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PUERTO RICO NUCLEAR CENTER

THE RAIN FOREST PROJECT

ANNUAL REPORT

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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,

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SECTION I

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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 equili-
brium 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

?Decause tritium is a tracer for water, but also because tritium will be a principal product of eny thermonuclear reaction used to excavate a new canal through Central Anerica.

?The secondary successional study vas initiated in the sunner 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 ani information are presented in section two.

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PART A - ISOTOPE CYCLES

The movenent of radioactive and stable elenents through an eco-system often is termed "mineral cycling" or "biogeochemical cycling". Both these terms are misleading. "Mineral cycling? is misleading decause to earth scientists, minerals are substances composed of tvo or more elenents, usually having a definite atomic arrangenent. These minerals do not cycle through plants and animals. The tern "biogeochemical cycling" also is misleading, because it implies cycling over millions of years whereby an elenent 1s deposited on the ocean bottom, decones sedimentary rock, there is land uplift, erosion, ani then the elenent is again avatisble for cycling through biological systems. The studies at the tropical rain forest 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 rain forest 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

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Fig. 1. Block diagram showing major storage

compartments and transfer routes

in the tropical rain forest.

Table 1. List of water collectors used for studying rate of element

movement between compartments.

Fix Number of collectors

Rainfall, 2

Throughfall 10

Stemflow 18

Out of litter 18

Through 5 inch soil depth 23

Through 10 inch soil depth 6

Runoff, during storms 2

Runoff, between storms 4

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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

receeded, 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 the

first reading and .2 on the second, resulting in an average concentration of .15 with a standard deviation of .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 were 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.

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Table 2. Standard deviation as a percentage of mean concentration.

Percentage

Samples, ca Ya, Me

Rain oT 34 5

Throughfall 45 3T 6

Stenflow 87 ST 9

Out of litter 3h 35 39

Through mineral. soil a 3T 49

Run off ab 9 a

?Table 3. Concentration of elements in water collected from the A horizon (5 in. deep) and
?Bhorizon (10 in. deep) of soil in the rain forest near HI Verde,

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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

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aay, 1968 ob 06 18 ae 6 9

be) 1968 Cd 2g MS 2 »

Bert, 1968 LL 10 aT 5h

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Table 5

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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 river-bed,

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, an 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 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) Ke/ta/ve

Total amount of isotopes moved is given on a weekly basis since collections were always made on the same day of the week (Von.). 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 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

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LEAF FALL

----- RAIN

OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP

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AWO/W/: 'S3AV31 SWVYS

Fig. 2. Average rates of rainfall and leaf fall at the El Verde site.

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?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 phenomena 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 m³ water/ha/wk by the relationship

$$(\text{cm water/wk})(100) = \text{m}^3 / \text{ha/wk}$$

Fig. 2 shows m³/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 total amount of rain.

Gains and losses of isotopes to the ecosystem are calculated by subtracting rate of loss by runoff from rate of input by rain (Table 13 and Figs. 7 and 8). 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 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 times weight of the upper layer of soil (Table 14).

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Fig. 3. Average rates of calcium movement through the ecosystem.

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OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP

Fig. 4, Average rates of magnesium movement through the ecosystem,

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OcT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP

Fig. 5. Average rates of sodium movement through the ecosystem,

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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

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Table 13, Met monthly rates of element gain and loss from ecosystem,
determined by subtracting rate of loss by runoff from rate
of input ty 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

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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.

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KG HA WK, TOTAL SOLUBLE SALTS

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MJJASONDJFMAMJ JAS

1967 1968

Fig. 8, Rates of gain and loss of total soluble salts to
and from the ecosystem.

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analyzed by atomic absorption spectrophotometry.

Leaves, wood, roots, organic matter and fresh litter were prepared for analysis by the following procedure: they were prepared

- 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 Ks
?final concentration of La should be 1f and K 500 pa.
- 10) Divide every ΔA 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 NH_4OAc 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, NH_4OAc 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 to a total volume of 50 ml. with 1 W NH_4OAc .

19) Filter through Whatman 40 filter paper.

1a) Run for Cu, Fe, K, Nn.

2) for Ca and? Mg, dilute 1:1 with a solution 2f La; 1000 pom K to obtain a final concentration of 1 La, and 500 ppm K in the sample.

13) Divide every \$ A by scale expansion, if any, and convert

absorbance.

1b) Prepare a standard curve of absorbance (Y) va concentration

(x) with the standards. Determine concentration in the samples and multiply by dilution factor, 1f ary.

?19+

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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 ty plants, as well as total elements as determined by the combustion technique. Therefore, an extraction procedure for the organic material vas 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 H₂O₂ 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. H₂O₂ 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 (H₂O₂) stays clear after shaking.

9) Filter through Whatman No. 1 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 2% la, 1000 pm K to obtain a final concentration of 1% fa, and 500 ppa K in the sample.

12) For Sr, use the method of addition, in which a standard 1s faded to the sample; two equal volunes of sample are @iluted in a 1:1 proportion, one with a known concentration standard prepared in 26 La, 1000 pom K, ani the other with Just a solution 2% la, 1000 py K. Compare the absorbance of the tvo samples using the following proportion.

Concentration sample Cone, sample + Conc. standard
?Absorbance sample ?sSsorbance of Cemmpie + atantard)
solving the proportion for Conc. sexple,

Asample C standard

Cone. °: (GS Se eee

semple A (sample + standard) - A sanple

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.

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4, Tree trunks for difference in sites.

5. Freshly fallen litter for difference in season.

&. Organic matter for difference in sites.

7. Leaves for difference in presence and absence of epiphyllas.

8, Leaves for difference caused ty 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, Mn, Fe, Sr, Ca, and Mg (Table 16). Presumably this is because when rain containing these elements enters the canopy, the elements are more efficiently ponded 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. *Panicum riparia* was excluded from the tests, because in many cages 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 in *Schinus molle* showed a difference, so it was checked again in *Sloanea*. There was no 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).

21+

---Page Break---

Baectatte a cf sites dentin

Wen arates sat

cs niger 3 omg 2

: 3 . i

8 3 a

e 3 i

5 i

3 : ?se ~ i

5 : : :

5 : : t

3 1 ectyyn cmt 2

3 : : i

3 : t

5 ; 5 : i

to) :

5 :

3 i

5 ?

1

a

"on lage top 3 eg. : og ime s

3 : at 3 ?

C 5 6 S oe : i

aa sites 53 trem auver = top of organo matter an Ler

Poorly drained sot

Te valley vote Legros cles untestory croton gonctati

{

A

i

---Page Break---

Table 16

Results of sign tests to test aiff in elenent concentration
ferences in elenent concentration between
eaves with and without epiphylls, Palicourea riparia excluied, ani. be-
?tween canopy and understory leaves.

Element Clean leaves vs. leaves Canopy leaves vs. under-
??sepipyiis ?story leaves
nr level of confidence nr _level of confidence

?that leaves plus that understory
epiphylls are higher leaves are higher

co woh 958 nok -

Ma ww 2 8 yok 5

Fe wo 9% m5 7

cu 2 8 - ak -

x 2 1 uo3 ot

a 2 8 - nos -

sr 2 2 99% nu 3 oH

co 2 2 99% nu 3 oh

Me 2 & 95% no 3 3

* clean leaves are higher in potassium

---Page Break---

?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

M6etioT 33942 setie

cu K Na

2.M6 \$1.02 1137 + 679 1482 + 190

sr ca %

8.2 £1.d1 3321 + 64h 1067 + 105

Dacryodes excelsa

understory

lean leaves (n = 4)

co Ma Fe

2,90 + 2.22 2.95+79 89 +16

cu K Ta

5.15 + 2.87 ? e7ho + 615 17074773,

sr ca %

6.45 \$2.54 3713 + 693 lae3Te

Dacryodes excelsa

ccancry

leaves + eptphylis (n = 3)

co Ye Fe

5.02 + 2.21 381+ 181 102 + 36

ou Kc Na

2,66 + .lh 981 + 283 1700 + 368

Br ca Me

10.2 + 1.8 4529 + 833. 1222 + 205

Dacryotes excelsa

understory

leaves + epiphylls (n = k)

co Yo Fe

4.39 43.34 NBT + 1N6 120+ 26

ou K ma,

2.72 + .26 1209 + 189 1529 + 6a

sr ca %

12.8 + 2.96 5173 41534 1320 + 232

2h

---Page Break---

eS

Continued Table 17

ee

Yantkara bidentate

canopy

clean Leaves (n = 2)

co Ye Fe

Toh+0.22 33412 she 9

ou x ma

4.95 \$0.64 2656 +12 315k + 364

se ca Ne

22.6 \$16.1 4991 \$582 2019 + 3m.

