITY BROAD-LEAVED FORESTS
WITHOUT *Rhizophora* UNDERSTORY
WITH *Rhizophora* UNDERSTORY
WITH GRAMINOID UNDERSTORY
WITH UNDERSTORY OF SALT TOLERANT SUCCULENTS
1 PEATY MANGROVE FOREST
2 PEATY MANGROVE WOODLAND
3 DWARF MANGROVE MUDFLAT
4 GRAMINOID SUPRATIDAL SCRUB
5 SUCCULENT SUPRATIDAL SCRUB
6 CORDGRASS SALTMARSH
7 FRESHWATER MARSH/SWAMP
8 TRANSITIONAL THORN WOODLAND
9 PINE ROCKLAND FOREST
10 LOW PRODUCTIVITY ROCKLAND HAMMOCK
11 MEDIUM PRODUCTIVITY ROCKLAND HAMMOCK
12 HIGH PRODUCTIVITY ROCKLAND HAMMOCK
13 COASTAL STRAND FOREST
ECOLOGICAL SITE UNITS

TABLE 2. *Physical characteristics of the 13 Ecological Site Units.*

| ESU | Elevation (cm) *N* | Elevation (cm) $\bar{x}$ | Elevation (cm) Range | Mean annual ground water salinity (‰) *N* | Mean annual ground water salinity (‰) $\bar{x}$ | Mean annual ground water salinity (‰) Range | Soil depth (cm) *N* | Soil depth (cm) $\bar{x}$ | Soil depth (cm) Range | Major soil material[a] | Location[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 3 | 34 | 9–47 | 2 | 34 | 33–35 | 4 | >120 | 22–200+ | O | U, M, L |
| 2 | 4 | 34 | 16–54 | 2 | 38 | 32–44 | 5 | >100 | 22–200+ | O | U, M, L |
| 3 | 2 | 22 | 17–28 | 2 | 28 | 24–33 | 3 | 20 | 11–30 | FM | U, M, L |
| 4 | 3 | 65 | 60–72 | 1 | 34 | — | 8 | 5 | 1–16 | FM | L |
| 5 | 9 | 59 | 30–94 | 3 | 20 | 17–22 | 13 | 5 | 0–23 | FM | U, M |
| 6 | 4 | 97 | 61–119 | 0 | — | — | 4 | 45 | 20–100 | FM | M, L |
| 7 | 3 | 43 | 31–50 | 3 | 6 | 2–16 | 7 | >40 | 1–200+ | FM, O | U, M, L |
| 8 | 8 | 70 | 51–91 | 3 | 14 | 11–19 | 10 | 6 | 0–13 | O | U, M, L |
| 9 | 3 | 84 | 67–113 | 3 | 6 | 2–11 | 6 | 4 | 1–10 | O | L |
| 10 | 2 | 102 | 73–132 | 2 | 8 | 3–14 | 12 | 11 | 2–35 | O | L |
| 11 | 12 | 114 | 71–200 | 2 | 10 | 5–15 | 21 | 8 | 4–15 | O | U, M, L |
| 12 | 7 | 245 | 132–328 | 3 | 19 | 17–23 | 11 | 10 | 4–16 | O | U |
| 13 | 2 | 160 | 132–187 | 0 | — | — | 8 | >60 | >60 | CM | U, M, L |

[a] O = organic; FM = fine mineral; CM = coarse mineral.
[b] U = Upper Keys; M = Middle Keys; L = Lower Keys.

sulted in subdivisions which were insufficiently well-represented or well-defined to meet the criteria that had been established. Further divisions of tidal wetland groupings did meet those requirements, however, yielding an additional three units at Levels 5 and 6. Thus, the classification procedure ultimately identified 14 major compositional units (Fig. 3).

Relationship between ecological site classification and vegetation classification.—Of the 14 compositional units outlined in Figure 3, only one was not considered to represent a distinct physical setting. That unit appeared to occupy the same sites as other supratidal *Conocarpus erecta* communities with succulent understories, and was distinguished from them primarily by an abundance of the exotic *Thespesia populnea.* The two groups were consequently combined. The remaining 13 vegetation categories formed the basis for an equal number of Ecological Site Units (ESUs) identified in Figure 3. Inclusion of site features in the definitions of ESUs (Appendix 1) necessitated reassignment of 18 of the 113 sample plots to groupings other than those indicated by vegetation alone. The physical characteristics, species composition, vegetation structure and productivity of these Ecological Site Units are detailed in Tables 2, 3, and 4, and described in the next section.

