Eutrophic overgrowth in the self-organization of tropical wetlands illustrated with a study of swine wastes in rainforest plots

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Abstract

The relationship of plant species diversity to cultural eutrophy in tropical wetlands was studied in Puerto Rico with experimental plots, a survey of 25 eutrophic sites developing from the wastes of society, and a simulation mini-model. The model is a quantitative hypothesis which contains the mechanisms to maximize empower (gross production) by reinforcing low diversity, net production overgrowth when resources are in excess, but switches to high diversity efficiency and recycle to maximize gross production when excess resources are absent. To study self-organization with eutrophy, six wetland plots (3×2 m) were seeded with many plant species and treated for five months with pig wastewaters and control plots with groundwater. Vegetation was seeded: (1) with seed bank; (2) with ten species of local rainforest and wetland trees (60 individuals in each plot); and (3) with weedy species invading from fertile surroundings. The fertilized waste plots filled in with vegetation in less than half the time (9 weeks) required for the clear water control plots (21 weeks). Vegetative diversity in both waste and control plots was maximum (2.73–3.34 bits per individual) shortly before 100% cover was reached, and then declined with the competitive overgrowth of a few species (mixed grasses and *Commelina diffusa*). Of the planted seedlings, there was little growth, and individuals of only four species survived. Survival of *Andira inermis* and *Cyrilla racemiflora* was 42 and 53%, respectively. Dominants of oligotrophic wetlands (*Pterocarpus officinalis* and *Prestoea montana*) were displaced. A survey of 25 other wetland sites, receiving high nutrient waters from developments, found low diversity overgrowth, but different species prevailing. Eighty-five species were involved in wetland self-organizational processes and ecological engineering management. Eutrophic wetlands, such as those released from sugar cane closure in Puerto Rico and elsewhere, may be in a state of marshy, arrested succession because there may not be a forest species already adapted for rapid reforestation of the excess nutrient habitat. The study provides evidence of the overgrowth principle as the natural means for ecological engineering of eutrophic interfaces between the current civilization and environment.

1. Introduction

Understanding cultural eutrophy (excess nutrient condition) is an important problem in developing interfaces between civilization and environment. A common ecological engineering technique provides seeding of many species to accelerate the self-organization of ecosystems symbiotic with society. But what principles determine the nature and diversity of the organizational process, when there is an excess of unutilized resources such as nutrients? This paper examines the 'overgrowth hypothesis' in rain forest areas of Puerto Rico where eutrophic waters are generating new kinds of wetlands. The paper includes: (1) a study of rain forest plots receiving wastes from pig farming; (2) a survey of other examples of eutrophic wetlands in the rainforest area; and (3) computer simulation of a minimodel of the vegetation start-up to show how the relationship of net production and diversity follows from the maximum empower principle.

1.1. Reforestation of eutrophic tropical wetlands

Understanding eutrophic self-organization is of practical importance in restoring forests associated with economic development, an objective of ecological engineering. Because of the intensive urban development and intensification of agriculture, Puerto Rico represents many aspects of tropical reforestation (Wadsworth, 1997). On uplands, 36% of the area in towns and abandoned agricultural lands had spontaneously self-organized forest cover by 1992. In many areas it started with fast growing exotic leguminous trees, a few of the many species that had been imported and tested for suitability in Puerto Rico earlier in the century. Underneath the exotic canopy a diversity of native species has been observed growing up in further succession (Lugo and Parrotta).

The situation with wetlands is different. Most of the original wetlands had been in sugar cane for a century. Since there were few unused wetland areas, the testing of imported tree species by the US Forest Service did not include wetland species (F.W. Wadsworth, personal comment). But in the last decade the sugar cane industry closed, leaving large flat lowland areas to the spontaneous self-organization of vegetation with available species. In many areas marshy vegetation developed in arrested succession without trees.

Before economic development few Puerto Rican wetlands were eutrophic. Wetlands with anaerobic soils form within rainforest climate in the Luquillo Mountains wherever the slope of land is small. With torrential rains, and leached clay soils, high nutrient conditions were not common before development. The principal native freshwater wetland tree *Pterocarpus* develops climax forest but colonizes slowly (Alvarez-Lopez, 1990). It does not easily invade fully developed eutrophic marshes (Rio Mar Associates, 1994 and Aide). In forested wetlands at higher altitude, the sierra palm (*Prestoea montana*) predominates along with a few of 28 other species (Frangi and Frangi).