Maniikara bidentate

understory

clean leaves (n = 4)

0 Ma Fe

4,78 42.84 32413 136+ 8b

ou K Na

8.00 + 2.59 3663 + 1099 haB5 + 2116

sr ca Ne

30.7 \$ 13.1 6651 + 2047 3080 + 506

Mantikara bidentata

canory

leaves + epiptyiis (n = 2)

co os Fe

8.254+0.36 Moree 8429

ou x Ma

Tho + L9T 18a HIB 3263 472

sr ca, Me

38.5 + 10.5 6496 th53 2647 ¥2TO

Vanilkara bidentate

understory

leaves + epiphyils (n= h)

co Ma Fe

4.96 \$3.bh 0456 253 + AT

cu K Ya

1.85 + 0b 1359 + 323 3828 + 2589

se ca Xe

Mae + 13.5 8070 + 1690 3539 + 502

25+

---Page Break---

Continued Table 17

Sloanes berterts

canopy

clean leaves (n = 2)

co Ma Fe

4.394132 M5 heh os Th

ou K Ta

9.10 \$6.50 2224 +922 510 + 180

Sr ca %e

16.4 + 9.4 5698 43069 2008 + 608

Sloanea berteriana

understory

clean leaves (n = 5)

co Ym Fe

4.70 43.29 1Sh+ 85 TT + 38

ou K ta

10.22 + 3.k 28h + 607 685 + 197

sr Ca %

25.38 + 4.65 4587 + 797 1596 + 152

Sloanea berteriana

conory

leaves + epiphyllis (n = 1)

co Yn Fe

5.2 nn 123

cu x Na

43 ant ate

sr ca Xe

MT eo 2678

Sloanes berteriana

understory

leaves + epiptyllis (n = 4)

co Xa Fe

5.354595 2554121 139 +29

ou K Na

5.32 + 1.50 1979 + 359 1135 + 22h

Sr ca Me

24.0 + 4.95 THB + B43 2039 + 185

---Page Break---

Contimiea Table 17

Palicoures riparia

clean leaves (n= 5)

co ry Fe

7.32 £3.24 1Tht 93 he iy

cu K Ya

13.96 £3.78 4596 + 954 2202 #1062

Sr ca Me

U8 ¢ 32 1092T + 983 5300 + 523

Croton poeetlantius

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 + epiphyllis (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

Groton poectianthus,

leaves + epiphyllis (n = 1)

co Mn Fe

3.37 1204 a

cu x Ma

6.0 3202 8025

sr ca Me

68 8586 eB

---Page Break---

??_

Continued Table 17

©

115

w.2

Sr

23.7

Buterpe globosa

lean leaves (nel)

Ya Fe

305 23

x Yo

4387 926

ca %

wt20 2958

Buterpe globose

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 ant standard deviations of concestrations of elesents 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 sites

han, /dence. F Level of stant

Tested _?Shecten Element «of Patio? «ratio fleant Atterences

Spectes ?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

Reoulte of analysis of variance to teat aifferences in concentrations

of elements in yoo! between sites.

mm./tence, PF Level of stgntfi~

tested Gpecten © Elenent? «of Prratio? 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 were 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 sites]. 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, Fe, 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 element in soil extracts are given in Table 23.

Concentrations of exchangeable and total elements in the organic matter 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),

Results of analysis of variance to test soil differences

between sites and depths.

Depth, un. /aencn. Level of signifi.

Tested inches Element _F ratio cant difference:

all sites 0-2 Mn 5/18 2.64 90%

5 well drained sites 0-8 Ya ins 3.08 958

?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 3.28 958

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 3.05 958

5 well drained sites 5-1 sr ins 0150 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 standart deviations of

ou

x

%

Re

oo

%

se

me

Table 24

Se

concentrations of elements in organic

matter on top of soil,

Parts per million

29

a

o

?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 ø 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 signifi-

Tested Element _F ratio" ratio cant difference

All sites, extractable elements

BRE OTR Re

elements

SERESTE Re

orennns

A

8

gw

HOTEL

e

* ? sr 2/38

2? R38888

---Page Break---

Table 26

So

Results of analysis of variance to test differences in soil

nitrogen concentration of elements in freshly fallen litter

Mean and Standard Error of

the Mean Ratio of Nitrogen

to Carbon in Litter

Month (Jan., Feb., Mar., May, July,

Sept., Oct., Nov., Dec.)

Sample Size = 4

Standard Error = 0.15

Mean = 1.5

Month (Jan., Feb., Mar., May, July, Sept., Oct., Nov., Dec.)

Mean = 1.5

Standard Error = 0.15

Sample Size = 98

00

Table 27

?averages an standard deviations of concentrations

?of elements in freshly fallen litters

element Parts per million

© 8.52 ± 6.10

a Mbt out

% mt

o 5.72

© 30

m 05

or os

ce sick

% 2200

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Ne

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33

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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 is 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 time:
? 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 turn-over 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. These tests test 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 topscast at the site? on from the bottom-most understory leaves of three species of five sites. In addition, clean and epiphyllae-covered leaves were

As it was difficult to find and reach all the desired samples at all the sites, more targeted samples were obtained (Table 28). No additional species were sampled at 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 epiphyllae were made using ^{137}Cs , ^{134}Cs , and ^{95}mTc ,

First, averages of ^{137}Cs , ^{134}Cs , and ^{95}mTc were calculated for the canopy and understory, for clean and epiphyllae covered leaves, by species and site (Tables 29-31). Then differences were tested by analysis of va-

yainee Scchmiquée for apectes, attes, clean vs. epiptyll coven, aed ranegy
Pomitterstory (Table 32).. Ditterences at the of error level or nae
found between species for 1370s and Illice on clean understory leaves, and
Cresent species for all isotopes on epiptyll covered understory tees
(ieble 5). Since tables 2,3 and k show that average levele or fence on
Feltcourea riparia are most different from the rest, species tn tre wdc
Har? He Gin eteed for alfferencen, this tine without, Pultosnres siea-
Hig, Mo dttferece between other speciés vas evitent. The eee ee
Gifferece between species in the canopy,

Ivo differences between sites, out of the 12 tested (table 32), vere
significant. Tis is not enough to'state that there are difference) bene
sites.

---Page Break---

Table 28, Actual sampling schene for deteraining fallout attribution.

Montara Slonnea *Palicouren Buterpe _Croton

Bidentata berterfana ?iperia globose poecflantius

canopy + eptptyll x x

Sitel understory clean x

understory +

epiphyt x x x

canopy clean x x x

canopy + epiphyt x x =

Site 2 understory clean x

understory +

epiphyt x

canopy clean

canopy + epiphyt.

Site 3. understory clean

understory +

epiphyt x x x

canopy clean

canopy + epiphyt2L

Site 4 understory clean x x x x

understory *

epiphyt x x x x

canopy clean

canopy, + eptptyli

Site 5 understory clean x x x x

unlerstory +

epiphyt

understory clean gq

Site 6 unterstory +

epiptyl. x

swnderstory epectes

-3T-

---Page Break---

Je 2. Tnt}ynce of species, site, canny postion an eptptylia

mee on ?7'Cs distribution, Average values are picocuries per

ee.

