Plant and Soil **253:** 479–492, 2003.

Soil-productivity relationships and organic matter turnover in dry tropical forests of the Florida Keys

M.S. Ross[1,4], C.L. Coultas[2] & Y.P. Hsieh[3]
[1]*Associate Research Scientist, Florida International University, Miami, FL, USA.* [2]*Professor, Florida A & M University, Tallahassee, FL, USA, retired.* [3]*Professor, Florida A & M University, Tallahassee, FL, USA.* [4]*Corresponding author**

Received 14 June 2002. Accepted in revised form 30 January 2003

Key words: aboveground production, Carbonate islands, Histosols, limestone bedrock, nutrient cycling, tropical hardwood hammocks

Abstract

Soils and aboveground production in five types of upland forest in the Florida Keys were examined. Throughout the habitat gradient represented by these forest types, the soils were predominantly shallow and organic, forming in place directly on the limestone bedrock. However, the well-drained soils in the most productive broadleaved forests were deep enough to qualify as Histosols (Folists). Soils decreased in electrical conductivity and increased in nutrient content with increasing aboveground production. At 3–12 Mg ha^{-1} yr^{-1}, production was within the range reported for dry tropical forests. Measured rates of decomposition were moderate or fast, and estimates of the organic C turnover of several soils based on their bomb radiocarbon signature were 100 years or less. In the face of these rapid turnover rates, we attribute the development of organic soils to the absence of mineral residues from weathering of the underlying limestone bedrock. Fast turnover of organic matter, and rapid and efficient cycling of nutrients are necessary to sustain the high production rates obtained on these shallow organic soils.

Introduction

Among the remarkable aspects of Florida Keys terrestrial ecosystems are the variety and stature of the forest communities that may be supported on very thin soils. A soil survey conducted in 1987 by the Soil Conservation Service of the Department of Agriculture categorized soils of Florida Keys into 17 series (USDA, 1995). Several of these soil series occurred in upland settings, i.e., sites that typically do not flood except during major storm events. The most common were Pennekamp silt loam (8 cm of black muck over l2 cm of dark gray marl over limestone), Matecumbe muck (15 cm of black muck over limestone), Saddlebunch silt (13 cm of grayish-brown marl over 30 cm of light gray marl over limestone), and Keyvaca silt loam (10 cm of dark brown gravelly marl over limestone). Florida Keys upland soils can also be divided into four categories on the basis of their dominant constituent, i.e., rocky soils, organic soils, fine mineral soils (marls), and coarse mineral soils (carbonitic sands). With few exceptions, these soils are <20 cm in depth and lack strong horizonation. The plant communities that occupy them include open slash pine (*Pinus elliottii* var *densa*) forests or denser forests comprised primarily of broadleaved tree species of West Indian origin. The latter are known locally as tropical hardwood hammocks. Among the thirteen Ecological Site Units defined by Ross et al. (1992), the upland or transitional units exhibited a broad range in structural characteristics, e.g., in basal area (20–40 m^2 ha^{-1}) and canopy height (6–13 m). The authors attributed this variation in part to differences in soil characteristics. In this paper, we explore further the relationships between these diverse tropical forests and the properties of their thin soils, especially the carbon (C) and nutrient cycles by which the plant communities are sustained.

* FAX No: 305-348-4096. E-mail: rossm@fiu.edu

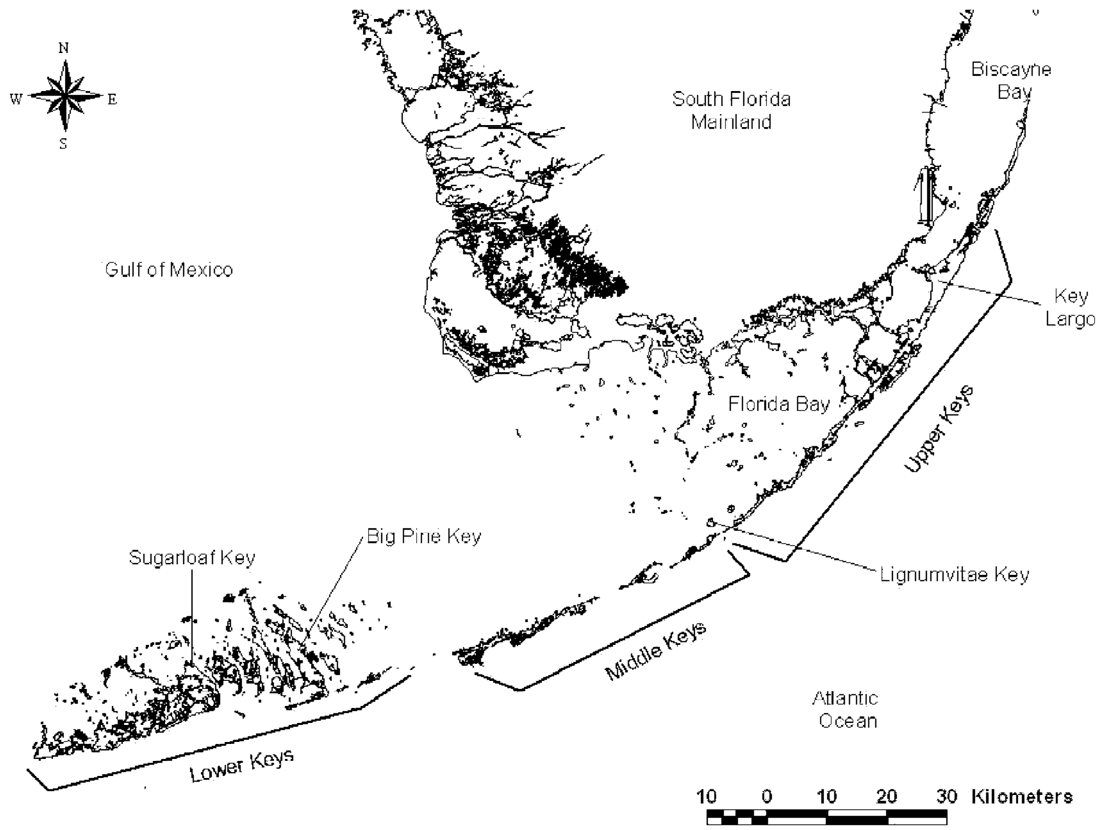

Figure 1. Location of study sites in the Florida Keys.

Materials and methods

Study area

The Florida Keys are a 210 km chain of islands running southwest from Soldier Key (25° 36′ N, 80° 10′ W) to Key West (24° 33′ N, 81° 49′ W) (Figure 1). The islands may be grouped into Upper, Middle and Lower Keys, which differ in climatic, geologic and geographic features. Despite their position several degrees north of the Tropic of Cancer, the Keys are characterized by a tropical climate. Mean annual temperature exceeds 25 °C, with no recorded freeze events throughout most of the area. However, brief periods of freezing temperatures have occurred in the northernmost islands closest to the Florida mainland. Rainfall is seasonal throughout the Keys, with two-thirds occurring during the months June–October. Conditions become progressively drier and warmer with increasing distance from the mainland. For instance, mean annual rainfall and temperature are 1.8 m and 25.1 °C at Tavernier in the Upper Keys and 1.2 m and 25.4 °C at Key West in the Lower Keys (Ross et al., 1992). The climate of the Keys closely resembles that of Cuba, the Bahamas, the Yucatan Peninsula and the north coast of Jamaica (Kapos, 1986; Walter, 1985).