With spreading development of human settlements and intensive agriculture, high nutrient runoffs and wastewaters are becoming common in rainforest areas. Adding more water to rain forest areas often generates anaerobic wetland conditions. Are any of the native species such as the pterocarps and palms adapted to reforest these eutrophic wetlands? The experimental plots in this study were planned to measure the adaptability to eutrophic wetlands of tree species already in rain forests of Puerto Rico and to understand how diversity is related to net production in early self-organization.

1.2. Overgrowth hypothesis and the maximum empower principle

Working in the Silver Springs Project, Yount (1956) proposed that ecosystems receiving excess nutrients generated rapid competitive overgrowth by a few dominant species with low diversity. Overgrowth dominance occurs in agar plate cultures of microbes. Low nutrient media cause slow growth and maximum diversity, whereas high nutrients cause immediate overgrowth by a dominant species (Henrici, 1939). Margalef (1958) related high diversity to oligotrophy and dominating blooms to eutrophy. He described individuals increasing faster than diversity in temperate oceans in the spring when nutrients are in excess. The association of low diversity with rapid net production of cultural eutrophy in wetlands is often taken for granted now, but regarded as a pathological effect rather than a normal property of ecosystems with excess inputs.

In contrast, where excess unused resources no longer exist, climax conditions develop maximum ‘gross production’ made possible by efficient recycle of nutrients by ‘high diversity’ division of labor in plants, animals, and micro-organisms (Odum, 1964; Odum; Odum and Beyers).

The maximum power principle (Lotka and Lotka) explains both conditions. (Those system designs that maximize energy incorporation and use are reinforced and displace alternative designs.) Where nutrients are in excess, power (gross production) is maximized by expanding overgrowth of fast growing ‘weed’ species with high ‘net production’. Where nutrients are not in excess, maximum power (gross production) is achieved by using products to support a high diversity, division of labor of specialists, that recycles materials efficiently.

We usually substitute the term ‘empower’ (=rate of emergy production and use) for the word power so that the concept becomes the ‘maximum empower principle’. Since emergy puts all energy flows in units of one kind of energy, the principle is made to apply to all levels and scales at the same time. Otherwise maximizing energy flow might imply maximizing the base of the food chain.

Recent literature contains many ideas on the relation of diversity to production and spatial patterns. After relating diversity to support energy in 1964, Connell and Orias (1964) retracted this view, instead attributing diversity to populations competing in changeable conditions. Tilman (1993) related diversity to productivity. Rosenzweig and Abramsky (1993) suggest maximum diversity at intermediate productivity. Margalef and Margalef, 1997 discusses a plethora of factors possibly affecting diversity.

1.3. Model of factors relating diversity and production

Sometimes, a systems minimodel helps understanding by showing the interplay of several causal mechanisms. A minimodel PIONINFO (Odum, 1999) includes material cycles, mature structure, fast turnover pioneers, and diversity. When simulated with excess input of unused materials (or excess initial stock of materials), pioneer overgrowth and net production results. When simulated with small inputs of materials, high gross production, high diversity and structure results. When simulated with intermediate inflow of materials, diversity and production characteristics are intermediate like those often observed in ordinary conditions. The model shows how choice can occur by reinforcement of alternate pathways within a system design that maximizes empower for different conditions. This class of model is a dynamic hypothesis relating productivity and diversity.

1.4. Related studies

Wetlands have been widely tested as useful filters of nutrients and sometimes a means to increase tree growth (Odum; Kadlec and Kadlec). Hubbard et al. (1994) filtered wastes from swine lagoons with grassy wetlands. However, few studies have been in tropical climates. Morris (personal papers) constructed artificial, non-discharge wetland for wastewater treatment in Humaco, Puerto Rico. Nelson (1998) obtained very high plant diversity in constructed wetlands containing limestone gravels that received hotel wastewaters in Akumal, Yucatan, Mexico.

1.5. Plan of study

In order to anticipate vegetation growth where rainforest lands receive wastewaters, experimental plots and control plots in eastern Puerto Rico were supplied wastewaters from swine pens. Natural seeding and invasion of vegetation was allowed, and tree seedlings from the rain forest areas of the Luquillo mountains were planted in order to observe their suitability for these conditions. Included were species occurring in wetland conditions. Control plots received only well water. Both treatment and control plots had an excess of unused light at the start.