Unteratory

Tiean leaves Teaves plus epiipiyils

en Heats __Teaves plus epiphyllis

" 1 et. deviation "

Site 1 3 3.03 2.02 2

Site 3 2 Mor 2:59 2

Site & 3 3:8 0.22 3

site 5 3 B59 1.30 3

Dacryodes excelsa w 3.62 2.9 4

Manflkare bidentate = 3.73 0:90 4

Slonnea 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 excelen 3 3.50 0.35 3 kage 0.50

Mantikara bidentate 1 © 218h 2 2 3:5 0.92

Sloanea berterians = 22.37, 0.32 2 kt 0.80

=38-

---Page Break---

Tuble 30. Infhugnce of species, atte, canony position ant epiptylis

en 1iMGe"ataertbuticn. ?Average vues are ploocurien Der

eran,

underat

Teaves plus epiyiis

" 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

Dacrycdes excelsa ath 1.72 » Beta

Yaniikera bidentate 1:09 0162 4 465

Bloanea berterians = 3 a5 0.8T 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

Wantizara bidentate 1 ag 0:86 2 an 3119

Sloanea berterians = 2 ore : 2 5.78 2136

---Page Break---

?table 32

site 1

Site 2

Site 3

Decryodes excelen

Sloanes berterian

oor

oe.

of opectes, site, canopy position ant epttylis

?Metribution:

iean eaves

x

Beas ERaT

RSE

Unters

Lat, deviation

0.

3

0,

°.

0.

0:

9,

0:

BEER

BbSE

Teaves

mx

2 1

2 0.92

3 1:05

3 Lot

Bake

wong

2 ot

5 kB

3 Las

3 0196

L139

3 Lp

2 166

2 0.68

?average values are picocuries per

ius pips

1 et, deviation

---Page Break---

?Tile 52, Femulte of analvaia of variance to detemine algnftficanca of differences in fallout,

(SR _ ier ee Degg eterno

syectes ?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 Campy, cies tem TD ve

ee

TE meta

os tetay, cnn begs she an

we haart oe sie

site Cancry, 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 taeeiny eR! AY the ve

cumyotervioy Cleese OSh th as

cumvmtentey ian iglla eka Oa ns

= atgteteant at 5f level

+ = wtgnitican at 24 level

aha

---Page Break---

Table 33. Average values of fallout within and

where no significant aifferences ext:

lean Leaves,

between compartnents

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 IWige 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 differences

between clean and epiphyll cover

leaves in the understory, for all dates, and for USPS Ue eee

Differences between

open canopy and understory were not significant

Hine (1967, P-R.M.C. Annual Report) reported differences between open canopy and understory leaves for 137Co, with the understory leaves higher. Epiphyll covered leaves in the understory showed a higher burden than those in the open canopy (Table 33), but the difference is not significant. Perhaps

Differences were obscured because 137Cs levels were lower by a factor of

about 4 from the time at which Kline took his samples. See table *

Averages values of fallout within and between compartments where significant differences existed are summarized in Table 3300

TRITIUM MOVEMENT THROUGH A TROPICAL RAIN FOREST ECOSYSTEM

Movement of tritium through ecosystem is of interest for two reasons:

1) Tritium is a tracer for water, and thus aids in water balance studies of the ecosystem, especially in transpiration studies. 2) Tritium is a major by-product of thermo-nuclear reactions, and could contaminate the environment as a result of both peaceful and military uses of thermonuclear power.

A series of experiments were undertaken to determine rates at which tritium moves through a tropical ecosystem, and the proportion of tritium that is immobilized and thus becomes a long-term radiation hazard in the ecosystem. The experiments were done in cooperation with Dr. Jerry Kline, Argonne National Laboratory, and Dr. John Koranta and Mr. John Yartin of Lawrence Radiation Laboratory.

The first experiment involved applying tritiated water to a 20.9 m² 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 rain forest.

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 deter.

shout @ variety

moves uniformly

in xylem.

Elements move through trees at the same rate as tritium.

Note the variation in tritium movement through tree through!

of meteorological conditions. 3) to determine if tritium

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, Carl Jortan, 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 adds 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.

Previously with PRIC, now with Argonne National Laboratory.

Lawrence Radiation Laboratory, Livermore, Ca.

Lawrence Radiation Laboratory, "i

Puerto Rico Nuclear Center, Rio Piedras, Puerto Rico,

hha

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Three tropical trees representing two species were injected with tritiated water through holes bored in the trunk near ground level. 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 exchange of leaf tissue water with uncontaminated rain water 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 Tiel. (2) Tritiated water persists in tropical trees with appreciable residence times even though large amounts of rainfall occurs in the rain forest. (3) Rains bearing tritium will probably cause leaf tissue water to become labeled immediately due to the exchange of water on leaf surfaces. (h) 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

A plot of ground,
side of the plot was cut away,
lysimeters", Jordan 1968, Soil Science 105,

hs.

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lysimeter collected water from a 2h 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 gareinifolia*, 2.06 inches basal diameter eg *Mantikara bidentata*, 1.14 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 so that 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 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 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.

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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.

x12 in. trough type rain gauges. Wet and dry bulb temperatures were measured on every permanent gages.

Water samples were analyzed by

standard liquid scintillation techniques. Known standards were included with the samples and results were converted to disintegrations 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 wind 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 made for the 4 cm collection because of the short distance from the soil surface. The half life of tritium (12.32 years).

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 ml in 1 liter equals 1.1×10^7 dpm in 4000 ml. equals 2.75×10^7 apm/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 catiefactorily. Therefore, specific activity of water vapor at ground level at tines after application vas estinated ty extrapolation

Of the curves of Fig. 1 (Table 35), using a flexicurve.

Specific activity of water vapor at ground level, (Table 35) vas then plotted ac a function of tine after application, using three dif-ferent tine scales (Figs. 10, ll,and 12).

Average specific activity for each given tine period vas then taken from Figs. 10, 11 and 12 (Table 36).

?aun and Jordan (1969) estimated evaporation from the soil to be

36 g/m2/aay. If evaporation occurs only during the deytine, the average is 3e/ne/nr, during the daylight hours. Since the tritiun plot was 3.68

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Table 35. Specitic activity of tritiated water at sotl surface as dete

ty extrapolation of curves.

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s/s 16:30 4.0 x 105

SAT 16:00 1.2 x10

sa 15:00 ko x13

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Fig. 9. Specific activity of tritium in the water vapor above the
@xperinental plot as a function of distance sbove the plot.

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Fig. 10, Specific activity of tritium in the water vapor at ground level as a function of hours since tritium application,

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Fig. 11, Specific activity of tritium in the water vapor of ground level as a function of days since tritium application.

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Fig. 12, Specific activity of tritium in the water vapor at
ground level as a function of months since
tritium application,

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TABS

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n2, 11,04 mi/hr evaporated from the entire plot. Specific activity given time period (Table 36) was multiplied times length of time period, times 11 mi/hr to give total dpm evaporated during the time period. Total tritium evaporated was 10.7107 dpm, or .09 percent of the total tritium applied.

Fifty one percent of the total evaporation took place during the

Evaporation at sea level 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

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Fig. 13. Specific activity of tritium in the water leaving the Litter layer as a function of time since tritium application,

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Fig. 1h.

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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 cell depths could be explained by

inch depth, the clay particles are

differences in soil structure. At the 5 inch depth,

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, inverted 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 activity (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. 1, 1967, (Kline and Jordan, 1968), the tritium has a retention 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 rainfall pattern following tritium application. In the earlier experiment, only 0.24 inches of rain fell during the first 2 days following the

The pattern of tritium movement through the trees is influenced by the pattern of movement through the soil. Since tritium has a long residence time in the litter and soil, the roots of trees are exposed to tritiated water for a relatively long time. Specific activity of tritium in the transpiration water is affected by several factors: 1) Distance of roots with depth in the soil 2) Specific activity of tritium at depth 3) Water vapor deficit of the air, which affects 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, since 20% of the plot is contaminated).

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Dew TmTUM ML SOL WATER,

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Fig. 15. Specific activity of tritium in the soil water at four depths as a function of time.

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DDSTANCE BELOW SOL SURFACE (NCHES)

specific activity of tritius in the soil water as a

Fig. 16.

6 eight days after tritiun application,

fimation of depth,

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Fig. 17. Specific activity of tritium in the soil water as a function of depth, at intervals following tritium application,

0.5 m

0.1 m

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,

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spread fallout situation). As a result of these factors, data points of specific activity of tritium in leaf or wood meristem 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). Sivity in the Uivtes ee

In the roots of the larger trees, yet another phenomena sens to

be involved (Fig, 21). The fret litte peat nay sebrecent water taken out of the Litter by rootlets in that layer, vile the second, more dif- fuse peak, may represent vater 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 rain forest ecosystem is increased ty a factor of five to ten.