Ecological Site Units.—ESUs 1 and 2, Peaty Mangrove Forest and Peaty Mangrove Woodland, are characterized by organic soils which are nearly always saturated with high-salinity water. Unit 1 is dominated by red mangrove, with admixtures of black and white mangrove. The forest canopy is high (7–12 m) and closed, and litter production is very high. Unit 1 communities are usually found in intertidal locations along island peripheries, but sometimes occupy depressions in interior locations. In such positions, the otherwise sparse forest understory may include vines, epiphytes, or ferns of the genus *Acrostichum.* In comparison to the tall Unit 1 forests, the black mangrove-dominated canopies of Unit 2 are low (4–10 m), uneven, and relatively unproductive. Unit 2 understories range from open and parklike to a dense tangle of mangrove or saltwort (*Batis maritima*). Mangrove Woodlands are usually located landward of Unit 1 forests, where higher salinities or reducing conditions in the organic soils may influence stand structure or the relative abundance of the three mangrove species.

Sites classified as Dwarf Mangrove Mudflats (ESU 3) are found along low-energy shorelines or in shallow bedrock depressions in island interiors. Once these interior locations become inundated, they usually remain submerged for several months at a time. These are not peat-producing environments, but are favorable sites for the accumulation or production of calcareous muds, which range in depth from a few centimeters to 30 cm or more. Unit 3 is typically a community of low shrubs less than 2 m in height, gnarled individuals of the same species which reach heights of 6–15 m in Unit 1.

Sites classified as Supratidal Scrub (ESUs 4 and 5) are inundated by high tides at certain times of

TABLE 3. *Species composition of the 13 Ecological Site Units. Dominant species (mean cover > 10%) are listed in order of abundance.*

| ESU | Dominant species | Other characteristic species |
|---|---|---|
| 1 | *Rhizophora mangle* | *Avicennia germinans*<br>*Laguncularia racemosa* |
| 2 | *Avicennia germinans*<br>*Batis maritima*<br>*Rhizphora mangle* | |
| 3 | *Avicennia germinans*<br>*Salicornia virginica*<br>*Rhizphora mangle* | |
| 4 | *Sporobolus virginicus*<br>*Conocarpus erecta*<br>*Monanthochloe littoralis* | *Salicornia virginica*<br>*Avicennia germinans*<br>*Borrichia frutescens*<br>*Borrichia arborescens* |
| 5 | *Batis marttima*<br>*Sesuvium portulacastrum*<br>*Salicornia virginica*<br>*Conocarpus erecta*<br>*Laguncularia racemosa*<br>*Borrichia frutescens* | *Thespesia populnea*<br>*Suaeda linearis*<br>*Avicennia gemrinans*<br>*Philoxerus vermicularis* |
| 6 | *Spartina spartinae*<br>*Sporobolus virginicus* | *Borrichia frutescens* |
| 7 | *Cladium jamaicensis*<br>*Conocarpus erecta* | *Laguncularia racemosa*<br>*Aster tenuifolius*<br>*Fimbristylis castanea* |
| 8 | *Conocarpus erecta* | *Pithecellobium keyense*<br>*Manilkara bahamensis*<br>*Eugenia foetida*<br>*Metopium toxiferum*<br>*Jacquinia keyensis*<br>*Pisonia discolor*<br>*Bumelia celastrina* |
| 9 | *Thrinax microcarpa*<br>*Pinus elliottii*<br>*Metopium toxiferum*<br>*Coccothrinax argentata* | *Myrtus verrucosa*<br>*Pisonia rotundata*<br>*Serenoa repens*<br>*Myrsine guianensis* |
| 10 | *Eugenia foetida*<br>*Metopium toxiferum*<br>*Thrinax microcarpa*<br>*Eugenia axillaris* | *Byrsonima lucida*<br>*Ernodea littoralis*<br>*Manilkara bahamensis*<br>*Myrsine guianensis*<br>*Chiococca pinetorum*<br>*Randia aculeata* |
| 11 | *Eugenia foetida*<br>*Coccoloba diversifolia*<br>*Metopium toxiferum*<br>*Gymnanthes lucida*<br>*Bursera simaruba*<br>*Thrinax floridana* | *Krugiodendron ferreum*<br>*Reynosia septentrionalis*<br>*Pisonia discolor*<br>*Pithecellobium keyense*<br>*Bumelia celastrina*<br>*Capparis flexuosa*<br>*Randia aculeata* |
| 12 | *Coccoloba diversifolia*<br>*Gymnanthes lucida*<br>*Bursera simaruba*<br>*Krugiodendron ferreum*<br>*Eugenia axillaris*<br>*Piscidia piscipula* | *Mastichodendron foetidissimum*<br>*Amyris elemifera*<br>*Guettarda elliptica*<br>*Psychotria nervosa* |
| 13 | *Eugenia foetida*<br>*Bursera simaruba*<br>*Pithecellobium keyense* | *Pisonia discolor*<br>*Reynosia septentrionalis*<br>*Casasia clusiifolia*<br>*Metopium toxiferum*<br>*Rivina humilis* |