The simulation model PIONINFO was simplified as the model NUTRSPEC and calibrated for the experimental conditions (see Fig. 4). Equations were derived from the energy systems diagram, a methodology given in detail elsewhere (Odum and Odum, 2000). The model simplified to represent the plot experiments is a quantitative systems hypothesis for the concept that diversity is inverse to eutrophic net growth. The numbers used for calibration of coefficients (*k*s) were values of light absorbed, and turnover time where nutrient stock is 1 ppm nitrogen, biomass 2000 dry g/m^2, and maximum developed diversity as 100 species per thousand individuals counted.

For comparison, a survey was made of other eutrophic wetland sites in the rainforest area of Puerto Rico where self-organization has occurred spontaneously to see if patterns of diversity and eutrophy were consistent with the hypotheses.

1.6. Experimental plots and treatments

The experimental site on the swine farm was on clayey soils at approximately 200 m elevation in rainforest climate in northeast Puerto Rico. The ecological life zone of the area is classified as subtropical moist forest by Ewel and Whitmore (1973). Annual rainfall is greater than 2500 mm.

Six 3×2-m plots were cleared and dug on the site (Fig. 1). The sloping plot design allowed for a range of water depths and wetland condition for each species. The unlined plots were dug to form a gradient along the long axis (0 cm depth at the upper end and 20 cm at the lower end. Berms of approximately 20 cm height were constructed around each plot. Starting July 19, 1995, plots were monitored after the first and second week and then at 2-week intervals until December 1.

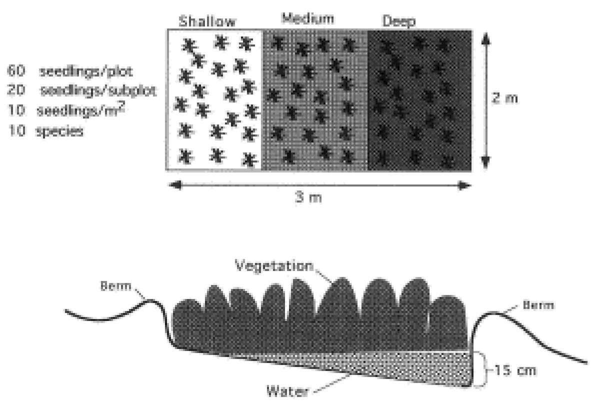


Fig. 1. Sketch of plot setup.

2. Methods

2.1. Planting

For planting and measurements each plot was divided into three subplots: a shallow subplot in the first meter, a medium depth subplot (10 cm), and a deep subplot (10–20 cm). Forest litter from 42 m^2 of the adjacent Luquillo Experimental Forest was distributed on the bottom of the plots to provide organic matter and some rainforest seedbank.

Thirty-six seedlings of each of ten chosen species were planted in waste and control plots. Seedlings 8–50 cm high were collected, measured, and transported in planting bags with available forest litter as mulch, and planted with numbered tags between June 21 and July 15.

The species planted included: successional pioneers in normal upland succession: trumpet tree: *Cecropia peltata* L., Balsa: *Ochroma pyramidale* (Cav. ex Lam.) Urban, and

Calophyllum calaba Jacq., found on degraded upland sites. Motillo: *Sloanea berteriana* Choisy and Tabonuco: *Dacryodes excelsa* Vahl are species dominant in mature, well-drained rain forest.

Wetland species included: Sierra palm: *P. montana* (Graham) Nicholson, swamp bloodwood: *Pterocarpus officinalis* Jaccq, Titi (Colorado): *Cyrilla racemiflora* L., Rose apple: *Syzygium jambos* (L.) an exotic observed in northeastern Puerto Rico and Cabbage angelin: *Andira inermis* (W. Wright) DC., Maria, a wetland legume adapted to a variety of conditions with bright sunlight Weaver (1989).

2.2. Application of waters

Starting June 22, 1995, control plots (1, 3 and 4), were filled with clean well water from the farmer's hose. The flow rate was measured using a stopwatch and a graduated bucket. The waste plots (2, 5 and 6), were filled from a black water pond containing runoff from swine pens, using a graduated bucket. A Taylor 11″ Clear-vu rain gauge was installed on the site to record the rain inputs. The plots were filled as needed to maintain the shallowest part wet, but out of the standing water, the deep ends between 10 and 15 cm deep, and the middle section about 4–7 cm deep.