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 and Shinn, 1991). Today the highest elevation (at Windley Key in the Upper Keys) is only 5.5 m above sea level, while most of the land area is below 2 m. Bedrock consists of two types of Pleistocene-aged limestone of marine origin (Hoffmeister and Multer, 1968). The Key Largo limestone, developed around a fossil coral reef skeleton, forms the surface rock substrate in the Upper, Middle and southeasternmost Lower Keys. The Miami limestone surfaces throughout the remainder of the Lower Keys. It is formed of poorly cemented carbonate grains (ooids), and is underlain by Key Largo Limestone. While both rock types are highly porous, the Key Largo limestone is much more permeable than its oolitic counterpart (Hanson, 1980).

Table 1. Several physical and biological characteristics of forest stands within five Florida Keys habitat types. Habitat types: TTW, Transitional Thorn Woodland; PRF, Pine Rockland Forest; LPH, MPH, and HPH, Low, Medium, and High Productivity Hammock, respectively. Stand ID's: K = Key Largo, L = Lignumvitae, B = Big Pine, S = Sugarloaf. Data from Ross et al. (1992)

Habitat Type	Stand ID	Elevation (m)	Mean ground water salinity (‰)	Dominant tree species
TTW	K4	0.64	11.4	*Conocarpus erecta*
	S4	0.77	11.4	*Manilkara bahamense*
PRF	B2	0.67	1.6	*Pinus elliottii var densa*
	S3	0.73	9.2	*Pinus elliottii var densa*
	S5	1.13	2.3	*Pinus elliottii var densa*
LPH	S2	0.73	10.4	*Thrinax morrissii*
	S7	1.32	2.6	*Metopium toxiferum*
MPH	L2	0.76	13.6	*Eugenia foetida*
	K1	0.86	3.8	*Coccoloba diversifolia*
	B3	0.79	10.7	*Coccoloba diversifolia*
HPH	L3	2.91	19.0	*Bursera simaruba*
	K5	1.32	15.2	*Coccoloba diversifolia*
	K9	3.28	24.0	*Coccoloba diversifolia*

Ground water throughout most of the Keys is fresher than the surrounding seawater. Ground water salinity is determined by the recharge rate, bedrock permeability, and the size and shape of the island (Meadows et al., in press; Vacher, 1978). Due to the relative impermeability of the Miami limestone, a fresh water lens is often maintained near the center of the larger Lower Keys islands, but brackish groundwater is the rule in most other Keys environments (Table 1). The elevation of the water table changes seasonally and with the semi-diurnal tide cycle (amplitude usually less than 1.25 m). In general, mean ground water level is slightly higher than mean sea level, because the fresher and less dense ground water floats on the underlying sea water. This difference is usually 30 cm or less, so ground elevation is a useful approximation of distance to the water table.

Sampling focused on five Ecological Site Units (hereafter designated by the more familiar 'habitat type'): Transitional Thorn Woodland (TTW), Pine Rockland Forest (PRF), and Low, Medium, and High Productivity Hammock (LPH, MPH, and HPH, respectively) (Ross et al., 1992). Sample locations representative of these habitat types were distributed among protected natural areas on Key Largo (Plots K1, K4, K5, and K9), Lignumvitae Key (Plots L2 and L3), Big Pine Key (Plots B2 and B3), and Sugarloaf Key (Plots S2, S3, S4, S5, and S7) (Figure 1, Table 1). Based on historical aerial photographs, none of the sites had undergone substantial clearing or other major human disturbance for at least 60 years prior to sampling. Scattered stumps present in several sites indicated that limited extraction of individual trees had taken place, however.

Soil physical and chemical properties

Soils were examined, and a modal site was selected, described and sampled following procedures outlined in the U.S.D.A. Soil Survey Staff (1993). After air drying and sieving through a 2 mm sieve, the following soil properties were measured, without replication: pH in H_2O (Jackson, 1958); electrical conductivity (EC) using the solution extracted from a saturated paste (Jackson, 1958); organic matter by low temperature (450 °C) combustion (Jackson, 1958); organic C by Walkley Black procedure (Jackson, 1958); total nitrogen (N) by semi-micro-Kjeldahl (Bremner, 1965); and total phosphorus (P) by perchloric acid digestion and colorimetry using ammonium molybdate (Olsen and Sommers, 1982). Calcium carbonate equivalence (CCE) was determined by titration with HCl (Soil Survey Staff, 1972). Extractable elements were determined using ammonium bicarbonate – AB-DTPA on calcareous soils and Mehlich 3 extractant on neutral or acidic soils (Mehlich, 1984; Soltanpour and Schwab, 1977). The extracted solutions were analyzed on a Jarrell-Ash model 750 ICP mass spectrometer. Bulk density was determined by excavating the soil within successive horizons, lining the hole with plastic, and measuring the volume of water required to fill each portion of the hole. The weight of the oven-dried (70 °C) soil removed from each horizon was used for calculation of bulk density. Available water was estimated using soil moisture pressure plates at appropriate pressures (Klute, 1965).

Decomposition and soil organic matter turnover

In May 1990, sets of three nylon [2 mm] mesh litter bags were placed at three randomly selected locations on the forest floor in each of the thirteen stands. Freshly fallen or senescent leaves were collected, dried at 65 °C, analyzed for N and P concentration, and a weighed amount (>20 g) inserted in each bag. One bag from each group was collected, dried, and reweighed in November 1990, May 1991, and May 1992, i.e., 6, 12, and 24 months after placement in the field.

Turnover time of soil organic matter

We used bomb ^{14}C as a tracer to infer the turnover time of the soil organic C, according to the method of Hsieh (1993). The basis of the method is that the ^{14}C signature of the active soil C pool integrates the ^{14}C input of the atmosphere over the past five decades, a period for which the trajectory of atmospheric ^{14}C is well known. Because the soil ^{14}C signature is a function of both turnover time and the timing of sample collection, knowledge of the sample ^{14}C content and its time of collection allows one to deduce the turnover time of the carbon pool.

Air-dried soil samples from a representative subset of sites were sieved through a 2-mm sieve to remove gravel and plant tissue debris. A 10 g sample of the sieved soil was weighed into a glass beaker, followed by the addition of 10 mL increments of 2 *M* HCl solution to remove carbonates. Increments of HCl were added to soil until no apparent reaction with carbonates was observed. The beaker was then covered with a watch glass and placed on a hot plate at 70–80 °C for 3 h. The beaker was allowed to cool to ambient temperature overnight. If the pH of the final solution was greater than 2, the sequence was repeated until pH 2 was reached. The acidified soil samples were washed twice with 20 mL distilled water by centrifugation and dried at 60 °C. The prepared sample was sent to the NSF/AMS facility at the University of Arizona for ^{14}C dating analysis. The ^{14}C was reported as percent modern (i.e., 1950) C (pmC) after correcting for ^{13}C content. All ^{14}C values were greater than 100 pmC, indicating significant incorporation of bomb carbon in the soil organic matter since 1950.

