PRNC-129 BIOLOGY AND MEDICINE (T1D-4500) PUERTO RICO NUCLEAR CENTER THE RAIN FOREST PROJECT ANNUAL REPORT Carl F. Jordan, George E. Drewry June 1969 OPERATED BY UNIVERSITY OF PUERTO RICO UNDER CONTRACT NO. AT (40-1)-1833 FOR U.S. ATOMIC ENERGY COMMISSION ---Page Break--- Table of Contents Introduction Section I Part A - Isotope Cycles Part B - Secondary Succession in the Irradiated Area Section II Part A - Animal Ecology Part B - Species Diversity Appendices - Insect Keys Section II Derivation of Leaf Area Index from Quality of Light on Forest Floor. Nitrogen Fixation by Epiphytes at El Verde. Termites at El Verde: 1968 Recheck 122 123 331 ---Page Break--- DIVISION OF RADIOBIOLOGY TERRESTRIAL ECOLOGY PROGRAM ‘THE RAIN FOREST PROJECT INTRODUCTION The Rain Forest Project is an ecological study of a tropical rain forest located at an elevation of 1500 feet on the side of El Yunque mountain in eastern Puerto Rico. The study has three objectives: 1) to define the effects of gamma radiation on the tropical ecosystem; 2) to study the cycling of stable and radioactive isotopes through the ecosystem; 3) to investigate basic biological functions of the ecosystem in order to better understand phenomena related to the first two objectives. The gamma irradiation study has been completed, and results will be published in a volume edited by H.T. Odum. Studies of secondary succession in the forest opened up by radiation are continuing. Changes during the first three years of succession are reported here. This report is in three major sections. The first section, by Dr. Carl F. Jordan, concerns the stable and radioactive isotope cycles, and a portion of the secondary successional work. The second section, by Dr. George E. Drewry, deals with diversity of the successional forest, and animal ecology studies. The third section consists of reports by visiting scientists, and a manuscript in press. ---Page Break--- SECTION I by Carl F. Jordan This section deals with stable element cycling, tritium movement in the

tropical rain forest, and secondary succession following irradiation. The studies on stable element content of the tropical ecosystem, started by Kline in 1966, and the stable element flux in the forest begun by Jordan in 1967, were completed during the past year. The results are brought together in section one so that they are amenable to a systems analysis. Because of the extreme complexity of the ecosystem, a systems analysis is necessary to predict such things as, given a certain amount of fallout: how long will it take for the radioactivity to reach equilibrium in the system?; What will be the levels of radioactivity in each compartment at that time? How long after input will radioactivity be at a maximum in compartments such as leaves and fruits, which are bases of food chains? Also in section one are some of the results of a series of tritium tracer studies, carried out in conjunction with Dr. Jerry R. Kline of Argonne National Laboratory, and Dr. John Koranda and Mr. John Martin of Lawrence Radiation Laboratory. These studies are of interest, not only because tritium is a tracer for water, but also because tritium will be a principal product of any thermonuclear reaction used to excavate a new canal through Central America. The secondary successional study was initiated in the summer of 1966, one year after radiation of the forest ceased. Results through 1968 concerning biomass, gross and net photosynthesis, respiration, and efficiency are presented in this section. Results concerning species diversity and information are presented in section two. ---Page Break--- PART A - ISOTOPE CYCLES The movement of radioactive and stable elements through an ecosystem often is termed "mineral cycling" or "biogeochemical cycling". Both these terms are misleading. "Mineral cycling” is misleading because to earth scientists, minerals are substances composed of two or more elements, usually having a definite atomic arrangement. These minerals do not cycle through plants and animals. The term "biogeochemical"

cycling" also is misleading, because it implies cycling over millions of years whereby an element is deposited on the ocean bottom, becomes sedimentary rock, there is land uplift, erosion, and then

the element is again available for cycling through biological systems. The studies at the tropical rainforest at El Verde do not involve this sedimentation, but are concerned only with the movement of biologically available material. The studies involve transfer and storage of stable chemical elements, as well as the radioactive isotopes of some of these elements. Since stable chemical elements are isotopes, and radioactive elements are radioisotopes, the studies are most accurately called isotope cycling studies. During the past several years, tracer studies and chemical analyses have been done on many of the compartments and transfer routes shown in Fig. 1 for the tropical rainforest at El Verde. Within the next year, a mathematical model of Fig. 1 will be programmed for a computer, so that with a given input of fallout of stable or radioactive isotopes, concentration in any compartment at any time after the input can be computed. Studies relevant to the model, that were completed during the last year by the Terrestrial Ecology Program follow. Transfer of Stable Isotopes by Water Water is a principal means of isotope transfer in the ecosystem, as shown in Fig. 1. Concentration of stable isotopes was measured in the water fluxes given in Table 1, and multiplied times the volume of these water fluxes to give total weight of elements moved. Rainfall was collected in plastic barrels on the top of a tower 12 feet above the top of the canopy. Throughfall was collected in similar barrels placed on the forest floor. Collars around trees to collect stem flow were made with polyvinyl tubing and sealed to the trees. The tubes led to collection barrels. Water moving out of the litter and through the soil was collected with "Tension-free" lysimeters (C.F. Jordan, Soil Science 105: 81-86). Runoff water from the Sonora

River between storms was taken directly from the river. Runoff water from the river during storms was collected in plastic bottles placed on the bank at a level of about one foot higher than the normal river level. When the river rose, the bottles filled, and when the river receded, the water could be collected. Collections were made once a week. Weekly water samples from each separate collector were pooled proportionately to the amount of water collected. For example, 1/500 of the weekly volume of throughfall collector number three gave a reasonable-sized sample for analysis. Therefore, every week, 1/500 of the total amount of water collected in throughfall collector no. three was poured into a plastic bottle labeled "throughfall collector no. three". At the end of the month, the pooled samples were analyzed for conductivity with a conductivity meter; Ca, K, Mg, Mn, Fe, and Cu by atomic absorption, and Na by sodium electrode. Due to various problems, not all the elements could be analyzed every month. All the concentrations of one group of samples (for example, all the throughfall samples) were averaged each month, and the standard deviation was obtained. While it is desired to give the reader an indication of the variation in samples, a listing of averages and standard deviations consumes too much space. Therefore, for each group for each month, the standard deviation was taken as a percentage of the mean concentration. Then the 12 percentages for the year for Ca, Na, and Mg were each averaged, and are shown in Table 2. Rain shows a fairly high

variation in the calcium samples. This was probably because the concentrations were near the lower limit of detection. For example, the same sample could give a concentration of 0.1 ppm in the first reading and 0.2 ppm in the second, resulting in an average concentration of 0.15 with a standard deviation of 0.071, 47 percent of the mean. Stem flow shows a very high variation between samples. Last year, Jordan (1968, The Rain Forest Project Annual Report) showed that larger trees generally have a higher concentration of isotopes, especially trees of the species Dacryodes excelsa. Variation in runoff is lowest, as might be expected, since samples are taken in virtually the same spot at the same time, while other samples are taken over a wider area. Concentrations of isotopes in the various water fluxes can indicate certain things about the isotope cycles. Concentrations of Ca, Na, and Mg were compared in water from the A horizon (5 in depth)

and B horizon (20 in depth), in river runoff during high and low water levels, and between the B horizon and river runoff. Average monthly concentrations are shown in Table 3 and, utilizing analysis of variance (Table 5), no differences can be shown between the A and B horizons, the low and high levels, or between the B horizon and the high water level. However, the ranked sign test showed a difference at the 5 percent level between low water and high water for Ca and Mg (Table 6). In this case, the signed rank test might be slightly more sensitive than ANOVA, because while there are moderate month-to-month variations, the concentration in the low water is usually just slightly higher than the high water concentrations. Since sodium is a more mobile element than Ca and Mg, it is not surprising that it is not diluted by rising water, whereas Ca and Mg are. ne ---Page Break--- Table 2. Standard deviation as a percentage of mean concentration. Percentage Samples, Ca 34 5 Throughfall 45 3T 6 Stemflow 87 ST 9 Out of litter 3h 35 39 Through mineral soil 3T 49 Run off ab

9 a ‘Table 3. Concentration of elements in water collected from the A horizon (5 in. deep) and B horizon (10 in. deep) of soil in the rain forest near Hl Verde, Cones sintion oe te ost. 1967 ke 16 ko m6 ers, 1967 ot 8 35 BS a Dees, 1967 186 6h 58 a Jan. 1968, oe 68 60 6S Fer. 1968 a3 89 ws ae La a mary 1968 Moe wear fe far, 1968 Lr 6 Th 60 aan Lo ayy 1968 neo 28 38 2 8 de, 1968 os Bas 0 aay, 1968 ob 06 18 ae 6 9 be) 1968 Cd 2g MS 2 » Bert, 1968 LL 10 aT 5h ---Page Break--- Lo 60 an sh st oz go6t ‘*3d08 ro 90 &9 9s ort ot eget “SRY et at ve st 60 ot eget “Arne £0 vo gt ae aT ve 996t ‘ome 20 60 ot ae oT vt 996t “Aad UT ot we sh ge ae g96t (dy ot at UE ez ez sz 996t “TH vt gt ve he ve oe g96t ‘a0E sro 20 on sn at ot gg6t fruee sto ero €9 ay at se Ag6t £1990 so sro oe oe ot at 1960 «Aon 20 sto ors on st ore Ag6t °390 xeqvaaay08 soqvaoqan s9y0A equa ‘ry__not yore oT wiry AoT oF =(sazoqe woangaq) TeAot xoqeA ACT Supp pe (eutoge SUMP) TeAS soon wiry Burm saKhy exopeIOg aun wAy yoRoeTTOD HOGeM UF SquDLeTS go WoRIeeUS, + oo 6. ---Page Break--- Table 5 me moet DFS. uemicteimitione mart sak ws eer ee Abert te tee i i i i peeareareeroarcae & an Dk Aer te owe ---Page Break--- Although there is a lower concentration of dissolved Ca and Mg when the river is high, the river also carries suspended soil material when it is in flood stage. This soil material represents loss of Ca and Mg, but it is probably a loss as a result of erosion of the riverbed, and does not represent material being carried away from the vicinity of the roots. The fact that there is no difference in concentration of elements in water moving through the soil at the 5 in. level, the 10 in. level, and river runoff indicates that all the isotopes which are recycled by plant roots are taken up by the roots before the isotopes reach a five-inch depth. This evidence is in agreement with the hypothesis of Went and Stark (BioScience 18, 1035-1039) who feel that in the tropics, elements are transferred directly from litter to roots by mycorrhiza. Total amount of

Isotopes moved by rain, throughfall, stemflow, out of litter, through mineral soil (average of A and B horizons) and runoff (high water only, since that is when the bulk of runoff occurs), were calculated by multiplying isotope concentration in each flux times the volume of the flux. Units are: (Volume of flux) (concentration in pm) Quantity of isotope moved 6 v 10° grams of water equivalent to 1 3 Z 7 a5 /na/ie) (e/n3) Relative 1000 Total amount of isotopes moved is given on a weekly basis since collections were always made on the same day of the week (Monday). Such weekly collections result in some months with four full weeks and some with five full weeks. A month with five Mondays but only 30 days would then have an error of about 14 percent, if there was a monthly base. Although in reality the rain falls in discrete storms, it is more practical to calculate results on the basis of a steady continuous drizzle throughout the year. Then the total moved for each week is a rate function, and the total amount for each month can be calculated by multiplying rate times the number of weeks plus tenths of a week per month. Rainfall is measured above the canopy with a

standard U.S. Weather Bureau recording rain gauge. Throughfall is measured in 12 collectors on the forest floor, each measuring 5 ft, by 2 in. by 12 in. Jordan (1968, The Rain Forest Project Annual Report) estimated stem flow to be 18 percent of rainfall, and transpiration to be 105 m3/ha/wk. Evaporation from the soil surface averages 2.5 m3/ha/wk (Odum and Jordan, A Tropical Rain Forest, in press). Water moving through litter equals throughfall plus stemflow minus evaporation from the surface. The same amount of water moves through the mineral soil as out of the litter. Most of the mineral soil lysimeters collect more water.

than the litter layer lysimeters except on ridge tops, where amounts are roughly equal. This phenomenon is caused by the subsurface flow parallel to the sloping soil surfaces described by Jordan (1968, The Rain Forest Project Annual Report). Runoff reaching the river is equal to throughfall plus stem flow minus evaporation minus transpiration. Centimeters of water flux is quickly converted to m^3 water/ha/wk by the relationship (cm water/wk)(100) = m^3/ha/wk. Fig. 2 shows m^3/ha/wk of rain on a monthly basis for the study period. kg/ha/wk of isotopes moved by the fluxes on a monthly basis are given in Tables 7-12 and Figures 3-6. Ca, mg, and na moving out of the litter follow the trend of rainfall; the more rain, the more loss from the litter (compare Figs. 3, 4, and 5 with 2). Input of these isotopes into the system via rain does not follow the rainfall pattern. Highest inputs occur around December and January and are probably more closely associated with the frontal passages that occur at that time of year than with the total amount of rain. Gains and losses of isotopes to the ecosystem are calculated by subtracting the rate of loss by runoff from the rate of input by rain (Table 13 and Figs. 7 and 8). The largest loss from the system occurred during the heavy rains of May, and gains of na and ca around December occurred as a result of the high inputs during that time. Total yearly difference between input and runoff is presumed to be made up by weathering of parent soil material. Element Concentrations in Ecosystem Compartments Leaves, wood from trunk, roots, soil, litter, and organic matter in the forest were sampled to determine stable element concentration in each compartment. Concentration, when multiplied times biomass of the organic components, gives the total amount of elements in each compartment. Biomass of the leaves, trunks, and roots will be calculated from the regressions in Odum (A Tropical Rain Forest, In Press). Biomass of the freshly fallen litter will be taken from the data of the 55 litter collection stations.

which are sampled monthly. Biomass of the partially decomposed organic material was measured by collecting 300 square meter samples, drying, and weighing them. Average weight was 360 grams per square meter, with one standard deviation of 176. Concentration of elements in the soil extract will be multiplied by the weight of the upper layer of soil (Table 14). -10- ---Page Break--- ————————___ after one, 1967 . ap. on above, 2967 a oto 16 ees, 1967 8 aah a0 a san 1968 1 0 19 on Fea, 1968 5 0.36 0.35 oat mas, 1968 3 0.9 0.88 a Aer 1968 8 0.2 1.00 aa 209 ey, 1968 » oat ak on on ne, 1968 ‘ 065 099 0.6 7 1.8 000 say, 1968 1 om 0.tT . 6 doa. 1968 3 0.30 1.06 . 0s Sept. 1968 5 sp 10 02.038 e000 018, ‘early average 8.00 Ae nd 0.35 0.095 1.8L 0.012.000 013 cet. 1961 8 oat Lk ost or 2961 » 08 16 95 dees, 1961 wo 0.70 1.68 295 an. 1968 » oth 2.03 3 Fe. 1968 8 og 0.5 a0 mar. 1968 3 01 1st 286 nor. 1968 3 om 1st 288 0. ny, 3968 8 oab 0.8 ato oor ane, 1968 » 05h 0.53 1.86 035 1.98 005 aay, 1968 » oat 0.33 . 200 tog, 1968 8 onto 0.6 208 009 septa, 1968 9 ob 0,88 1.23 10 00.013 O15 early average 1058 OME 2.228 1.5 ah Ligh ook 01S IS -1- ---Page Break--- mae 9. Bee. 1968 » mer. 1988 a pe, 1968 » May, 1968 a ae, 1968 2 July, 2968, ry bea, 1958 6 Bape. 3968 % early average 08 afte oom Kom PF oe 0.30 03 0.5 0.36 2 as 0.30 028 08 ots 055 0s ons 08 06 0.50 08 010 0.00 0g oak 0.30 er oak 0.23 1.50 016 0.78 oa 0.08 . ons . 0.25 Ler .0@ 0.29 1.38 0.009 0.18 0.83 1s ae 282 2.06 1.88 16 136 Lw 6 1.08 sts 29 89 333 3 3.03 aes ATs aah us aor 0 1.6 “ der 139 te eae 113 0.656 BEREBRE 68 632 Inte cf movement of elements by

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090 ost. 1967 Yor. 1967 bres, 1967 Jan. 1968 Fe, 1968 Mars, 1968 dor, 1968 ay, 1968 sme, 1968 say, 1968 tog.» 1968 Sept, 1968 ‘Yearly average ovat soluble sale o 1 ot w 0.96 ‘ ote a 0.88 » 0.32 5 on ry 0.6 2 ase ve ont 6 Ler 6 1.08 0.29 0.83 aat 130 ate 0.08 ae 0.88 2aT aoe 135 aar 0.4 2b 13+ 5 a 3 as 0 0.7 ath 2 2” 0.10.23 0.t0 0.29 ase 2.52 000 BRB 203 008 og wo ---Page Break--- — RAIN 3] 1 OUT OF LITTER — THROUGHFALL STEM FLOW I = 52 3 z c e OcT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP Fig. 3. Average rates of calcium movement through the ecosystem. x = S ¢ z < > = ° @ g OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP Fig. 4, Average rates of magnesium movement through the ecosystem, ---Page Break--- — RAIN THROUGH FALL sl eT STEM Flow — —1— OUT OF LITTER \ KG of No /HA/WK OcT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP Fig. 5. Average rates of sodium movement through the ecosystem, —e— OUT OF LITTER THROUGHFALL — pan 4oF\ Stem FLOW A KG/HA/WK, TOTAL SOLUBLE SALTS wo AS OND JFMAMJJAS 1967 1968 6. Average rates of movement of total soluble salts ‘the ecosystem. Fig. 6 through a15- ---Page Break--- Table 13, Met monthly rates of element gain and loss from ecosystem, determined by subtracting rate of loss by runoff from rate of input by rain, oct., 1967 125 +aT +.02 Tov. 1967 -.56 4.16 2h Dec., 1967 +452 +12 ol Jan, 1968 2h +436 “5 Feb. 1968 +08, +01 406 Mar. 1968 -.62 =136 7.25 Apr. 1968 kT +e 216 May, 1968 -LuT 71.33 -5T June, 1968 12 012 nal duly, 1968 os 1.08 =.25 ‘Aug. , 1968 ~ -a +239 Sept., 1968 +001 +256 <16- ---Page Break--- KG/HA/WK OcT NOV DEC JAN FES MAR APR MAY JUN JUL AUG SEP g. T. Rates of gain and loss of isotopes to and from the ecosystem. hose iS KG HA WK, TOTAL SOLUBLE SALTS ae MJJASONDJFMAMJ JAS 1967 1968 Fig. 8, Rates of gain and loss of total soluble salts to ‘and from the ecosystem. aT ---Page Break--- gVP4 HET = czoryat = £570 x CODES Hoots 4san0g 30 gu/B = gHo/B x “TOA @ o00'HEz = gD OOOOT x "HO H°EE Hoots aeaHos Jo zi 40d Tos Jo oAST seddn 50 “toa = at T x wadap a9uraKe Co ar 3 £50

ez 69 F Hee seats TT « Lot ¥ 192 equa UOTAVTPEE or ar F Lao 4 OTE le (su073, -rpuoo TyO8 poonpat) SqULE pus sOTTEA ot ov F 20'r or 60° ¥ 1S*0 co T9Fe'te —— (suoTaTpUOD TTo8 pezTpTx0) se8pTa suoyyearosqo —Ayysu0p suoygearoego Ayyetep — suoyyeaxosqo “to 30 “OH ara Jo “on rng 30 ‘ON ‘uadap emazane oparano aeuroK9 Thor Fo RT TT ‘soya some ed Tr08 Jo s926t sadn 30 4uGen pu ‘Ty08 Jo eeTareuep ammq pe Yadeq at stam, ---Page Break--- ALL elements were analyzed by atomic absorption spectrophotometry. Leaves, wood, roots, organic matter and fresh litter were prepared for analysis by the following procedure: 1) Put 2 grams of plant material into a 50 ml beaker. 2) Burn in the furnace at 250°C for 3 to 4 hours. 3) Increase the temperature to 450°C and ash for 12 hours. 4) Let cool, add 5 ml of concentrated HCl and evaporate to dryness (Don't let boil). 5) Let cool; add 25 ml of 0.1 HCl and stir. 6) Let sit for 30 minutes. 7) Stir again and filter through Whatman No. 1 filter paper (Do not wash filter paper). 8) Run for Co, Cu, Fe, K, Mn. 9) For Ca, Mg, and Sr dilute 1:1 with a solution 2% La; 1000 ppm K final concentration of La should be 1 and K 500 ppb. 10) Divide every reading by scale expansion, if any, and convert to absorbance. 11) Prepare a standard curve for absorbance (1) vs concentration in the samples and multiply by dilution factor, if any. Note: Same procedure as above is used for the complete analysis of organic matter, except for Sr, which has to be analyzed using the method of additions. Elements were extracted from the soil for analysis by the following procedure: 1) Weigh 2.00 grams of ground, oven-dried soil into a 50 ml plastic centrifuge tube. 2) To the soil in

the tube, add 15 ml of 1 N NH4OAc and shake at full speed for 30 minutes. 3) Centrifuge at full speed for ten minutes. 4) Decant and save the supernatant. 5) Add another 15 ml of NH4OAc and shake again at full speed for 15 minutes. 6) Repeat step 3. 7) Decant, adding supernatant to the supernatant.

from step 4. 8) Repeat steps 5, 6, and 7. 9) Make a total volume of 50 ml. with 1% NH4OAc. 10) Filter through Whatman 40 filter paper. 11) Run for Cu, Fe, K, Na. 12) For Ca and Mg, dilute 1:1 with a solution of 2% La; 1000 ppm K to obtain a final concentration of 1% La, and 500 ppm K in the sample. 13) Divide every absorbance by scale expansion, if any, and convert absorbance. 14) Prepare a standard curve of absorbance (Y) vs concentration (x) with the standards. Determine concentration in the samples and multiply by dilution factor, if any. “19+ ---Page Break--- Since available elements in the decomposing organic matter may be important in the element cycle, an attempt was made to get an indication of what quantity of elements were available for immediate uptake by plants, as well as total elements as determined by the combustion technique. Therefore, an extraction procedure for the organic material was used, similar to the extraction procedure for the soil. It is as follows: 1) Put 4.00 grams of oven-dried organic matter into a 50 ml. plastic centrifuge tube. 2) Add 20 ml. of 0.1 M HCl and shake at full speed for 30 minutes. 3) Centrifuge at full speed for ten minutes. 4) Decant and save the supernatant. 5) Add another 20 ml. of HCl and shake again at full speed for 15 minutes. 6) Repeat step 3. 7) Decant, adding supernatant to the one from step 4. 8) Repeat steps 5, 6, and 7 until the extracting solution (HCl) stays clear after shaking. 9) Filter through Whatman 40 filter paper. 10) Run for Co, Cu, Fe, K, Mn, Na (dilute, if necessary). 11) For Ca and Mg, dilute 1:1 with a solution of 2% La, 1000 ppm K to obtain a final concentration of 1% La, and 500 ppm K in the sample. 12) For Sr, use the method of addition, in which a standard is added to the sample; two equal volumes of sample are diluted in a 1:1 proportion, one with a known concentration standard prepared in 2% La, 1000 ppm K, and the other with just a solution of 2% La, 1000 ppm K. Compare the absorbance of the two samples using the following proportion.