TABLE 3. *Continued.*

| ESU | Dominant species | Other characteristic species |
|---|---|---|
| | | *Hymenocallis latifolia*<br>*Lantana involucrata*<br>*Capparis flexuosa* |

the year, but are dry for much longer periods. Supratidal Scrub soils are usually rocky, without continuous soil cover, and buttonwood (*Conocarpus erecta*) is often the leading woody species. Vegetation structure is variable, ranging from shrub communities not very different in composition and structure from Dwarf Mangrove Mudflats to open woodlands up to 7 m in height. Units 4 and 5 are distinguished primarily on the basis of ground cover. Unit 4 sites are characterized by the presence of salt-tolerant graminoids (*Sprorobolus virginicus, Monanthochloe littoralis*), while twining, succulent shrubs and herbs (*e.g., Sesuvium portulacastrum, Batis maritima, Philoxerus vermicularis*) are important in the understory of Unit 5 sites. Litter production is very low in Succulent Scrub (ESU 5), which is most often found in narrow, rubbly bands immediately behind coastal mangroves in the Upper Keys. Graminoid Scrub (ESU 4) is more typical of extensive supratidal areas in the Lower Keys, with smooth-surfaced bedrock and shallow pockets of mineral soil.

ESU 6, Cordgrass Salt Marsh, is found in supratidal environments affected by only the highest nonstorm tides. Cordgrass (*Spartina spartinae*) forms a continuous sward, which appears quite resistant to invasion by woody plants. ESU 6 is characterized by deep (>30 cm), fine-textured mineral soils, with pore water salinities consistently above 20‰. Cordgrass Salt Marsh is relatively uncommon in the Keys. It is found in the center of a few mud islands in Florida Bay, along the axis of two Middle Keys peninsulas extending into the Gulf of Mexico, and in a narrow zone landward and upslope of the supratidal scrub zone on several of the Lower Keys.

ESU 7, Freshwater Marsh/Swamp, occurs most frequently in depressions in the interior of islands. Where the depressions are deep, they are filled by peat, but where they are shallow, soils may be little more than a thin layer of calcitic mud. In either case, fresh water is generally ponded during the wet season, and rarely far from the soil surface at any time of year. Although salinities may range as high as 20‰ in the dry season, ground water in ESU 7 sites remains the freshest on an island. Unit 7 is typically an open marsh characterized by an abundance of sedges, especially sawgrass (*Cladium jamaicensis*), but may take on the appearance of a low, swamp forest following invasion by a number of woody species. It is primarily a Lower Keys habitat, but is also present in narrow bands in several Upper Keys locations where the islands are unusually wide.

As the name implies, Transitional Thorn Woodland (ESU 8) shares elements of both uplands and wetlands. These sites include the most upslope locations to be inundated in the absence of a major tropical storm. Water may be ponded for a short time in Transitional Woodland sites when high tides and periods of heavy rain coincide, particularly during the late summer. A recognizable feature of this Unit at any time of year are the very shallow soils, without significant accumulations of organic matter. The Unit 8 forest is low (3–7 m) and well-lit, with multi-stemmed and thorny plants which make passage difficult. Litter production is low in comparison to Units further upslope. Buttonwood remains an important component of the canopy, but is mixed with upland species like *Eugenia foetida, Metopium toxiferum,* and *Pisonia discolor. Bumelia celastrina, Manilkara bahamensis,* and *Jacquinia keyensis* are other characteristic species not present in all stands.