Forest structure and production

We estimated three elements of forest stature (canopy height, basal area, and total tree biomass) and two components of aboveground production (annual litterfall and tree biomass increment).

Estimates of tree biomass, basal area, and canopy height were based on trees within a single 600 m^2 (10 × 60 m) plot located within relatively homogeneous vegetation representative of each site (Ross et al., 1992). The species and diameter at breast height (1.45 m above the ground) of all stems >2.54 cm diameter were recorded in the spring of 1989. Basal area was calculated on the basis of all measured trees, but total tree biomass was estimated by applying published regression equations to trees over 5 cm diameter only. For broad-leaved species we used a general equation developed by Brown et al. (1989) for dry tropical forests. For pines, we used an equation developed for *Pinus elliottii* throughout its range by Clark and Taras (1976). Palm species (*Thrinax radiata, Thrinax morrissii*, and *Coccothrinax argentata),* which represented 0–33% of stand basal area, were not included in biomass calculations because no published regression equations were available. Canopy height estimates were based on the total height of all trees >10 cm DBH, measured with a telescoping height pole. Mean canopy height was defined as the modal (50th percentile) tree height within this distribution.

Estimation of tree biomass increment was based on regular monitoring of radial growth. During the fall of 1989 aluminum band dendrometers (Liming, 1957) were established at 1.45 m height on a small subsample of each abundant canopy species per plot. Diameter growth was monitored monthly on a total of l08 trees through December 1992. Using the regression equations described above, we determined initial biomass, final biomass, and mean annual biomass growth for each sample tree. Mean growth rates

Table 2. Some physical and chemical properties of upland soils in Florida Keys. OM=organic matter; OC=organic carbon; EC= electrical conductivity; CCE=calcium carbonate equivalent; BD=bulk density. This determination was performed only if the soil sample effervesced with 10% HCL; – = no data

Vegetation type	Site	Depth (cm)	pH	OM (%)	OC (%)	Total N (%)	Total P (ppm)	EC (mS cm^{-1})	CCE (%)	BD (g cm^{-3})
TTW	K4	0-5	–	72.6	18.9	0.98	344	22.0	–	0.14
		5–12	–	57.4	18.0	0.90	722	31.0	–	0.35
	S4	0–7	7.9	33.1	12.1	0.63	440	20.0	31.8	–
PRF	B2	0-5	8.0	19.8	15.7	0.37	325	3.8	57.0	–
		5–10	8.1	14.7	8.0	0.40	272	3.2	>62	–
	S3	0–3	6.2	85.3	24.9	0.87	475	6.2	–	–
		3–12	7.7	22.0	12.2	0.37	205	12.4	51.5	–
	S5	0–7	7.9	36.7	17.5	0.62	337	20.0	35.4	–
LPH	S2	0–5	6.0	86.8	24.0	1.40	–	4.9	–	0.06
		5-10	7.7	28.7	10.8	0.5	–	18.0	55.9	0.61
	S7	0–5	6.7	87.7	23.5	1.28	221	4.9	–	0.06
		5–14	7.4	65.3	19.6	1.10	828	7.2	17.4	0.61
MPH	B3	0–5	7.4	74.4	27.0	1.32	1760	1.9	–	0.35
		5–14	7.7	62.4	20.1	1.24	3220	2.6	28.8	0.48
	L2	0–5	6.8	80.8	26.1	1.30	744	8.0	–	0.12
		5-10	7.4	54.3	18.7	1.22	1840	18.0	–	0.50
	K1	0–7	6.7	77.5	19.3	1.21	181	5.0	–	0.10
		7–12	–	–	–	–	–	–	–	–
HPH	K5	0–10	7.3	78.8	23.4	1.30	503	2.0	–	0.13
	K9	0–7	7.6	76.1	22.7	1.39	378	1.4	–	–
		7–18	7.6	68.3	23.2	1.32	1100	1.5	–	–
	L3	0–5	7.6	72.6	25.1	1.42	1060	1.2	–	0.16
		5–10	7.5	59.2	24.5	0.36	1810	2.2	30.4	0.57

were calculated by species in each stand, and applied to the initial stand tables on a species-specific basis. Dendrometer design allowed detection of diameter changes as small as 0.2 mm, but did not enable sampling of several important understory tree species that never attained the minimum diameter of 10 cm. Species present in the stand but not represented in the dendrometer sample were assigned the mean growth rate of all species. The method does not account for ingrowth into the tree stratum, and assumes that all trees survived the three-year period. Since leaf populations tend to reach an asymptote early in stand development (e.g., Covington and Aber, 1980), tree increment calculated in this way is primarily wood production.

Litter production estimates were based on leaves, small twigs, and reproductive parts collected in three 1 × 1 m litter traps per plot over the period December 1989–November 1991. A stratified random process was used to determine trap locations. Accumulated material was collected at two-month intervals, then dried at 65 °C for 48 h before weighing.

Results

Soil physical and chemical properties

Most upland soils in the Florida Keys develop on flat (0–1%) surfaces, and are shallow (<20 cm) over limestone except above occasional small sink-holes. Due to the uneven limestone surface, micro-relief is substantial. The large volume of medium and fine live roots, the presence of limestone gravel, and the patchy exposure of limestone bedrock further reduce the effective volume of these thin soils.

Soil profiles from our thirteen study sites are described in the Appendix. The soils in all five habitat types are similar in that they are thin and include organic horizons with or without marl. The organic materials have negligible fiber content. The soil surface is usually covered with 2–5 cm of undecomposed organic material (leaves and stems). Soils are deepest in the hammock forest types, and thinnest in the TTW and PRF units. There are extensive areas in the latter

Table 3. Extractable nutrients from some soils of the uplands in the Florida Keys and adequacy for agronomic crops. Extractants: M = Mehlich III; A = AB – DTPA; Ca and Mg concentrations are meaningless for AB-DTPA extractant. Availability or sufficiency levels of Ca, Mg, K, or P are indicated by H (high), M (medium) and L (low) for agronomic crops

Habitat Type	Location	Depth (cm)	Extractant*	Ca	Mg	K	P
				—(‰ or	mg dm^{-3}	with Mehlich III)—	
TTW	K4	0-5	A	–	–	252 H	11 H
		5–12	A	–	–	433 H	19 H
	S4	0–7	A	–	–	287 H	11 H
PRF	B2	0–5	A	–	–	34 L	6 M
		5–10	A	–	–	40 L	8 H
	S3	0–3	M	2410 H	886 H	120 H	17 M
		3–12	A	–	–	163 H	8 M
	S5	0–7	A	–	–	78 M	–
LPH	S7	0–5	M	2780 H	1170 H	254 H	19 H
		5–14	A	–	–	183 H	10 H
MPH	B3	0–5	M	6130 H	1260 H	127 H	6 L
		5–14	A	–	–	55 L	8 H
	L2	0–5	M	3160 H	1400 H	156 H	28 M
		5–10	M	6610 H	2440 H	400 H	45 M
	K1	0–7	M	3560 H	1280 H	233 H	6 L
		7–12	A	–		–	
HPH	K5	0–10	M	5790 H	1150 H	115 H	23 M
	K9	0–7	M	8500 H	629 H	124 H	26 M
		7–18	M	11400 H	719 H	127 H	30 M
	L3	0–5	M	8240 H	726 H	147 H	26 M
		5–10	A	–	–	62 M	14 H

two types where little or no soil is present and trees are rooted in fissures in the limestone. This is particularly evident on Big Pine and Sugarloaf Keys, where slash pine has made fair growth in a soil-less environment.