Concentration sample Cone, sample + Conc. standard ‘Absorbance sample ‘sAbsorbance of Sample + standard) solving the proportion for Conc. sample, Asample C standard Cone. °: (GS Se eee sample A (sample + standard) - A sample 13) Divide every $A by the scale expansion, if any, and convert to absorbance, 14) Prepare a standard curve of absorbance (1) vs concentration (X) with the standards. Determine concentration in the samples and multiply by dilution factor. ‘The sampling scheme was designed so that the following statistical tests could be made: 1. Soil, for difference in sites, 2. Soil, for difference in depth. 3. Tree trunks for difference in species. ---Page Break--- 4. Tree trunks for difference in sites. 5. Freshly fallen litter for difference in season. 6. Organic matter for difference in sites. 7. Leaves for difference in presence and absence of epiphylls. 8. Leaves for difference caused by location in ‘canopy or understory. ‘The exact sampling scheme is shown in Table 15. All statistical tests were made with the analysis of variance technique, except for the leaves, where it was necessary to use a non-parametric sign test. Results Leaves with epiphylls contained greater amounts of Co, Ma, Fe, Sr, Ca, and Mg (Table 16). Presumably this is because when rain containing these elements enters the canopy, the elements are more efficiently bound to the leaves when epiphylls are present. It is not surprising that the epiphyll covered leaves did not contain more K and Na, since these are very mobile elements and are less likely to be bound by the epiphylls. It is surprising that Cu showed no difference. Perhaps there is no significant input of Cu via rainfall. Pulicoures riparia was excluded from the tests, because in many cases it showed tendencies opposite to that of the other species. ‘There is a tendency for understory leaves to be slightly higher in element concentration than canopy leaves

(Table 16), but the differences are not great enough nor consistent enough to be statistically significant.

Averages and standard deviations of element concentrations in leaves of each category are given in Table 17. Differences in element concentrations between species are very great in some, but not all, species (Table 18). However, differences are sufficient for each species to require different treatment in the model. Calcium differences between three species were checked, and the differences are highly significant (Table 19). There were no differences in six element concentrations in Dacryodes between sites, but there were differences in Mn, Mg, and Na. Therefore, the sites were checked again for these elements using Manilkara. Magnesium showed a difference, so it was checked again in Sloane. There was a difference between sites (Table 20). For purposes of the model previously discussed, we can assume no difference between sites. There are apparent differences in concentrations of elements in the roots of the various species (Table 21).

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Table 16 Results of sign tests to test differences in element concentration between leaves with and without epiphylls, Palicourea riparia excluded, and between canopy and understory leaves.

Element	Clean leaves vs. leaves with epiphylls	Canopy leaves vs. understory leaves	nr level of confidence	nr level of confidence
K	95%	99%
Fe	95%	99%
Cu	95%	99%
Sr	99%	99%
Mg	95%	99%

* Clean leaves are higher in potassium.

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Table 17 Averages and standard deviations of element concentrations

in leaves of each category. All values are parts per million. Dacryodes excelsa canopy clean leaves (n = 3) co Mn Fe 6.39 + 2.42 3.42 + 1.37 6.79 + 1.82 cu K Na 2.76 + 0.12 1.37 + 0.67 1.48 + 0.19 sr ca % 8.2 + 1.01 3.32 + 0.64 10.67 + 1.05 Dacryodes excelsa understory clean leaves (n = 4) co Mn Fe 2.90 + 2.22 2.95 + 0.79 0.89 + 0.16 cu K Ta 5.15 + 2.87 0.67 + 0.15 1.70 + 0.77, sr ca % 6.45 + 2.54 3.71 + 0.69 1.83 + 0.12 Dacryodes excelsa canopy leaves + epiphylls (n = 3) co Mn Fe 5.02 + 2.21 3.81 + 1.81 1.02 + 0.36 ou K Na 2.66 + 0.18 9.81 + 2.83 17.00 + 3.68 sr ca % 10.2 + 1.8 45.29 + 8.33 12.22 + 2.05 Dacryodes excelsa understory leaves + epiphylls (n = 4) co Mn Fe 4.39 + 4.34 1.20 + 0.26 0.00 + 0.00 ou K Na 2.72 + 0.26 12.09 + 1.89 15.29 + 0.68 sr ca % 12.8 + 2.96 51.73 + 4.53 13.20 + 2.32 ---Page Break--- Continued Table 17 Yantlkara bidentata canopy clean leaves (n = 2) co Mn Fe 0.80 + 0.22 3.34 + 1.2 0.00 + 0.00 ou K Na 4.95 + 0.64 26.56 + 1.2 31.50 + 3.64 sr ca % 22.6 + 16.1 49.91 + 5.82 20.19 + 3.00. Yantikara bidentata understory clean leaves (n = 4) co Mn Fe 4.78 + 4.84 3.24 + 1.36 0.00 + 0.00 ou K Na 8.00 + 2.59 36.63 + 10.99 13.85 + 2.116 sr ca % 30.7 + 3.1 66.51 + 20.47 30.80 + 5.06 Yantikara bidentata canopy leaves +

epiphylls (n = 2) co Mn Fe 8.25 + 0.36 9.00 + 8.42 0.00 + 0.00 ou K Na 0.00 + 0.00 0.00 + 0.00 0.00 + 0.00 sr ca % 38.5 + 10.5 64.96 + 5.3 26.47 + 2.0 Yantikara bidentata understory leaves + epiphylls (n = 4) co Mn Fe 4.96 + 3.58 4.56 + 0.53 0.00 + 0.00 cu K Na 1.85 + 0.08 13.59 + 3.23 38.28 + 2.589 sr ca % 0.00 + 0.00 80.70 + 16.90 35.39 + 5.02 ---Page Break--- Continued Table 17 Sloanes berteriana canopy clean leaves (n = 2) co Mn Fe 4.39 + 1.32 5.55 + 0.00 0.00 + 0.00 ou K Na 9.10 + 6.50 22.24 + 9.22 51.00 + 18.0 sr ca % 16.4 + 9.4 56.98 + 43.69 20.08 + 6.08 Sloanes berteriana understory clean leaves (n = 5) co Mn Fe 4.70 + 3.29 1.50 + 0.85 0.00 + 0.00 ou K Na 10.22 + 3.10 28.00 + 6.07 68.50 + 19.7 sr ca % 25.38 + 4.65 45.87 + 7.97 15.96 + 1.52 Sloanes berteriana canopy leaves + epiphylls (n = 1) co Mn Fe 5.20 + 0.00 0.00 + 0.00 0.00 + 0.00 cu K Na 0.00 + 0.00 0.00 + 0.00 0.00 + 0.00 sr ca % 0.00 + 0.00 26.78 + 0.00 Sloanes berteriana understory leaves + epiphylls (n = 4) co Mn Fe 5.35 + 4.95 25.54 + 12.1 0.00 + 0.00 ou K Na 5.32 + 1.50 19.79 + 0.00 0.00 + 0.00

359 1135 + 22h Sr ca Me 24.0 + 4.95 THB + B43 2039 + 185 ---Page Break--- Continued Table 17 Palicourea riparia clean leaves (n= 5) co ry Fe 7.32 £3.24 1Th 93 he iy cu K Ya 13.96 £3.78 4596 + 954 2202 #1062 Sr ca Me U8 ¢ 32 1092T + 983 5300 + 523 Croton petiolatus clean leaves (n = 1) co Mn Fe 2.87 828 8 ou K No 8.8 5250 6130 sr ca ¥e st eet Hoel Palicourea riparia leaves + epiphylls (n = 5) Co. Yn Fe 7.32 £2.95 ll+ 68 277 + 126 ou K Na, 18.98 418.25 3171 41228 5344 41012 sr ca, Me aah + 53, 10368 sukgh 5239 + 803 Croton petiolatus, leaves + epiphylls (n = 1) co Mn Fe 3.37 1204 a cu x Ma 6.0 3202 8025 sr ca Me 68 8586 eB -21- ---Page Break--- ——_ Continued Table 17 © 115 w.2 Sr 23.7 Butterpea globosa clean leaves (n=1) Ya Fe 305 23 x Yo 4387 926 ca % wt20 2958 Butterpea globosa leaves + epiphylls (n=1) © Me re 4.87 06 22h ou x me 12.5 2665 315 sr ca % 19.6 3981 ‘687 Table 18 SS ‘Averages and standard deviations of concentrations of elements in tree trunks POPE R RE 5.62 wo 29 178 258 3.38 ats has, ah ale m3 na 188 31st a8 wah 33 48 25 3.36 as ast 90 m & 2 = 33 £388 3.502 200 29 tL 5502 AB tr BT Tt 39 rw Leos art uss hae we: sete ase wet ca wot art ba 15 1.80 + 0.50 83 + wt ee 6 set we ao 20 oh 2.98 6 aus aa cc ---Page Break--- Table 19 Results of analysis of variance to test differences in concentrations of calcium in wood, between species. F Level of significance Tested - Shecten Element of ratio fleant Differences Species - De-De ca 1/38 3h.o 9.8 Mao ca 1/38 12.0 9.58 . De-Sb ca 8 06 9 Table 20 Results of analysis of variance to test differences in concentrations of elements in wood between sites. mm./tence, PF Level of significance tested Species © Element of ratio ratio cant difference sites be ca bas wer a . De x aps 158 - 0 be c 4As 1.88 e . De % aps 1.80 9.56 . be Br aps ua a . De % As 6.22 9.58 . be re aps 1.8 5 0 be ca eho 0.00 o . be Ma ans 2.62 sof . me a aps 1.53 - . Ys % aps abe sot . % Ma aAs 0.62 - . > 6 4s ade S ---Page Break--- Differences in element concentration in the soil

extract very tested, between the five well-drained sites, and all six sites including the poorly drained site. Differences between sites occurred only in Mn and K (Table 22) for the soil 0-2 inches deep, but these differences occurred within the well-drained sites, and not necessarily between the well and poorly drained soil. However, with soil from the 5-7 inch level, differences between the well and poorly drained soil existed for Mn, Ca, Mg, and Sr (Table 22). Since differences increase with depth, differences are likely to be caused by differences in parent material. There are differences in element concentration between the 0-2 and 5-7 inch level for Mn, Ca, Mg, Na, and K. Iron, Cu, and Sr appear to be equally distributed in the soil down to the 7 inch depth (Table 22). Average and standard deviations of concentrations of elements in soil extracts are given in Table 23. Concentrations of exchangeable and total elements in the organic material are given in Table 24. In the extractable elements, there is a difference between sites only in Mn and Na, and for the total elements, in Mn and Co. There is a strong difference between total and extractable elements for all

but Sr (Table 25). Seasonal differences in freshly fallen litter exist only for Na and Mn (Table 26). Exceptionally high sodium concentrations occur during the January collection. This coincides with high sodium input to the ecosystem via rain during January. Manganese is low in the litter in the May collection. Yearly averages of elements in the litter are given in Table 21. Table 21 Average and standard deviations of concentrations of elements in litter, and the results are summarized as follows. The results show that the sodium concentrations are notably high at certain times of the year. The analysis also indicates the variation in element concentrations across different sites and depths, highlighting the importance of soil drainage characteristics. ---Page Break--- Table 22 Results of analysis of variance to test

soll differences between sites and depths. Depth, un./aencn. Level of significance. Tested inches Element F ratio significant difference: all sites 0-2 Mn 5/18 2.64 90% 5 well-drained sites 0-8 Ya ins 3.08 95% all sites 0-2 ca 5a 1.01 - non 0-8 Me 58 2.09 - nos 0-2 Fe 5s 1.88 = B 0-2 ou 5/8 1.00 : 0-2 Sr 581.55 5 0-8 Xa ip 0.55 = as 0-2 K 5s 3.28 95% 5 well-drained sites one K As 3.38 95% all sites 5-1 Ma 5182. 90% 5 well-drained sites 5-1 Ma ns 1.60 E all sites 5-1 ca 5fie 22h 8 5 well-drained sites 5-1 ca ins 0.92 : all sites 5-7 My sib 3.96 oth 5 well-drained sites 5-7 Mg is 1.37 5 all sites 5-1 Fe sb 8.67 oot 5 well-drained sites 5-1 Fe ins 9:16 59% all sites 5-7 cu 5/18 0.50 = all sit 5-1 Sr 5B 3.05 95% 5 well-drained sites 5-1 sr ins 0.150 fs all sites 5-1 ia ya ong : all sites 5-1 K sng 0.9 a Ma a6 00 99% ca Ue +23, 91% " Mg 1/6 75, 99% Q Fe 3/6 35 es o ca ane 25 : G Sr ase 32 : G Ta ifs 6 90% " afu6 50 9% Be ---Page Break--- Table 23, oo i Fre evaes Averages and standard deviations of ou x % Re oo % se me 155 Table 24 Se concentrations of elements in organic matter on top of soil, Pacts per million 29 a ° ‘8 determined by to sethote, Sree Mi\OAe extraction 2.85 + 1.60 2+ at x aa t 30.2 amo + gh em sats 30.9 t Bb wet 5 32 3m ¢ as mot we ht x wart bs nak 2 ono 9.68 fa wee E 25.6 25+ ast aie 30.3 n.6. 16.5 x 105 a6oe 32 a & 1.29 3.06 o& out as ---Page Break--- Table 25 Results of analysis of variance to test differences between sites, and between analytical methods, for organic matter on top of soil. tun./denom, F Level of significance- Tested Element F ratio" ratio significant difference All sites, extractable elements BRE OTR Re elements SERESTE Re orennnns A 8 gw HOTEL e * ” sr 2/38 2’ R38888 ---Page Break--- Table 26 Results of analysis of variance to test differences in monthly concentration of elements in freshly fallen Litters Ma/aenoe. oP Level of estea Rest P'iatio” ratio gaan alge Month (San. 5 Mars, May July, Sept, Nov. 5 ca sh 0.50 - some ee = . Ar . wee ee = on 4 e+e» « a s a . some ee o . a . Month

(Jan., Mars, Suny, Hoy.) ne 3/6 2.32 - rar x = a . hoe ee Ss . oO - she m . ser 98 oo Table 27 ‘averages an stantant deviations of concentrations ‘of elements in freshly fallen litters est Parts per million © 8.52 ¢ 6.10 a Mbt oot % mt o 5.72 © 30 m 05 or os ce sick % 2200 ots * Ne ag asse 33 ---Page Break--- ne ak 1b. TRANSFER AND STORAGE FUNCTIONS FOR STABLE AND RADIOACTIVE ISOTOPES IN ‘THE TROPICAL RAIN FOREST ECOSYSTEM Input of isotope into system by rainfall is a function of volume of rainfall times concentration of isotope in rain. Isotope movement by throughfall is a function of volume of throughfall times concentration of isotope in throughfall. Isotope movement by stem flow is a function of volume of stem flow times concentration of isotope in stem flow. Isotope movement by leaf fall is a function of biomass of leaf fall times concentration of isotopes in undecomposed litter. Isotope movement from litter to soil is a function of volume of water leaving the litter times concentration of isotope in that water. Isotope movement through the soil is a function of volume of soil water times concentration of isotope in soil water. Isotope loss through runoff is a function of volume of runoff times concentration of isotope in runoff. Loss of isotope through sediment movement is a function of the volume of water during flood stage times concentration of sediment times concentration of isotope in sediment. Turnover time of

isotope in canopy is the biomass of the canopy times the concentration of the isotope in the canopy divided by the loss rate from the canopy. Turnover time of isotope in the understory is the biomass of the understory times the concentration of the isotope in the understory divided by the loss rate from the understory. Turnover time of isotope in the litter is the biomass of the litter times the concentration of the isotope in the litter, divided by the loss rate from the litter. Increase of isotope in biomass of canopy is a function of the rate of canopy increase times concentration.

of isotope in the canopy. Increase of isotope in biomass of stem is a function of the rate of stem increase times concentration of isotope in the stem. Increase of isotope in biomass of roots is a function of the rate of root increase times concentration of isotope in the roots. Transfer rate from epiphyllae to leaves determined by tracer experiment. 35+ ---Page Break--- 16. Transfer rate from canopy to root through phloem determined by tracer experiment. A. Transfer to roots calculated by subtracting loss from ecosystem from total movement into litter. Influence of Species, Site, Canopy Position, and Epiphylls on Fallout Distribution To construct a model which will predict pathways, rates, and turnover times of stable and radioactive isotopes in the tropical rain forest ecosystem, it is necessary to understand inputs to the system. Fallout, of course, is an important input. Once fallout is carried into the ecosystem by rain, a variety of factors might influence its subsequent behavior. The study tests the importance of four of these factors: species, site, location of leaves in canopy or understory; presence or absence of epiphyllae on leaves. The sampling plan was to take one sample of leaves heavily covered with epiphyllae, and one sample devoid of epiphyllae from the topmost of the site; on from the bottom-most understory leaves of three species of five sites. In addition, clean and epiphyllae-covered leaves were also sampled. It was difficult to find and reach all the desired samples at all three sites, so suggested samples were obtained (Table 28). Two additional species were sampled at a sixth site for additional comparison (Table 26). Samples were oven-dried, and counted in bulk by gamma scintillation spectrometry. Data were corrected by computer solution of simultaneous equations. Comparisons between sites, species, canopy position, and presence or absence of epiphylls were made using 137Cs, Li, and 95Sr. First, averages of 137Cs, Li, and 95Sr were calculated for the canopy and understory, for clean and

epiphytic covered leaves, ty, egesin and site (Tables 29-31). Then differences were tested by analysis of variance Schemes for aspects, rates, clean vs. epiphytic cover, and range Posteriority (Table 32). Differences at the level of error or none found between species for 1370s and lilice on clean understory leaves, and Crescent species for all isotopes on epiphytic covered understory trees (Table 5). Since tables 2, 3 and k show that average levels or fence on Fulicourea riparia are most different from the rest, species in the wide Har” He Gin eteed for differences, this time without, Pulsatres sia- Hig, no difference between other species was evident. The ee ee difference between species in the canopy, two differences between sites, out of the 12 tested (table 32), were significant. This is not enough to state that there are differences between sites. ---Page Break--- Table 28. Actual sampling scheme for determining fallout distribution. Montara Sloanea *Palicouren Buterpe _Croton Bidentata berterfana —iperia globose poecflantius canopy + epiphyll x x Site 1 understory clean x understory + epiphyll x x x canopy clean x x x canopy + epiphyll x x = Site 2 understory clean x understory + epiphyll x canopy clean canopy + epiphyll. Site 3. understory clean understory + epiphyll x x x canopy clean canopy + epiphyll Site 4 understory clean x x x x understory + epiphyll x x x x canopy clean canopy + epiphyll Site 5 understory clean x x x x understory + epiphyll understory clean gq Site 6 understory + epiphyll. x understory species -3T- ---Page Break--- Je 2. Influence of species, site, canopy position and epiphyll on “7'Cs distribution. Average values are picocuries per ee. Understory Mean leaves Leaves plus epiphylls on Heats __Leaves plus epiphylls " 1 et. deviation " Site 1 3 3.03 2.02 2 Site 2 3 2.59 2 Site 3 3 3.8 0.22 3

Site 4 3 3.59 1.30 3 Dacryodes excelsa w 3.62 2.9 4 Manilkara bidentata = 3.73 0.90 4 Sloanea berterfana = 33.88 on 2 Fulicourea riparia = 55.65 159 5 Canopy Site 2 2 2.62 0.67 3 b.80 0.48 Site 2 3

3.03 0.55 3 123 Bite 3 i 36 + 2 wT : Dacryodes excelsa 3 3.50 0.35 3 kage 0.50 Mantikara bidentata 1 © 218h 2 2 3:5 0.92 Sloanea berteriana = 22.37, 0.32 2 kt 0.80 =38- ---Page Break--- Table 30. Influence of species, site, canopy position and epiphytes on "Average values are picocuries per gram, under leaves plus epiphytes" x deviation 1 st, deviation Bite 1 3 2.38 1.26 2 6.46 Site 3 2 2154 2125 2 W10 site & 3 LIS 0.08 3 wat Bite 5 3 0.63 0.86 3 49 Dacryodes excelsa ath 1.72 » Beta Mantikara bidentata 1:09 0.162 4 465 Sloanea berteriana = 3 a5 0.87 2 4gT Falicoures riparia 5 6.59 3.26 5 15.88 canopy site 1 2 2.92 ak 3 5.99 LAS Site 2 3 21h6 2:70 3 619 6205 Site 3 L 8.06 + i ea : Dacryodes excelsa 3 5.19 aT 3 8.19 4.23 Mantikara bidentata 1 ag 0.86 2 an 3119 Sloanea berteriana = 2 ore : 2 5.78 2136 ---Page Break--- Table 32 site 1 Site 2 Site 3 Dacryodes excelsa Sloanea berteriana oor oe. of species, site, canopy position and epiphytes ‘Distribution: mean leaves x ERaT RSE Unters Lat, deviation 0. 3 0, °. 0. 0: 9, 0: BEER BbSE Leaves mx 2 1 2 0.92 3 1:05 3 Lot Bake wong 2 ot 5 kB 3 Las 3 0.196 L139 3 Lp 2 166 2 0.68 ‘average values are picocuries per gram, deviation ---Page Break--- Table 52, Results of analysis of variance to determine significance of differences in fallout, (SR _ ier ee Degg eterno species ‘Understory clean Dey8o, Majop, Pr 3.338 5.10" 2h ape a Ten eae 8 va m9 eee oe e a ee TrogaE™ aaeme aseokA on seiee Canopy, species tem TD ve ee TE meta os tetay, cnn begs she an we haart oe sie site Canopy, clean Dein, 1.20 2.31 2.6 3 Bee cone Pyle ‘De Mn, Bb o.2h 0.16 1.29 of Clean-epiphyll Canopy Dein, Sb 1b. 6e4 2.5 2.83 ya Ceara taaeeiny eR! AY the ve cumyotervioy Cleese OSh th as cumvmtentey ian iglla eka Oa ns = atgnteteant at 5f level + = wtgniticant at 24 level aha ---Page Break--- Table 33. Average values of fallout within and where no significant differences exist: mean Leaves, between compartments st. NK 1 etadeviation » & 122 sites ana toecfggs except Pr, fer Ge. 2337 as

25.30 Fulicomen riparia, for 137s 5 5.65 1.59 5 7.82 Wa sites and cpeclepe exmeyt Pr for hk, ie 1.65 1.27 na 4.50 Pullcopren riparia for se 5 6.59 3.26 5 15.88 2 sites and gpectes, except Pr for Ber" 220.58 0.08 nou Palicomea riperta, for ir 5 15h 0.98 458 canepy man ottes, fpeles furs 6 ga 0.68 1 kst san sites, species for lWige 6 3.54 2.83 647 m2 sttes, aan species for 952r 6 0.79 0.65 T 1.31 le- underst Se eet ____ a a ST 2 stedevtatice La 1B 1.6 hag ob 2.78 0.81 38 0.61 ---Page Break--- There are strong aisteren me erences tetveen clean and eptphyll cover leaves in the unerstony, for ail destopes, and for USPS Ue eee Differences betve “en canopy and understory vere not signtficen Hine (1967, P-R.M.C. Aamual Repore) peported differences teereen eato and understory leaves for 137Co, with the understory leaves higher. Ppl plyll covered teaves in the understory shoved a higher burien than those pas eenonva Cieble 33), but the difference is not significant. Perhaps Fences vere obscured because 1370s levels were lover ty a factor o about 4 from the time at which Kline took his samples. Sr ye tac * Averages values of fallout within and betveen conpactnents vhere x0 significant differences existed are tumarize! In Table 3300 TRITIUM MOVEMENT THROUGH A TROPICAL RAIN FOREST ECOSYSTEM Movenent of tritiun through ecosystem 1s of interest for two reasons: 1) Tritium is a tracer for water, and thus aids in water balance studies of the ecosysten, especially in transpiration stulies. 2) Tritium is a major by-product of thermo-nuclear reactions, and could contaminate the environ~ nent as a result of both peaceful and military uses of thernomclear pover. A series of experinents were undertaken to determine rates at which tritium moves through a tropical ecosystem, and the proportion of tritiun that 1s immobilized and thus becnes 0 long-term radiation hazard in the ecosystem. The experiments vere done in cooperative vith Dr. Jerry Kline, ‘Argonne National Laboratory, ana Dr.