Each week control plots received rain (5.4 cm±S.E. 0.7) plus clear water (12.2 cm±S.E. 0.9), and fertilized plots received rain plus clear water (4.1 cm±S.E. 0.6) plus wastewater (4.6 cm±S.E. 0.15).

2.3. Monitoring vegetation and sediment

Plants on the site prior to the experiment were inventoried by examining 1000 stems along transects that radiated out from the center of the site in four directions. When seedlings were collected, their height and diameter were measured, and leaf counts were made on the last three species collected. Seedling height in the plots was measured from a metal washer, which was anchored by the forester's flag locating each seedling, to the top of the stem. Diameter was measured 10 cm above the metal washer, and leaves on each seedling were counted. Diameters were measured with a caliper. Percent cover was measured in two square meter subplots.

Sediment that accumulated above the metal washers anchored on the seedling locator flags, was measured on each planted seedling at the midpoint and the endpoint of the study.

2.4. Plant diversity

The diversity of the invading community over time, was measured in two ways: (a) the total number of species observed in the plot; and (b) the Shannon–Weaver–Wiener diversity index $H=-\Sigma P_i \log_2 P_i$ with P_i being the relative frequency of each species observed (Krebs, 1978).

2.5. Chemical methods

Dissolved solids, sediments, nutrients in water and sediments, and dissolved oxygen in daytime were analyzed. Surface grab samples (0–3 cm) were collected from each plot at the beginning and end of the experiment. Black pond water was collected during the middle of the study and allowed to evaporate in a solar oven at approximately 65°C until it reached a consistency of soil. The dry pond residue and surface soils were then analyzed for nutrients at the International Institute of Tropical Forestry using techniques that are standard for the laboratory. See Silver et al. (1994) for detailed description of extraction techniques. All samples were air dried, ground in a Wiley mill, and passed through a 2-mm sieve. Subsamples were dried at 104°C to determine moisture content. Other subsamples were extracted with 1 M KCL for exchangeable Ca, Mg, and Al and with a modified Olsen solution ($NaHCO_3$ with EDTA) for exchangeable P, K, Mn and Fe.

Extraction solutions were analyzed using a plasma emission spectrometry (Beckman Spectra Span V). Available phosphorus, manganese, and iron were analyzed with a modified Olsen's method (Hunter, 1982). Total C and N were determined on a LECO CNS analyzer that combusts samples at 1300°C. Soil pH was measured on fresh soils in a 1:1 water:soil solution. Dissolved oxygen in waters in the plot was measured in daytime using an Orion 820 oxygen meter. Total dissolved solids were measured using a Corning PS 18 total dissolved solids probe.

2.6. Survey of other sites

The plant communities of 24 wetland sites in the region were surveyed, recording the type of wetland (Cowardin et al., 1979), canopy cover, overall pattern of vegetation (e.g. zoned, patchy, clumped, uniform, or irregular), dominant species, and surrounding factors including type of discharge, topographic setting, earth substrate, and daytime water quality parameters (dissolved oxygen and total dissolved solids of standing water, if any). Daytime dissolved oxygen was measured and percent saturation recorded including the effects of elevation and water temperature.

3. Results

After 5 months the lush vegetation in the wastewater plots had formed a closed canopy waist high. Colored photographs included by Kent (1996) show much less growth in the control plots. There were differences in chemistry, sedimentation, and diversity.

3.1. Dissolved solids, dissolved oxygen, and sedimentation

The following comparisons show statistically significant differences between waste plots and control plots; means differ by several standard errors of the mean (S.E.).

As might be expected with the regular input of highly organic pig wastes, total dissolved solids in the waste plots was much higher, 356 ppm (18 analyses, S.E. 56.9), than in control plots, 93 ppm (16 analyses, S.E. 1.9).

The average daytime dissolved oxygen values in waste plots was 0.8 ppm (12 analyses with S.E. 0.20), significantly less than 2.5 ppm in control plots (13 analyses with S.E. 0.3). Values in both sets of plots were much lower than saturation (about 8 ppm), indicating an excess of underwater respiration over photosynthesis and inward diffusion of oxygen from the air. There was little algal productivity compared to the high respiration of the underwater surface of soil, sediment and roots, as might be expected with overgrowth of emergent plants. Wastewaters in the plots receiving the pig wastes were nearly anaerobic.