Some physical and chemical properties of the soils are presented in Table 2. Soil reaction in most soils is near neutral, though pH 8 is approached in some marl horizons. Soils in the three hammock types have the highest organic matter content as well as the highest concentration of N and P. Organic matter content is inversely related to bulk density. Where little $CaCO_3$ is present, most organic horizons have a bulk density around 0.1 g cm^{-3}. Soils high in marl have a bulk density of 0.5 g cm^{-3} or higher. Electrical conductivity of the soil solution is generally lowest in MPH and HPH hammocks (1.2-5.0 mS cm^{-1}, but 18.0 in L2 (5–10 cm)), intermediate in LPH and PRF (3.2–20.0 mS cm^{-1}), and highest in TTW soils (20–31 mS cm^{-1}). Electrical conductivity is directly related to salt content; 4 mS cm^{-1} is considered a saline soil and is harmful to most agronomic crops (USDA, 1954).

Soil testing is not widely used for determining nutrient deficiencies in forest crops (Pritchett, 1979). With the exceptions listed below, the concentrations of extractable Ca, Mg, K, and P presented in Table 3 indicate that these elements would be adequate for agronomic crops (J.B. Jones, pers. comm.; Soltenpour and Schwab, 1997; Sims and Johnson, 1991). Inadequate K is indicated at sites B2 and in the subsoil of B3, and inadequate P at B2 and B3 (surface) and K1.

Soil moisture at field capacity (−0.033 MPa) and permanent wilting point (−1.5 Mpa) was determined on three soil horizons: an organic soil with no $CaCO_3$; a soil with 62% organic matter and 29% $CaCO_3$; and a soil with 24% organic matter and >60% $CaCO_3$. Available moisture (difference between moisture content at field capacity and permanent wilting) was 112%, 40%, and 22% of dry soil weight, respectively. However, adjusting for bulk density and gravel content, there was little difference in water-holding capacity among these soils; assuming a 10 cm soil thickness, total water storage capacity was 1.45 cm

Table 4. Measures of structure and productivity for 5 vegetation types: Transitional Thorn Woodland (TTW); Pine Rockland Forest (PRF); Low, Medium and High Productivity Hammock (LPH, MPH, and HPH, respectively)

Vegetation Type	Location	Canopy Height (m)	Basal area (m^2 ha^{-1})	Total tree biomass (Mg ha^{-1})	Annual litterfall (Mg ha^{-1})	Annual wood production (Mg ha^{-1})
TTW	K4	4	4.4	4.7	2.9	–
	S4	5	14.4	35.4	4.26	0.38
PRF	B2	12	12.1	47.5	2.76	3.05
	S3	10	21.0	39.6	2.24	3.31
	S5	12	15.2	33.8	2.17	3.32
LPH	S2	5	22.2	45.3	5.73	2.04
	S7	6	24.3	102.0	5.01	1.76
MPH	B3	8	32.5	109.0	7.99	2.96
	L2	8	15.0	27.4	5.61	2.60
	K1	8	27.5	75.7	5.31	2.05
HPH	K5	13	35.8	136.0	7.35	5.02
	K9	10	33.9	120.0	6.85	4.29
	L3	8	39.4	163.0	6.79	3.27

in the highly organic soil, 1.54 cm in the soil with intermediate organic matter content, and 1.51 cm in the soil with highest carbonate content.

Forest structure and production

The dominant species in each habitat type are listed in Table 1. Forest structure varied widely among sites, with canopy height ranging from 4 to 13 m, basal area from 4 to 39 m^2 ha^{-1}, and tree biomass from 5 to 163 t ha^{-1} (Table 4). Stand basal areas generally followed the sequence TTW < PRF< LPH < MPH < HPH. Canopy heights also followed the same order, with a single exception: the PRF canopy was taller than that of all other units except HPH, which was about the same. Habitat types were not clearly distinguished on the basis of stand biomass, except that HPH was consistently the highest.

Annual litterfall and wood production (biomass increment) both varied considerably, with the former ranging from 2.9 to 7.4 Mg ha^{-1} yr^{-1}, and the latter from 0.4 to 5.0 Mg ha^{-1} yr^{-1}. Litter production exceeded wood production by substantial margins in all stands except the three PRF sites. Total (wood + litter) annual production was less than 6 Mg ha^{-1} yr^{-1} in TTW and PRF sites, but exceeded 7 Mg ha^{-1} yr^{-1} in all LPH, MPH, and HPH stands. The highest productivity observed was 12.4 Mg ha^{-1} yr^{-1} at HPH site K5.

Table 5. Correlations (Pearson's r) between several soil variables and total annual production (litter + wood) in Florida Keys upland forests ($n = 11$)

Soil variable	r	p
pH	−0.35	0.330
EC (mS cm^{-1})	−0.89	0.001
Nitrogen concentration (%)	0.74	0.009
Phosphorus concentration (%)	0.55	0.081
Effective soil depth (cm)	0.41	0.214
Total soil nitrogen (kg ha^{-1})	0.59	0.056
Total soil phosphorus (kg ha^{-1})	0.42	0.203

Correlations of total annual production of litter and wood with several soil variables are listed in Table 5. The strongest association was a negative one with soil conductivity ($r = -0.89$; $p = 0.001$), but strong positive correlations between productivity and several measures of nutrient content were observed (%N, $r = 0.74$; total N, $r = 0.59$; %P, $r = 0.55$). However, because these statistics were based on only 11 sites, only the correlation with %N was significant at $p < 0.05$. Associations with other soil variables were weak.