John Koranta and Mr. John Yartin of Lawrence

Radiation Laboratory. ‘The first experiment involved applying tritiated water to a 0.9 sq. meter plot by simulated rainfall, and collecting runoff water beneath the litter and at a depth of five inches. Results were published in Science 160, 550-551, and the 1968 Terrestrial Ecology Annual Report. The second experiment consisted of injecting two Dacryodes excelsa and one Sloanea berteriana with a pulse of tritium, and determining the length of time it took for the pulse to reach the canopy, the residence half-time of tritium in the free water, and the amount of tritium bound in the leaves by photosynthesis. ‘The third experiment was called a micro-systems experiment because it was an attempt to measure tritium movement through all portions of a micro-ecosystem, a plot of 3.7 square meters in the middle of the tropical rainforest. ‘The fourth experiment was a combination of a multi-isotope experiment and a pulsed tritium experiment. The objectives were: 1) to determine if certain gamma-emitting isotopes which are similar to nutrient -13- ---Page Break--- 2) to determine how a variety of elements move uniformly through xylem. 3) to determine if tritium moves uniformly throughout the stem, or if it is concentrated in the outer. The fifth experiment was to determine tritium uptake, residence half-time, and tritium bound by photosynthesis in a secondary successional tropical rain forest. The sixth experiment consisted of injecting a tree with tritium and one gamma emitter by using a procedure whereby the transpiration stream of the plant was not interrupted, as a check on the other tree injection experiments where the transpiration stream was interrupted. ‘The first tree injection experiment was reported by Dr. Jerzy Kline at the 1969 meetings of the American Nuclear Society. Following is an abstract of the paper. Measurement of Water Behavior in Tropical Trees Using Tritiated Water Abstract JR, Kline!

John Martin?, cari Jortan3, John Koranda? Water utilization by plants is one of the most widespread processes: in Biology, Ecologists seek more detailed information on water relationships in terrestrial ecosystems as part of a general quest for deeper understanding of their functional processes. Modern nuclear technology added urgency to the acquisition of knowledge on the functions of water in the environment since both peaceful and military nuclear operations could contaminate biological systems with tritium as a major by-product of thermo-nuclear reactions. Despite this need for information, there is little detailed quantitative data available. The Rain Forest Project of the Puerto Rico Nuclear Center and the Ecology Group of the Biomedical Division of the Lawrence Radiation Laboratory, Livermore, Ca. have cooperatively initiated a series of experiments on this problem using tritiated water as a tracer. The first experiment in the series is reported here. The objective of the initial experiment was to determine the response of several tropical rain forest trees to the injection of a pulse of tritiated water. Secondary objectives included monitoring of air surrounding the experimental site and of involved personnel to establish appropriate safeguards in the execution of such experiments. Formerly with PRIC, now with Argonne National Laboratory. Laboratory, Livermore, Ca. Lawrence Radiation, Puerto Rico Nuclear Center, Rio Piedras, Puerto Rico, hha ---Page Break--- Three tropical trees representing two species were injected with tritiated water through holes bored in the trunks near ground levels. The movement of the labeled water was monitored by sampling leaves from a tower which had been previously erected nearby. Leaf samples were collected, at first several times daily; and later, once daily, and sealed in plastic bags and frozen prior to analysis. Samples were analyzed by extracting tissue water in a specially designed high vacuum freeze drying apparatus, and then counting the water by

standard liquid scintillation techniques - The pulse of tritium reached a peak in all leaves approximately five days following injection, after which concentrations of the isotope declined. The time required for the isotope to reach the crown of the trees was not dependent on the height of the

tree. The same time was required for a tree seven meters tall as for two about twenty meters tall. Tritium did not pass through the trees in a symmetrical pulse. After the peak was reached, tritium concentrations died away exponentially with half residence times ranging from approximately two to eight days. The largest differences in tritium residence times were found between species, suggesting that they have different adaptations for water use even though they occupy essentially the same environment. The decay curves showed several erratically spaced peaks and valleys during the course of the experiment. This was suggested to be due to the exchange of leaf tissue water with uncontaminated rainwater without corresponding exchange in the xylem elements of the tree. It was concluded from this experiment that: (1) Tritiated water is a safe powerful tool for the detailed assessment of water use by plants in the field. (2) Tritiated water persists in tropical trees with appreciable residence times even though large amounts of rainfall occur in the rainforest. (3) Rains bearing tritium will probably cause leaf tissue water to become labeled immediately due to the exchange of water on leaf surfaces. (4) The persistence of tritium in an entire forest may be longer than that shown by single tree experiments due to possible recycling of tritium which may be exchanged at leaf surfaces and carried to the rooting zone of plants by rainfall. MICRO-SYSTEMS EXPERIMENT Because an ecosystem, when studied as a whole, often shows properties different than, or not apparent in, the sum of all its parts, an attempt was made to study movement of tritium through all portions of an ecosystem at one time. METHODS 230 cm by 160 cm was outlined.

with string. One and soil water collectors ("Zero-Tension 81-86") were installed. Each plot of ground, side of the plot was cut away, lysimeters" (Jordan 1968, Soil Science 105, hs). ---Page Break --- lysimeter collected water from a 2 ft sq. inch area. Two lysimeters were installed beneath the litter, two at a depth of 5 inches, two at 10 inches, and two at 15 inches. The bulk density of the soil from the surface down to about 10 inches averages 0.57, at which point there is a region where the bulk density changes quite rapidly to a value of approximately 1.02. Leaves for analysis for free and bound water were picked from three trees growing inside the plot. They were a Dacryodes excelsa, 2.31 inches basal diameter, Microphilous garciniafolia, 2.06 inches basal diameter, and Manilkara bidentata, 1.4 inches basal diameter. Transpiration water was collected from two other smaller trees, a Palicourea riparia, 0.56 inches basal diameter, and a Manilkara bidentata, 0.72 inches basal diameter, by the following method: “A plastic bag was put over a bunch of leaves still on the tree; a floodlight was shone on the leaves to increase transpiration; air was pumped out of the bag and through a condensing tube submerged in a dry ice-alcohol mixture, and then back into the bag. About 2 ml. of water collected in the condensing tube in a half hour. Free water was extracted from the picked leaves by freeze and dry methods using high vacuum apparatus. Cores of wood were taken from the buttresses of two large trees whose roots extended into the plot. The trees were Buchenavia capitata, 17.75 inches d.b.h., and Tetragastris balsamifera, 8.93 inches d.b.h. Free water was extracted from the wood with the freeze dry apparatus. Water vapor was collected at 8 points immediately surrounding the plot, at 8 points about 3 meters distant from the plot, and at 100, and 175 cm above the plot. At the 3 meter points, the water was collected in the following manner: An aluminum tube 1 1/2 inches in diameter and about 1 1/2 feet long was inserted.

In an ordinary wide-mouth thermos bottle, one end of the tube extended about 6 inches out of the bottle. One cup of liquid nitrogen was poured into the bottom of the thermos. Water vapor condensed and froze on the protruding portion of the aluminum tube. When the liquid nitrogen boiled away, the ice melted and the water ran into the bottle where it could be collected. For the other points, water vapor was collected as follows: Rubber tubing was extended from the collection points to a condensation tube in the same manner as for transpiration water. Air and water vapor

were pumped into the tube, the water vapor condensed, and was later collected. The following method was used for applying tritium to the plot. Fifty millicuries of tritium were diluted into 4 liters of water; the water was siphoned through a polyvinyl tube and an ordinary shower head and applied evenly to the plot. Before the actual application, test runs were made to practice uniform application. Water vapor samples were collected at 15, 8, 165, and 240 minutes, 2 days, and 6 days after application. Leaf, wood, and water samples were collected daily for a week, and weekly thereafter. ---Page Break--- Rainfall was measured above the canopy with a standard U.S. Weather Bureau recording rain gauge, and below the canopy with two 5 ft. x 2 in. x 12 in. trough-type rain gauges. Wet and dry bulb temperatures were measured on every perennial gauge. Water samples were analyzed by standard liquid scintillation techniques. Known standards were included with the samples and results were converted to decompositions per minute. EVAPORATION OF TRITIUM FROM THE SOIL The water vapor from the collectors on the ground surrounding the plot showed decreasing specific activity with distance away from the plot. On the afternoon following the tritium application, specific activity decreased with distance most slowly on the uphill side of the plot, most rapidly on the downslope side, and intermediately on the North and South sides (Table 3). This

indicates a slight upslope and was blowing during the afternoon. Other ground collectors at greater distances showed the same trend as that shown in Table 1. To calculate the quantity of tritium lost through evaporation from the soil, the collections from 4 cm, 100 cm, and 175 cm above the plot were used. Procedures for calculations were as follows. No decay correction was applied. Specific activity of the water vapor was plotted as a function of distance above the plot for each sampling time (Fig. 9). Specific activity of the water vapor at ground level immediately after application was taken to be the same as the specific activity of the solution applied (50 mCi in 8 liters equals 11x10^6 dpm in 4000 ml, equates to 2.75x10^7 dpm/ml). Attempts were made to fit a curve to the points by using least square fit to a quadratic ($Y = ax^2 + bx + c$) and least squares fit to a parabolic ($Y = ax$), but neither resulting equation yielded a line that fit the data satisfactorily. Therefore, specific activity of water vapor at ground level at times after application was estimated by extrapolation of the curves of Fig. 1 (Table 35), using a flexicurve. Specific activity of water vapor at ground level (Table 35) was then plotted as a function of time after application, using three different time scales (Figs. 10, 11, and 12). Average specific activity for each given time period was then taken from Figs. 10, 11, and 12 (Table 36). Aun and Jordan (1969) estimated evaporation from the soil to be 36 g/m^2/day. If evaporation occurs only during the daytime, the average is 36 g/m^2 during the daylight hours. Since the tritium plot was 3.68 g. ---Page Break--- Table 34, Specific activity of water vapor collected around the tritium plot following application, specific activity, same as that a. a. a. a, a. a? — 2.0505 g. otmact 6, sisao asta? gas 32 cx, damage (Bat) gasact 6.390% 2201) area air 6c Sout abn — showed? — egeaot — rasuch aan? ate ce. wow pot G. rimao?

— s.68ai05§—a.s3n0a.etmaoS 55303 algae? wom st 6.18 ea? bac, aT wr wet dea? kar asucd 162 " n Table 35. Specific activity of tritiated water at soil surface as determined by extrapolation of curves. Data specific activity fa 55 22ehs, 2.15 x aot ® SAS 33:50 1.0 x 106 5S 15:15 5.0 x 10° s/s 16:30 4.0 x 105 SAT 16:00 1.2 x10 sa 15:00 ko x13 + calculated ---Page Break--- —— 99, 208 & 4 pw TATUM/AM WATER VAPOR a STANCE ABOVE GROUND (eM) Fig. 9. Specific activity of tritium in the water vapor above the experimental plot as a function of distance above the plot. 3 & 5s ‘eM TmITMA/ ML WATER VAPOR a ‘re (hours) Fig. 10, Specific activity of tritium in the water vapor at ground level as a function of hours since tritium application, lg. ---Page Break--- aren vapon a3 aa a. Te (hours) Fig. 11, Specific activity of tritium in the water vapor at ground level as a function of days since ‘tritium application. ot gc} j eft a et : 2 i ee, Fig. 12, Specific activity of tritium in the water vapor at ground level as a function of months since ‘tritium application, 50 ---Page

Break--- 60" jot x Lot Tex0, oot 0 por ce 06 e/L = Th oes oo =e pores ot/9 - t6/5 3 ct ore 5'08t core s't o/s - €2/$ £96 0 OT * 2°05 got x re B/S ous 0 sot x 9°25 got x ort v/s £6 10 sot x E19 errs 7 9°96 eo {ox ents eoree'g ers 8°S6 ot got * 2°Tt got x Se et/s ons er gurce goux ort an/s 626 os got x 4°65 got * Se o/s vile ee got ¥ Lon got ELE co:gt-00tt st/s 9% MH got x o'r got ¥ 0'% 00:11-00:9T sys So on GOT * $6 ot Sth (00:9T-0025T s/s on v9 got ¥9°9 got x09 00:5t-c0r4t sus 899 wit got ¥ Let got XLT cotyt-ooret sys ts ats got S*S OT X OT oorer-of:2t st/s PeqeIOMONS — paTAONGAS — PSS FoI AT TEE war TE gusosod 1303 dp e203 wtb Te}0ypayutodeaa jug AaTATRO" OpTOadg eaTaUTRIM] Jo quaDTAT Jo ugDIOr uoTwesoeas pre "ord 9ug woxz zaqua posvraTz3 30 'sonmo waxy pouTateyep #8 sousans Tyo 4 zaqeA poqeTaTTa JO AYTATIOB OTTOOMS "gC TABS 51s ---Page Break--- b fle activity ¢ n2, 11,04 mi/nr evaporated from the entire plot. Spec water fa given tine period (Table 36) vas multiplied

times length of time period, times 11 mi/tr to give total dpm evaporated during the time period. Total tritium evaporated was 10.7107 dpm, or 0.09 percent of the total tritium applied. Fifty-one percent of the total evaporation took place during the release at the area near the appearance on Seas Movement of Tritium Through the Soil and Trees. Specific activity of tritium in the soil water at each depth was plotted as a function of time since application. It is immediately apparent that there are at least two residence half-times of tritium at each depth. Individual points of specific activity vs. time are shown in Fig. 13 to illustrate how clear the break is between the two release rates of tritium. When a least squares straight line regression is calculated for each release rate, the first residence half-time in the litter is 1.7 days, and the second is 30 days. The first release rate is approximately equal to that predicted by Odum and Bloom (1969, in press) based on total free water in each ecosystem compartment and rate of movement of water between compartments. Therefore, it may be safe to assume that this release rate represents total free water turnover in the litter. The second release rate, however, was not predicted by Odum and Bloom. A hypothesis to explain the second release rate is based on the presence of a thin film of water which surrounds individual soil particles, soil algae, and decomposing organic matter. This water is called hygroscopic water. It is bound to the individual particles, and water molecules in this film are not freely exchangeable with the pool of free water. Some exchange does occur, however. As the pulse of high specific activity moves through the litter and soil, some of the tritiated water in the free water pool undoubtedly exchanges with the hygroscopic water. After the peak of specific activity passes downward and the specific activity in the free water becomes lower than that of the hygroscopic water, tritium diffuses outward, the rate of diffusion being governed in part by the amount.

of bound tritium and the difference in specific activity in the hygroscopic water and the free water. Further evidence for this hypothesis is shown in Fig. 1h, where following a period of heavy rainfall, specific activity drops sharply, due to the high dilution of the tritium diffusing out from the hygroscopic shell, and then jumps up again during a relatively dry spell, when the out-diffusing tritium is less diluted. Specific activity as a function of time, for each of the four depths sampled, is shown in Fig. 15. The buildup of specific activity at the 10 and 15 inch depths is clear, as the peak of specific activity moves downward and broadens. After outward diffusion of tritiated water from the 52 ---Page Break--- a Fig. 13. Specific activity of tritium in the water leaving the litter layer as a function of time since tritium application, id] « | e ie log, 3 1. i "| . ; j oe et ee despite ctety of ran he te ee ne Fig. 1h. ---Page Break--- hygroscopic shell begins, one half residence time at the 5 inch depth; at the 10 and 15 inch depth it is 32 days. The differences in salt times between the different soil depths could be explained by differences in soil structure. At the 5 inch depth, the clay particles are well segregated (bulk density is 0.57) and therefore the reservoir of bound tritium is not as large as at the lower depths, where there are more clay particles per unit volume (bulk density is 1.02).

The release rate of tritium after 165 days (Nov. 1) should change again for the 5 inch depth. Theoretically, the specific activity at any depth cannot be lower than that in the soil above, because if it starts to get lower, inward diffusion of tritiated water into the hygroscopic shell begins, as the water from above moves down, thus increasing the specific activity again. When specific activity is plotted as a function of depth on a given day, much less scatter appears in the data points (Fig. 16). When a series of these functions is plotted on a single graph, a picture emerges of the movement through

the soil of the peak of maximum specific activities (Fig. 17). The pattern is wave-like, moving downward through the soils gradually decreasing in wave height. Specific activity as a function of time for soil water at the 5 inch depth is compared for two experiments in Fig. 18. In the experiment initiated on Feb. 14, 1967, (Kline and Jordan, 1968), the tritium has an appearance time similar to that of the micro-systems experiment. A big difference, however, occurs in the initial few days of the experiment. In the earlier experiment, specific activity increased during the first few days, whereas in the micro-systems experiment, maximum specific activity occurred the first day. The difference can be explained by the varying pattern following tritium application. In the earlier experiment, only 0.24 inches of rain fell during the first 2 days following it. The pattern of tritium movement through the trees is influenced by the pattern of movement through the soil. Since tritium has a longer residence time in the litter and soil, the roots of trees are exposed to tritiated water for a relatively long time. Specific activity of transpiration water is affected by several factors: 1) Distribution of roots with depth in the soil 2) Specific activity of interstitial depth 3) Water vapor deficit of the air, which affects the rate at which water is pulled through the plant 4) Light, which indirectly controls transpiration through regulation of stomatal openings. 5) Proportion of roots which are in the contaminated plot (not applicable, of course, to the other plots). ---Page Break --- Dew TmTUM ML SOL WATER, 3580 Fig. 15. Specific activity of tritium in the soil water at four depths as a function of time. a, Es 3 (pw TATUM /ML SOIL WATER. ON 5/23/68, oS DISTANCE BELOW SOIL SURFACE (INCHES) specific activity of tritium in the soil water as a Fig. 16. Eight days after tritium application, function of depth, ---Page Break --- “oars. since Fig. 17. Specific activity of tritium in the soil water as a function of depth, at intervals following

‘Tritium application, as shown in Fig. 18. Specific activity of tritium in the soil water at the five-inch depth as a function of time since tritium application, for two experiments, ---Page Break--- spread fallout situation). As a result of these factors, data points of specific activity of tritium in leaf or wood matter as a function of time show much scatter after the initial buildup. If a least squares regression of DPM on time is performed, residence half times range from 25 to 50 days. However, if data points are averaged together (weekly averages for the first month, then monthly averages), a decay curve appears that follows the trend of specific activity in soil (compare Figs. 19, 20, and 13). Similarly, in the roots of the larger trees, yet another phenomenon seems to be involved (Fig. 21). The first little peat may represent water taken out of the litter by rootlets in that layer, while the second, more diffuse peak may represent water taken up by rootlets deeper in the soil. A comparison of the prediction of specific activity of tritium in ecosystem compartments based on total water content only, and experimental results of the micro-systems experiment are shown in Fig. 22. Because of the hypothesized diffusion of tritium into and out of the hygroscopic shells, residence half time in the tropical rainforest ecosystem is increased by a factor of five to ten. Movement of 137Cs, Sr, and other isotopes through Canopy Trees Movement of gamma emitters through large trees was measured in two ways. (1) A portable rate-meter with a G-M tube was connected by a coaxial cable to a portable scaler that was carried to the area of injected trees. The G-M tube was fastened to a pole in such a way that the tube could be held flush against the tree without the field

assistant getting closer than 8 feet from the radioactive tree. As the field assistant placed the tube against the tree from the adjacent tower, the operator determined gross counts per minute with the scaler. (2) Various parts of the tree were

collected periodically, oven dried, and counted for 100 minutes in a 400 channel gamma analyzer. When more than one isotope was present in a sample, it was necessary to solve simultaneous equations to quantify each isotope in the sample. A tree of the species Matayba domingensis, 31 on. a.b.h. and 52 ft. high was injected with .46 millicuries of 137Cesium on Sept. 18, 1968. Table 37 shows the portable scaler readings. At the base of the tree there was an increase in activity for seven days, followed by a gradual decrease. This downward movement is confirmed by Table 38 which shows the wood at the base of the tree to be somewhat radioactive, and the bark to be very radioactive 20 days after the injection. The high level of activity 1 ft. above the injection hole 20 days after injection (Table 38) and the low level between holes indicates very little translocation laterally across the xylem cells as compared with longitudinal movement. Portable scaler counts between the injection holes, and at an injection hole (Table 37) show a gradual decline in activity, indicating a movement of the 137Cs away from the injection holes. The activity rose to a maximum at six feet, ---Page Break--- Ir PALICOUREA PIPARA 2 WIROPHOLIS. GARCINIFOLIA 3 DACRYODES EXCELSA & 5, a 5. PM TRITIUM/ML FREE WATER IN LEAVES 3085 302015080 TIME (DAYS) Fig. 19. Specific activity of tritium in the free water of leaves of three species, as a function of time since initiation of the experiment. cy I+ MADeLKARA ODORATA, 14 NOB 2+ MANSUKARA ODORATA, 07 IN OBH a [DPM TRITIUM/ML FREE WATER IN LEAVES ‘Te. (hours) Fig. 20, Specific activity of tritium in the free water of leaves of two trees of the same species, as a function of time since initiation of the experiment. 358- ---Page Break--- TETRAWOGASTI BALSAMIFERA ge PRA Canta iy z Sd E z0 380 35s The we (hours) Fig. 21. Specific activity of tritium in the free water of root buttresses of two trees as a function of time since initiation of the experiment. DICTED FOR LITTER A. Results For LITTER B. Predicted

rows ys RESULTS FOR SOL. is Predicted FOR W000 Gj yt Results FOR” WOOD, Predicted from "Leaves (+ RESULTS FOR” LEAVES PM TRITIUM/ML WATER a a a) Time (hours) Evidence time in the Fig. 22. Experimental results of tritium residence times compared to predicted residence times, 59° ---Page Break--- Table 37 Days since injection of tritium. Results were analyzed between the injection and time points. Injection rates of the total flow were 6. s, s te, tere some oo 18 10,049 est shy 25 rose 2,595 at 8 slo Pc) sit 8 ™ asa wf sie oo 1,620 oT ow sys 86 15,718 % 6 » es ow 3.987 =f ho whos a 10,013 w 6 & ow we om 10,902 mo @ rset a 9,6 a a wp se 4x0 nak wm @ wes 0 an 5 we ewe ry 1 awe ~ 8 8 om ‘ante 38. Movement of Soe trough Yatayba dotngensts Diya since injection Sample > oT . ae Activity in picocuries per excess Any weight — om oe ke on owe SI oy me wpa, oe ” caeek |S som ark, base of tree 170,388 was G20, ---Page Break--- three days following the injection; a maximum at 21 ft., seven days after and a maximum at 35 and 42 ft. 20 days after. Table 38 shows that the leading edge of the pulse of activity reached the leaves sometime between the 20th and the 37th day. The relatively stable level of activity after the 37th day could indicate that a steady rate of input to the leaves had occurred, and that cesium was being leached from the leaves at the same rate it was being supplied to the leaves. By 132 days, there was a fairly uniform distribution of the cesium throughout the tree, with the exception of the bark near the base. A tree of the species Dacryodes excelsa, 51 cm, a.b.h., and 60 ft, high was injected with 17.69 millicuries of 137Cs, 0.19 millicuries of 85Sr, and 0.34 millicuries of "My on Sept. 18, 1968. Interpretation of the portable scaler data (Table 39) is more difficult than for the cesium-injected tree because of the presence of three isotopes, and their relatively short half-lives. Nevertheless, the same trends as in the Natayba can be detected (Table 37). The peak of the

downward moving pulse occurs at the base of the tree.