Novenent of ^{13}Tcs , Sp, sr, ana in through Canopy Trees

Movenent of gama emitters through large trees vas measured in two vays. (1) A portable rate-neter with a G-M tube was connected by a co- axial 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 vay 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 tover, 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 in. a.b.h. and 52 ft. high was injected with .46 microcuries of ^{137}Cs 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 ^{137}Cs away from the injection holes. The activity rose to a maximum at six feet,

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PM TRITIUM/ML FREE WATER IN LEAVES

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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.

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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.

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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.

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Fig. 22. vrimental results of tritium res:

Ss coat compared to predicted residence times,

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Table 37

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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 ^{137}Cs , 0.19 millicuries of ^{85}Sr , and 0.34 millicuries of ^{131}I on Sept. 18, 1968. Interpretation of the portable scaler data (Table 39) is more difficult than for the ^{137}Cs 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, and 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 ^{137}Cs showing the fastest movement. At 132 days after injection, ^{137}Cs was still increasing in the leaves (Table 40). Data for day 132 indicates that the peak of upward moving ^{137}Cs 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 ^{137}Cs and ^{131}I data after the 75th day. However, it is clear that both isotopes had only reached approximately 20 ft. (20 ft. above injection holes) by the 75th day.

^{11}C 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 ^{14}C , 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 ^{14}C were present.

A curious phenomena 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 132 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 TO for . No explanation is apparent for this phenomena.

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Table 39

Portable scaler reading on *Dacryodes excelsa*

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Table M1, vovenent of sr through Dacryodes excelsa

Days since injection

Semple © 2 B

Activity in plecuries per gran, dry weight

Leaves 6.0 2.0,

tree 23.6

Wood, 20 ft. above

Injection hole ea

Wood, 1 ft, above hole 0.0

Wood, base of tree 0.0 22

Bark, base of tree 3,385

Table 42, Movement of pin through *Dacryodes excelsa*

Days since injection

Sample 2 B

Activity in pleocurtes per gran, dry weight

Leaves 19 16.9

Tree wT

Wood, 20 ft. above

Injection hole wT 68.1

Wood, 1 ft. above

Anjection hole 5h

Wood, base of tree 0.0 erg

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PART B - SECONDARY SUCCESSION IN THE IRRADIATED AREA

METHODS

Description of Site

The study area is located near El Verde, in the Luquillo Experimental Forest of eastern Puerto Rico. The site is at an elevation of 1500 feet, in a forest described as Tabomuco type (Wadsworth 1951). Annual rainfall is approximately 240 in. per year, with more than 10 in. every month. The terrain consists of a series of sharply sloping ridges and ravines, Average height of the forest top is 65 feet.

The studies of early succession were made in the area affected by gamma radiation. 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 had ceased (Table 1).

There are two distinct soil types in the irradiated area, one red-

dish 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.

Gria

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 axis, a strip of squares two meters wide was run cut to 30 meters from the source.

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LEAF AREA INDEX

DISTANCE FROM CENTER

Fig. 2. Leaf area index of the irradi

Leaves directly at the center are

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?*~radiation by the plug above

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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. a

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 dieback 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/n@/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

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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.

x x Correlation coefficient

basal diameter weight ST

basal diameter height 98

height weight 9h

height weight (adjusted for dia.- .2h

wt. correlation)

basal diameter @ diameter, 30 cm.

99,

~68-

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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 were 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 dia-

meter 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 illinoense*, biomass was determined by digging up 10 individual square meters of each type, and regressing biomass on the quantity (% coverage) \times (density). Biomass was directly proportional to this quantity.

Regressions were programmed into a desk-top computer, and total biomass 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 times 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/sizeclass/hectare for each size class was added together to give total biomass/hectare.

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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 rate of biomass increase in palms is different from rate of biomass increase in other species, an error was introduced. It is not known if the rates differ.

Respiration

Leaf respiration of successional vegetation was determined during night time hours only, using the following technique. A plastic bag was inverted over the leaves to be studied; the bottom of the bag was soft

open. Air was slowly pumped from 92 feet above ground (to ensure a source of air with a stable CO₂ content) through a plastic tube into the top of

the bag. A relay switch attached to a timer set for 15 minute periods directed air into an infra-red CO₂ analyzer, alternately from the external

air source, and from the bottom of the bag. Differences in CO₂ concentration between 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:

$$TLR = ax + by$$

where $\lambda = 1$, when leaf area index ≥ 1

leaf area index, when leaf area index < 1

$= (\text{leaf area index}) - 1$

= respiration rate of top leaves

= respiration rate of bottom leaves

Skewes

---Page Break---

Gross Photosynthesis

Gross photosynthesis was calculated for the study area

using the following equation:

GP.

$\text{GP} = \text{biomass} + \text{leaf fall} + \text{leaf respiration} + \text{root respiration}.$

Biomass and leaf fall were converted into carbon by multiplying times

0.44 (carbon = Hf OG, 205). nko conven Wy mltignyins

Gross photosynthesis of the mature forest was calculated by adding

change in biomass to total forest respiration (Odum and Jordan, In Press).

Solar Radiation

Solar radiation above the canopy was measured with an Epply pyrano-

meter 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),

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Total chlorophyll (Cy) in the successional ecosystem was calculated by the equation

$$Ch = a \times t \times y$$

and for the mature forest by the equation

$$cy = ar \times ts$$

where

$$= 1, \text{ when leaf area index} = \text{or } 1$$

= leaf area index, ven leat a¥ea Index < 1

(ear area index) ~ 1

chloroplyl1 concentration of sun leaves, successional plante

chloroplyll concentration of shale leaves, successional plants

chloroplyl1 concentration of sun leaves, trees in mature forest

chloropiyi1 concentration of shade leaves, trees in nature forest

BHdKoe

"Equivalent" Age of the Nature Forest

To plot long term changes in ecosystem functions with succession, it was necessary to establish an age for the forest surrounding the irfa~ diated area. the forest, however, had been affected in the past by hurri- canes, and come selective logging, with the result that it 1s an uneven aged stand, Therefore, an "equivalent" age was determined by dividing the biomass of the mature forest (22,853 g/m² fron Table 3) by the average of the four values of assinilation/year (Table 5). The equivalent age of the forest in 1966 vas? 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 10 most common species in the mature forest, in decreasing order of importance, are *Butyrpe globosa*, *Croton poseLiantina*, *Dacryodes eucetss*, *Gecropia peltata*, *Sloanea berteriana*, and *Wentia nitida* (see et). *Gecropia* is a secondary successional species, while the *Teet proae* seeks to be germinable beneath a closed canopy, and thus can be called "climax" species. The standing crop of the five most important climax

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?ON oxinzeED

BIOMASS, GRAMS /M?

CLIMAX SPECIES

r 3 10 30100

TIME (YEARS)

Fig. 3. Change in biomass of plant material during succession.

?ble 3. total standing crops (Dionase) of vegetation in the ttrailated ares ant the surrounding forest.

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Table 4. Percentage of standing crop contributed by vegetation in vartous categories.

Years fron

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

Figure 5. Net photosynthesis (assimilation) in the irradiated area and mature forest,

Table 2/any

Table 3/any

Table 4/any

Table 5/any

Table 6/any

Table 7/any

Table 8/any

3 oe 3.86 0.800 0.0095 o.35e ote

9 186 3.23 asst ute 0.585 one

The

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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, percentage of total biomass of sprouts decreased, percentage of climax species increased, and 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 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 rate of soil respiration between the mature forest and the secondary successional area (Table 7). The

see meter soil respiration in the mature forest on Feb. 11, 1968 may have been slightly an unusually dry condition on the floor of the mature forest.