Upland locations which are only flooded during major storm events comprise Site Units 9–13. ESU 13 (Coastal Strand Forest) is primarily an edaphically defined category. These forests, which feature deep, coarse-grained mineral soil and woody plant species with upland forest affinities, are not extensive in the Keys. They usually consist of narrow (5–20 m wide) bands adjacent to a Straits of Florida-side shoreline, or immediately landward of a paralic Mangrove Forest. Coastal berms in the Florida Keys range in elevation up to about 3 m. As a group, the species composition of Coastal Strand Forests is far from uniform, and their most common tree species not very different from those of other upland Site Units. Coastal Strand communities are characterized by a relative abundance of shrubs and herbaceous plants (*e.g., Rivina humilis, Hymenocallis latifolia, Lantana involucrata, Capparis flexuosa*) well adapted to the high light and exposed mineral soil conditions.

TABLE 4. *Structural and fine litter production in 13 Ecological Site Units.*

| | | Basal area (m²/ha) | | | Canopy height[a] (m) | | | Fine litter production (g/m²/yr) | |
|---|---|---|---|---|---|---|---|---|---|
| ESU | *N* | $\bar{x}$ | Range | *N* | $\bar{x}$ | Range | *N* | $\bar{x}$ | Range |
| 1 | 4 | 22.8 | 16–30 | 4 | 9.5 | 7–12 | 2 | 913 | 588-1237 |
| 2 | 5 | 12.8 | 5–22 | 5 | 6.4 | 4–10 | 2 | 300 | 212–388 |
| 3 | 3 | 0 | — | 3 | 1 | 1–1 | 0 | — | — |
| 4 | 8 | 1.5 | 0–9 | 8 | 2.1 | 1–4 | 0 | — | — |
| 5 | 13 | 6.5 | 0–18 | 13 | 4.2 | 1–6 | 3 | 261 | 176–376 |
| 6 | 4 | 0 | — | 4 | 1 | 1–1 | 0 | — | — |
| 7 | 7 | 0.7 | 0–3 | 7 | 2.1 | 1–4 | 0 | — | — |
| 8 | 11 | 6.6 | 2–20 | 11 | 4.1 | 2–6 | 3 | 387 | 307–469 |
| 9 | 6 | 18.3 | 12–23 | 6 | 10.7 | 9–13 | 3 | 361 | 281–409 |
| 10 | 12 | 21.8 | 15–28 | 12 | 5.8 | 4–8 | 2 | 472 | 460–485 |
| 11 | 21 | 26.9 | 15–37 | 21 | 7.1 | 6–10 | 3 | 557 | 452–693 |
| 12 | 11 | 32.1 | 24–39 | 11 | 9.4 | 6–10 | 3 | 610 | 603–620 |
| 13 | 8 | 18.2 | 8–26 | 8 | 6.1 | 4–10 | 0 | — | — |

[a] For stands with more than 200 trees/ha, the ninetieth percentile of tree heights; for stands with fewer trees, the height of the 20th tallest tree/ha.

Unlike Coastal Strand Forests, the soils of the other four upland Site Units are shallow and organic-rich. There is also considerable inter-group overlap in physical characteristics such as elevation and ground water salinity. The rockland forests represented by these four Site Units have different geographic distributions, with Units 9 and 10 restricted to Lower Keys locations, Unit 12 restricted to the Upper Keys, and Unit 11 found throughout the islands.

Pine Rockland Forest (ESU 9) is found in medium elevation (70–130 cm) environments in the interior of several of the Lower Keys large enough to support a significant fresh water lens. Although mature slash pine (*Pinus elliottii* var *densa*) stems are clearly able to survive at a mean annual ground water salinity of 11‰, salinity in the most extensive Pine Rocklands is 2–3‰. The slash pine canopies characterizing these forests are relatively high (7–13 m) and open, but understory composition and soil characteristics depend on fire history. Pine Rockland understories that have burned regularly are rich in shrubs, grasses, and herbs, and soil is found in pockets among the outcropping limestone. In the absence of fire, a dense subcanopy of broad-leaved trees forms within 3–5 decades. Few herbaceous plants are present, and soils may include a foot or more of organic material. Litter production in Pine Rockland Forests is low in comparison to other Rockland sites.