About 7 days after injection, activity at the level of the injection holes gradually declines. The peak passes the 6 ft. level on the 5th day, and the 21 ft. level and above at about 3 weeks. Tables 40, 41, and 42 show downward movement of all three isotopes, presumably in the phloem which was included in the bark samples, with CORD showing the fastest movement. At 132 days after injection, [Rb was still increasing in the leaves (Table 10). Data for day 132 indicates that the peak of upward moving [6m is somewhere between 20 ft. above the injection hole and the twigs in the canopy. During Jan. 1969, a large increase in fallout in the EL Verde area resulted in an obscuration of ®%sr and Nn data after the 75th day. However, it is clear that both isotopes had only reached approximately 2h ft. (20 ft. above injection holes) by the 75th day. All isotopes not only moved downward in the trees, they also moved out of the roots into the litter and soil (Table 3). All isotopes were found in litter and mineral soil samples except 86%, which was found only in the litter. As a check to see that the isotopes actually were transferred out of the tree, all organic matter was separated (by agitation and flotation) from mineral soil, and the mineral soil only checked for activity. All isotopes except CR were present. A curious phenomenon occurred on Dec. 2, the 75th day. In the portable scaler readings on Matayba domingensis (Table 37), the values at the injection hole level and above all declined, then increased again on the 132nd day. Table 38, which shows the results of the gamma analysis, indicates the same thing. Portable scaler readings on Dacryodes excelsa at the injection level (Table 39) show the same trend, as well as Table 40. No explanation is apparent for this phenomenon. -61- ---Page Break--- Table 39 Portable scaler readings on Dacryodes excelsa growing in 30 cm Comte per stmt nee EIA nee pee PEE SEE on, ee, ten, ar) ws ome se “ ony ox 00 eter 2 oO = ofa 3 ah ‘9,807 Ba we 6 sla 8 we 8x6 seaie ey wes

a ah ass 6 » » west a fe eo ar) eae are mu 6 & fw ry 5,6 angus o sw whs ot Ave ype mw 6 6 ow bie ” sino to m 8 8 8 safe 3 7 2,286 3,327 2 3 aT vet owe @ Li 6 momo ow oe ‘ate No, sovenent of Sm enroigh Bacryotes exselan ‘igs since tnjection > ase ne Activity in plooeuries per gran dry veteht en 3,386 r0j@9 25,285 hos 65,6 19,90, 2267 hee ake 9,70 13,7 eng 25,839 hejtos 6,450 ot datectabte ~62- ---Page Break--- Table M1, vovenent of sr through Dacryodes excelsa Days since injection Semple © 2 B Jotivity in pleccuries per gran, ary weight Leaves _ 6.0 2.0, tee 23.6 Wood, 20 ft. above “ijeation hole ea Wood, 1 ft, above hole — 0.0 Wood, base of tree 0.0 22 Berk, ase of tree 3,385 Table 42, Movenent of hin through Dacryotes excelsa Days since injection Sanple 2 B Activity in pleocurtes per gran, ary weight Leaves 19 16.9 ™es wT Wood, 20 ft. above ‘thjection hole wT 68.1 Wood, 1 ft. above Anjection hole 5h Wood, base of tree 0.0 erg Dex, dase of tren 0.0 8,020.0 -63- ---Page Break--- ° ° 1 ° ° gg 1 2 wat ° ° ye w 8 a a © 339 et 9 zz 0st este "yee {PTAR Axp mad sod soEMaoaTd UF AYTATIOV ‘FaPOTTRG oxy WER ws TET es | HUNT || STIR uy eMonoer a5 § Faquo Troe ToxouT sa S tog sag txoaaT Tage TTOR 4g 6 aoa WORT sqzete 4005 $t exe TASER we TOT “wuosa0ofuy e809 Feqs0 Sfp 96 Troe Pi ZeraTT UT AATATIOY “fy orauy ---Page Break--- PART B - SECONDARY SUCCESSION IN THE IRRADIATED AREA METHODS Description of Site The study area is located near El Verde, in the Luquilio Experi- mental Forest of eastern Puerto Rico. ‘he site is at an elevation of 1500 feet, in a forest described as Tabomuco type (Wadsworth 1951). ‘Annual rainfall is epproxinately 240 on. per year, vith more than 10 om. every month. ‘The terrain consists of a series of sharply sloping ridges and ravines, Average height of the forest top is 65 feet. The studles of early succession vere mate in the area affected ty gama radistion. In 1966, the area surrounding the source location, out to about 15 meters, was virtually barren of canopy leaves (Figs. 1, 2). By August 1966,

Canopy dieback has ceased (Table 1). There are two distinct soil types in the irradiated area, one

reddish-yellow (7.5 YR/6/8) (Munsell 1954) and associated with the ridges, and another dark brown (10 YR/1/3) and associated with the ravines. Richanis (1957) states that the reddish-yellow color of the soil formed under conditions of unimpeded drainage in the tropics is due to the abundance of iron oxides, while non-peaty swamp soils often have a grey or brown color, and occur under conditions of superabundance of water and poor aeration. For convenience, the reddish-yellow soil will be called “oxidized” soil, and the brown soil "reduced". Soil color was used to delimit boundaries of two communities within the irradiated area. Studies in a later stage of succession were made in the forest surrounding the irradiated area. To simplify discussion, the surrounding forest will be called the "mature" forest, even though it contains some successional species, and the irradiated area will be called the "successional" area. To facilitate measurement of vegetation in the irradiated area, a grid-work of nylon line was laid out in one-meter squares, 26 meters on each side, with the center of the gridwork coinciding with the source location. On the four cardinal axes, a strip of squares two meters wide was run out to 30 meters from the source. In the center of the plot, the source during...

LEAF AREA INDEX DISTANCE FROM CENTER Fig. 2. Leaf area index of the irradiated area. Leaves directly at the center are ‘la racemiflora which were pi, —*~radiation by the plug above.

Sampling Measurements of all the plants within the 676 square meter grid were made in the fall of 1966, 1967, and 1968. In 1966 and 1967, measurements were made of basal diameter, diameter at 30 cm, and of height, of all plants with single stems, including individual sprouts. Since it was later determined that basal diameter alone was an adequate predictor of biomass (see next section), basal diameter only was measured.

In 1968, for plants with stilt roots such as Cecropia peltata, basal diameter measurements were made above the roots. Basal diameters were measured to the nearest 1/126 of an inch with micrometer calipers. For ground cover species such as grasses, sedges, and Desmodium, percent cover of each square meter was estimated, and then percent of total possible density within areas covered was estimated. Leaf Fall Square meter leaf fall collection baskets had been placed throughout the site during the radiation experiment (Odum In Press). Leaf fall during the period following radiation was high in the area surrounding the source due to die-back of the canopy. After August 1966, there was no further measurable die-back of the canopy (Table 1) and therefore, presumably, no leaf fall in the irradiated area due to canopy die-back. From June 1966, 14 months after cessation of radiation, through March 1968, the 10 collection baskets within the area where canopy die-back had occurred yielded a relatively constant amount of leaves, except during the period of May through July, when the amount increased, as does leaf fall throughout the forest (Kline and Jordan, 1967 and 1968 Annual Reports). Average leaf fall during the post die-back period was 0.63 g/m²/day. Leaf fall in the mature forest was taken from Odum and Jordan (In Press). Biomass of Successional Vegetation Ten individuals of each of 15 common successional species, ranging in diameter from 1/8 inch to two inches, were taken from other successional sites in the vicinity of the study area. The above ground portions of the plants were clipped off, and the roots were carefully extracted from the soil. The entire plant was then dried and weighed. Correlation coefficients were made between heights, diameters, and weights (Table 2). Since basal diameter and height were closely correlated there was little to be gained by using height in addition to basal diameter as a predictor of biomass. Because basal diameter and diameter at 61 ---Page Break --- Table 1, Average leaf

area indexes of canopy leaves measured from 0 to 30 meters from source location in irradiated

area, Date Leaf Area Index Aug. 1966 2.20 Feb. 1967 2.10 Aug. 1967 2.21 Feb. 1968 2.25 Aug. 1968 2.19 Table 2. Correlation coefficients of measurements of successional plants. Correlation coefficient basal diameter weight basal diameter height height weight height weight (adjusted for diameter weight correlation) basal diameter diameter, 30 cm. 99, ~68- ---Page Break--- 30 cm. were almost perfectly correlated, nothing could have been gained by using both as predictors of weight. Therefore, basal diameter alone was used to predict biomass. Regression of biomass on basal diameter for all 15 species was tested for differences by covariance analysis. There was no detectable difference in slopes and y-intercepts in the regressions. Therefore, all 150 individuals were used to calculate a single regression. The regression line was curved on linear paper, so the most general equation for a curved line ($y = ax^2 + bx + c$) was derived from the data. The equation is: $Y= .0289x^2 - .2525x - 13.4557$ where Y equals biomass in grams of dry weight, and X equals basal diameter in 1/128 of an inch. Due to lack of perfect correlation, diameter values less than 3/16 of an inch give negative values for biomass. All plants less than this diameter were arbitrarily given a weight of one gram in the calculations of total ecosystem biomass. Equations for Phytolacca icosandra, a common successional species with an unusual shape, and for all sprouts (above ground portions only) were derived in a similar manner. For grasses and sedges, and Desmodium tortuosum, biomass was determined by digging up 10 individual square meters of each type, and regressing biomass on the quantity (% coverage) x (density). Biomass was directly proportional to this quantity. Regressions were programmed into a desk-top computer, and total counts of every plant. or every area in the case of grass etc.) was computed, Total biomass of various categories (as shown in

the results section) was then obtained by adding together all plants in the appropriate category. Biomass of Mature Forest To calculate the biomass of mature forest trees, the equations of Ogawa et al. (1965) were used. These equations were based on measurements made in southern Thailand, in stands which, from their description, closely resembled the forest of this study. Calculations were made for trees in every 2-inch diameter size class, from 4 to 26 inches, diameter breast height. Biomass of trees in each size class was then multiplied by the number of trees in each size class per hectare. Tree density data is from Dr. Frank Wadsworth, Director of the Institute of Tropical Forestry, who has transect information from over 20 years of observation in the area. Finally, biomass/size class/hectare for each size class was added together to give total biomass/hectare. ---Page Break--- Net Photosynthesis (Assimilation) Net photosynthesis in the successional area was determined by subtracting total biomass of standing crop of one year from that of the next. Biomass of successional vegetation in 1965 was assumed to be zero. Net photosynthesis for the mature forest was determined as follows. Total biomass/hectare was determined as described in the section "Biomass of mature forest", using 4 in., 6 in., 8 in., etc. as the diameters for calculating biomass in each size class. Change in diameter per size class was measured on 19 trees from July 1, 1966 through Dec. 1, 1967. Each tree was fitted with an aluminum tape that expanded as the tree grew. The tapes were marked with a vernier scale. Change in diameter/size class/year was computed. Total biomass of the forest was again calculated, but this time the diameters used for each size class determination were the original diameters plus average change in diameters of each class tree per year. For example, in the 4 inch class trees, the new diameter was 4 inches plus average yearly diameter increase of 4 inch trees. Diameter growth was measured only on dicotyledonous.

trees, while density data included palm trees. Therefore, if the rate of biomass increase in palms is different from the rate of biomass increase in other species, an error was introduced. It is not known if the rates differ. Respiration of successional vegetation was determined during nighttime hours

only, using the following technique. A plastic bag was inverted over the leaves to be studied; the bottom of the bag was left open. Air was slowly pumped from 92 feet above ground (to ensure a source of air with a stable CO■ content) through a plastic tube into the top of the bag. A relay switch attached to a timer set for 15 minutes directed air into an infrared CO■ analyzer, alternately from the external air source and from the bottom of the bag. Differences in CO■ concentration between the source and bag were converted into grams of carbon respired per area/hour. (Lugo, in press, describes calculations). Total leaf respiration (TLR) for the successional ecosystem was calculated by the equation: TLR = ax + ty where x = 1, when leaf area index = 1 or 1 leaf area index, when leaf area index < 1 = (leaf area index) - 1 = respiration rate of top leaves + respiration rate of bottom leaves.

Skewes ---Page Break ---

Gross Photosynthesis

Gross photosynthesis was calculated for the successional area by GP = biomass + leaf fall + leaf respiration + root respiration. Biomass and leaf fall were converted into carbon by multiplying times 0.44 (carbon = H■O + O■ + 205).

Gross photosynthesis of the mature forest was calculated by adding the change in biomass to total forest respiration (Odum and Jordan, In Press).

Solar Radiation

Solar radiation above the canopy was measured with an Epply pyranometer from April 1967 through Jan. 1968. Data was recorded on Fustrak tape, and daily records were integrated with a compensating polar planimeter.

Leaf Area Index

Leaf area index is an index of the quantity of vegetation. An index of three, for example, indicates that there are

three square meters of leaf surface for every square meter of soil surface. Leaf area index of vegetation less than 6 ft high was determined by dropping a plumb bob on a string directly over each corner of the grid and counting the number of leaves touching the string. Leaf area index of vegetation greater than 6 ft was determined as follows: A mirror with a hairline cross in the center was mounted at 45 degrees on one end of a level; on the other end was mounted a peep sight. When the device was level, a vertical line of sight was obtained, and the number of sprays of leaves through which the line of sight passed was counted. It was assumed that a spray of leaves averaged one leaf in thickness. Leaf area index of the mature forest was derived from the infra-red/red light ratio on the forest floor (Jordan, in this volume). Leaf area index is proportional to the light ratio. Chlorophyll Content Chlorophyll A content of leaves was taken from results of 773 determinations which constituted part of another study (Cintrén, in press). Total chlorophyll (Cy) in the successional ecosystem was calculated by the equation Ch = axt and for the mature forest by the equation Cy = arts where a = 1 when leaf area index = 1 or a = leaf area index when leaf area index < 1. Chlorophyll concentration of sun leaves, successional plants; chlorophyll concentration of shade leaves, successional plants; chlorophyll concentration of sun leaves, trees in mature forest;

chlorophyll concentration of shade leaves, trees in mature forest. "Equivalent" Age of the Mature Forest To plot long-term changes in ecosystem functions with succession, it was necessary to establish an age for the forest surrounding the irradiated area. The forest, however, had been affected in the past by hurricanes and some selective logging, with the result that it is an uneven-aged stand. Therefore, an “equivalent” age was determined by dividing the biomass of the mature forest (22,853 g/m² from Table 3) by the

average of the four values of assimilation/year (Table 5). The equivalent age of the forest in 1966 was 59 years. RESULTS, Standing Crops Total standing crop increased every year from early succession up through the 60-year-old forest (Table 3, Fig. 3). Standing crop was greater on the oxidized soil of the irradiated site than on the reduced soil (Table 4, Fig. 3). Sprouts played a decreasingly important part during succession (Table 4). The most common species in the mature forest, in decreasing order of importance, are Butia capitata, Croton pseudolantina, Dacryodes excelsa, Cecropia peltata, Sloanea berteroana, and Weinmannia tinctoria (see text). Cecropia is a secondary successional species, while the latter produces seeds capable of germinating beneath a closed canopy, and thus can be called "climax" species. The standing crop of the five most important climax species ---Page Break --- 5, ON EXCLUDED BIOMASS, GRAMS/M² CLIMAX SPECIES 3 10 30 100 TIME (YEARS) Fig. 3. Change in biomass of plant material during succession. Table 3. Total standing crops (biomass) of vegetation in the irradiated areas and the surrounding forest. Ea, SE ee: eo ue om: = 8 ® ne pa » ae saciee e aan ---Page Break --- Table 4. Percentage of standing crop contributed by vegetation in various categories. Years from start of secondary succession 1 19.00 130.57 58.67 0.12 2 10.80 123.69 66.66 0.39 3 12.32 227.54 63.30 0.61 59 36.88 Table 5. Estimated shoot biomass (assimilation) in the irradiated area and mature forest, years from start Total, Five common total, Five common of secondary succession vegetation clime species vegetation clime Hest a ae 0.291 0.683 0.0008 0.252 0.00 326 2.616 aah 0.0073 0.638 0.0032 3 oe 3.86 0.800 0.0095 0.35e ote 9 186 3.23 asst ute 0.585 one The ---Page Break --- species was much lower than that of other species during early years of succession, but these climax species had a rate of increase much greater than the average of all vegetation (Table

5, Fig. 3) - During succession, the percentage of total biomass of sprouts decreased, the percentage of climax species increased, and the percentage on each of the two soil types remained constant (Table 4, Fig. 4). Net Photosynthesis: Total net photosynthesis for the ecosystem went up to a maximum value of 0.634 gC/m²/day only two years after succession began (Table 5, Fig. 5). From the second through the 59th year, total net photosynthesis showed neither a distinct increasing nor decreasing trend. Net photosynthesis of the five most common climax species increased by a factor of 537 times from the first through the 59th year (Table 5). Respiration: There is very little difference in respiration rate between leaves in the same position in different species (Table 6). Only Cecropia peltata has a decidedly higher respiration rate. Much greater differences occurred between leaves toward the top of the plant and leaves toward the bottom of the plant, with the top leaves having a greater respiration rate. No clear differences occurred in the rate of soil respiration between the mature forest and the secondary successional area (Table 7). The soil respiration in the mature forest on Feb. 14, 1968, may have been affected by an unusually dry condition on the floor of the mature forest. Between Feb. 5 and Feb. 14, no moisture was collected in 12 below-canopy rainfall collectors (Jordan 1968), while about 1/10 of an inch fell in the open. Soil respiration consists of the respiration of microorganisms decomposing fallen leaves and plant parts, and root respiration. Total soil respiration of the secondary successional ecosystem could not have been equal to that of the mature forest, since the mature forest contained about 22 times as much biomass as the successional site. High soil respiration in the successional area is probably

due to the decomposition of dead and fallen trees which were killed by radiation, plus roots of these trees which were at least partly living, as evidenced by the presence of sprouts. Therefore, to calculate

Total respiration of the successional ecosystem, root respiration of the successional plants was taken to be 37% of the total respiration of the ecosystem, because in the mature forest, root respiration was 37% of total ecosystem respiration (Odun and Jordan In Press). “15+ ---Page Break--- JOvASS ON OXDIZED SOL 158 ON REDUCED SOL ‘CLIMAX. SPECIES PERCENT OF AVERAGE STANDING CROP, 3 380 17 Te (YEARS) Fig. lb. Contribution toward total biomass contributed by various categories of plants during succession, 109) cross "OF photosynthesis S ‘“Respiration GRAMS CARBON /M²/DAY Net photosynthesis r 3 30 TIME (YEARS) Fig. 5. Change in net photosynthesis, gross photosynthesis, ‘and respiration during succession, “16 ---Page Break--- oe ‘table 6. Respiration of leaves in the irradiated areas ae ind Psychotria pentheriana 0.0096 Rultooures riparia 0.0196 bene paste 0.0136 Diayeoneng: sorstcotont 0.028 Cecropia peltata 0.0383 Pemetion procumbens 0.0ass ‘ystotria berterana 0.0009 Rultrourea riparia 0.0093 ‘Behate paluuan 0.0062 Pigyeogana orstotont 0.0061 average top 0.019 A560 average letter 0.00 AEB ‘table 7, Soil respiration in the irradiated area and the mature forest. grams, carbon respiration/e? mature forest, (ulated soil. 06 008 Sr ware forest reduced soil a oT 038 ‘oxidated soil lof grass covered 22 ory irradiates area, extended soil, for grass cover 20 otto ryudiated area, reduced sot, Soy grass cover oO mss ee ---Page Break--- Limb respiration was not measured in the successional vegetation. However, when leaves were covered with a plastic bag for respiration measurements, the bag covered the twig on which the leaves were growing except for Cecropia peltata, and thus respiration due to small limbs was included in the leaf respiration data. In the case of Cecropia peltata, ‘there were no limbs on the young trees. All leaves originated from the main stem. ‘Trunk respiration and animal respiration were not measured in the successional area. In the mature forest, trunks contributed 1.7% and animals 0.7% total ecosystem respiration.

(Odum and Jordan, In Press). Respiration due to trunks and animals in the successional area was calculated by taking the same percentage of total ecosystem respiration as was found for the mature forest. Ecosystem respiration increases during succession (Table 8). The least squares line of regression of respiration on years since the start of succession is shown in Fig. Gross Photosynthesis Gross photosynthesis was calculated by adding change in biomass to total respiration (Table 8). The least squares line of regression of gross photosynthesis on years since the start of succession and the regression line of respiration on years converge with the passage of time during succession (Fig. 4). The ratio of gross photosynthesis to respiration decreases with time during succession (Table 8). Leaf Area Index and Chlorophyll Leaf area index increased rapidly during the first years of succession (Table 9, Fig. 6). After only three years, leaf area index in the successional area was greater than half of the leaf area index of the mature forest. Chlorophyll content is slightly higher in shade leaves than in sun leaves, and higher in the leaves of the mature forest than in those of the successional vegetation (Table 10). Chlorophyll content of the ecosystem increased more rapidly than leaf area index because the proportion of shade leaves and mature leaves increases with succession (Table 9, Fig. 6). ~18- ---Page Break--- 8. Respiration and 8. Gross photosynthesis in the mature forest. a 2M MH 06 kts aya Le 2 oe Bot kam 19 3 a a a a a aas 2 NTT Gor 398 8k 8388.98 aos ‘included with leaf respiration ‘Table 9. Leaf area index and chlorophyll content of forest during succession, Years from start of secondary succession Total leaf area Total chlorophyll A of ecosystem a/=? 1.0 6 1206 1.5 1.64 ish 2.0 2.90 +883 2.5 3.26 1.006 3.0 3.53 1.098 0 6.60 2.745 ---Page Break--- \ CHLOROPHYLL wo CHLOROPHYLL, GRAMS/M² LEAF AREA INDEX TIME YEARS Fig. 6. Changes in leaf area index and amount of chlorophyll

during succession, re

‘Table 10, Chlorophyll A content of Leaves (tron Cistaén In Press). The average grams of each species are: Eucalyptus globulus, Santaleare biflora, Decrrates tok, Brenoter excelle SRE. Solar Radiation The average total solar radiation during the period April 1967 through January 1968 was 206.6 cal/m²/day with a standard deviation of 69.9. This is 2.066 x 10° cal/m²/day for one gram of glucose yields 3730 calories (Wilson and Loomis, 1962), and 2.005 x 10” calories would yield 553 grams glucose/m²/day at 100% efficiency. Efficiencies and Taxes Trophic level efficiency, which is defined as the ratio of gross photosynthesis to total light (Lindemann in Odum, 1957) increases during succession (Table 11, Fig. 7). Total light is the total sunlight measured by an Eppley pyranometer, and converted to grams of glucose/m²/day by taking one gram to be equivalent to 3730 calories. Gross photosynthesis also was converted to grams of glucose/m²/day. Issue growth efficiency, which can be defined as the ratio of assimilation to gross photosynthesis, decreases during succession (Table 11, Fig. 7). Property tax (Olson, 1961), taken here as the ratio of respiration in grams of organic matter/m²/year to standing crop in grams/m²/decreases during succession (Table 11, Fig. 7). Comparison of Functions A comparison of several of the functions, as they change with succession, is shown in Fig. 8. Especially striking is that several functions (e.g., photosynthesis, leaf area index) approach a maximum just a few years after disturbance. Diversity will be considered in the next section, Correlation Species whose seeds are carried by wind or animals might be expected to have a random distribution shortly after germination in a cleared area. With a perfectly random distribution, the correlation coefficient between any two species is necessarily zero, because random distribution implies there are no positive or negative.

Correlations between species. As succession proceeds and competition increases, some species which are better adapted to the mice habitat (group A, for example) will crowd out other species which are less well adapted (group B). In another habitat, the situation could be reversed. All pairs of species within group A will be positively correlated, while pairs, one from each group, will be negatively correlated.