Between Feb. 5 and Feb. 11, no moisture was collected in 12 below-canopy rain fall 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 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 sprout:

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+

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JOvASS ON OXDIZED SOL

158 ON REDICED SOL

?CLIMAX. SPECIES

PERCENT OF AVERAGE StANOING CROP,

3 380

17

Te (YEARS)

Fig. 1b. Contribution toward total biomass contributed by various categories of plants during succession,

109)

cross

"OF photosynthesis

S

??Respiration

GRAMS CARBON /W?/DAY

Net photosynthesis

r 3 30

TIME (YEARS)

Fig. 5. Change in net photosynthesis, gross photosynthesis,
and respiration during succession,

16

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oe

Table 6 . Respiration of leaves in the degraded areas

ae ind

Psychotria pertertana 0.0096

Rutooures riparia 0.0196

bene paste 0.0136

Diayoneng: sorstont 0.028

cecropin peltata 0.0383

Pemetion procumbens 0.0093

ystotria bertertane 0.0009

uttoouren riparia 0.0093

Bbehate paluan 0.0062

Pigyeogana orstotont 0.0061

average top o.019 A560

verage etter o.oo AEB

?ble 7, Sola respiration in the irradiated area ant the mature forest.

rams, carvan reepirea/e?

sure forest,

(ulated soll. 06 008 Sr

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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 were 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 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 start of succession and the regression line of respiration on years converge with passage of time during succession (Fig. 4).

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 of the proportion of shade leaves and sun leaves increases with succession (Table 9, Fig. 6).

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8. Reeptration ant

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2 oe Bot kam 19

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2 NTT Gor 398 8k 8388.98 aos

?rineiuded with leat respiration

?Table 9. Leaf area index and chlorophyll content of forest during succession,

Years from start teat area Total chloroptyy A
of secontary succession inter in ecosysten 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

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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 (from Cistaén In Press).

leaves

grams/m² of leaf area

leaf area

See ES page 236-35

ious ?

Eucalyptus

Scoroparia

Slows berteriana

Euterpe glstose.

Santieare bifereata

Decrrates tok 388 sas

Brenoter exeiee

SRE

a

33h

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Solar Radiation

me average total solar radiation duris B 1

yeriol April 1967 through January 1968 vas 206.6 cay ee tan wink

Pie standard deviation of 69.9. This 1s $2.066 \times 10^{\circ}$ eal/n@/aay

fone gran Of glucove yields 3730 calories (\itlson ant Loomis, 1962),

en 2.005×10^7 calories would yield 553 grins glucose /at/any? at 100k 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 to the total sunlight was measured by an Epply pyranometer, and converted to grams of glucose/day by taking one gram to be equivalent to 3730 calories. Gross photosynthesis also was converted to grams of glucose /a?/aay.

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/n@/year to standing crop in grams/n®/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

Joss eter stack ch guesession. Divercity 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 one niche 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.

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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 trenis of varlous

?Tunctions during succession.

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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 m² 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 *Cynantherus 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 Snith, 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 desk top computer.

Apparently there is no increase or decrease in correlation in the area studied (Tables 12 and 13),

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

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Tangeiatons cost tctene

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2 Paychotrie bertertane Lénocierm doningensis «0.02.05

2 ? ?Tabebuia palliga 0.19 0129

3 . : Tenanthus? pallens ont oor

geen picate ole

3 : eee ese 033 ok

é " Palicourea rij -0.08 0.16

1 : 0 Digymopanax morototons 0. 0.28

a Parerngiony oe fer

wctgra dewingenate ??Bbebuie pitts 085

20 " Tcnanthud pallens 0106 0:31

a " = Zecropia peltata 0.03 0.38

i i . Alchornia latifolis 0.15 0.18

: Falicourea riparia 0.03 0.01

Fs a. 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

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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

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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

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Table13. Correlation coefficients between species in the mature forest.

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To, Species x Species ¥ 2énequadrats ?Ghnéguadrate

2 Dacryodes excetse Ruterpe globose 0.01

2 Menigies sxcgiee Wniikars bidentate Soa

3 an Higienia 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

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Fr 4 Bat 1

i c G ont one

a5 G 5 0.07 0.33,

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ye cols. ?0.46

B 5 : 0.39 0.39

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a a a Groton porctlanthus 70126 70.38

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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

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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 .

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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 bielimination 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 2 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 bielimination 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 foci is indicated in this comparison as giving a curvature to the normally linear relationship between number of species and log number of individuals,

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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 Drevry, 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.

Possible ecological role of the call of male *eleutherodactylia*

frogs as a population spacing device is presently being studied. Mate attraction as one primary role is well documented, but recent observa-

tions of increased calling activity after 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,

and comparative data of ecological, evolutionary,

and comparative data of ecological, evolutionary,

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?Table 1

chromosome counts of Puerto Rican leptodactylid frogs.

Diplota Chromosome Count

Leptodactylus albilabris 22

Bleutherodactylus unicolor 30

E, portoricensis 26

E, antdliensis 26

brttont 26

E. wightmamnae 6

E, rlotmonat 30

E, snetdse 26

E. hedriki 26

E, Locustus 26

ak

E. gryllus

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PART B - SPECIES DIVERSrry

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 rela-

tionship that governs the complex ratio of numbers of individuals of

various species to one another. Very little has been published of cau-

sative 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 (1966) 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 use of a set of computer generated nomographs, 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 OG , 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.

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Willians 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.

Pielou (1957) has introduced a new (to biologists) measurement of species diversity that does not rest on prior assumptions of relationship 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.

No 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:

$$H = -\sum_{i=1}^N p_i \log_{\phi} p_i$$

where H is mean diversity or information content per individual, ϕ is a scale factor to convert to any number base desired (binary bits are often used in information theory where $\phi = 3.321928$), N is total individuals in the sample and n_i 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

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of individuals of each, of individuals of each. Because of the large range of categories, the level of the rarer species, Resolution can be improved by plotting on a log scale, Resolution can be improved by plotting on a log scale, Figure 1 shows the results of the analysis. Recovery area, labelled cumulative species richness, would normally be, viewed with the effect of the number of species, so species represented by one individual are more common than those represented by two individuals. Information available in the sample and the number of species to be made about structure. The curve can be inverted by axis X. The total number of individuals in the sample, for the number of taxa

individuals in each species. The curve so formed is labelled 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 Shimlance curve biomass division to sigmoidally mubervative en 8 106 Scale, but differs from the relative abundance curve in that given $\int U_{ae}$ composite ratio of species ceion courtant ar repleteiee 12 Increased, each point on the relative abundance curve moves to the left as sample size increases while the composite ratio curve Only Eide points at the upper ends, Points on this curve representing species say be real ap a ratio, 20:12:15 or aa ene pact in 20) 12) 15 et The SSuposite ratio curve in this focus te ainitory but not iaentiesly to'8 Sisbeauty inten curve developed by classical evneds or to Wiiiieá?® log etse Ciera tie wager Thave head goiahs vhaeh eercesente © single Siacien in the composite setio, also represents total species fd 10s strcied dtaintais Bo will be dwed'ea trance petnt an ony eiverslty TOaet SOSA Sache nay date potrt normally used ah WinIdan'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 species 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 any method is a rigorous exercise in probability theory and has been substituted here by an empirical correlation method covering the range of curves and slopes encountered in this study (some are not linear at any point). An example of the theoretical complexity is provided by the fact that the probability that a single species whose frequency is one part in one hundred will be missing from a random sample of one hundred is its probability of absence in a sample of one (.99) raised to the 100th power (approximately 36%). The probability that it will be absent, but replaced by a still rarer species, involves all of their probabilities. This is almost too complex for computation. Common sense indicates that for even a single sample there is not one but an indefinite family of diversity index curves depending on the order of sorting and recording individuals, and that there is a maximum likelihood curve having the highest probability of occurrence that will best represent this family.

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Such a curve should run approximately parallel to the composite index curve, always to the left of it (randomly varying individuals). It may converge with it because it is subject to the same error as the log series curve at low number. It must be emphasized that no theoretical reasons exist for linearity of diversity curves. The composite ratio curves in any type of graph. Semi-log plots are merely a representational convenience.