Based on canopy height, ESUs 10–12 represent a clear sequence of increasing forest stature (Table 4). Because the sampled stands were all beyond the age at which Florida Keys hammocks cease to increase in height (Carrington & Ross 1991), the relative heights of these three compositionally defined Site Units may also reflect differences in site potential. This view is further supported by the litterfall data in Table 4. Ecological Site Units 10, 11, and 12 are therefore designated Low, Medium, and High Productivity Rockland Hammocks, respectively.

ESU 10 (Low Productivity Rockland Hammock) overlaps broadly in elevation and ground water salinity with Pine Rockland Forest. When the two are found together, hammock is generally located seaward of pineland, and in areas of slightly higher salinity. ESU 10 forests are typically dense and short in stature (4–7 m), with an abundance of low-branching stems. Like Pine Rockland, Low Productivity Rockland Hammock is today restricted to the area west of GEO 155. Characteristic species include *Byrsonima lucida, Ernodea littoralis, Myrsine guianensis,* and *Myrtus verrucosa.*

Sites included in ESU 11 (Medium Productivity Rockland Hammock) typically have a higher canopy (6–9 m) and more open understory than Unit 10 hammocks. Like their Unit 10 counterparts, however, Medium Productivity Hammocks occupy mid-elevational (70–200 cm) locations of low-to-intermediate ground water salinity. *Gymnanthes lucida, Thrinax floridana,* and *Krugiodendron ferreum* are among the species which distinguish ESU 11 from ESU 10.

High Productivity Rockland Hammock (ESU 12) is found in Upper Keys locations at elevations above 150 cm. Mean annual ground water salinity is high (17–23‰) in comparison to other upland forests. High Productivity Hammocks are relatively tall (6–10 m) forests with open understories. *Mastichodendron foetidissimum, Amyris elemifera, Guettarda elliptica,* and *Psychotria nervosa* are characteristic ESU 12 species.

Figure 4 depicts the distribution of many of the Ecological Site Units described above on one Upper and one Lower Keys island. Most notable is the fine scale of topographic difference which elicits major changes in plant community structure and composition, especially at low elevations. Comparison of the two profiles illustrates the contrast in topographic relief and ground water salinity between Upper and Lower Keys, as well as the associated difference in the habitat mosaic.

Species diversity.—Plant species richness and diversity (H′) generally increased along an elevational gradient from simple intertidal communities along island peripheries, through supratidal communities fronting on the mangroves, and finally culminating in upland forest communities (Table 5). However, the most species-rich communities were Pine Rocklands, not the High Productivity Rockland Hammocks occupying the highest elevations (though those sites generally contained the most tree species). Among Pine Rocklands, the richest were those lacking the continuous broad-leaved subcanopy characteristic of stands not recently burned. Given the overall elevational trend, the open Transitional Thorn Woodland was also a surprisingly rich community.

TABLE 5. *Plant species diversity in 13 Ecological Site Units.*

| ESU | *N* | Species number (per site) | Species diversity[a] |
|---|---|---|---|
| 1 | 4 | 5.3 | 0.61 |
| 2 | 5 | 5.0 | 0.88 |
| 3 | 3 | 5.3 | 0.73 |
| 4 | 8 | 13.1 | 1.50 |
| 5 | 13 | 15.1 | 1.76 |
| 6 | 4 | 14.3 | 1.25 |
| 7 | 7 | 16.4 | 1.10 |
| 8 | 11 | 28.9 | 2.20 |
| 9 | 6 | 34.7 | 2.33 |
| 10 | 12 | 28.6 | 2.24 |
| 11 | 21 | 24.4 | 2.20 |
| 12 | 11 | 23.2 | 2.33 |
| 13 | 8 | 22.6 | 2.15 |

[a] Shannon-Wiener $H^1$: $(-\Sigma p_i \ln p_i)$.