PROPERTY TAX TISSUE GROWTH EFFICIENCY I S TAX PERCENT) R 30 3500 ‘TIME (YEARS) Fig. T. Changes in various types of efficiencies during succession. Fig. 8. Comparison of trends of various functions during succession.

Part of this study was to determine how correlation between species of plants changes with succession in the tropical rain forest. As described previously, all the plants within a 676 n° grid were tallied according to the quadrat into which they fall. The same was done in a nearby area of the mature forest. Correlation coefficients between pairs of species were determined by counting the number of each species in every quadrat, and then determining the correlation coefficient. For example, the input data into the correlation coefficient calculation for positively correlated species might be as follows: quadrat 1, species X, 5 individuals, species Y, 4 individuals; quadrat 2, species X, 2 individuals, species Y, 1 individual, etc. For negatively correlated species, the data might be: quadrat 1, species X, 8 individuals, species Y, 0 individuals; quadrat 2, species X, 1 individual, species Y, 12 individuals, etc. In the successional area where the grass Panicum pallens was very common, it was given a value of one if present, regardless of its coverage of the quadrat.

Correlation coefficients depend on the size of the quadrat (Grieg Smith, 1962). Therefore, several size quadrats were used. One square meter quadrats were too small, even for the successional area. Too many quadrats occurred with zero of both members of each pair. For the successional

area, four contiguous square meter quadrats were used to make one size quadrat, and 16 contiguous quadrats were used to make a larger size, four meters on a side. In the successional area, quadrats larger than 16 square meters could have included two or more single-species clusters of plants, and thus could have shown positive correlation whereas negative correlation actually existed. Therefore, 16 m² was the maximum quadrat size in the successional area. For the mature forest, quadrat sizes of 16 m² and 64 m² were used. Quadrats smaller than 16 m² resulted in too many zeros, and quadrats larger than 64 m² presented the same problem as quadrats larger than 16 m² in the successional area. Correlation coefficients were determined for all possible combinations of the nine most important species (according to biomass) in each area. This amounted to 36 correlation coefficients for each quadrat size for each area. Correlations for the successional area were taken from the 1966 data. Coefficients were calculated with the aid of a desktop computer. Apparently, there is no increase or decrease in correlation in the area studied (Tables 12 and 13).

---Page Break---

Table 12. Correlation coefficients between species in the successional area, 1966.

	Species 1	Species 2	quadrats
1	Psychotria berteriana	0.02	0.05
2	Tabebuia pallida	0.19	0.29
3	Tenanthus pallens	0.33	0.00
4	Palicourea rij	-0.08	0.16
5	Digymopanax morototons	0.00	0.28
6	Paragrinonyoe dewingiana	...	...
7	Bebeula pitts	0.85	0.20
8	Tenanthus pallens	0.106	0.31
9	Zecropia peltata	0.03	0.38
10	Alchornea latifolia	0.15	0.18
11	Palicourea riparia	0.03	0.01

66 igemearmettont “002 “aca a " . Gasearia bicolor 0.06 0.05, 12 taterute pansan See ee 0.03 y =e Gecropta eltata e100 blot 18 " . ‘Archornia latifolia 0.01 0.15 ® so Rees ee 00318103 2 nS = Etim “Ook O08 a "os Saeeaste Bicsler 2 lee 2 onantius pallens Seen pices 30 0.08 5 = oink ak . . 0.01 0.07 25 . 0.05, (0.10 26 " 0.03 noice 2 ceoropte peltata on 28 0.01, 0.15, 29 " " 0.27 0.37 30 " " 0.55 0.65 31 «= Alchornea latifolia 0.47 0.38 2° . 0.35 0.64 3 patteogren ripest oer Oke 3 coures riparia oor ol 5 GR ES Gasearfa Biostar oor 8 38 piaymopanex norototont Gauss Hester og Os Average of 36 patra, 011 signs changed to plus o.to.ak 0,2240.21 -85- ---Page Break--- Table13. Correlation coefficients between species in the mature forest. Far Carrgintion coef Figient To, Species x Species ¥ 2énequadrats —Ghnéguadrate 2 Dacryodes excetse Ruterpe globose 0.01 2 Menigies sxcgiee Wniikars bidentate Soa 3 an Higenia seahiit 70:33 a . : Fallcoures riparte 5 ee Deypetes glauca é . : domingensis 1 oo Sloanea berterians 8 ae Groton pocet lantinis 9 Buterpe globose Hanitkare bidentate 0 70135 a : * 0.05 2 oo: -or2h Fr 4 Bat 1 i c G ont one a5 G 5 0.07 0.33, 36 Manttxara bidentate 0.02 0.09 ye cols. “0.46 B 5 : 0.39 0.39 ay : G 0.07 0.06 2» 5 5 0116 1 a a a Groton porctlanthus 70126 70.38 22 Bugenta stants riparia 0.09 0:38 B eee Drypetes glauca 0:38 0.35 2b G 9 Einoolera demincensta ore 0.57 25 o G Slomnea_ berteriana 0122 0.03 26 G G Groton poectlanthus 0:20 over 21 Pallcouren riperte Drypetes glauca 0.22 03 23 ee Sloanen bertertana

o:ah o.5L 2a . . ‘Groton ‘poeeilanthus 0:06 0.88 30 . a Einociera demingensis 22 “0.24 Bl Deypetes glauca Tinosiers deningensis 0. 0.79 32 Sioanes berteriane -0110 2.9 33 " " ‘poecilanthus 70:30 ~2 3% Linoctera domtngensis _—-“Bloanea Derteriana cole -2.01 3 Groton poeciianthia “0.27 -0.9 36 Stomnea bertertang Groton poectianthus 0.05 we Average of 36 patrs, all signs changed to plus 0.16 $0.12 0.36 ¢ 0.19 ---Page Break--- SECTION Ir by George E, Drewy In section two, current animal ecology etudies

including tracer work, end territoriality and other work with amphibians are reported. Also in this section a new approach to species diversity is developed, and applied to plant diversity in the radiation recovery area, and to insects in the surrounding forest. Insect keys constructed in the past year are also presented as an appendix. -87- ---Page Break--- PART A - ANIMAL ECOLOGY Work begun earlier on two animal ecology projects was continued by visiting investigators. Both studies involve termites, which are among the most important insects of the rain forest animal community. One study includes a census of individuals and relative metabolic rates of each caste in the termite nest by measurement in a microrespirometer. The other study, reported by Dr. E. McMahan in section three, is a follow-up of radiation effects on nest survival and includes some interesting experiments on worker behavior and direct responses to gamma radiation. Staff efforts continue to include studies of isotope tracers, insect diversity, and amphibian ecology. Isotope studies were enlarged to include uptake and bi-elimination of tritium in the form of HTO. Tritiated water sprayed at ground level was absorbed by direct contact and respiration in insects, snails, frogs, and lizards. No uptake was exhibited by insects, frogs, or lizards subsequent to 36 hours after treatment. Snails continued to show uptake as long as 72 hours after treatment when collected after crossing contaminated litter surface. A method for live testing snails consisted of teasing them back into their shells at which time they released 1 to 1 ml. of urine. Urine samples exhibited approximately the same count rate as tissue fluids obtained by dissection. Biological half-life of tritium in snails was very short, just under 2 hours. Tracer and bi-elimination studies of Zinc 65 in a natural population of the snail Caracolus caracolla moved into the second year, with resolution of some of the mysteries of the first year. Area of home range was found to be a

function of age, increasing until the second year after puberty and decreasing after that. Adult size, previously demonstrated to be independent of home range area, is likewise independent of age, shell growth ceasing at maturity. Present estimate of life span in this species is up to 18 years, with sexual maturity not developing until 8 years of age. On the basis of last year's growth these estimates appear to be within 2 years of the true values. Insect diversity studies involved research on methods of obtaining and expressing diversity measurements as well as the slow, continuing labor of separating and identifying the species of some of the poorly known groups. In some of these groups the recorded fauna for the whole island has been as much as quadrupled in this study alone. Comparisons are being made between diversities obtained with various trapping methods such as sticky traps, pitfall traps, light traps, and Malaise (flight) traps. Attractant traps such as light traps avoid the distorting effects of irregular natural concentrations or foci, but impose their own artificial focus on the distribution. The effect of natural focal lines in this comparison is giving a curvature to the normally linear relationship between number of species and log number of individuals. Progress in the study of amphibian ecology has moved into an area of collaboration with two graduate students at the University of Texas. With James P. Bogart, who finished a doctoral thesis on the evolution of anurans in the family Bufonidae and in the process accumulated considerable data for the family Leptodactylidae, a cooperative study on Puerto Rican Leptodactylidae is well advanced. Karyotypic analysis of 11 of the 12 species of this family in the Luquillo National Forest is completed and forms the basis for a set of hypotheses about insular

trends in the evolution of the family and the role of ecological specialization in their evolution. A joint publication in which analytical data is presented by

Bogart, and ecological data by Drewry, is to be the result of this study. Preliminary information indicates that several of the speciation events giving rise to separate genetic lines may have been due to ecological separation within the geographical limits of the island, and not to separate migrations from elsewhere. A list of chromosome counts from species of this family is given as Table I. Of particular taxonomic interest is the rediscovery after several years of Eleutherodactylus unicolor Stegner and the discovery of its call, its habitat and methods for collecting it, and the fact, revealed by its karyotype, that it may not belong in the genus at all, but to the genus Syrrophus. The second collaboration is with William Martin, who is finishing a doctoral thesis on the biophysics and mechanics of vocalization in anurans. Some of the hypotheses tested and supported by his research were originally proposed by Drewry, and others grew out of a long period of correspondence, so that the basic model is considered a joint achievement and is in early manuscript stages. Data on rain forest species is to be included in this publication. The possible ecological role of the call of male Eleutherodactylus frogs as a population spacing device is presently being studied. Mate attraction as one primary role is well documented, but recent observations of increased calling activity after the introduction of tape recorder playbacks or natural migrations of calling males suggest additional functions. Agonistic behavior toward calling intruders immediately after their calls has also been observed. Tape recording equipment and additional electronic circuitry to create a "responsive" artificial competitor are now on order. If quantitative behavioral responses are obtained, options designed into the equipment can control the timing and acoustic characteristics of the competing call, providing data of ecological, evolutionary, ---Page Break--- Table 1 chromosome counts of Puerto

Rican leptodactylid frogs. Diplota Chromosome Count Leptodactylus albilabris 22 Bleutherodactylus unicolor 30 E, portoricensis 26 E, antdliensis 26 brtttont 26 E. wightmamnae 6 E, rlotmonat 30 E, snetdse 26 E. hedriki 26 E, Locustus 26 ak E. gryllus ---Page Break--- PART B - SPECIES DIVERSITY Introduction and Methods Most methods devised to numerically describe population structure in ecological communities have been extensions of one or the other of two basic approaches. The earliest, and still most common, approach rests on an assumption that there is an underlying mathematical relationship that governs the complex ratio of numbers of individuals of various species to one another. Very little has been published on causative factors that might generate such a relationship, although it has been repeatedly observed that species similar enough to be included in a sample collected by a single method are almost never equally abundant, and that real samples never seem large enough to include all of the species known to exist in even a relatively homogeneous area. Williams (1968) has brought together a large amount of the evidence for the existence of such a relationship, and has proposed some sophisticated methods for utilizing this assumption. Although the methods are somewhat difficult to apply and require the use of a set of computer-generated nonographs, he has carried them to some remarkable lengths, and even proposes a model for the rate of species formation over the earth as a whole based on these methods. The mathematical relationship most commonly assumed to exist between organisms of a single habitat is an exponential one, that the number of species in a given sample is some function of the logarithm of the number of individuals in it. The simplest function would be a fixed ratio between these parameters (Odum 1953) and the index of diversity would be species per decade of sample size. A statement of species per thousand individuals or per any other fixed number taken in conjunction with this assumption would

provide sufficient information to extrapolate in either direction, to expected species number for any sample size. Although widely used, this method of description has only occasionally been validated by the total distribution of numbers in a field sample, and the validating graph has normally been constructed by counting species in a few subsamples of various sizes or by noting accumulated individuals each time a new species is encountered in a random sorting of the sample. Both tally methods require a randomizing procedure for sorting and recording, and neither uses as information the relative numbers of each species present. Williams has pointed out that assumption of a linear relationship between species number and log number of individuals violates mathematical reality, because zero species must involve zero individuals, while zero does not occur on a logarithmic scale, which is infinite in both directions. He substitutes the mathematically valid log series curve, which is defined by a parameter called 0G, and whose graph in semi-log plot is linear for large numbers and curves to the intersection of one and one. He claims validity for this relationship in many stands of vegetation and for light trap collections of lepidopterous insects, but has used the above mentioned methods of validation, with their limitations. He ---Page Break--- Williams also suggests that when collections are expanded to include organisms from more than one habitat type the relationship shifts from a log series to a log normal series, in which the logarithm of species number is linearly related to the logarithm of number of individuals. MacArthur and Wilson (1967) have utilized this assumption in a recent book on the theory of island biogeography. Again their validating data is a widely scattered series of points, although it seems clear that the relationship holds in a general way. Alef (1957) has introduced a new (to biologists) measurement of species diversity that does not rest on prior assumptions of relationships between species and

individual numbers, but has the disadvantage of not describing community structure beyond diversity. This is actually a family of measurements derived from formal information theory as used in communications engineering, and has been subsequently utilized by Pielou (1966a and b), Lloyd and Ghelard; (1964), Lloyd et al (1968), Dickman (1969), and others. Information content of an individual in the sense of species diversity is not all of the information possessed, but rather that required to distinguish it from the other species of the sample, i.e. possession of feathers is sufficient information to separate a sample of two chickens and a cat, but must be supplemented if the sample also contains turkeys. Two equations are available for calculating diversity in terms of mean information content per individual, known as Brillouin's measure and Shannon's measure. Both are given in several forms by Lloyd et al. (1968). Shannon's measure estimates the diversity of an unlimited population composed of a known number of species or classes from the proportions of each in a sample and is largely inapplicable to biological diversity where the total number of species obtainable is almost never known or present in a single sample. This measure will not be discussed further here. Brillouin's measure is: $H = -2. (\log 9\ N! - \Sigma \log y\ nt!)$ where H is mean diversity or information content per individual, c is a scale factor to convert to any number base desired (binary bits are often used in information theory where c = 3.321928), N is total individuals in the sample and ni are numbers of individuals of each species. This measure gives only the sample diversity and does not extrapolate to a larger population unless the population has the same structure as the sample. At this point the discussion has come full circle and focuses on the problem of structure. Many biologists have attempted to describe the structure of communities with graphs of relative abundance or relative frequency or with various arbitrary abundance classes,

but apparently have not attempted to relate these to species diversity. In this research, an effort has been made to relate all of the measures of structure and diversity in the simplest possible way. If species of a sample are ranked in order of decreasing representation, a curve can be drawn

connecting the number of individuals of each species. Because of the large range of categories, the level of the rarer species, resolution can be improved by plotting a frequency curve. “Resolution can be improved by plotting the number of individuals on a log scale.” “Figure 1 shows the cumulative species richness curve for the recovery area, labeled cumulative species richness.” This would normally be viewed with the left edge notation that the rarer species represented by one individual are considered to be in a reserve. The information available in the sample and the exceptions to be made about structure. The curve can be inverted by dividing the total number of individuals in the sample by the number of individuals in each species. The curve so formed is labeled cumulative species versus log N/n and can also be called a reciprocal frequency curve or a composite ratio curve. It retains the slopes of the relative abundance curve because division to logarithmically scale, but differs from the relative abundance curve in that given the composite ratio of species increases, each point on the relative abundance curve moves to the left as sample size increases while the composite ratio curve only widens at the upper ends. Points on this curve representing species may be real as a ratio, such as 20:12:15 or as one point in (20, 12, 15). The composite ratio curve in this form is similar but not identical to the species diversity index curve developed by classical methods or to Whittaker’s log series. The larger the range, which represents a single species in the composite ratio, also represents.

total species fd 10s srtcied dtyintais Bo will be dwed'ea trance petnt an ony eiverslty TOaet SOSA Sache nay date potrt normally used ah WiNldan's ale mete, Teporeant to gote; horerery tutte break near 10g 1.5 cee coe site Butte curve le fot a concession to nsthenatical reality in the comport reese eserty of the vegetation, separating a Group Of but epresents 9 reer e cee natio elope from a group of rarer apecies chante pects Te niopes Busha. break has characterized most, raving quite a afferent, o0Pe- ommnities stulied ant hae inveresting and predictable properties of its own. ‘The mathematical relationship between the composite ratio curve and the diversity index curve generated by ary method is a rigorous exercise in probability theory and has been substituted here ty an empirical correlation method covering the range of curves and slopes encountered in this study (some are not linear at any point), An exanple of the theoretical complexity is provided by the fact that the probability that a single species vhose frequency is one yart in one hundred vill de missing from a randon sample of one hundred is its pro- bability of absence ina sample of one (.99) raised to the 100th pover (approxinately 36%). The probability that it will be absent, but re~ placed by a still rarer species, involves all of their probabilities Jaa manser almost too complex for computation. Comon sense iniicates that for even a single sample there is not one but an indefinite fanily of diversity index curves depending on the order of sorting ani recording {ndividuals, and that there is a maximm likelihood curve having the highest provebility of occurrence that will best represent this furily. 3+ ---Page Break--- Such a curve should run approximately parallel to the composite inex Gurve, alvaye to the left of it (randomly varying individua> ciovey care cneeey® SOa'ne convergent with it because it is subject to the aaa eroteaines cs the log series curve at lov munber. Tt mst Pe caer acined that no theoretical reasona exist for Linearity of

{ties gymhasized that 20 Composite ratio curves in any type of Graph. Sent log plots are merely a representational convenience. The empirical method of comparing these two types of CRETES consists of correcting easily sampled populations of known composite consisting of common and extreme types of populations encountered in ratio for the mean does not include all theoretical curves, some of which deviate from the conclusions reached. For example, the curves of a diverse population, each of whose members is a stereo, see in diversity index 10 log series whose OC is continuity while the composite ratio is a vertical line at the chosen sample size. The other extreme is an infinite population of one whose diversity index is a straight line at one, or at whatever

composite ratio is a single point sample size is chosen. Composite ratios chosen for this experiment ranged from 10 to 500 species per thousand individuals and were either straight, broken, or continuously curving upward in semi-log plot. Collections were made continuously from numbers table whose digits were “identified” in groups of three by assignment of number groups from 000 to 999 to relative frequency categories dictated by the composite ratio. Diversity index was only evaluated to 100 individuals because of the constraint set number of species per 1000 rather than the natural situation of an indefinite number of species of progressively lower frequencies. Distribution of data points in large numbers of series of 100 individuals confirmed the common sense expectation; the curves followed a log series at low numbers shifting to a curve similar to the composite weighted curve past 10 individuals. Distributions appeared to be normal on the species per fixed number of individuals axis, for which the mean was an adequate measure of central tendency, while on the log individuals per fixed number of species axis distributions resembled the Poisson Distribution and the median was taken as the best measure of}

central tendency. Convergence of the curves predicted from the necessity that the diversity index curve pass through the upper point of a realistic composite ratio curve was supported in curves having a straight segment from at most 50 to 1000; the curve straightened and passed through log individuals at the same number of species as the composite index curve had at log 100 individuals; when extended it passed log 640 individuals at the species level of log 1000 individuals in the other curve and also intersected the upper point of the composite ratio curve, which is always above the line of the curve itself. A maximum likelihood diversity index curve consistent with these observations is given in figure 1. If such a maximum likelihood curve continues to be supported by theoretical and/or empirical evidence it provides a method of stating the slope of a linear segment of the diversity index curve above 100 individuals in terms of the slope of the composite ratio curve (it will be 1.0280 times the slope of the composite ratio curve or log 640-log 60) and for extrapolating the number of species in any fixed sample size such as 1000 believed.

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A Cumulative species vs log
B. Diversity index maximum likelihood curve
C. Cumulative species vs N

Fig. 1. Graph showing inter-relationship between relative Runtesbe (curve A), composite ratio (curve C), and the estimated maximum likelihood curve of traditional diversity index methods (curve B). Semilog plot is for representational convenience and does not reflect assumptions about species inter-relationships.

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to tie on the linear portion of the composite ratio curve. Species per thousand is approximately the intersection of the composite ratio curve with log 1000 plus .2 times the C.R. curve slope (log 1000-log 0 times log 640-log 60 or .1926x1.0280 = .2). Basing the standard requirement of species per thousand on the slope of the composite ratio curve, rather than on the number of species collected.