?the empirical method of comparing these two types Of CRETES
considers comparing easily sampled populations of known composite
consisted of common and extreme types of populations encountered in
ratio for the mean do not include all theoretical curves, some of which
deviate from the conclusions reached. For example, the
diverse population, each of whose members is a stereo-
secret diversity Antex 100 log series whose OC is unity
while the composite ratio is a vertical line at whatever sample size

is a line at

is chosen. The other extreme is an inde-

finite population of one

species diversity index is a straight line at one, or there, one

at whatever 9%

composite ratio is a single point sample size is chosen.

sample ratios chosen for this experiment ranged from 10 to 500

species per thousand individuals and were either straight, broken, or

seen only curving upward in semi-log plot. "Collections" were made

continuation 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

of finite number of species per 1000 rather than the natural situation

OF on 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
weibull curve past 10 individuals. Distributions appeared to be normal

on the species per fixed number of individuals axis, for which the mean
is 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

the 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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Cr)

A Cumulative species

vs log

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B. Diversity index

?maximum,

likely hood,

curve C. Cumulative

species vs

N

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Fig. 1. Graph showing inter-relationship between relative

Runtsebe (curve A) composite ratio (curve C) and the
seetatoted marimm Likelihood curve of traditional
Weereity index methods (curve B). Semilog plot is
fon representational convenience ani does not reflect
asamptions about species inter-relationships.

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fo tie on the linear portion of the composite ratio curve. Species

Per thousand 1s approximately the intersection of the composite ratio

Curve with log 1000 plus .2 times the C.R. curve slope (10g 1000-10g

$0 \text{ times } \log 640 - 1 \log 60 \text{ or } .1926 \times 1.0280 = .2$). Basing the standard
Reaouement of species per thousand on the slope of the composite
ratio curve, rather than on the munber of species collected in a sample
of 1000 individuals, hao already proved to be a valuable strengthening
Of the foundation for this useful measurerent. When notified that the
number of rare epecies in a certain collection vas theoretically inade~
quate, one collector vac reninded that a small group of very rare species
hhad been put aside for detailed identification and forgotten, The re~
lative taxononic abilities of several collectors have siso been evaluated
by thie method and the evidence obtained has been consisted with other
evidence available. Extrapolation of such measuresnts as species per
thousand upward beyond the Limits of the sample has for far been confined
to communities having Linear composite ratio curves, but dovnvard extra~
polation 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
fa simple way to the above measurements of diversity. Independence of
sample size has been found ina very few cases where the composite ratio
curve vas linear and the usual group of comuon species exhibiting ©
@ifferent elope vas absent. Mormally 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

$$\log n! = (n + 0.5) \log n - 0.4342944819 \log 2\pi n + 0.39894228$$

which can be written into a computer program. For rigorous accuracy, 10-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 desk top 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 cal-

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 $\log n$ for each species in pairs. By utilizing Sterling's approxi-

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nation they calculate $\log n!$ on a continuum rather than as discrete volume numbers and thus avoid rounding errors. Species are entered from commonest to rarest and treatment 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, design-

nated 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 upwards, 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 and information content for samples scaled
downward to 100, 500 and 1000 individuals where appropriate designated
 $F_{0.9} \approx \#500 \approx H_{0.9}$ and $\text{Int.}/100$, $\text{Int.}/500$ and $\text{Inf.}/1000$.

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 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 indi-
viduals, 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.

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?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, having decreased 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 fH is calculated for the abundant species only

?At the same time the number

increasing to 5,133.

?the drop in diversity is from 3.62h to 3.097.

of rare species was extended from 79 to 109, and while rare individuals increased 1,24 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 41.1h 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 number of abundant species with further increase

in number of their individuals; and a slower increase of species and indi-

viduals 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 can not 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 3 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

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Fig. 2. Composite ratio curves for total vegetation in a radiation

?cles data points cited.

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Oo 2400 20400 2040020 400

Species

Fig. 3. Composite ratio curves of seedlings (4.5 ft.

?Hecoverly area one ani tvo yearo after irradiation. Ordinate

?and absoisea have been reversed fron figure one and spe-

20,

Das

1968

2040

tall)

and saplings (> b,5 ft. tall) of tree species one, two

fan three years after trraiation. Slopes given? to

nearest whole munber. Scale of species axis

shorter than figure 2.

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The B curve is not well differentiated and contains only 20 species.

Species per thousand at 35 is the lowest registered for seedlings.

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 2.113 and the slope Likewise decreased to 8.0h 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 H_{90} 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 H_{90} ,

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
& large percentage of successional species that will be replaced in the
mature canopy by other species, should in three years time establish each
@ 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
has gone from zero to 2,923 to 3,196, Slope A has been 0, 5, and 6; white
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. Tate 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 overshoot
and subsequent correction are probably to be anticipated among the pioneer
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,

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and although a great deal of labor was involved, trends in the two were so similar as to warrant little discussion here. Development proceeded 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 anoxic 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 (Odum 1959) seems to require qualification. The SEttint seem to be very true for the more abundant species, which

are 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, and 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 taken as a measure of diversity, for the growth process itself dic-

tates that a large percentage in early colonists can not 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 initial Mitule do the same as diversity in terms of area must be strongly restricted to situations in which size and/or density are equivalent. ~

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ings in well and poorly drained soils.

(A) well drained (B) poorly drained.

Comparison of composite ratios for 1967 tree

Seeali

Fig. 4.

?Table 1

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In summary, the seedling by

population of this recovery area was able

in three years to produce a diversity structure comparable to that of

sae ee nen erat 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

Fach ©Tevel rear 92 pees per tonal ibivadiae Wy the tte

Several studies have aimed at discovering community structure and diversity of lower montane rain forest in Puerto Rico. Snith (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 spiralling 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 has 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 *Butterpe globosa*, which was also a dominant in the *Croton* group but had a couple of species almost absent from the other groups, including *Wyreia Gefiexa*, *Trichilia pallida* and *Ixora ferrea*. The habitat of this group seems to be gentle slopes having mostly soils of high moisture content, and is not 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,

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---Page Break---

empos re 6

the ratio curves obtained for nature forest. (A)

M16, dave nevers in ruitation control center (B) 1000 trees growing
in poorly drained (reduced) sites (?) 1000 trees from red oF
Fellow (presumably well drained soils).

Fig. 6, Further breakdown of figure 5C into three apparent tree associations
which correlate with topography. Lower curve characterizes

flat areas and is dominated by *Croton poecilanthus*, Middle
curve includes steep slopes and river bank and is dominated
by *Sloanea berteriana*, Upper curve includes gentle

slopes with *Heterpe globosa* and *Dacryodes excelsa*

as dominants but has *Trichilia pallida* and *gnetum*

glauciflexa as exclusive subdominants,

-10h-

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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* ~ *Trichtlia* group (upper curve in figure 6).

Me A segment of this group has only three species; *Buterpe 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 inatequate in mumber. ?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 dis-

couraged by temporal physical diversity of the environment from exerting

strong competitive presoures, leaving the habitat relatively open for

sub-optinal, subsistence utilization by any comer. Such a situation

could lead to development of a coniiition of maximn 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 te

doubtful that so mary sufficiently unspecialized species are available.

In analogous situations exist 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 824 in 1966 to 386 in 1967, the number of species from 54 to 10, etc.

olated species per thousand from 51 to Wk, and H from 3.821 to?3.4Si

Te number of species in the A segment decreased from 8 to 5 enl'ite.?

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oe

aa aa a ar

Figure 7, Composite ratios of old vegetation surviving

?from before irradiation until 1966 and 1967, one

and tyo years respectively.

=r

Figure 8, Composite ratio curves of sprouts populations

one ani tvo years after irradiation,

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---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 perennating 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 decrease 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. Meristematic diversity may be the factor most responsible for the fact that sprouts have a lower diversity than old vegetation as the sprout lists are very similar to the old vegetation lists but lack certain of the species completely. The 1966 anomaly in composite ratio, on the other hand, seems to be probably a function of sprouting rate, as several rarer species did not join the sprout community until 1967. Other factors may have also operated to correct 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

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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 fami-

Lies 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 purpose, 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 not 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 Hymenoptera with 9 species, 32 Lymanoptera 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 has been used. Crude extrapolations for H at 100 were made on Trichoptera and Coleoptera, yielding values of 1.6 and 2.8 respectively. 100 for Homop-

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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) Hsing tropic Sept. 24, 1965. (B) malaise flight trap Yarr, but note scale on species axis is very different from previous curves,

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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 $1/125$, 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 uncer-

cal 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,

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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 is the result of single breaks at different

points in many combined community curves, but this is unlikely in view

of curvature in 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 samplings

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 nature 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 H' 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

?couparable,

Reduction of diversity in vegetation showing radiation damage dia
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

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Dezrmes 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

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?Appendix A

to Dolichopods of the Rain Forest at HL Verde by George Drewy
ot at HL Verde ty George Drewy

(Gientittentions ty taroia Tobinwon, UeSy National Suseus). abbreviations

a: A ~ anterior, P- posterior, ?D = dorsnis V - ventral, TI ~ protibia,

Ws mesotibia, 1 netavibin, ? m

Wing veins efter Curran (Worth 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 Scutellm with 4 strong bristles (Condylostyius)

2 Soutellim with only 2 strong bristles (Scien)

3. Wings ploturea ...,

3* Wings clear .