## DISCUSSION

The vegetation ordination described above indicated that Florida Keys terrestrial plant species assemblages are arranged along two major gradients. The first is the local gradient encountered moving inland and upslope from an island periphery. The second is the complex geographic gradient encountered moving south and west, away from the Florida mainland along the arcuate Keys archipelago. The local zonation within low limestone islands has previously been described for the Sand Keys by Davis (1942), and for Bimini by Howard (1950). Our primary contribution in this regard is to define and describe site units along this gradient, as well as to quantify the small elevational scale across which major changes in vegetation are visible. The geographic gradient in the Florida Keys, on the other hand, has received little attention in the scientific literature, although naturalists working in the area have long been familiar with it.

The vegetation analysis illustrated in Figure 3 further suggests that at a basic level, Florida Keys plant communities are of two very distinct compositional types: assemblages of species adapted to frequent tidal inundation, and groups rarely confronted with such conditions. Whereas elevation and ground water salinity are the strongest environmental correlates with vegetation over all terrestrial habitats, other factors may influence patterning within each of the categories mentioned above. Working in the second of these categories, nontidal upland and transitional communities in the Lower Keys, we recently used stable isotope analysis to identify the source of water used by plants (Sternberg *et al.* 1991, Ish-Shalom *et al.*, in press). During nondrought periods, plants only a few decimeters above the ground water table utilized soil water almost exclusively, and responded physiologically to seasonal changes in soil moisture and salt content. These results indicate that the droughty or skeletal organic soils of uplands and transitional environments (ESUs 8–13) (Table 2) represent a very limited and precious storage capacity for water and nutrients to fuel plant processes. In a climate of high evaporative stress, characteristic of the Florida Keys (Fig. 2), it is not unreasonable to expect species affinities to be patterned along a gradient of available soil volume. By the same token, one might expect plant communities with limited moisture storage capacity to arrange themselves along even the modest climatic gradient illustrated in Figure 2.

The within- and between-island vegetation gradients described in the preceding pages are expressed not only in terms of species composition, but also with respect to community structure and fine litter