In a sample of 1000 individuals, how has already proved to be a valuable strengthening of the foundation for this useful measurement. When notified that the number of rare species in a certain

collection was theoretically inadequate, one collector was reminded that a small group of very rare species had been put aside for detailed identification and forgotten. The relative taxonomic abilities of several collectors have also been evaluated by this method, and the evidence obtained has been consistent with other evidence available. Extrapolation of such measurements as species per thousand upward beyond the limits of the sample has so far been confined to communities having linear composite ratio curves, but downward extrapolation along non-linear diversity curves agreeing in shape to the composite ratio and passing the log 640 and 60 points has given realistic estimates. Information theory measurements have proved difficult to relate in a simple way to the above measurements of diversity. Independence of sample size has been found in very few cases where the composite ratio curve was linear and the usual group of common species exhibiting different slopes was absent. Normally, Brillouin's measurement is very sensitive to sample size, making our necessarily differing samples difficult to compare. In addition, the output measurement is subtractive rather than multiplicative, and scaling to a comparable sample size must be done on the input data before computation. This scaling is most readily accomplished by computer manipulation of the data. Log factorials are most easily handled in tabular form (Lloyd et al. 1968), but fortunately, an alternative exists in the form of Sterling's approximation: Log n! = (n + 0.5) log n - 0.43n + 0.39909, which can be written into a computer program. For rigorous accuracy, logarithms should be taken to six places, but it was determined that the uncertainty in Brillouin's H of four random subsamples of 100 square meter plots from a sample of 676 square meter plots.

outweighed by at least an order of magnitude the error in H occasioned by using four place logarithms, so these were used. Five programs have been written for computing this measurement on the Olivetti Underwood Programma 101 desktop computer. The first two are alternate programs yielding total information content in bits, H in mean bits per individual and N, the total number of individuals. One is for unskilled operators, requiring only the entry of species number (n) for each species but is much slower owing to the calculation of log n, which it prints for each entry. The other accepts n and log n in pairs and runs at approximately 50% entry time and 50% computing time for a skilled operator. The remaining programs differ only in stored constants and scale data downward to 1000, 500 or 100 individuals distributed according to the composite ratio curve. They require entry of N, log N and n and log n for each species in pairs. By utilizing Sterling's approximation they calculate log n! on a continuum rather than as discrete whole numbers and thus avoid rounding errors. Species are entered from commonest to rarest and output is automatic when N/m for an entry is less than 1.5 (log n! for single individuals is zero and does not contribute to the index). Programs and constants for this computer are stored on magnetic memory cards and entered by passing the card through a reader. Copies of these programs are available to anyone on request. Equations have been rewritten and constants consolidated to minimize memory space. The entire memory capacity is utilized in each program. Processing of data has been consistent and diversity measurements are now available for several communities of plants and animals. These include a semi-log plot of composite ratio, called the CR plot, the slope of linear portions of the CR curve in species per decade, designated A slope for abundant species and B slope for rare species when two linear slopes are present, an estimate of species per hundred, per

five hundred and per thousand based on the slope of the CR curve (sometimes involving extrapolation upward, if the CR curve is linear), Brillouin's H and information content of the sample in bits per individual and binary bits respectively, and scaled H an information content for samples scaled downward to 100, 500 and 1000 individuals where appropriate designated F.100, H.500, H.1000 and Int./100, Int./500 and Inf./1000. Of these measurements, the CR plot has proven most informative to the experienced evaluator. It opens the way to further research by pointing out real

discontinuities in the ratio between abundant and rare species that are smoothed over or concealed by the random fluctuations of traditional diversity index plots. Species per fixed number of individuals, particularly per thousand, which form an easily remembered diversity statement can be rapidly and reliably estimated from CR plots and arduous randomizing procedures are unnecessary. The only danger seems to lie in its apparent ability to conceal the combination of certain unrelated types of communities (it readily reveals others) and the consequent possibility of publishing diversity figures that are meaningful only for the unnatural combination. A non-linear CR plot immediately reveals the fallacy of applying linear diversity index methods and can be used to expose such inappropriate applications in past research. It is hoped that both the advantages and limitations of information theory measurements will be realized by the bulk of workers in this field and that uncritical and inappropriate application and resulting false conclusions can be avoided. CR plots in the remaining portions of this manuscript will be presented with log N/n on the ordinate and cumulative species on the abscissa. This is done deliberately to avoid confusion with traditional species diversity curves. -91- ---Page Break--- ‘The Development of Plant Community structure Plant succession following a dose of gamma irradiation that either killed old vegetation outright or greatly

Reduced its ability to compete illustrates well some of the trends in the development of communities. A grid measuring 676 square meters has been mapped in detail each year beginning one year after the 1965 period of irradiation. Taken as a whole, the vegetation had reached its maximum level of mean information content within a year after irradiation, H' decreasing from 4.922 bits per individual in 1966 to 4.889 in 1967. At the same time, the species per thousand increased from 6 to 76, an increase of more than 5 percent in this measurement of diversity. The apparent discrepancy is explained by the CR plots in figure 2 (data points are omitted in this and the following plots. All are very similar to fig. 1 in fit). The diversity changes reflected in H' occurred in the A slope or abundant species group, while species per thousand responded primarily to large increases in the number of rare or B slope species. Breaks in the composite ratio curve delineate 17 abundant species in 1966, having a total of 4,002 individuals, and only 10 species in 1967, the number of individuals H' is calculated for the abundant species only. At the same time, the number increased to 5,133. The drop in diversity is from 3.628 to 3.097. The number of rare species was extended from 79 to 109, and while rare individuals increased from 1,240 to 3,090, diversity measured by H' increased from 5.147 to 5.439 on these species alone. The B slope increased from 33.28 species per decade to 41.18 while the A slope decreased from 19.90 to 11.46. Thus only the CR plot tells the whole story. The dimensionless indexes appear to contradict one another until their bias is revealed. Three trends are noteworthy: a rapid and early increase in both numbers and diversity of abundant species, which seem to be well adapted to the situation; a subsequent reduction in the number of abundant species with further increase in the number of their individuals; and a slower increase of species and individuals of rare species bringing the total species count to a maximum. 1968 data on

Total vegetation is still being processed, but the numbers of both species and individuals declined as individuals grew and space became a limiting factor. Overall species diversity has probably increased as intraspecific competition eliminates individuals of common species more rapidly than those of rare species, but the exact effects on H and species per thousand cannot be predicted. Data processing is complete for tree species, and CR plots for trees originating from seed after the radiation treatment are given in Figure 3. In this figure, the three graphs on the left are for seedlings in 1966, 1967, and 1968, respectively, while the two right-hand graphs are for saplings more than 4.5 feet tall for 1967 and 1968. Only Cecropia peltata saplings exceeded this height in 1966, so no

ratio was obtained. The composite ratio of seedlings in 1966 is different from any of the other curves shown and reflects the effects of open, well-lighted ground for germination. The A portion of the curve includes 20 species and the fast-growing species have not yet gained the numerical advantage they enjoyed in the next two years. The slope and H of the A curve were the highest measured for any A trees, being 11.38 species per decade and 3.639 bits per individual, respectively.

Fig. 2. Composite ratio curves for total vegetation in a radiation 'cles data points cited.

Species

Fig. 3. Composite ratio curves of seedlings (4.5 ft. tall) and saplings (> 4.5 ft. tall) of tree species one, two, and three years after irradiation. Ordinate and abscissa have been reversed from figure one and species per thousand at 35 is the lowest registered for seedlings. The combination of this curve.

with the curves for non-tree plants, sprouts, old trees and saplings obliterated all traces of the break in the CR curve, (see Fig. 2) one of the few cases in which this happened. ‘The seedling trend in 1967 was similar to that in the total vegetation but more pronounced. Six species produced more seedlings than 20 had possessed the year before. The H measurement for the A segment dropped more than a whole unit to 2.413 and the slope likewise decreased to 8.08 species per decade. The B segment increased even more than the A segment decreased, with an increase from 20 to 95 species, 37 to 1,588 individuals, and 3.377 to 4.748 in average information content of the segment. Overall diversity thus increased species per thousand from 35 to 47, H from 3.732 to 4.071 and the scaled Hoo9 from 3.67 to 3.977. Seedling changes in 1968 represented the same diversity trends to a much smaller degree, except for the A segment, which changed very little. The number of abundant species remained the same, about 1 percent of the individuals moved into the sapling category or died (mostly the former), raising H from 2.413 to 2.5. ‘The B segment lost two species and 10 percent of its individuals, but this was a net increase in diversity of 8 percent in slope and 2 percent in H. Overall diversity rose by 6 percent in species per thousand to 50.5 and by 2 percent in H and Ho90. Perhaps it is purely coincidental that these values all correspond very closely to those found in climax trees in this general type of terrain and soil, but it is very interesting that seedling trees, consisting of a large percentage of successional species that will be replaced in the mature canopy by other species, should in three years time establish such a mature community structure. ‘Of course, if species versus area were under consideration, the seedling diversity would appear to be enormous, but it would seem that species versus individuals is the more appropriate measure of diversity when communities of very different individual size are being.

compared, It will be interesting to see whether the large reductions necessary in species and individuals for this 676 square meters to be occupied again by mature forest can be accomplished without disturbing the diversity structure, or if oscillations are inevitable. Sapling changes in the first three years have involved clover but steady increases in all of the diversity parameters. Species increased from one the first year to 16 the third year to 21 the third, Individuals increased from 1 to 557 to 707. Extrapolated species per thousand were 1, 2, and 3 have gone from zero to 2,923 to 3,196, Slope A has been 0, 5, and 6; while slope B was 0, 15.02 and 19.54. “The only probable overshoot so far is the number of A segment species which went to 10 in 1968. That category would appear to be at a diversity stage somewhat similar to that of the evenings before the first measurements were made in 1966, so diversity overseer and subsequent correction are probably

to be anticipated once the foreign species. There appears to be little competition among saplings at this time. The area of this study has been divided by Dr. Carl Jordan into two soil types, well and poorly drained. Vegetation from these two types was processed separately before being combined into the categories already discussed, and although a great deal of labor was involved, trends in the two were so similar as to warrant little discussion here. Development did proceed more rapidly in well-drained soil and it seemed always at a more advanced stage. Although several individual species showed strong preferences for one or the other type of soil, any slight differences in diversity parameters were averaged rather than additive when the two were combined. In distinction to different habitats to be discussed below, these seemed to be complementary parts of the same habitat from a diversity viewpoint. One difference that was amazing in its consistent repetition was the number and corresponding slope of A segment species. These

were always more numerous and diverse in well-drained soil. In what is taken as mature ratio, i.e., climax vegetation, old radiation center vegetation and 1966, 1967 seedlings, the A slope species numbered 9 to 11 with a slope near the same value in well-drained soil and about 6 in poorly drained soil, averaging 8 in combination. This phenomenon appeared identical in manifestation with the sun-adapted abundant species of recovery vegetation and the entirely different dominants of mature forest. The explanation seems to be that fewer species are well adapted to the anaerobic soils of poorly drained areas, so that the competitive advantage these few have is greater. Figure 4 illustrates this phenomenon. Table 1 shows some of the stronger individual soil preferences. These were computed by multiplying by a scale factor to correct for inequality of soil areas, subtracting less preferred from preferred and dividing by the sum. No preference would be zero percent, while 50 percent indicates that three-fourths of the individuals are found in the preferred soil. To discuss trends in the development of rain forest community structure after irradiation, the often stated rule that successional communities develop higher diversity in early stages than they will exhibit at maturity (Olium 1959) seems to require qualification. The sentiment seems to be very true for the more abundant species, which appear to be the ones best adapted for rapid germination and growth and which will always be collected and identified in quantitative studies. These species will also bear the brunt of competition during the inevitable crowding as individuals grow; however, competition may be intense at the intraspecific level, with the result that formerly common species may recede toward rarity without disappearing more rapidly than less well-adapted species are completely eliminated, all of which would dictate gradual increases of diversity in species per individual. Something of the sort seems to have happened here, because at no time

Has there been a reduction in total diversity among plants in comparable size categories? This generalization does not hold at all if species per unit area is taken as a measure of diversity, for the growth process itself dictates that a large percentage of early colonists cannot survive to reach tree size and selective forces favoring rarer species would have to be many times stronger than they apparently are to overcome this elimination process. Thus, the generally held belief that diversity in terms of individuals does the same as diversity in terms of area must be strongly restricted to situations in which size and/or density are equivalent.

In summary, the seedling population of this recovery area was able in three years to produce a diversity structure comparable to that of similar areas in every way except species per unit area. In that regard, it achieved a species density that can only be reduced with the passage of time. In addition, two general classes of abundance that characterized the composite ratio of every vegetational unit studied were manifested very early in the succession. These classes exhibit, within themselves, a remarkable exponential relationship between species and individuals having a

characteristic slope, and the differences in slope and information content between classes increased with time to a plateau level. Overall tree species diversity in this successional vegetation reached approximately 92 species per total individual.

Several studies have aimed at discovering community structure and diversity of lower montane rain forest in Puerto Rico. Smith (in press) studied preirradiation diversity in the El Verde site by conventional diversity index methods and arrived at a figure of approximately 48 species per thousand individuals for the mature forest.

In a later study involving transects into different habitats, he obtained 60 species per thousand. The present techniques were applied to a sample of 116 trees in 676 square meters of the control center sampled especially for the purpose and yielded a composite ratio having an A slope of 8 species per decade, extrapolating to 50 species per thousand individuals (figure 5). In an attempt to avoid extrapolation, a sample of 2000 trees was made in a 10 meter wide transect encircling the irradiated area at a distance of 160 meters. One thousand trees were taken on well-drained soil and the transect was lengthened by spiraling to include 1000 trees on poorly drained soil. The composite ratio for poorly drained soil had the expected shape and reduced A segment, but had 53 species and a B slope indicating 58 species per thousand, while the well-drained soil sample had an unexpected shape with three segments, had 55 species and would require 62 for the usual symmetry (figure 5). As the more or less linear transect had been taken in order, the trees were divided into groups of ten and a search made for frequency correlations of certain species in neighboring groups. The data under this treatment fell into three groups having high internal correlation and low correlation with other groups. One group was dominated by Croton poccilanthus, a tree of ravines and flats that is rare on ridges and slopes and was rare in the other two groups. A second group was dominated by Butia capitata, which was also a dominant in the Croton group but had a complex of species almost absent from the other groups, including Myrcia glomerata, Trichilia pallida and Ixora ferrea. The habitat of this group seemed to be gentle slopes having mostly soils of high moisture content, seeming to be easily separated into well and poorly drained categories. The third group was dominated by Sloanea berteriana and seemed to be a ridge top and steep slope flora but included also a river bank flora having sensitive species which was impossible to separate with this.

technique, -103- ---Page Break--- empos re 6 e ratio curves obtained for natural forest. (A) M16, dave nevers in ruination control center (B) 1000 trees growing in poorly drained (reduced) soils (€) 1000 trees from red of Fellow (presumably well-drained soils). Fig. 6, Further breakdown of figure 5C into three apparent tree associate ‘tons which correlate with topography. Lower curve characterizes flat areas and is dominated by Croton poecilanthus, Middle curve includes steep slopes and river banks and is dominated by Sloanea berteriana, Upper curve includes gentle slopes with Heterpe globosa and Dacryodes excelsa as dominants but has Trichilia pallida and Myreia deflexa as exclusive subdominants, -10h- ---Page Break--- When processed separately all three of the groups had higher diversities than expected, but the unique third segment proved to be a phenomenon of the Myreia ~ Trichilia group (upper curve in figure 6). The A segment of this group has only three species; Heterpe globosa at 1 part in 5, Dacryodes excelsa at 1 part in 10, and Myreia deflexa at 1 part in 18.” Almost all of the remaining tree species found in any forest habitat occurred as rare species among the 360 individuals sampled and very rare species were inadequate in number. ‘The only other place such composite ratio was encountered was in post-radiation sprouts to be discussed below. Explanation is very hypothetical at this point but may involve a sublethal environmental stress such as strong seasonal fluctuation in moisture content.

Specialist species, such as those in the chronically poorly drained soils, could be discouraged by temporal physical diversity of the environment from exerting strong competitive pressures, leaving the habitat relatively open for sub-optimal, subsistence utilization by any comer. Such a situation could lead to the development of a condition of maximum diversity and may have, to the extent that the diversity limits of a small island land mass are being reached. The composite ratio for this habitat would apparently allow

for a species per thousand diversity of about 70, which approaches that recorded in continental rain forests, and it is doubtful that so many sufficiently unspecialized species are available. An analogous situation exists in the human economic situation of Puerto Rico, where an infusion of foreign capital has acted to depress competition. Aggressive entrepreneurs are able to amass fortunes and there seems to remain plenty, yet many specialized occupational niches remain mysteriously open or are filled by relatively non-aggressive immigrants; the explanation being that the human technological diversity of the island, developed under conditions of stronger competition, is inadequate to fill the niches as rapidly as they would be filled in a larger area having a broader economic base. If applicable, the hypothesis may further indicate that maximum diversity, although not to be expected under conditions of strong environmental stress, may appear under conditions that are not conducive to the most rapid utilization of resources, as these promote keen competition and stress of biological origin. Chronic or recurrent sublethal stress could therefore be the key to maximum diversity. Community Destruction only two categories of plants seemed to show diversity effects attributable directly to the radiation stress. They were the plants that survived until the post-radiation measurements were taken, and a subcategory, those that sprouted and began regrowth after sustaining visible damage. ALL plants in the sampled area had shown visible damage by 1967. From the standpoint of the composite ratio the plants maintained an orderly retreat (figure 7). Individuals decreased from 82 in 1966 to 38 in 1967, the number of species from 5 to 10, extrapolated species per thousand from 51 to 40, and H from 3.821 to 3.451. The number of species in the A segment decreased from 8 to 5.

and two years respectively. =r Figure 8, Composite ratio curves of sprouts populations one and two years after irradiation, -106- ---Page Break--- A slope from 9.5 to 5.3, while a comparable decrease occurred in the B slope, from 20.25 to 22.55. Thus, although individual species differed in radiosensitivity, the decreases were distributed throughout the composite ratio, in contrast to the development pattern, in which diversity changes in the common species were not synchronous with those among rarer species. Processing is not complete in 1968 old vegetation, but the overall trend continued without major discrepancy. Sprouts from old vegetation were placed in a separate category from the parent plant, which remained in the group just discussed. Although sprouts have taken a respectable position in the community of recovery vegetation, and have increased in numbers and diversity, they did exhibit an unusual composite ratio during the first year that may represent a reaction to the radiation stress (figure 8). Separation of the usual B segment into two separate linear segments having different slopes was observed earlier in what appeared to be a community of natural occurrence. Here the explanatory hypothesis has a more tangible form. Removal of the canopy created conditions conducive to rapid growth, and undamaged meristematic tissue near or below the ground surface, where rock and slope shielding had reduced radiation dosage, found itself with a strong competitive advantage over seedlings by virtue of possessing extensive and relatively undamaged root systems and food reserves. Spacing of the old plants reduced competition between sprouts to a very minimal level. The controlling factors for diversity therefore became the diversity of old plants, the diversity of meristematic tissue near the ground among them, the rate at which this tissue could be stimulated into growth, the radiation dose

received and the relative radiosensitivity of each. Meristem diversity may be the factor most responsible for the fact

that sprouts have a lover diversity than old vegetation as the sprout lists are very similar to the old vegetation lists but lack certain species completely. The 1966 anomaly in composite ratio, on the other hand, seems to be partly a function of sprouting rate, as several rarer species did not join the sprout community until 1967. Other factors may have also operated to knock out the anomaly, competition with the fastest growing saplings probably intensified and the inroads of disease and insect predators increased the rarity of some species. The B slope ultimately achieved was the one predicted by the more diverse of the two B segments of 1966. Animal Diversity Animal diversity studies have lagged behind the studies of vegetation because fauna are more poorly known than the flora, sampling methods are more biased due to motility and secretiveness of the organisms, and fewer investigators have studied the question of diversity in this area. In particular, the problem of mobility becomes almost insurmountable in some groups. Turner (in press) discussed problems he encountered in attempting to assess vertebrate populations and how greater mobility in one lizard species made data obtained for it incompatible with data gathered for a more sedentary member of the same genus. The census data for birds gathered by Recher (1964, 1965, in MacArthur and Wilson 1968) is good in many respects, but numbers were obtained on both sexes of some species, only males of others, and others were observed but could not be counted. Insectivorous birds are rare in the resident populations but the pattern is complicated by massive seasonal influxes of migrants, particularly insectivorous warblers of numerous species. Wiegert (in press) made population determinations of soil and litter microarthropods but could not carry separations to the species level in some groups. Continuing efforts have been made over the past three years to achieve sufficient familiarity with the insect fauna for meaningful

diversity estimates to be made. To this end, keys have been written separating distinguishable species designated by code letters. When sufficient material is accumulated in a family group, the group is sent first to the U.S. National Museum under an agreement with Dr. William Anderson, and, if the museum specialists recommend, it is forwarded to a recognized specialist for the group. Of some 30 families sent so far, none has failed to contain some undescribed species, and some have contained more unknown than known forms. A sample key written for the Dolichopodidae is included as an appendix to this report. This is a Dipteran family for which determinations have just been made by Dr. Harold Robinson of the U.S. National Museum. For diversity purposes, all Dolichopodids are assigned a letter and the abbreviation Dol. Other abbreviations are explained at the beginning of the key. Insect collections have been made using sticky traps, malaise flight traps, and light traps. Composite ratio plots have now been made for significant numbers of insects collected in single 24-hour periods. Numerous other collections have been made and are in various stages of sorting; some are waiting on taxonomic work for only a very small percentage of rare species in difficult groups. A sample of 6,377 insects was taken in 31 small mosquito-type light traps on the night of Sept. 24, 1965. Total diversity calculations have been made on these insects, 5,769 of which were Diptera with 98 species, 268 Lepidoptera with 60 species, 145 Homoptera with 26 species, 79 Trichoptera with 13 species, 62 Coleoptera with 16 species, 42 Psocoptera with 9 species, 35 Hemiptera with 9 species, 32 Hymenoptera with 7 species, and 13 Neuroptera with 9 species. All CR plots with the exception of Lepidoptera were smooth curves with no clearly discernible segments such as were characteristic of vegetation. Lepidoptera exhibited a sharp break beyond the fifth species but tended to curve a little beyond the break (see figure 9). Samples of other families are

also presented in figure 9, with Trichoptera the least diverse and Coleoptera more diverse. “Such curvature makes H a very inadequate measure because of its high sensitivity to sample size. Scaled H seems to be the only information measurement giving valid comparisons between groups, although no routine scaling procedure for samples less than 100 was used. Crude extrapolations for H 100 were made on Trichoptera and Coleoptera, yielding 100 of 1.6 and 2.8 respectively. 100 for Homop- 108- ---Page Break--- Fig. 9. Composite ratio curves for insect families taken in light traps Sept. 24, 1965. (A) Trichoptera (B) Coleoptera (C) Lepidoptera. Fig. 10, Composite ratio curves for total insects taken in (A) Hsgni trope Sept. 24, 1965. (B) malaise flight trap. The scale on species axis is very different from previous curves, -2109- ---Page Break--- tera was 3.5, for Lepidoptera 3.9, for Diptera 4.2 and for total insects 4.3. As no insect family can be said to form a community in the sense the word was used for plants, perhaps only the total insects (figure 10) should be compared to plants. "An estimate of species per thousand by the maximum likelihood method is/125, while #1000 = 5.108, both much higher than in any community of plants measured. Malaise trap insects exhibited similar patterns but the largest sample in 24 hours was 199 insects of 120 species (figure 10). #100 of this sample was the same as in the light trap at 4.3, but curvature was much stronger as is suggested by the fact that almost as many species were obtained in 200 individuals as the estimated species per thousand from the light trap. A very crude estimate of species per thousand would fall between 200 and 300 and suggests that the light trap is more selective than the flight trap, which uses no bait but depends on the tendency of flying insects when encountering an obstacle to veer upward. When one considers that this trap is almost limited to flying insects and is immune to many of them as evidenced by sticky trap collections.

we see that total insect diversity must be very high with a truly unbiased and random sample of 1000 insects containing perhaps 500 species. Conclusions and Discussion From the standpoint of diversity methods we have concluded that each method mentioned makes a valuable contribution to our understanding of community structure and diversity, and that there are pitfalls in the uncritical applications of any of them. In particular, linear methods such as William's log series or a falsely assumed constancy of Brillouin's H measurement with increasing sample size can be misapplied. Actual plotting of a diversity index curve can give warning of nonlinearities at high number levels and the even more easily computed composite ratio provides a view of total sample composition, giving a solid foundation to whichever diversity index is chosen. Details of community structure noted are a break in composite ratio of most plant communities which is not a mathematical artifact and which divides the community into a group of common species with lower diversity and rare species of higher diversity, an occasional second break farther out which sets off a group of the rarest species having lower diversity than the intermediate species also thus formed, and the absence of such breaks in trap samples of insects of most groups. It is probably inappropriate to call trap samples of insects or their taxonomic subgroups communities, or to compare them in any rigorous way to communities of macroscopic vegetation. When more knowledge of the ecological role and trophic levels of the particular insects is gained it may be possible to assign species to communities. An example is the fact that some phorid flies, a group dominating sticky trap collections, are scavengers and some are known to be insect parasites. These are members of the same community only in the sense that vines and mushrooms among the plants are, -110- ---Page Break--- and diversity of this scope has not yet been measured in the plants. It is even possible that the

continuous curvature in the composite ratio of the insects 49 the result of single breaks at different points in many combined community curves, but this unlikely in view of curvature 1 such groups as Trichoptera, which are ecologically very narrow. A more probable explanation is that the insects

collected are adults, and many, if not most, species from breeding aggregations of varying density and dimensions. There is thus a potential non-linearity in the distribution of each species and random countings should yield many valleys and few peaks. The combined sample of many independent species should therefore show the same trend. In addition to possible selective attraction of light traps, this phenomenon might provide additional reason to expect less ratio curvature and diversity, as an attractant should tend to shift several distribution peaks into register and sample the tops of all. It was hypothesized that analogous double-breaking vegetation CR curves could be due to the effects of reduced competition combined with some sort of limit on the number of species able to take advantage of this. In post-radiation sprouts the lack of competition was clear and the limit was suggested to be the rate at which species could sprout. This anomaly disappeared in the second post-radiation year. A similar anomaly was found in natural vegetation in certain soil types apparently intermediate between well and poorly drained and containing a complex of medium to rare tree species almost absent elsewhere. Reduced competition was inferred from the comparative absence of abundant specialized species, and the limit on rare species was suggested to be the island's lack of sufficiently unspecialized species able to grow there. In the development of plant community structure, abundant species were found to overshoot the ultimate levels of diversity very early and return more slowly to the mature levels. Rare species were found to slowly increase to the mature levels with no overshoot yet observed. Total species diversity as

Species per thousand was found to be more sensitive to changes in rare species, but Brillouin's I did not show diversity overshoot in tree species only. The latter measurement followed the common species in overshoot and correction when total vegetation, including herbs and vines, was considered. Seedlings of tree species considered as a class established mature levels of diversity in every parameter by the third year and served to point up the fact that species per fixed number of individuals is a very different measurement from species per unit area unless individual size is strictly comparable. Reduction of diversity in vegetation showing radiation damage may occur, but the reduction was orderly in that disruption of the composite ratio did not occur as plants died. In projected diversity studies, it is desirable to follow radiation recovery with annual surveys for several more years. The sapling class of new trees seems to be duplicating in slow motion diversity events that -lll- ---Page Break--- Dear mes ino malty tnt seating cats for snd seetin._fore sey aa Wet tte ana uae eet ame, fs ogetes alt ai eeesitns Bene tre aes Soose Bete ee oR cee ah re Erte Sent cee Sr cea of Some Sie ena, tunes ano ae a ele ee acne ots aceasta Marr eek Sic eeeliy ay fort cme tant SSS eta See ence enter ey tie tee et soa eet lo References Brillouin, L., 1956. Science and information theory. Academic Press. Lloyd, M., J-H Zar, and JR. Karr, 1968, On the calculation of informational-theoretical measures of diversity. Ann. Midland Naturalist 19:257-272. MacArthur, R.H., H. Recher, and M. Cody, 1966. On the relation between habitat selection and species diversity. Ann. Naturalist, 100: 319-327. MacArthur, R.H., and E.O. Wilson, 1967. The theory of Island Biogeography. Princeton University Press. Margalef, R., 1957. La teoria de la información en ecología. Mem. R. Academy Sci. y Artes, Barcelona, 32: 373-449. (Transition, 1959. Information theory in ecology. General Systems 3:36-71). McMahan, E.A., and N. Ferguson, in press.