The association of soil nutrients and forest production is a reciprocal one. Concentrations of N and P in litter fall were consistently higher in the more

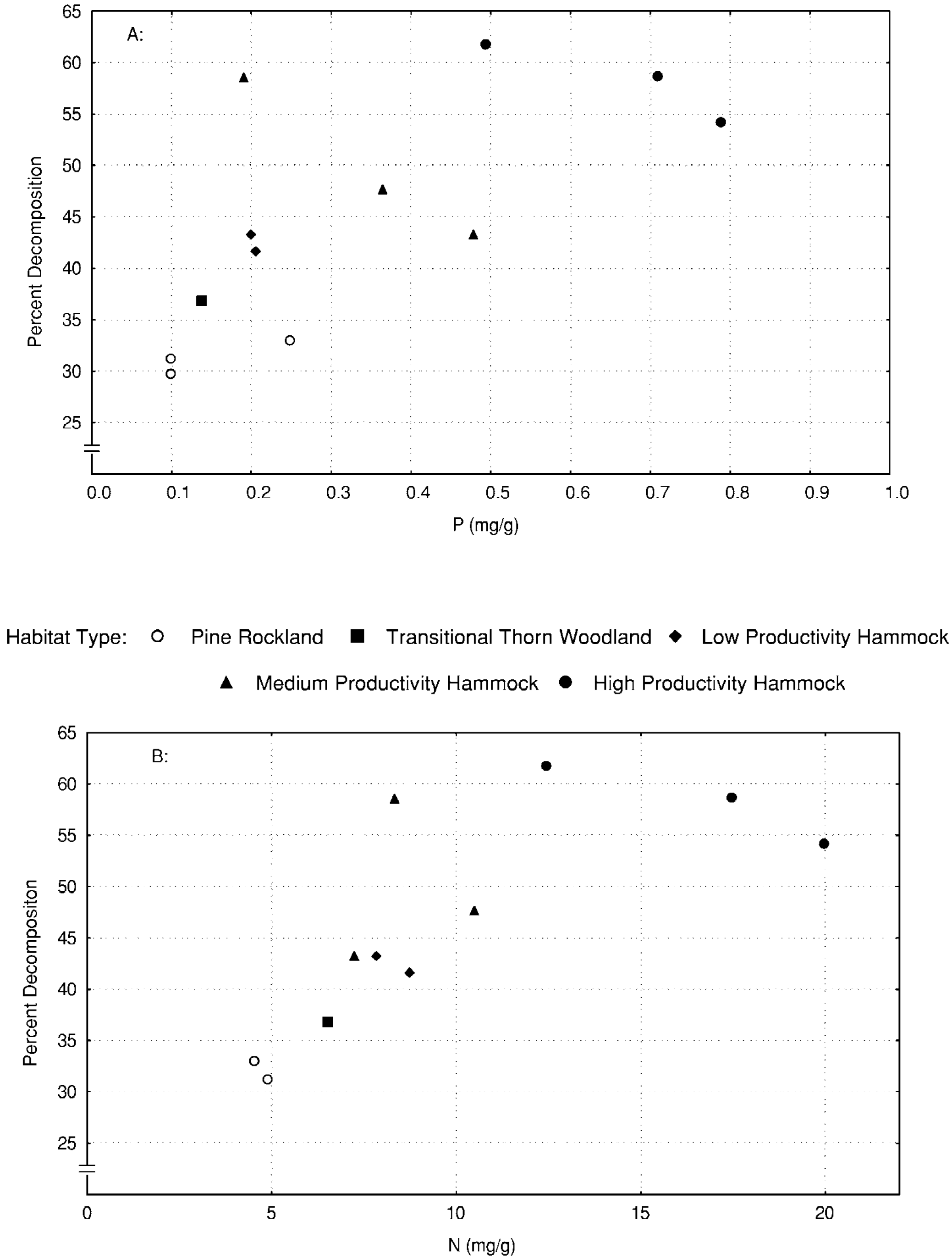

Figure 2. Relationship of initial leaf nutrient content to total decomposition over 24 months in five Florida Keys habitat types. (A) Phosphorus ($n = 12$). (B) Nitrogen ($n = 11$).

productive upland habitats (Figure 2), and the total N and P returned to the soil on an annual basis clearly increased with forest productivity (Table 6). For instance, the total amount of N in yearly litterfall was 3–10 times higher in the HPH sites than in the TTW or PRF sites. The corresponding range for P was 4–25 times. Current-year litterfall represents a substantial proportion of the total N and P stored in the forest floor, ranging as high as 6% for N (plot S7), and 5% for P (plot K5) (Table 6). Assuming that the source of most soil N and P is litterfall, minimum estimates of N and P turnover times are therefore of the order of 20 years.

Decomposition and soil organic matter turnover

Measured litter decomposition ranged from 18% to 52% during the first year the newly senesced material was exposed to field conditions, and from 30 to 62% after two years (Figure 2). Decomposition was most rapid in the HPH, MPH, and LPH habitat types. The slow decomposition observed in the TTW and PRF types was associated with litter N concentrations <7 mg g^{-1} dry weight and litter P concentrations <0.25 mg g^{-1} (Figure 2).

Radiocarbon dating from a total of five sites indicated that all soil organic matter contained significant amounts of bomb radiocarbon produced by the nuclear bomb testing since 1950 ($^{14}C > 100\%$ pmC), signifying that the turnover time of the soil organic C was relatively short. Using the bomb radiocarbon signature to quantify these rates (Hsieh, 1993), it was determined that the turnover times of the total soil organic C pool at two locations within site B2 (PRF) were 20 (124.7 pmC) and 29 (122.5 pmC) years for the 0–5 cm soil layer, and 52 (116.4 pmC) and 55 (115.5 pmC) years for the 5–10 cm soil layer. The turnover times of C in the entire soil profiles to bedrock at sites B3 (MPH), L3 (HPH), K5 (HPH), and K9 (HPH) were 100 (107.7 pmC), 67 (113.5 pmC), 30 (121.4 pmC) and 29 (122.5 pmC) years, respectively. For these five sites, we also found that the radiocarbon-inferred C turnover rates were strongly correlated to the ratio of total soil organic C content/annual litterfall C (Figure 3), another measure of organic turnover (Hsieh and Weber, 1984). This ratio provides a minimum estimate of the turnover time of soil organic C, because much of litterfall consists of rapidly recycling materials (turnover time < 2 years) that need to be eliminated from the calculation of turnover times, which usually are on the order of decades or centuries (Hsieh, 1989). Figure 3 indicates that the radiocarbon-inferred turnover time was about twice as large as that implied by the ratio of soil to litterfall C. This result suggests that less than half of the litterfall is incorporated into bulk soil organic C, along with contributions from belowground production. The rapid turnover rates determined by both methods indicate that organic matter decomposition is not inhibited in Florida Keys forests.

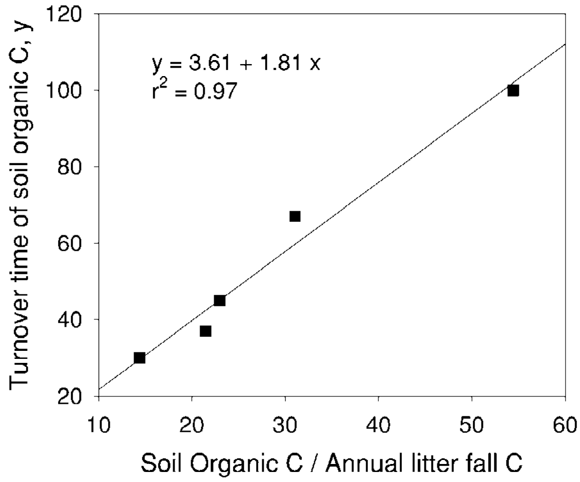

Figure 3. Relationship between the turnover time of soil organic C and the ratio of soil organic C content to annual litterfall C content.