4 Wing pattern Atstinets PY bristles of TL elongate. C, pLlosus (Loe¥)

Do

4" Wing pattern indistinct; AD bristles of TI elongate.

c. aiffusus Wied . & sesteseees DOL AR

5 AD and AY bristles of 12 greatly elongated; 2 long PY bristles on

.C. prunosus (Cog.) «. perms seeeere DOLW

5" j2 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+ ?Titr? and fourth vein 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) sssereersereerasereee 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 on 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 8. *innequalis* (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 «eeeeeeeee

13 Posterior ezocevein 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 pronotu yellow « %

15* Front of pronotun metallic?. B

26 Sixth (anal) vein present; a large, round green spot in frontot

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; postscutellum dark and a thin dark
line down postnotum. X. sp. » oon

18 Posterior crossvein would intersect third vein if extended forward
by its own length; bristles yellowish; very small, Thrypticua 19

18! Posterior 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, l. 5p. 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

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ge Basal ebaominal sternites yellow.. setoous il, Robinson «

2. pasal ebdominal 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, *Symycterus* +25

Wot exactly as above., +2

Basal metatarsal segment about as long as second segment; 3 pre

© Meal 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

zenales almost touching below antennae, Chrysotus «+...

er"

+35

seers 29

32

28 Front coxae yellow .

28" Front coxae dark05

29 A strong ventral aristae on 12, 12 also with 2 AD and 2 PD pre-
apical bristles; legs yellow with a distal dark band on metafemora,
2, dimidiatus Ald. + Dol 88

29" Tio strong ventral br: 30

92} mostly small speck

30 Avistae of male apical on a slender neck, pleura dark; wing tip

Behind long axis of wing; female unknown. D, flavipes Ald. ..

3L Wot as above, Chrysotus females ...+-,

- contiguus Ald. ...44e. DoI R

32, Hyes contiguous above base of antennae.

32! Byes not contiguous above antennae ..

33 A medion AD bristle on 72 about half way between upper AD and epex

of leg, but median D or PD of TI, if present, is much smaller than basal D of TM; third segment of antennae little higher in lateral view

Second segment; basal metatarsal segment of males with a strong

g: Yenttal 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 TI that is as long as upper

>. *Crysotus* females .

+ 3h

-15-

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3h Median AD of 72 more than half as long as upper AD. ?Third vein of males not strongly arched. *D. sp.* . ++. DoI DD

3M" Median AD of 72 less than half as long as upper AD, ?Third vein of males strongly arched. *D. simplex* ...

35, Ab 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 72, C. sp. seseeeees Dol C

36" Distance between tips of second and third veins almost twice that

between third and fourth . pasceneesens

37 Pleura, legs, and antennae yellow; very small flies 1-2 m. long;

third antennal segment of male with slender processes above and

below arista. C. sp. + ae

31" Pleura and antennae dark; usually with some dark shading on

femora pale

38 A small PD bristle opposite or basal to upper AD on T2.

36" Any PD bristle on 72 distal to upper AD; profenora 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 sssesssssseeeers +

39' All femora yellow; second antennal segment yellow, third darks of male normal, C, mexicans H, Robinson ...

40 A median AD bristle on 72 and 73, although minute in males;

dark bands on femora variable but usually strong on mesofemora of

males. *C. flavohirtus* Van Duzee eeeeeea

40! Upper AD only noticeable bristle on T2 and 13; dark distal band on

metafemora only. *G. sp.* «

41 At least basal three fourths of all femora dark sesesees 2

41! Metafemora 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. ϕ .

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 ..., seseeseae

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; metatibies 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

absent; basal metatarsal segment of male lacking a ventral bristle.

C. proximus Ald. .

us: Head of male not recessed

metatarsal segment of male; female not discovered but possibly

indistinguishable from *C. 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 mm. long .., see 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 TI 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 seeeeeeeeeee

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; arista barely subapical. C. sp.

-t-

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Appendix B

Key to Muscidae (sensus lotus) of the Rain Forest at El Verde (Anthonyiidae
gna 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. Anthomyiidae..... 2

1! Lower calypter broad, somewhat flattened posteriorly and triangular
dorsally (Muscidae). Arista bare. *Synthesomyia 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; palpt broad, flat and yellow;

+ Anth U

tibiae yellow, fenora black. Probably Euryouma sp.....++

3" No preepical AD on TI; pmipi cylintrical ent black; heel
bristles all shorter than third antemal segment; color shiny

Diack overall. Fannia sp.

4 Less than two presutural doreocentral bristle:

Coenosiinse

4' Oo presutural a:

5, One pair of presutural dorsoventral bristles. *Atherigona exelsa*

5+ Dorsocentral bristles not differentiated from thoracic halva

profenora black, meso and notauli yellow. *Atherigona exelsa*

Thomson + +.+++ Sissesseseseseeee vererersee Anth W

6, two pairs of postutural dorsoventral bristles. *Bithorachaeta* 1

6! More pairs of postutural dorsoventral bristles. *Necleniopsis* sp. 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 postoutural TA (intralar) bristles; procoxae yellow 10

9" wo pairs of postsutural IA bristles; procoxae yellow or black

10 Palpi and third segment of antennae yellow (males presently

10? ?Third antennal segment dark below arista; 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 apteral

eighth of 133 male with an additional PD bristle on 13 basal to

the other 3. N, rex Curran

---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 *Ne rex*, on 5 sieve Anth G

tit One large median anterior bristle on mesofemur; proboscis

female with all femora yellow; same 13 bristles as

rex but distal AD on apical fourth, Mop. undescribed near

- *tees* Anth

12 Procoxae gray or black and same color as adjacent mesopleura.....+. 13

! Procoxae yellow and much lighter than adjacent mesopleura

13 A preapical AV bristle on 13 .. Beeeerserses

13' Wo 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); indtinct longitudinal stripes on thorax; tibiae black; median parafrontal bristles reclinate, N. ditiportus Snyder.sesesereeseee

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 sessesereeses:

15" A cnall AV near median AD of 73; paipi yellow; third antennal segment dark with a prominent yellow band basally (nale unknown); fenora of fenale yellow with posterior of profenora 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 # preapical 13

bristles (AD, D, 2D, AD); 13 of male with numerous long,

bristly hairs, 'N. colvaiaata Snyder (probably a synonym of W,

nedine Snyder) .

LT Fenora, all coxae and palpi dark, tibiae light ...

LT" Fenora, coxae and palpi yellow se++++ee

19

18 one pair of postoutural TA (intralar) Bristles} median para

frontal bristles cruciate; 3 preapical bristles on 13 (AD, D, AD).

fale trknow. 'N. ebintemir Styler seecessesseneee 2 hnth 0

18" to pair of ?tsutural IA bristles; median parafrontals ??

reelinatey ?preaploal 3 bristles (AD, A, TD, D, AD, PD).

Ty maldonadel Sryeer. peecst neces aes + Ante N

19 Stignatal and propleural bristles duplicated (It snall bristles

near base of front coxse); 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 sequent 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 patr then FD, D, AD, on 73; sides of

male abdomen shiny with few setulae, two postoutural TA on at

east some opecinens, one in listed for holotype. MH. srleplacta

Snyder. co Anth 4

21 One pair posteutural intralar bristles; male with 1A and 3D

bristles on 12, numerous curly hairs on 73 and dorsum of basal

metatarsal segnent; posterior hairs of oral margin yellow in

fenale. N. sp. undescribed + Anth R

21! Two pair postusutural intralar bristies; 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 next two

species. N. sp. undescribed or possibly hybrid sees AnthW

22! Wo AV on 13. pcaeenee iene

23 Males with one A to AD bristle on 72, merous 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, abdo-

minal setulae normal; female with posterior hairs of oral

margin light, two posterior bristles on 2, N. crassicrumus

Snyder .