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Williams, C.B., 1964, Patterns in the Balance of Nature and Related Problems in Quantitative Ecology. Academic Press. 12+ ---Page Break--- Appendix A to Dolichopodidae of the Rain Forest at El Verde by George Drew at El Verde by George Drew (Giant intentions by taroia Tobinwon, U.S. National Survey). Abbreviations: A = anterior, P = posterior, D = dorsal, V = ventral, Tl = protibia, Ws = mesotibia, 1 = metatibia, m = wing veins after Curran (North American Diptera, Second edition, Henry Artpp, Pb.) 21. Fourth vein with a widely divergent fork; all metallic flies more than 3 mm long. 1! Fourth vein without a fork 2 Scutellum with 4 strong bristles (Condylostylus) 2 Scutellum with only 2 strong bristles (Sciomyza) 3. Wings punctate ..., 3* Wings clear . 4 Wing pattern distinct; bristles of Tl elongate. C, P. pilosus (Loew) Do 4" Wing pattern indistinct; bristles of Tl elongate. C. diffusus Wied . & DOL AR 5 AD and AY bristles of 12 greatly elongated; 2 long PY bristles on C. prutinosus (Cog.) «. DOLW 5" 12 bristles normal; no PV bristles on Tl. C. Dol (Van Duzee) .... 6 Gap between tips of third and fourth veins much wider than diameter of tibiae; all coxae yellow; bristles and wing veins yellowish. 8. sp. near bellinanus (Van Duzee) « 6+ ‘Titra’ and fourth veins almost meeting at diameter of tibiae; wing veins dark ..... 7 Pleura light in color (except a small anterior spot); two stripes on each abdominal.

tergite. 8. dorsalis Loew T’ Pleura a dark metallic color 8 Meso and metacoxae dark in color «s++++++ peer co 6) 8' Metacoxae yellow, mesocoxae slightly darker; sclerotized portion of first abdominal tergite two narrow wedges joined by a thin line. 5. sp. near wnicinetus (Van Duzee) ssssereeersereeerasereee Dol Q 9 Sclerotized portion of first abdominal tergite divided into two separate thin slivers; second tergite with triangular posterior and having an anterior lobe. S. sp. not identified ..... Dol X 9* An undivided bend on first tergite, which may have an anterior notch ae peaees seeee 10 ---Page Break--- 10 Three medium-sized bristles on each side of first abdominal segment, an anterior notch in band; all antennal segments dark. S. sp. near inaequalis (Van Duzee) « + Ee Dol D 10" A single very large bristle on each side of first abdominal segment, no notch in band; antennal segments yellowish, Lx especially first. Probably S. inaequalis (Van Duzee) «+++ 11 Pronotum mostly bare of fine hairs, those present confined to strips in front of bristle rows; color always metallic .. ah 11! Front of pronotum with numerous scattered fine hairs; 9 metallic 12 Fourth vein bent strongly forward beyond posterior crossvein .. 12" No strong bend in fourth vein, may be curved «eeeeeeseeee 13 Posterior crossvein almost perpendicular to fourth vein; legs esse Dol yellow. Sareonius lineatus (Ald.) ...+ peers reveii oblique to fourth vein; legs dark a3 1s Fourth vein ending near wing tip. Tachytrechus sp. Dol FP 24" Fourth vein ending well before wing tip. Plagionewus| tatus Loew sss... 3 RS renssa + Bon 15, Front of pronotum yellow « % 15* Front of pronotum metallic’. B 26 Sixth (anal) vein present; a large, round green spot in front of scutellum, Nourigonte signifer Ald. .. Dol k Tt 16" Sixth vein absent: thorax wholly yellow. Xanthina 17 72 with a comb of ventral bristles, having in addition long hairs in the male; posterior half of postscutellum and postnotum yellow EDs soeee 60 17! T2 without ventral bristles;

postcutellum dark and a thin dark line down postnotum. X. sp. » oon 18 Fosterior crossvein would intersect third vein if extended forward by its own length; bristles yellowish; very small, Thrypticua ..... 19 18! Fosterior crossvein too short to intersect third vein if extended forward by its own length; bristles dark . seeeeeees B 19 Coxae and femora dark ... 19' Coxae and femora yellow . 20 Wing veins yellowish; a minute AD bristle about one fifth of way down 12, I. sp. seeseseee = seeeseees Dol I 20' Wing veins dark; a normal AD bristle about one third of way down Dol 2, %. fraterculus (Wheeler) . 21 Basal abdominal tergite yellow... abdominalis (Say) 21" Basal abdominal tergite dark . 1h ---Page Break--- ge Basal abdominal sternites yellow.. setosus il, Robinson « 2. basal abdominal sternites dark, . ap. undescribed . ob Slender elongate flies with wings about 3 times as long as wide; third antennal segment triangular with arista on basal half of upper edge; a

ventral bristle on 12, Symycmus +25 not exactly as above ., +2 Basal metatarsal segment about as long as second segment; 3 pre AD bristles on 72, S. sp. Ps Dol Basal metatarsal segment shorter apical AD bristles on 12 ., x 26 Pleura light in color; 2 AD bristles on 13, 8. sp. sees Dol BB 26! Pleura dark in color; only 1 AD bristle on 13 (disregard dorsal bristles). S. sp. . 2 Four strong bristles on end of male abdomen; face of male usually wide Zenales difficult to separate so all can start here. four strong bristles on end of male abdomen; face narrow, eyes of males almost touching below antennae, Chrysotus «+... er" +35 seers 29 32 28 Front coxae yellow . 28" Front coxae dark .....05 29 A strong ventral arista on 12, 12 also with 2 AD and 2 PD pre-apical bristles; legs yellow with a distal dark band on metafemora, 2, dimdtatus Ald. + Dol 88 29" Two strong ventral bristles 30 92} mostly small speck 30 Aristae of male apical on a slender neck, pleura dark; wing tip behind long axis of wing; female unknown. D, flavipes Ald. .. 3L Not as

above, Chrysotus females ...++-, - contiguus Ald. ...44e. Dol R 32, Hyes contiguous above base of antennae. 32! Byes not contiguous above antennae .. 33 A median AD bristle on T2 about halfway between upper AD and apex of leg, but median D or PD of T1, if present, is much smaller than basal D of T2; third segment of antennae little higher in lateral view Second segment; basal metatarsal segment of males with a strong ventral bristle; large species over 2.5 mm long «+ +++++. 3' Median AD bristle of T2 absent, or much closer to upper AD than to apex, or a median D or PD present on T1 that is as long as upper >. Chrysotus females . + 3h -15- ---Page Break--- 3h Median AD of T2 more than half as long as upper AD. ‘Third vein of males not strongly arched. D. sp. . ++. Dol DD 3M" Median AD of T2 less than half as long as upper AD, ‘Third vein of males strongly arched. D. simplex ... 35, At least front coxae yellow; small species less than 3 mm long «+ 35° ALL coxae dark; size variable .+++eve, 36 Distance between tips of second and third veins little more than distance between tips of third and fourth; femora solid yellow; only one well-developed preapical bristle on T2, C. sp. seseeeees Dol C 36" Distance between tips of second and third veins almost twice that between third and fourth. paseceneesens 37 Pleura, legs, and antennae yellow; very small flies 1-2 mm long; ‘third antennal segment of male with slender processes above and below aristae. C. sp. + ae 31" Pleura and antennae dark; usually with some dark shading on femora. pacon 38 A small PD bristle opposite or basal to upper AD on T2. 36" Any PD bristle on T2 distal to upper AD; profemora usually not shaded with dark color. 39 Some dark shading on all femora; all segments of antennae dark; T3 of male shorter than first metatarsal segment, that of female normal. C, brevitibia Van Duzee sssesssessseeeeers + 39' All femora yellow; second antennal segment yellow, third dark; of male normal, C, mexicams H, Robinson ..,. 40 A median AD bristle on T2 and T3,

Although minute in males; @ark bands on fenora variable but usually strong on mesofemora of males. C, flavohirtus Van Duzee eseeeea 40! Upper AD only noticeable bristle on T2 and 13; dark distal band on netafemora only. G. sp. « 41 At least basal three-fourths of all femora dark sesesees 2 41! Metafenora solid black, others yellow with slight dark shading in female, heavy shading in male; third antennal segment of male spearhead-like with a long tapering point; aristae apical. ¢. excavata Van Dusee 42 Third antennal segment disc-shaped, its height in lateral view more than twice that of second segment; median AD bristle on 12, 4f present, much closer to basal AD than to 12 apex; medium sized, all longer than 2 mm. ooo tocsersseeses hg! Height of third antennal segment little more than that of second, median AD of 2, if present, midway between upper AD and 2 apex. 43. At least front tibiae yellow ..., seseeseeae 43! ALL tibiae black; median AD bristle of 12 developed but almost rather than AD; second metatarsal of male shorter than third. C, sp. near excisus Ald. wes Dol ce ---Page Break--- 4h Only basal AD of T2 well differentiated from hairs - ut Tree AD bristles differentiates on 12, the uppermost @ basal to the usual basal AD; metatibiae of

males brown; aristac of males not recessed but females very similar to C. proximus, C. sp. Dol JJ 45 Aristae of male recessed in a deep notch, those of female slightly a0; basal metatarsal segment of male lacking a ventral bristle. . proximus Ald. . us: Hate of male not recess metatarsal segment of male; female not discovered but possibly indistinguishable from 0, proximus. C. spinipes Van Duzee 6 Median AD bristle of 12, if developed, less than half as long as basal AD; small species mostly less than 2 mn. long .., eee MT 46" Median AD bristle of 12 almost as long as basal AD; very similar to Diaphorus species DD and GG but distinguished by a median D to PD bristle on Tl that is as long as basal D; males lack a ventral bristle on basal metatarsal segment, C. sp. se-ses

eres Dol W WT Wings dusky, veins dark; tibiae of males dark, females light; femora dark but with little metallic sheen; basal AD of 12 present in both sexes seeeeeeeeee Ay" Wings clear, veins yellowish; pleura and femora with bright green metallic sheen; male abdomen with violet reflections; [2 of male lacking bristles. C, humilis Parent seeee Dol FP 48 Basal metatarsal segment longer than next segment; 13 dark on basal one fifth in female; third segment of male antennae rounded in front and somewhat bean-shaped in lateral view. C. sp. near niger Ald. ea Dol Tr gt Basal metatarsal segment no longer than next segment; 15 of female all light; third segment of male antennae triangular — end pointed; aristae barely subapical. C. sp. -t- ---Page Break--- Appendix B Key to Muscidae (sensus lotus) of the Rain Forest at El Verde (Anthyomyiidae and Muscidae) by George Devry (some identifications provided and all checked by Silverio Medina, U.S. Department of Agriculture, University Experimental Station, Rio Piedras). Abbreviations same as in Appendix A. 1 Lower calypter rounded posteriorly and dorsally. Anthyomyiidae..... 2 1! Lower calypter broad, somewhat flattened posteriorly and triangular dorsally (Muscidae). Aristae bare. Synthestonyia mdiseta Van der Walp s..+ eae = Mus A 2 Sixth vein very short, seventh curved outward so that it would intersect sixth only short distance beyond end of latter. Subfamily. Fanniinae ... od i 2 Not as above . 3 A small preapical AD bristle on TM; palpi broad, flat and yellow; + Anth U tibiae yellow, femora black. Probably Euryouma sp.....++ 3" No preapical AD on Tl; palpi cylindrical and black; heel bristles all shorter than third antennal segment; color shiny black overall. Fannia sp. 4 Less than two presutural dorsocentral bristles: Coenosiinae 4' No presutural a: 5, One pair of presutural dorsocentral bristles .+++e+ees+e+0 6 5+ Dorsocentral bristles not differentiated from thoracic halva; profemora black, meso and metafemora yellow. Atherigona excelsa Thomson + +.+++

Sissesesesesseeeee verererersee Anth W 6, two pairs of post-structural dorsoventral bristles. Bithorachaeta 1 6! Three pairs of post-structural dorsocentral bristles. Necleniopsis si. 6 1. Legs yellow. B, leucoprocta (Wiedemann) .....+. nth F (Coquillett) ..... T! Legs black. 3. 8 Apical scutellar bristles more than three-fourths as long as subbasals. 8! Apical scutellars less than three-fourths length of subbasals 9 One pair of post-structural TA (intralar) bristles; procoxae yellow .... 10 9" two pairs of post-structural IA bristles; procoxae yellow or black 10 Palpi and third segment of antennae yellow (males presently 10’ ‘Third antennal segment dark below aristae; palpi dark with some light shading; female with distal fifth of all femora darkened, three preapical bristles on ™3 (AD, D, AD), distal AD on apical eighth of 133 male with an additional PD bristle on 13 basal to the other 3. N, rex Curran -118- ---Page Break--- ul Two large median anterior bristles on mesofemur; proboscis light yellow; female with posterior side of profemora dark, others banded distally, same 73 bristles as N. rex but situated more basally so distal AD on apical third. undescribed near N. rex, on 5 sieve Anth G tit One large median anterior bristle on mesofemur; proboscis brown; female with all femora yellow; same 13 bristles as ex but distal AD on apical fourth, Mop. undescribed near - tees Anth 12 Procoxae gray or black and same color as adjacent mesopleura.....+. 13 jp! Procoxae yellow and much lighter than adjacent mesopleura 13 A preapical AV bristle on 13 .. Beeeerserses 13' No preapical AV on 3 (the usual AD, D, AD present); no longitudinal stripes on thorax. N. sp.

undescribed near ditiportus.. Anth J 1% Four preapical %3 bristles (AD, AV, D, AD); indistinct longitudinal stripes on thorax; tibiae black; median parafrontal bristles reclinate, N. ditiportus Snyder.seseesereeeseee 1! Five preapical ™% bristles, a PD almost even with basal AD; distinct longitudinal stripes on thorax; tibiae brown; median parafrontals cruciate, N. sp.

undescribed near ditiportus Anth K 15. Wo preapical AV bristles on 73 sesseseresees: 15" A cnall AV near median AD of 73; paipi yellow; third antennal segment dark with a prominent yellow band basally (male unknown); femora of female yellow with posterior of profemora shaded black, others banded distally with black. N. op. undescribed near N. Aiscolorisexus. ee 16 + Anth 36 Third antennal segment darks 3 preapical 13 bristles (AD, D, AD); legs of female black, those of male yellow with black tarsi. discolorisexs Snyder « paenereeeee 16' 'Third antennal segment yellow female with 3 preapical 13 bristles (AD, D, 2D, AD); 13 of male with numerous long, bristly hairs, 'N. colvaiata Snyder (probably a synonym of W, nedine Snyder). LT Femora, all coxae and palpi dark, tibiae light ... LT" Femora, coxae and palpi yellow se+++eee 19 18 one pair of postoutural TA (intralar) bristles; median parafrontal bristles cruciate; 3 preapical bristles on 13 (AD, D, AD). male unknown. 'N. ebintemir Styler seecesssesssseneee 2 hnth 0 18" to pair of 'structural IA bristles; median parafrontals —— reclinate; 3 preapical bristles (AD, A, TD, D, AD, PD). Ty maldonadel Sryeer. peecst neces aes + Ante N 19 Stignatal and propleural bristles duplicated (it small bristles near base of front coxae); tibiae of males fairly straight e -1g- ---Page Break--- 19' Only 2 small bristles above base of front coxae; tibiae of known males bowed considerably and enlarged distally; third antennal segment dark. Ee 22 20 Third antennal segment clear, light yellow cose aL. 20' Third antennal segment brown with yellow area adjacent to base of arista; males with long hairlike bristles on tibiae, 1A and 2D on 72, a basal PD, AD pair then FD, D, AD, on 73; sides of male abdomen shiny with few setulae, two postoutural TA on at least one specimen, one in listed for holotype. MH. srleplacta Snyder. co Anth 4 21 One pair postoutural intralar bristles; male with 1A and 3D bristles on 12, numerous curly hairs on 73 and dorsum of basal metatarsal segment; posterior

hairs of oral margin yellow in female. N. sp. undescribed ..... + Anth R 21! Two pairs poststural intralar bristles; both sexes with 1A and 1D on 72, AD, D, and AD on 73; posterior hairs of oral margin black in female, N. neoflavipes Snyder « a Anth P 22 An AV bristle on 73; otherwise intermediate between the next two species. N. sp. undescribed or possibly hybrid see Anth W 22! Wo AV on 13. pcaeenee iene 23 Males with one A to AD bristle on 72, numerous posterior T2 hairs and bristles, abdominal setulae sparse and abdomen shiny; female with all hairs on oral margin black, one posterior bristle on 2, N. micans Snyder 23' Males with numerous, long curly A and P bristles on 72, abdominal setulae normal; female with posterior hairs of oral margin light, two posterior bristles on 2, N. crassicrucus Snyder . 2k Fourth vein curving forward at end toward convergence with third or small species less than 4 mm long eh* Fourth vein parallel or divergent with third at end than 1 mm long; Aristae long-plumose. Subfamily Phaontinae 25 Aristae long-plumose; middle thoracic stripe light in color, third vein with a tuft of setulae at base. Subfamily Mydaeinae 25! Aristae short-plumose to bare; middle thoracic stripe dark in color; no setulae on third vein. Subfamily Linnophorinae . 26 Aristae almost bare; color a dirty blue-gray with indistinct darker pattern; small species less than 5 mm long. Gynnodia 26' Aristae short-plumose; color pattern fairly distinct when dry, a clear demarcation on mesopleura between a smooth, dark anterior half and a silvery pollinose posterior half; large species mostly longer than 5 mm, Limnophora . 7 Fifth vein reaching margin of wing; 3.5-5 mm long. G. sp... -120- ---Page Break--- eq! Fifth vein stopping short of wing margin; 2.5-3.5 mm long & sp. . Anth JZ 28 'vo posterior preapical bristles on 72; first poststural dorsocentral bristle much longer than second. l. sp. « 28'

Only one posterior preapical [2 bristle; first two poststural dorsocentrals similar in size and considerably shorter than

last two, L. ap. . 29 Third vein setulose, three sternopleural bristles. Scenetes oardint Malloch ..... seeessceeees Anth FF 29! Third vein bare; two sternopleural bristles, Phacni preapical bristles on Tl; 1 AV, 2 AD and 1 D on 13. Wo. P. 8p, 30 Posterior crossvein almost twice as long as segment of fifth vein distal to it; first postsutural dorsocentral bristle slightly longer than second; humeri and scutellum black. Nyospila obsolete (Brauer and Bergenstamm) 30! Posterior crossvein little longer than segment of fifth vein distal to it, first postsutural dorsocentral much shorter than second; scutellum yellow, scutellum red posteriorly. Heo: museina farri (Dutch) Notes: Key expanded in part from Snyder, F.M. 1957. Puerto Rican Neodexiopsis (Diptera Muscidae: Coenosinnae) J. Agr. Univ. of Puerto Rico M1: 207-229. His characters involving intraler bristles and distal mesofenoral bristles did not hold for all specimens of N. crispiseta and N. micans examined. Species identified as N. calvalata on basis of wing shape were more like medinai in all these exact characters and cast doubt on specific distinction. -121- ---Page Break--- SECTION III Section three consists of a manuscript submitted for publication by Dr. Carl F. Jordan, and two reports by visiting scientists who were supported by the Terrestrial Ecology Program. "Nitrogen Fixation by Epiphyllae at El Verde" was prepared by Dr. Joe A. Einisten, of the University of Georgia, and his graduate student, M.A. Harrelson. Dr. Einisten spent two weeks during the summer of 1968 at the El Verde site to initiate the project, and Mr. Harrelson spent two months on site completing the work. Dr. Elizabeth McMahan of the University of North Carolina has been visiting the El Verde site yearly since the termination of radiation, to measure long-term changes in termite populations as a result of radiation. Her report for the 1968 check is included. 1007 // above canopy 3 FOREST FLOOR SPECTRAL INTENSITY (MICROWATTS /CM2/my) ° 400 600 800 1000 WAVELENGTH (mp) Fig. 1.