Discussion

Two related questions are suggested by the results outlined above: (1) Why are organic soils maintained in upland settings in these coastal environments? (2) How can forests of substantial productivity be sustained on such limited soil resources? These issues are discussed below.

The organic soils

The development of organic soils (Histosols) such as those that form under closed, broadleaved forest canopies in the Keys (LPH, MPH, and HPH habitat types in Tables 2–4, 6, Appendix) seems to imply the dominance of above- and below-ground production over degradative processes (i.e., microbial decomposition and combustion in periodic fires). However, the organic layers are thin, such that the total accumulation of soil organic matter (mean soil organic C = 63±43 Mg C ha^{-1}; Table 6) lies within the normal range for well-aerated layers of mineral soils in Florida upland forests (e.g., USDA-SCS, 1990). Moreover, both the organic matter turnover and decomposition rates we found suggest that the formation of shallow organic soils in the Florida Keys cannot be attributed to inhibited decomposition, but instead may result from the lack of mineral matrix.

Worldwide, most Histosols are found on poorly drained sites where anaerobic conditions inhibit decomposition, allowing organic sediments to accumulate (Coultas, 1977). Folists are a relatively restricted

Table 6. Estimated organic C, total N and P content in soil and litterfall (SOC, soil N and P are adjusted for volume, gravel, and soil-less areas). – indicates missing data

Habitat Type	Site	Soil Depth (cm)	SOC (Mg ha^{-1})	Soil N	Soil P (kg ha^{-1})	Litter C	Litter N (kg ha^{-1} yr^{-1})	Litter P
TTW	K4	12	51.1	1.60	166	1160	16.8	0.58
	S4	7	30.5	1.10	77	1613	28	0.60
PRF	B2	10	25.4	1.79	188	1104	12.6	0.70
	S3	12	52.1	1.85	132	896	–	–
	S5	7	49.5	1.89	107	868	10.8	0.22
LPH	S7	14	26.7	0.79	320	2004	49.6	1.20
MPH	B3	14	174.0	6.13	1360	3196	39.0	1.00
	K1	–	–	–	–	2124	57.6	3.84
	L2	10	94.6	3.04	403	–	44.0	1.00
HPH	K5	10	42.3	1.69	65	2940	84.3	3.33
	K9	18	58.8	2.94	175	2740	140.6	5.85
	L3	10	84.4	4.22	510	2716	119.0	4.83

group of organic soils found in well-drained sites in humid climates from the Tropics to high latitudes (Coultas, 1977). In the United States, Folists with slightly lower pH than those found in the Florida Keys are reported from tropical environments in Hawaii, where the Kona and Honokohau series develop over hard volcanic rock (USDA, 2000). Kona soils form under forest cover on relatively steep slopes (2–40%) at high elevations (>500 m). Soils of the Honokahau series typically occupy more xeric sites at lower elevation, under grass cover. In contrast, the Folists we describe from the Florida Keys develop in place on coralline or oolitic limestone bedrock. The limestone is 99% calcium carbonate and leaves almost no residual mineral material upon dissolution, a process that is accelerated by tree roots through bioturbation and the production of organic acids (Duever et al., 1986). Saharan dust reaches the Keys via high elevation air currents (Prospero and Nees, 1986), but outside of some local depressions, these materials do not accumulate to a significant degree in the soil matrix.

Estimated rates of production and decomposition in Florida Keys hammocks are similar to values reported for other dry tropical forests, where organic soils are the exception. Litter production estimates in the three Florida Keys hammock types (mean = 6.3 Mg ha^{-1} yr^{-1}; Table 4) lie within the range of values reported from 34 dry tropical forests (range = 1.5–12.6 Mg ha^{-1} yr^{-1}; mean = 4.81 Mg ha^{-1} yr^{-1}; Martinez-Yrizar, 1995). Lugo and Murphy (1986) observed a decomposition rate of 41.3% per year at a dry forest at Guanica, Puerto Rico. This rate translates to roughly 65% decomposition over 24 months, which is slightly faster than observed litter decomposition rates in the relatively productive HPH and MPH types in the Keys (44–62%; Figure 2).

The litter decomposition rates cited above are based on short-term studies that assess the decomposition of only the least refractory element of the organic material that reaches the forest floor. For instance, Minderman (1968) found that the bulk of soil organic matter in a mor soil in Holland was comprised of a small portion of total litterfall, i.e., less than 25%. Our results from the Florida Keys suggest that less than half of litterfall became incorporated into soil organic C (Figure 3). In the dry tropical forests we studied, these bulk materials provided a mean C turnover time of 51 $\pm$ 11 (1 S.E.) years, as determined by the bomb radiocarbon signature (Hsieh, 1993). This rapid turnover of organic C implies that Florida Keys soils lack the stable soil organic C pool (turnover time $\geq 10^3$ years) usually observed in mineral soils (Hsieh, 1992), and is not consistent with the view that organic soils develop only where decomposition is slow. Organo-mineral association is believed to be the primary mechanism by which organic carbon turnover is extended beyond several hundred years (Adu and Oades, 1978; Hassink, 1992).

The presence of organic soils in the hardwood hammocks of the Keys also attests to the low frequency of fire in these forests. However, once ignited by lightning or human sources, fires may smolder for months in cavities within the limestone bedrock, emerging when conditions warrant to consume organic material accumulated over many years. Careful inspection of old aerial photographs indicated that, among the sites we sampled, only those in the PRF habitat type had burned during the last half century or more. The short turnover time of organic C in even the PRF soils, however, implies that the stock may be rebuilt within a time scale of several decades to a century.

Soil limitation of forest production

Though based on a small sample of Florida Keys forests, the correlations listed in Table 5 suggest a covariation of above-ground production with several fundamental soil resources, especially the size of the soil N pool. Furthermore, the association of decomposition rate with habitat type (Figure 2) suggests that these relationships may also extend to soil microbial processes. However, distinguishing cause and effect in the soil vs. vegetation relationship is not obvious, especially in light of the youth and thinness of the soil organic matter. The more productive forests return more nutrients and organic matter to the soil, enhancing the resources available to them and amplifying their relative productivity.

Several external factors may set the parameters of the cycle described above. The most productive forests are situated at relatively high elevations in the interior of the small islands, where they are least likely to be inundated by spring tides or storm surges. Salts deposited during these events may remain in place for long periods, with negative impacts on growth (Table 5). Although one might expect high groundwater salinity to negatively affect productivity, this apparently does not apply to Keys forests more than about two meters above sea level . In fact, our data (Table 1) show that the very productive HPH forests of the Upper Keys had the highest groundwater salinity (average 19 ‰), while the less productive PRF type of the Lower Keys had the lowest (average 4 ‰).