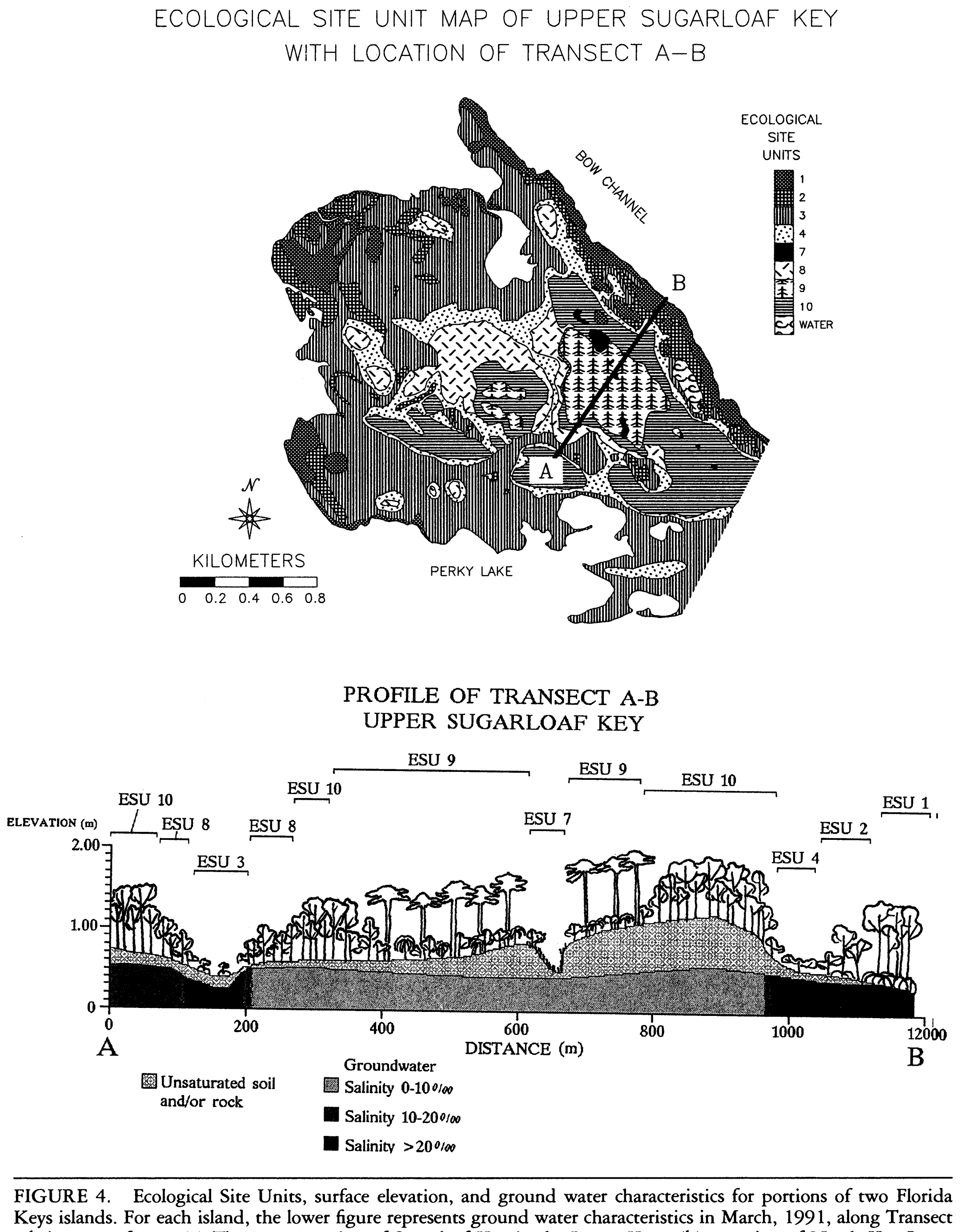


FIGURE 4. Ecological Site Units, surface elevation, and ground water characteristics for portions of two Florida Keys islands. For each island, the lower figure represents ground water characteristics in March, 1991, along Transect a-b in upper figure. (a) The upper portion of Sugarloaf Key in the Lower Keys; (b) a section of North Key Largo in the Upper Keys.