2k Fourth vein curving forward at end toward convergence with third or small species less than 4 m, 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 atetinct when dry, fa clear denarkation 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 posteutural dorsocentral bristle much longer than second. l. sp. «
28' Only one posterior preapical [2 bristle; first two postutural dorsocentrals similar in size and considerably shorter than last two, L. ap. .

29 Third vein setulos

three sternopleural bristles. Scenetes

oardint Malloch seeessceeees Anth FF

29! Third vein bare; two stemopleural bristles, Phacni preapical bristles on TI; 1 AV, 2 AD and 1D on 13.

Wo.

P. 8p,

30 Posterior crossvein almost twice as long as segment of fifth vein distal to it; first postautural dorsocentral bristle slightly longer than second; humeri; and scutellum black.

Nyospila obsoleta (Brauer and Bergenstann)

30! Posterior crossvein little longer than segment of fifth vein distal to it, first postsutural dorsocentral much shorter than second; ?tuner! yellow, scutellum red posteriorly. Heo: *museina farri* (Dutch?)

Notes: Key expanded in part from Snyder, F.M. 1957. Puerto

Rican *Neodexiopsis* (Diptera Muscidae: Coenosininae)

J. Agr. Univ. of Puerto Rico M1: 207-229. His charac-

ters 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.

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SECTION IIT

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 FI 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 // agove canopy

3

FOREST FLOOR

SPECTRAL INTENSITY (MICROWATTS /CM²/my)

o

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.

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DERIVATION OF LEAF AREA INDEX FROM QUALITY
OF LIGHT ON FOREST FLOOR

By

Carl F, Jordan

Introduction

Beosystem studies such as those of productivity and chemical
elenent cycling require measurement of the quantity of leaves in

the canopy. This quantity is often expressed as leaf area index,

that is, area of leaf 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 wavelength 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 radia-

tion by leaf pigments. The more leaves that are present, the greater

WEL be the aleference An red and infra-red radiation at? the forest
oor.

?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

183+

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@irectly at several points ina 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 trans-
mission 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 in-

fluenced 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.

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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.

Example 1, intensity of light of wavelength 600 at 5 wavelengths

a

Example Ramer ceatige Amat Me

Example 961.5 on 0.3

Example, 6 : ca

Example 5967 ; one

Example 36,961 a ar

Example 9,606 on

Example 5,961 ew

Example 25,961.5 ?

Example 8,962 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

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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 @ 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 oni

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 lamp 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

$$Y = 0.3813 + 0.0989X$$

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 (Oitun, 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

$$\log Y = 0.3813 + 0.0002908X$$

126:

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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

Slope

Ridge

Ravine

?Total for

forest

eat aren Average Light Ho, of readings Date of

index ratio, 600/675 m taken readings

6.68 10.51 16 tag. 15, 1968

6 dug. 19 1968

5.60 88h 4 May 2, 1968

4 uly 23, 1968

30 Aug. 15, 1968

10 fori 2h, 1968

8.60 w.3t % fort 24

8 Suly i, 1968

2.28 3.98 32 hug. 22, 1968

nak April 24, 1968

eee 0 133 Ney 2, 1968

130 July 26, 1968

% Value taken from Odum, Copeland ani Brown, 1963.

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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.

9

3

RATIO, 800/675

S.

1000 2000 5 3000

MGM CHLOROPHYLL "A"/M² 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,

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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 Brow (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,

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NITROGEN FIXATION BY EPIPHYLLAE AT EL VERDE

J.-A. Hamisten* and M.A. Harrelson?*

Abstract

Acetylene reduction techniques with gas chromatography have
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

Experiments 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

populations 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 test.

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 ^{15}N experiments, reported on a high rate of N-fixation by mixed epiphyllae on Citrus leaves and showed that some of the fixed ^{15}N 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 algal 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.

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Department of Biology, Gardner-Webb College, Boiling Springs, N.C.

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?TABLE 1

ee

Plants from El Verde Forest Used in Acetylene Tests

Genus Growth Habit Mische

Citrus small understory tree escaped

Groton slender canopy tree climax

Dacryodes large spreading canopy tree climax

Euterpe medium palm follows streams

Manitkare 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 epiphyllse 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 with:

drawn by mouth vacuum through a plastic tube and hypodermic needle,

The bag was then filled with a mixture of 22.6% O_2 , 17.95% CO_2 , and

Argon. The bag was again evacuated and refilled with the same mixture

to insure 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 .C. 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, CO and Argon mixture. Acetylene was added to make up one-tenth of the flask volume.

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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 30°C and pH 1.5.

?Aigee vere grom in go] extract media for flush growth, then to yefree media (Rutnen, 1965) for testing.

Fungi vere isolated by cutting strips of leaves 3x20 mi and placing them on Martin's Rose Bengal Mediun, sotl-extract medium, and ¥-8 juice medium. ?Transfers were made to N-free medium for testing.

?The surface of leaves vas scraped to get a mixture of Lchens ani Liverworts. ?These vere 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 mumber of cultures prepared for testing by gas chromatography were as follow

Whole leaves on trees...

Whole leaves in flasks

Whole leaves in flasks, scraped clean

Epiphyllae in Flasks, from scraped

leaves 5

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. 31 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

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Pylten (1965) when *Betula*, *Azotobacter* and *Herizobium* were found 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 4 led 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, of liverworts and lichens taken from leaves

Microscopic examination

have 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 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 Mantikara leaves with epiphyllae in a flask, while figure 6 shows very high conversion to ethylene by epiphyllae scraped from older Mantikara 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 experiments by Binisten and Kline (1968). The acetylene reduction tests represented by figures 7 and 8 were performed on leaves of the same grass tree that was used in the preliminary 15% test as well as on *Scenestea* climax species, Mantikara. In the Hi test, it was found that 104% of the total nitrogen as ^{15}N had been taken up from the atmosphere during the 48 hour exposure period and incorporated into organic form. Host Citrus leaves from which epiphyllae

lace had been scraped and washed had 15% of their total nitrogen or eke
stable isotope ^{15}N , 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 4 genera on leaves that showed
conversion of acetylene to ethylene. Figures 9 and 10 show the actual

Leaves in

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ane Patt

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,

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Fig. 8. Scale drawing of gas chromatograph tracings

?to show conversion of acetylene to ethylene

by a Yanilkara leaf in a plastic bag on tree.

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Fig. 9. Gas chromatograph tracings to show conversion

OF acetylene to ethylene by blue-green algae.

Fig. 10. Gas chromatograph tracings to sho conversion

of acetylene to ethylene by blue-green algae.

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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 .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 symusia 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 Vere, 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 micro-organisms 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, inex-

pensive acetylene reduction test for the ability to fix nitrogen is a
reliable tool as shown by the independent ^{15}N experiment. The acetylene

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reduction test was also performed

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 lau-
zing, Andira inermis, Neorudalphia 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. Puerto Rico Nuclear Center should support
studies in which various nitrogen fixing epiphylls are grown on
citrus, pineapple and sugar cane with their crop yields and nitrogen
contents compared to untreated control crops.

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?TTERMETES AT EL VERDE: 1968 RECHBCK

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P. Murphy and R. Wiegert made preliminary surveys of Nasutitemes

costalis nests at 1 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 (^{137}Cs) in the Radiation Center.

Methods

costalis nests within 8 m of point zero in the Radiation Center and in the South Control Center has 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 *Parvirhones discolor*; once *Glyptotermes* was found inside a stub on

which were P. discolor tunc:

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.

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But two more nests were found to be abandoned also in the 8. 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,

Results

The 1966 and 1967 studies had shown that about 10% 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

Costes Tani in the parcsennes| acta Sacceseel
1967.

The 1968 survey showed for the first time that reinvasion of 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

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Percentage of Tunnel Occupancy for the Three Centers

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Radiation 8. Control A, Cut

Year Center Center Center

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1968 23.6 ?AT 42.6

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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 discolor* 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,

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