In view of the limited soil resources available, recycling processes must be extremely efficient, and losses of water and nutrients through runoff or leaching must be small in order to sustain the high rates of production attained in the three Florida Keys hammock types (Table 4) in comparison to many other dry tropical forests (Murphy and Lugo, 1986). Economic cycling of water is particularly critical. For instance, if evapotranspiration is conservatively assumed to be 0.25 cm/day (e.g., Dolan et al., 1984; German, 2000), and, as our analyses indicate, a typical soil profile of 10 cm depth holds about 1.5 cm of available water, then it follows that rainless periods as short as one week may exhaust the soil moisture storage capacity. One mechanism that clearly limits water loss is uptake by the dense root mat that typically forms near the soil surface in these stands . Moreover, under some conditions, soil water and nutrient pools may be supplemented by condensation of water vapor on leaf surfaces, or by rewetting of the soil during peaks in the tidally-driven ground water cycle. Root penetration into the porous limestone has been observed, and could indicate that trees obtain substantial quantities of both nutrients and water from the aquifer. Evidence for this can be seen on Big Pine Key, where slash pines growing directly on limestone bedrock can maintain reasonable growth rates, though in very open stands. In contrast, hammock species in the Florida Keys are reported to utilize soil water exclusively, based on comparisons of the isotopic content of plant water to alternative water sources (Ish-Shalom-Gordon et al., 1992).

Conclusions

The tropical forests of the Florida Keys are supported by thin organic soils developed directly on limestone bedrock. These well-drained organic soils differ from poorly-drained Histosols in their limited depth and in their rate of organic matter turnover, which by several measures is extremely fast. Forest production on such sites appears to depend on a fine balance between accretionary and degradational processes. On the one hand, sustained production requires that soil volume be sufficient to maintain adequate water supplies. Conversely, our estimates of nitrogen and phosphorus pools make clear that plant demands can only be met if mineralization is rapid, especially since organic forms dominate the soil nutrient pool. For forest production to be sustained in such an ecosystem, it also appears that nutrient cycling must be extremely efficient, i.e., there can be little leaching beyond the rooting zone. Maintenance of the very diverse forests that grow on the most productive Keys soils may depend on a continuation of this efficiency in the face of threats such as forest fragmentation and sea level rise (Ross et al., 1994; Strong and Bancroft, 1994).

Appendix 1. Description of some soils of the uplands in the Florida Keys

Habitat Type	Site	Depth (cm)	Description—lithic contact (limestone) below deepest horizon
Transitional Thorn Woodland	K4	0–5	Black (10YR 2.5/1) organic with frequent medium and fine roots. 10% limestone gravel and shell.
		5–12	Very dark gray (10YR 3.1) marl with frequent roots. 10% limestone gravel
		Over 50% of this soil area is exposed limestone. The elevation is about 70 cm above mean tide.	
	S4	0–7	Very dark gray (10YR 3/1) organic with occasional shells and marl. Occasional medium and fine roots. 10% – 20% limestone gravel.
		About 50% of this area is exposed limestone.	
Pine Rockland Forest	B2	0–10	Brown (10YR 5/3) marl. Very abundant medium and fine roots. 20% limestone gravel.
		20% – 40% of area is exposed limestone. Burned in 1987.	
	S3	0–3	Dusky red (2.5YR 3/2) organic with abundant medium and fine roots. 5% limestone gravel.
		3–12	Dark grayish-brown (10YR 4/2) marl with frequent medium and fine roots. Fine and medium granular structure. 20–30% limestone gravel.
		Less than 10% of this area is limestone outcrop.	
	S5	0–7	Black (10YR 2.5/1) organic (calcareous) with abundant medium And fine roots. Fine granular structure.
		10% – 20% limestone outcrop in area	
Low Productivity Hammock	S2	0–5	Dark reddish-brown (5YR 4/2) organic with very abundant medium and fine roots.
		5–10	Dark grayish-brown (10YR 4/2) organic (calcareous) with abundant medium and fine roots. 50% limestone gravel.
	S7	0–5	Very dusky red (2.5 YR 3/2) organic with very abundant fine and medium roots. 25% limestone gravel.
		5–14	Very dusky red (2.5YR 2.5/2) organic with frequent fine and medium roots. 20–25% limestone gravel.
Medium Productivity Hammock	B3	0–5	Dusky red (10R 3/2) organic with abundant fine and medium roots. 5–10% limestone gravel.
		5–14	Dusky red (10R 3/2) organic with occasional fine roots. 30–50% limestone gravel.
	L2	0–5	Dusky red (2.5YR 3/2) organic with abundant medium and fine roots. 5–10% limestone gravel with occasional shell.
		5–10	Very dusky red (2.5YR 2.5/2) organic with frequent medium and fine roots. 30–40% limestone gravel.
	K1	0–7	Dusky red (2.5YR 3/2) organic with abundant medium and fine roots.
		7–12	Very dark grayish-brown (10YR 3/2) organic with abundant medium and fine roots. 20–40% limestone gravel. Occasional shell
High Productivity Hammock	K5	0–10	Dusky red (2.5YR 3/2) organic with frequent fine and medium roots. Occasional shell.
	K9	0–7	Dusky red (2.5YR 3/2) organic with frequent fine and medium roots. 5–10% limestone gravel.
		7–18	Dusky red (2.5YR 3/2) organic with frequent fine and medium roots. 10–20% limestone gravel.
	L3	0–5	Dusky red (2.5YR 3/2) organic with abundant fine and medium roots. Occasional shell.
		5–10	Dusky red (2.5YR 3/2) organic(calcareous) with abundant fine and medium roots. 10–20% limestone gravel and frequent shell.
		All soils have a 2–5 cm cover of undecomposed organic material (leaves and stems), and this litter layer is thicker with the soils at higher elevations.	

Acknowledgements

We wish to recognize that the National Audubon Society provided much of the financial support for this study. Joe O'Brien, Pablo Ruiz, and Josh Walters made important contributions to the success of the project in the field and/or in the lab. This is Southeast Environmental Research Center Contribution #193.

References

Adu J K and Oades J M 1978 Physical factors affecting decomposition of organic materials in soil aggregates. Soil Biol. Biochem. 10, 109–115.

Bremner J M 1965 Total nitrogen. *In* Methods of Soil Analysis, Part 2. Ed. C A Black. pp. 1149–1179. American Society of Agronomy, Madison, WI.

Brown S, Gillespie A J R and Lugo A E 1989 Biomass estimation methods for tropical forests with applications to forest inventory data. For. Sci. 38, 881–902.

Clark A III and Taras M A 1976 Comparison of aboveground biomass of the four major southern pines. For. Prod. J. 26, 25–29.

Coultas C L 1977 Soils of the Apalachicola National Forest wetlands. Part 2: cypress and gum swamps. Soil and Crop Sci. Soc. of FL. Proc. 37, 154–159.