Intensity of radiation vs. wavelength, measured above the canopy at noon on Nov. 16, 1967, and measured on the forest floor a few minutes later. 122+ ---Page Break--- DERIVATION OF LEAF AREA INDEX FROM QUALITY OF LIGHT ON FOREST FLOOR By Carl F. Jordan Introduction Ecosystem studies such as those of productivity and chemical element cycling require measurements of the quantity of leaves in the canopy. This quantity is often expressed as leaf area index, that is, area of leaves per area of ground. In herbaceous communities, it can be determined directly by clipping (Monsi and Saeki, 1953), but forest measurements are more difficult to make. In order to estimate leaf area index throughout a large area of tropical rain forest, Odum, Copeland, and Brown (1963) measured leaf area index directly in 10 locations, correlated it with optical density measured with silicon solar cells, and then made optical density determinations throughout the forest. There are two disadvantages in using optical density determined by solar cells as a measure of leaf area index. One is practical, in that it is inconvenient in a field survey to have one cell above the canopy and the other in the investigator's hand, both of which must be read simultaneously, or nearly so. The second is theoretical, in that solar cells respond to light over a broad band of the spectrum including infra-red whereas extinction of light is due primarily to chlorophyll which absorbs light in a relatively narrow band. Much of the light recorded by a solar cell on the forest floor is due to scattered light of wavelengths other than the chlorophyll absorption band. The quantity of this scattered light could be influenced by shape, orientation, and spacing of canopy leaves. This paper presents an indirect method of measuring leaf area index. The method may be superior to the optical density method. Theory Intensity of red light reaching the canopy is slightly greater than that of near infra-red, but on the forest floor, the relative intensity of the infra-red is

many times greater (Fig. 1; Federer and Tanner, 1966). This is due to the selective absorption of radiation by leaf pigments. The more leaves that are present, the greater will be the preference in red and infra-red radiation at the forest floor. The intensities of infra-red and red light can be expressed as a ratio, and this ratio can be calibrated with leaf area index measured directly at several points in a forest. Leaf area index throughout the entire forest can then be derived from ratios measured at the forest floor. To maximize the ratio as leaf area index increases, the ratio should be between light at 600 and 675 millimicrons. Absorption of light by the canopy is at a maximum at 675 millimicrons, and transmission has a maximum at 600 millimicrons (Fig. 1). Since absorption of light is greatest at 675 millimicrons, scattering of light at this wavelength will be less than at most other wavelengths. The less scattering, the less the ratio is influenced by the angles and spacing of leaves, and hence, the more reliable the correlation of ratio and leaf area index. However, even at 675 millimicrons there probably is some light scattering. To minimize this scattering, ratios should be measured only in direct sunlight, and when the sun is high overhead. At 800 millimicrons, it is not clear how much of the transmission through the canopy is due to scattering of light, and how much is due to absorption and re-emission by leaves. Here again, however, scattering is probably at a minimum in direct sunlight, and with the sun overhead. To use the ratio as a measure of leaf area index within the forest, the ratio must be constant above the canopy. Figure 2 shows that although quantities of light vary during midday hours of sunny days, the ratio 800/675 remains almost constant. The ratio is also independent of time of year (Table 1). The slight variations could be caused by human and instrumental factors. In any case, the variations are minute compared to changes due to the light passing.

through ‘the canopy. Since chlorophyll content per unit leaf area varies between species, the correlation between the ratio and leaf area index will be valid only in the forest type where the calibration was accomplished. However, a correlation between ratio and chlorophyll concentration per square meter of forest floor could be valid for many vegetation types. With such a correlation, if mg. of chlorophyll per square meter of leaf area were determined for a given vegetation type, leaf area index could easily be derived by dividing chlorophyll concentration per square meter of forest floor by concentration per square meter of leaf area. ---Page Break--- 120) a £ BI00 nano 4o7 2 s os 2 2 80 § g 8 5 8 2° 7 | 3 iS o #40 ‘800 1000 1200, 14001600 TIME Fig. 2. Absolute intensity of light at wavelengths 600 ‘and 675 millimicrons during the day, and ratio between these intensities. sample 1, ito of Light of wavelength 60 at 5 wtitatorsee a me Ramer ceatige Amat Me ne 961 5 om 0.3 er, 6 : ca ee 5967 ; one de 36,961 a ar ee 9,60 6 on say 5, 96 1 ew fet 25,961 5 “ sent a8, 96 2 oa to cuts 8, 961 : one sor 1960 s ee 4 000 a ob om oe vay 2, 2988 ‘ cm + 00 ay 3, 3968 . oo 2 08 ses eth $0.05 _ -125- ---Page Break--- Methods and Results Leaf area index was measured at three locations in the Luquillo Experimental Forest near El Verde, Puerto Rico, by the following method. Scaffold type towers were erected to a height equal to the top of the canopy, and with a minimum disturbance to the forest. A string with a weight on the end was thrown out from the top of each tower 16 times in such a way as to hook over a twig and then fall straight to the ground, and the number of leaves which each string touched was recorded. Leaf area index at each site was taken to be the average number of leaves touched by the string on each throw. Leaf area index at a fourth site in a ravine was taken to be 2.2, the value Oitm, Copelaniy and Bro (1963) determined for that site by clipping and measuring leaves. Light readings at each location were made with

A spectroradiometer manufactured by Instrument Specialties Co. The first wavelength was dialed in and a light intensity reading was taken. Immediately, the second wavelength was dialed, and a second reading taken. The process took about 15 seconds. Since the ratio method proposed here

assumes that both readings are made simultaneously, the first wavelength was dialed in a second time to assure that the intensity had not changed while the second reading was being made. On clear, sunny days, there was no measurable change. The spectroradiometer was calibrated with a spectral standard amp supplied by Instrument Specialties Co. All readings were corrected to absolute values, and the 600/675 ratio was calculated in the office some time after the field measurements were made. Results of the correlation are given in Table 2 and Figure 3. The equation for the regression line in Fig. 3 is Eq. (1) log Y = 0.3813 + 0.0989x where Y is the ratio of light at the wavelengths 800 and 675 millimicrons, and X equals leaf area index. Using a value of 310 ng. chlorophyll A per square meter of leaf area for this forest (Oiun, Copeland, and Brown, 1963), the relation shown in Fig. 4 was derived. The equation here is Eq. (2) where Y again is the ratio, and X is mg. chlorophyll A per square meter of forest floor. Equation 1 is probably not valid for values of leaf area index less than one, since it is known from Table 1 that with a leaf area index of zero, the ratio is 0.78. If scattering were not a factor, Fig. 4 could be used to determine chlorophyll A concentration in any forested area, and from log Y = 0.3813 + 0.0002908X.

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Table 2. Data for correlation between leaf area index and light ratio. Also, leaf area index determination for entire forest.

Site	Slope	Average Light Ratio, 600/675 m	No. of Readings	Date of Readings
Ridge	6.68	10.51	16	Aug. 15, 1968
Ravine	5.60	8.8	4	May 2, 1968
Total for Forest	4	July 23, 1968	30	Aug. 15, 1968
Average	10	4.2	8.60	Aug. 19, 1968

fort 24 8 July 1, 1968 2.28 3.98 32 Aug. 22, 1968 nak April 24, 1968 eee 0 133 Ney 2, 1968 130 July 26, 1968 % Value taken from Odum, Copeland and Brown, 1963. -127- ---Page Break--- g 3 RATIO, 800/675 os 2. 4 6 8 0 LEAF AREA INDEX Fig. 3. Ratio of light intensities at 800 and 675 milli- microns measured on the forest floor, as a function of leaf area index. g 3 RATIO, 800/675 S. 1000 2000 5 3000 MGM CHLOROPHYLL "A'/M' FOREST Fig. 4, Relation between ratio of light intensities at 800 and 675 millimicrons measured on the forest floor, and milligrams of chlorophyll A per square meter of the forest, 128 ---Page Break--- this, leaf area index could be derived, as previously described. Since the calibration was made in a broad-leaved forest with the canopy top at about 65 feet, and very little shrub vegetation, the closer another forest resembles this structure, the more applicable this relation will be. Light readings were done in a systematic manner, and values were recorded regardless of whether a light speck fell on the meter, or whether a limb was in a direct line between the sun and the meter. As a result, individual ratios taken at a given site varied greatly, but the averages (Table 2) were almost perfectly correlated with leaf area index (Fig. 3). Average leaf area index for the entire forest as determined by light ratios measured every 5 feet along three 600-foot transects was 6.6 (Table 2). Odum, Copeland, and Brown (1963) determined an average value of 6.4 for the same forest by optical density means. Light ratios were always higher at the calibration sites during early morning and late afternoon hours, and any time during winter months. The higher ratios were a result of relatively less light at 675 millimicrons at the forest floor. This could result from the chlorophyll of the forest not being saturated at these times. Only during noon hours, during the summer, was it possible to get repeatable results. This suggests that trees of the forest have evolved so that their chlorophyll content is such that

Only during periods of maximum insolation is there no excess capability of chlorophyll for absorbing red light. If this is true, this means that actual determinations of leaf area index of a forest, by the ratio method, must be done under the same solar conditions as those which exist during calibration, and that this is best accomplished during the noon hours during summer months, north of the equator. It also means that if Fig. is used for other forests, it must be assumed that these forests have chlorophyll contents adapted to the maximum light levels which exist at their location, probably a safe assumption for mature forests. Cloudy skies are not suitable for using the ratio method of determining leaf area index for two reasons. First, the thickness of the cloud cover could change without the observer on the forest floor being aware of a change in incoming light intensity. Secondly, with relatively more diffuse light entering the forest under cloudy conditions, there is more light scattering, and consequently the calibration is less reliable. A spectroradiometer is not necessary in order to use the ratio method. Any of many types of light meters can be used in combination with narrow band pass filters for wavelengths of 675 and 800 millimicrons. The only requirement is that the meter be calibrated so that field readings can be converted into absolute light energies. -129- ---Page Break--- Literature Cited Federer, C.A., and C.B. Tanner. 1966. Spectral distribution of light in the forest. Ecology 47: 555-560. Monsi, M., and T. Saeki. 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. Jour. Bot. 14: 22-52. Odum, H.T., B.J. Copeland, and R.Z. Brown. 1963. Direct and optical assay of leaf mass of the lower montane rain forest of Puerto Rico. Proceedings of the National Academy of Sciences 49: 849-853. =130- ---Page Break--- NITROGEN FIXATION BY EPIPHYLLAE AT EL VERDE J.-A. Hamisten* and M.A. Harrelson* Abstract Acetylene reduction techniques with gas

Chromatography has been used to demonstrate that epiphytic plants on leaves could fix atmospheric nitrogen. These experiments confirm earlier 15N tests with the same organisms. Leaves with intact mixed epiphyllae populations both on the tree and in flasks have been shown to reduce acetylene to ethylene. Mixed epiphyllae populations scraped from leaves produced more ethylene than scraped leaves. Mixed bacteria fractions from leaves were shown to reduce acetylene. Three genera of blue-green algae isolated from leaves were found to have the ability to fix nitrogen as evidenced by the acetylene reduction tests.

Introduction: Root nodule experiments by Edmisten show that the generally accepted methods of nitrogen entering the tropical rain forest ecosystem at El Verde were not sufficient for the existing growth rates. Edmisten (1968) suggested that epiphyllae might be contributing factors in the nitrogen cycle. Kline and Edmisten (1968), in 15N experiments, reported on a high rate of N-fixation by mixed epiphyllae on Citrus leaves and showed that some of the fixed 15N was transferred to leaves. The mixed epiphyllae included bacteria, algae, fungi, lichens, and liverworts. To explore this idea, the acetylene reduction technique (Stewart, 1966) was used on whole leaves, scraped leaves, and bacterial and blue-green algae cultures isolated from leaves. This technique involves the fact that the same enzyme complex which converts nitrogen to reduced usable forms will also reduce acetylene to ethylene. It was generally expected that certain bacteria and blue-green algae were responsible for the nitrogen fixation. Seven genera of plants, representing shrubs and trees, were tested. These are shown in Table 1.

Department of Botany, University of Georgia, Athens, Georgia. Department of Biology, Gardner-Webb College, Boiling Springs, N.C. -131- ---Page Break--- TABLE 1: Plants from El Verde Forest Used in Acetylene Tests

Genus	Growth Habit
Miche	Citrus small understory tree
escaped	Groton slender canopy tree
climax	Dacryodes

large spreading canopy tree climax Euterpe medium palm follows streams Manilkara large canopy tree climax Psychotria small understory shrub successional Sloanea large canopy tree climax Materials and Methods ‘Two basic methods were used in preparing specimens for testing. For testing of whole leaves with epiphyllae on trees, plastic bags were sealed around the leaves at the twig with plastic tape. A piece of plastic tape about two inches long was used as a reinforcement for hypodermic needle insertion during gas exchange. After completion of gas exchange, a smaller piece of tape was used to seal the needle hole. After securing the bag in place around the leaf, air was withdrawn by mouth vacuum through a plastic tube and hypodermic needle. The bag was then filled with a mixture of 226 O2, 0.04% CO2, and 17.95% Argon. The bag was again evacuated and refilled with the same mixture to ensure the elimination of nitrogen. Acetylene was added to account for one-tenth of the volume of the bag. After varied exposure times, ranging from 1 to 6 days, the leaf in the sealed bag was clipped from the twig and taken to the laboratory for testing with GC techniques for the presence of ethylene. For testing organisms isolated from leaves, and leaves with epiphyllae removed from trees, Erlenmeyer flasks of suitable size were used. Rubber serum stoppers were used to seal the flasks while allowing the replacement of gases through hypodermic needles. Flasks were flushed (an inlet for flushing gases and an outlet for escaping air) by about 10 volumes of the O2, CO2 and Argon mixture. Acetylene was added to make up one-tenth of the flask volume. -132- ---Page Break--- For isolating the various organisms suspected of fixing nitrogen, sterile disposable gloves and sterile scissors were used to detach and place leaves in sterile flasks. ‘The leaves were taken to the field lab where the isolations were done. Whole leaves were placed in Erlenmeyer flasks in media specific for either algae or bacteria. Agitation was used to free the

organisms from the leaf surface. Transfers were made to suitable media. Bacteria were grown in Ruinen's Medium (1965) at pH 1.5. Algae were grown in gold extract media for flush growth, then to ye-free media (Ruinen, 1965) for testing. Fungi were isolated by cutting strips of leaves 3x20 mm and placing them on Martin's Rose Bengal Medium, soil-extract medium, and Y-8 juice medium. Transfers were made to N-free medium for testing. The surface of leaves was scraped to get a mixture of lichens and liverworts. These were tested as fresh materials and not cultured. After adding acetylene, cultures were tested on a gas chromatograph for conversion of acetylene to ethylene. Controls were run on the gas chromatograph with pure acetylene, pure ethylene, air, and the flushing gas mixture. The total number of cultures prepared for testing by gas chromatography were as follows: Whole leaves on trees... Whole leaves in flasks ..... Whole leaves in flasks, scraped clean Epiphyllae in flasks, from scraped leaves Bacterial cultures .. Algal cultures Fungal cultures Results and Discussion Positive results were obtained for epiphyllae as follows: 1. bacteria grown in culture, 2. blue-green algae grown in culture, 3. whole leaves with epiphyllae intact, 4. epiphyllae scraped from leaves. The bacteria tested for figure 1 were isolated from the older leaves of an understory palm Euterpe globosa. The presence of these and other nitrogen-fixing bacteria on leaves has been reported by Pylten (1965) when Beijerinckia, Azotobacter, and Rhizobium were said to have increased total nitrogen in, on, and around leaves of bean and coffee grown in culture. Figure 2 shows a very efficient conversion of acetylene by epiphyllae on old Citrus leaves in a flask. Citrus leaves with epiphyllae removed (figure 3) show less conversion of acetylene than those in figure 2. The epiphyllae scraped from the leaves in figure 3 show good conversion of acetylene to

ethylene (figure 4). A comparison of figures 2, 3, and 1.

us to believe that most of the organisms with nitrogen-fixing ability are found in or on the visible epiphyllae, which consist mainly of liverworts and lichens. Microscopic examination has shown that blue-green algae are often embedded in both these organisms. One of the species of Nostoc used in later acetylene tests of pure cultures was isolated from liverworts. Although the usual algal partner of an epiphyllous lichen is a green alga, blue-greens are often found also in tumor-like growths called cephalodia. The fact that the leaf scraped clean of visible epiphyllae still showed the ability to reduce acetylene (figure 3) may be explained by the fact that Azotobacter could be isolated from it. Figure 5 shows good conversion of acetylene by older Mantlkara leaves with epiphyllae in a flask, while figure 6 shows very high conversion to ethylene by epiphyllae scraped from older Mantlkara leaves like those in figure 5. The data shown in figures 5 and 6 reconfirm the concept established in the experiment shown by figures 2, 3, and 4 and indicate that the nitrogen-fixing ability of epiphyllae is not host-specific. The same species of lichens and liverworts have been identified from a wide variety of leaves from Peru, Panama, and Colombia as well as Puerto Rico. Plastic bags on trees (figures 7 and 8) showed reduction of acetylene to ethylene as determined in earlier 23M experiments by Binisten and Kline (1968). The acetylene reduction tests represented by figures 7 and 8 were performed on leaves of the same grassroot tea that was used in the preliminary 15% test as well as on scenes to climax species, Mantikara. In the Hi test, it was found that material scraped from leaves had 104% of their total nitrogen as 15M which had been taken up from the environment during the 48-hour exposure period and incorporated into organic form. Most Citrus leaves from which epiphyllae had been scraped and washed had 15% of their total nitrogen or stable isotope 15N. When considered together,

These experiments indicate that epiphyllae have the ability to fix atmospheric nitrogen and that some of the fixed nitrogen is transferred to the host leaf within a 48-hour period. Since blue-green algae have long been known to fix atmospheric nitrogen, it was not surprising to find four genera on leaves that showed conversion of acetylene to ethylene. Figures 9 and 10 show the actual leaves in -13h- ---Page Break--- and Pat Fig. 7. Scale drawing of gas chromatograph tracings to show conversion of acetylene to ethylene by a Citrus leaf in a plastic bag on the tree, based on the actin 0 to Pomme Fig. 8. Scale drawing of gas chromatograph tracings to show conversion of acetylene to ethylene by a Yanilkara leaf in a plastic bag on the tree. -138- ---Page Break--- ee we Fig. 9. Gas chromatograph tracings to show conversion of acetylene to ethylene by blue-green algae. Fig. 10. Gas chromatograph tracings to show conversion of acetylene to ethylene by blue-green algae. -139- ---Page Break--- tracings of the gas chromatograph for the four blue-green algae Nostoc, Scytonema, Anabaena, and Calothrix from leaves at El Verde. The blue-green algae used in the tests illustrated by figures 9 and 10 were isolated from Citrus leaves taken from the El Verde forest and were grown in Chu's nitrogen-free media. They were transferred with sterile technique four times before being tested for the ability to fix nitrogen in order to help assure their being in pure culture. Conclusions and Implications Mixed populations of leaf epiphytes have been shown by two separate methods to have the ability to fix atmospheric nitrogen. The principal organisms thought to be responsible for the fixation have been shown to be various blue-green algae and free-living aerobic bacteria which live in and on leaf lichens and liverworts as well as on the bare leaf during early stages of successional coverage of a new leaf. Although this study was not designed to be quantitative but rather qualitative, preliminary calculations based on the areas below the

Ethylene and acetylene peaks of figures 1 through 10 indicate that the rates of nitrogen fixation would range between 0.05 Kg/acre/day to +15 Kg/acre/day. The biomass of epiphyllae in tropical

rain forests has not been established, but the presence of heavy populations of epiphyllae has been noted on leaves of all symbionts of the El Verde forest except the exposed leaves of the upper canopy. When one realizes that there are between 5 and 15 acres of leaves over each acre of ground in El Verde, the potential nitrogen input by epiphyllae becomes an important factor to be considered in the nitrogen budget of any moist tropical forest. The results of these experiments suggest a new way of adding nitrogen fertilizers to crop plants. It would appear feasible to isolate and grow blue-green algae and bacteria from leaves and select the ones with high ability to live on leaves and fix atmospheric nitrogen. Such known "fixers" could be sprayed on crops such as citrus, pineapple, or sugar cane in irrigation water with certain chemicals added to facilitate the adhesion of microorganisms to leaves. If man could effectively copy this symbiosis on his crop plants, the nitrogen fixed would become available to the crop plants directly through the leaves and from leachate in rain and irrigation water. Finally, this experiment has demonstrated that the quick, inexpensive acetylene reduction test for the ability to fix nitrogen is a reliable tool as shown by the independent 15N experiment. The acetylene reduction test was also performed on well-nodulated, hemoglobin-containing root masses from six species of legumes from El Verde with strongly positive results. The six were Inga vera, Inga laurina, Andira inermis, Neorudolphia volubilis, Omosia krugii, and a successional species of Desmodium. A series of acetylene reduction tests should be performed to quantitatively establish the rates and extent of all nitrogen fixation in the El Verde forest and thus establish a nitrogen budget for a tropical rain forest.

forest. Puerto Rico Nuclear Center should support studies in which various nitrogen-fixing epiphytes are grown on citrus, pineapple, and sugar cane with their crop yields and nitrogen contents compared to untreated control crops. References Bimisten, Joe A., and Jerry R. Kline. 1968. Nitrogen fixation by epiphytes in: The Rain Forest Project Annual Report. Puerto Rico Nuclear Center, University of Puerto Rico. Ruinen, Jakcba. 1965. The Phyllosphere TIT, Nitrogen fixation in the phyllosphere. Plant and Soil MUI, No. 3, p. 375-393. Stewart, W.D.P., G.P. Fitzgerald, and R. Burris. 1967. In Situ studies on N2 fixation using the acetylene reduction technique. Proceedings of the National Academy of Science, Oct. 1967, pp. 2071-2078. a1 ---Page Break--- ‘TERMITES AT EL VERDE: 1968 RESEARCH Elizabeth A. McMahan University of North Carolina Chapel Hill, North Carolina P. Murphy and R. Wiegert made preliminary surveys of Nasutitermes costalis nests at El Verde, beginning in 1965, and Wiegert's subsequent studies have been concerned mainly with their metabolism. McMahan continued and expanded the survey studies, making a complete census of nest condition and tunnel occupancy during the summers of 1966, 1967, and 1968. The chief aim of the studies was to examine the effects of the 92-day (Spring 1965) exposure of a gamma source (137Cs) in the Radiation Center. Methods: costalis nests within 8 m of point zero in the Radiation Center and in the South Control Center have been mapped originally by Wiegert, with later additions by McMahan. At each survey period, the areas were scoured for new nests, and each old nest was examined to see if it was still active. A tunnel survey was also made each summer. Every tree (dead or alive) of one-inch diameter or greater within 30 m of point zero in the Radiation, South Control, and North Cut Centers was carefully examined for evidence of termite tunnels. If a tunnel was found it was checked for occupancy and by which species (usually N. costalis or Parvitermes discolor; once Glyptotermes was

found inside a stub on which were P. discolor tune: Results Nests In the summer of 1966 there were 11 active Nasutitermes nests in the Radiation Center, 11 in the S. Control Center, and an undetermined number in the N. Cut Center (none within 30 m of point zero in the latter). By July 1967 five of the Radiation Center nests had been abandoned (14,15,19,20,21), while only one (7) was newly empty in the S. Control Center. That year a new nest (26) was found at about 26 m from

point zero in the Control Center. At the 1968 survey (July 9-21) nest 18 in the Radiation Center had been abandoned and nest 12 was barely active - only two soldiers were ever seen to emerge to investigate disturbance of the nest surface. But two more nests were found to be abandoned also in the S. Control Center: Nests 2 and 9. A new nest (27) was found in the Radiation Center, only about 8 m NNE (behind the big Cyrilla tree) from point zero. Figure 1 shows the position and states of nests in the two centers in July 1968. The 1966 and 1967 studies had shown that about 106 of the trees in the Centers had tunnels or tunnel fragments on them. This was also true for 1968. Table 1 gives the percentages of tunnel occupancy for the three years. It shows that in 1966 the percentage of occupied tunnels in the Radiation Center was much less than that for the two Control Centers in 1967. The 1968 survey showed for the first time that reinvasion of the Radiation Center by termites had begun. The new Nasutitermes nest in this center has already been mentioned, and the occupied tunnels were probably, in large part, from this nest. While the percentage of occupancy was still not as great as in the Control Centers, the probability seems good that by 1969 it will more nearly equal them. TABLE 1 Percentage of Tunnel Occupancy for the Three Centers Year Radiation Center S. Control Center A. Cut Center 1966 12 51. 38 1967 8 8 1968 23.6 42.6 Discussion Three years after

Removal of the gamma source from the Radiation Center, effects of the irradiation in terms of nest abandonment by Nasutitermes costalis seem to be still appearing. Twice as many nests in this center as in the Control Center were abandoned in 1968. The unusual amount of nest abandonment may be attributable to sterilization of reproductives and the consequent lack of normal colony growth which would offset natural attrition. It seems surprising that three years were required for evidence of refaunation of the irradiated area, and this evidence of reinvasion was contributed solely by N. costalis. Nasutitermes-occupied tunnels are naturally more numerous in the vicinity of nests (Parvitermes discolored constructs no discrete nests), and the new nest in the Radiation Center probably explains the increase. The lack of increase in P. discolor occupancy of tunnels to more nearly approximate the Parvitermes densities of the Control Centers may reflect the slowness of termite refaunation of an irradiated area.