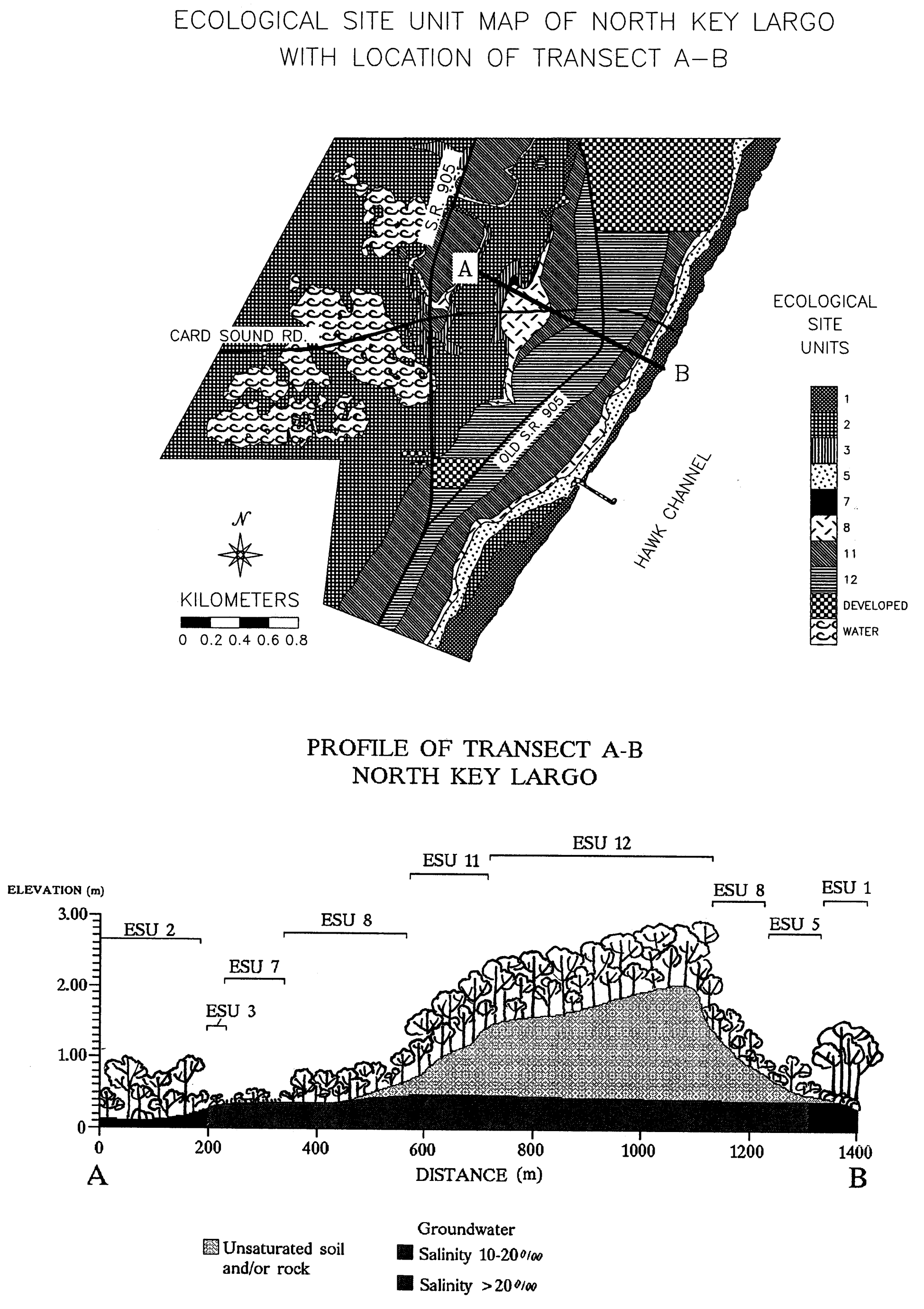


FIGURE 4. *Continued.*

production. Within islands, a pattern of increasing size and productivity both inland and seaward of a minimum located landward of the coastal mangrove fringe is illustrated by comparing ESUs 1, 2–6, and 8–12 in Table 4 and Figure 4. Between islands, an increase in forest stature and litter production from Lower to Upper Keys upland forests is best illustrated by comparing ESUs 10 and 12. In our view, these patterns are generally consistent with a model invoking available rooting substrate, the climatic water balance, and their interactions as the primary determinants for plant community structure.

Elaboration of this simple model should include some consideration of the quality of the substrate available to plant roots. For instance, elevated salinities in interstitial soil waters may create as inhospitable a growth medium for certain upland or wetland plant species as the limestone bedrock beneath. A recent examination of upland soils on six Florida Keys islands indicated that soil salinities may decrease dramatically with a small rise in elevation (C. L. Coultas, pers. comm.). Because of the concentration of aerosol salts in this coastal area, as well as the tendency for ground water and soil water to be decoupled, the dynamics of soil salinity are not well understood, but may have important effects on vegetation processes.

Finally, the interactions of disturbance, soil characteristics, and climate must be noted. The Lower Keys have a history of frequent fires which is at least in part responsible for their pine forests (Alexander & Dickson 1972, Snyder *et al.* 1990). In the wake of these fires, Pine Rockland Forests gradually develop a deeper and more continuous soil layer, and then either reburn or succeed to more productive broad-leaved forest types (ESUs 10 or 11) (Alexander 1967, Loope & Dunevitz 1981, Carlson 1989). Like fire, hurricanes are also a climatic fact of life in the Keys, and their winds have a great short-term impact on vegetation structure. When accompanied by a large storm surge, however, their most significant ecological effect may be the salinization of upland soils.

The objectives of our classification were to organize the remaining undeveloped areas of the Florida Keys into units that were easily recognized in the field, but also reflected the underlying environmental variables that controlled their distribution. It is therefore a site classification, which incorporates not only vegetation features, but also their hydrologic and edaphic underpinnings. Other environmental factors such as local climate and long-term disturbance history may affect vegetation structure, but are not easily assessed in the field. The site features that are explicit in the classification will be of particular value in mapping devegetated areas, or in projecting the effects of various sea level rise scenarios on the vegetation of the Keys.

## ACKNOWLEDGMENTS

This study was supported by grants from the John D. and Catherine T. MacArthur Foundation and The Nature Conservancy. We are grateful to Mary Carrington for field assistance, and Ann Williams for her taxonomic expertise and knowledge of Lower Keys plant communities. We thank two anonymous reviewers for constructive comments which helped the manuscript. We finally thank personnel of the Key Deer National Wildlife Refuge, Long Key and Bahia Honda State Recreation Areas, Key Largo Hammocks and Lignumvitae Key State Botanical Sites, and Everglades National Park, especially Debra Holle, Pat Wells, and Jeanne Parks.

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