Covington W W and Aber J D 1980 Leaf production during secondary succession in northern hardwoods. Ecology 61, 200–204.

Dolan T J, Hermann A J, Bayley S E and Zoltek J Jr 1984 Evapotranspiration of a Florida, USA, freshwater wetland. J. Hydrol. 74, 355–371.

Duever M J, Carlson J E, Meeder J F, Duever L C, Gunderson L H, Riopelle L A, Alexander T R, Myers R L and Spangler D P 1986 The Big Cypress National Preserve. Research Report No. 8, National Audubon Society, New York. 455 pp.

German E R 2000 Regional evaluation of evapotranspiration in the Everglades. US Geological Survey Water Resources Investigations Report 00–4217. Tallahassee, FL, USA.

Hanson C E 1980 The freshwater resources of Big Pine Key. US Department of the Interior Geologic Survey. Open file report 80–447.

Hassink J 1992 Effects of soil texture and structure on C and N mineralization in grassland soils. Biol. Fert. Soils 14, 126–134.

Hoffmeister J D and Multer H G 1968 Geology and origin of the Florida Keys. Geol. Soc. Am. Bull. 79, 1487–1502.

Hsieh Y P 1989 Dynamics of soil organic matter formation in croplands – conceptual analysis. Sci. Total Environ. 81/82, 381–390.

Hsieh Y P 1992 Pool size and mean age of the stable soil organic carbon in croplands. Soil Sci. Soc. Am. J. 56, 460–464.

Hsieh Y P 1993 The radiocarbon signatures of turnover rates in active soil organic carbon pools.Soil Sci. Soc. Am. J. 57, 1020–1022.

Hsieh Y P and Weber O J 1984 Net aerial primary production and dynamics of organic matter formation in a tidal marsh ecosystem. Soil Sci. Soc. Am. J. 48, 65–72.

Ish-Shalom-Gordon N, Sternberg L, Ross M S, O'Brien J J and Flynn L J 1992 Water utilization of tropical hardwood hammocks of the Lower Florida Keys. Oecologia 92, 108–112.

Jackson ML 1958 Soil Chemical Analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J.

Kapos V 1986 Dry limestone forests of Jamaica. *In* Forests of Jamaica. Eds. D A Thompson, D K Bretting and M Humphreys. pp. 49–58. Jamaican Society of Scientists and Technologists, Kingston, Jamaica.

Klute A 1965 Water capacity. *In* Methods of Soil Analysis, Part 1. Ed. C A Black. pp. 274–277. Amer. Soc. of Agronomy, Madison, WI.

Lidz B H and Shinn E A 1991 Paleoshorelines, reefs, and a rising sea: South Florida, U.S.A. J. Coast. Res. 7, 203–229.

Liming F G 1957 Homemade dendrometers. J. For. 55, 575–577.

Lugo A E and P G Murphy 1986 Nutrient dynamics of a Puerto Rican subtropical dry forest. J. Trop. Ecol. 2, 55–72.

Martinez-Yrizar A 1995 Biomass distribution and primary productivity of tropical dry forests. *In* Seasonally Dry Tropical Forests. Eds. S H Bullock, H A Mooney and E Medina. pp. 326–345. Cambridge University Press, Cambridge, UK.

Meadows D G, Caballero J P, Kruse S E, Vacher H L and Ross M S In press Variation of salinity in brackish-water lenses of two Florida Keys. J. Coast. Res.

Mehlich A 1984 Mehlich III soil extractant, a modification of Mehlich II extractant. Comm. Soil Sci. Plant Anal. 15, 1409–1416.

Minderman G 1968 Addition, decomposition and accumulation of organic matter in forests. J. Ecol. 56, 355–362.

Murphy P G and Lugo A E 1986 Ecology of tropical dry forest. Annu. Rev. Ecol. Syst. 17, 67–88.

Olsen J R and Sommers L E 1982 Phosphorus. *In* Methods of Soil Analysis, Part 2. Eds. R H Miller and D R Sommers. pp. 403–430. Amer. Soc. Agron., Madison, WI.

Pritchett W L 1979 Properties and management of forest soils. Wiley, New York. 500 pp.

Prospero J M and Nees R T 1986 Impact of the North African drought and El Nino on mineral dust in the Barbados trade winds. Nature 320, 735–738.

Ross M S, O'Brien J J and Flynn L J 1992 Ecological site classification of Florida Keys terrestrial habitats. Biotropica 24, 488–502.

Ross M S, O'Brien J J and Sternberg L 1994 Sea level rise and the reduction in pine forests in the Florida Keys. Ecol. App. 4, 144–156.

Sims J T and Johnson GV 1991 Micro-nutrient soil tests. *In* Micronutrients in Agriculture. Book Series no. 4. Eds. J Mortvedt, F R Cox, L M Shuman and B M Welch. pp. 427–476. Soil Sci. Soc. of Amer., Madison, WI.

Soltanpour P N and Schwab A P 1977 A new soil test for simultaneous extraction of micro-and macro-nutrients in alkaline soils. Comm. Soil Sci. Plant Anal. 8, 195–207.

Soil Survey Division, NRCS, U.S. Dept. of Agriculture 2000 Soil series description of Kona and Honokohau series. USDA, Washington, D.C.

Soil Survey Staff 1972 Procedures for collection of soil samples and methods of analysis for soil survey. Soil Survey Investigation Report, No.1. USDA. Soil Conservation Service, U.S. Govt. Printing Office. Washington, D.C.

Strong A M and Bancroft G T 1994 Patterns of deforestation and fragmentation of seasonal deciduous and mangrove forests in the Upper Florida Keys. Bull. Mar. Sci. 54, 795–804.

U. S. Dept. Agriculture, NRCS 1995 Soil survey of Monroe County, Keys Area, Florida. Supt. of Documents, Washiington, D.C.

U.S. Department of Agriculture, NRCS 2000 Kona series, Honokohau series. www.statlab.iastate.edu. Ames, Ia.

U.S. Dept. of Agriculture, Salinity Lab Staff 1954 Diagnosis and improvement of saline and alkali soils. U.S. Supt of Documents, Washington, D.C.

U.S. Dept. Agriculture, Soil Survey Staff 1975 Soil taxonomy: A basic system of classification for making and interpreting soil surveys. Handbook no. 436. U.S. Govt. Printing Office, Washington. D.C.

U.S. Dept. of Agriculture Soil Conservation Service 1990 Soil Survey of Polk County FL. U.S. Govt. Printing Office. Washington, D.C.

U.S. Dept. Agriculture, Soil Survey Staff 1993 Soil Survey Manual. Supt. of Documents, Washington, D.C.

Vacher H L 1978 Hydrogeology of Bermuda – significance of across-the-island permeability. J. Hydrol. 39, 376–426.

Walter H 1985 Vegetation of the Earth and ecological systems of the geo-biosphere. Springer-Verlag New York Inc., Secaucus, NJ, USA.

Section editor: R. Merckx