On September 21, average sediment accumulations were greater in waste plots (2.69 cm with S.E. 0.374) than in control plots (0.51 with S.E. 0.098), based on 180 measurements in each category. Results were similar on November 18: waste plots (4.89 cm with S.E. 0.552) greater than control plots (1.21 with S.E. 0.150). Some sediments were added with the pig wastes from the black water pond.

3.2. Chemical elements and pH

The analyses of chemical elements in dried soil from the plots (Table 1) show very high concentrations, ten to 100 times those usually found in a rainforest climate. The waters were hard, eutrophic, and organic in spite of being diluted by rains.

Table 1. Chemical analyses of soil and pond residues in experimental plots[a]

Item	Soil (mg/g)				Pond residue (mg/l; except pH)
	Before	Controls[b]	Test plots[b]	S.E.[c]	
Calcium	1.590	3.218	3.045	0.208	134.9
Magnesium	0.263	0.546	0.589	0.025	29.0
Sodium	0.078	0.174	0.161	0.032	117.9
Phosphorus	0.024	0.127	0.120	0.008	3.8
Iron	0.160	0.122	0.158	0.022	1.2
Manganese	0.048	0.067	0.056	0.005	1.6
Potassium	0.139	0.281	3.301	0.009	35.5
Nitrogen	1.244	5.080	5.917	0.180	348.8
Carbon	18.36	62.670	78.153	2.36	5494.4
C:N ratio	14.76	12.37	13.18	13.12	15.75
pH	6.14	6.36	6.08	0.22	6.37

[a] Means based on three replicates each.
[b] After 5 months; one sample from each plot.
[c] S.E., standard error.

Table 1 shows the levels of nutrients present in the clay soils before and after the experiment. In both the control and waste plots, all elemental nutrient concentrations in the soil were significantly higher in concentration than in pre-experiment samples. There was little if any difference between the waste and control soils after the experiment. Soil pH was somewhat acid before and after the plot experiment.

3.3. Results of vegetation measurements

On the experimental site prior to the study, twenty species were found among the first 1000 stems counted. Grasses, dominated by *Panicum laxum,* were just over half of the stems in the sample.

As indicated by graphs of percent cover in Fig. 2, vegetation invaded the waste plots in 2 months and the control plots in 5 months. Plants covered the shallower depths first in control and waste plots. Even after the test plots reached 100% vegetative cover, the number of stems per unit area still increased. Thirty different species of invaders were observed at some time in one or more of the experimental plots. Grasses were an important component, sometimes more than half of the vegetative coverage. Grassy species included *Digitaria sanguinalis*, *Eriochloa polystachya*, *Leptochloa filiformis*, *Paspalum conjugatum*, *P. laxum*, *Paspalum virgatum*, *Echinochloa colonum*, *Panicum maximum* and *Paspalum pleostachyum*.

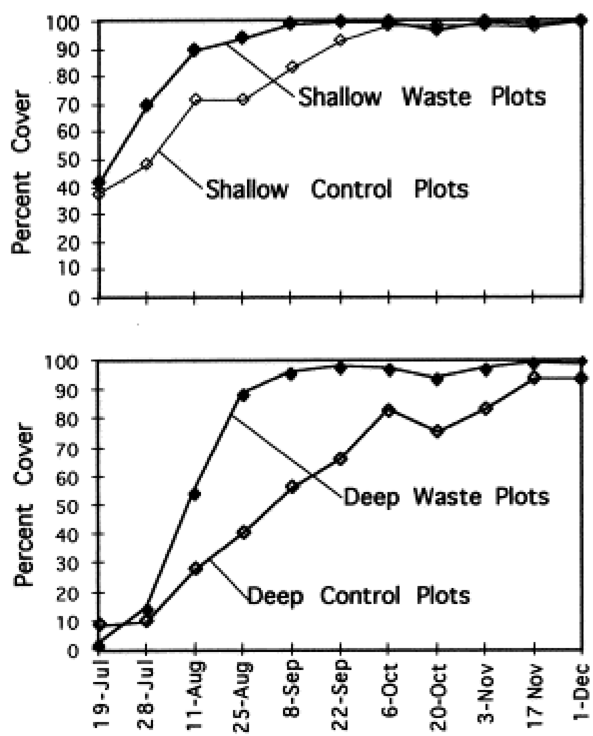


Fig. 2. Record of percent cover of vegetation with time, comparing control and waste plots.

Other important species in the plots included *Commelina diffusa*, *Cyperus odoratus*, *Colocassia esculenta*, *Malachra aceifolia*, *Mimosa pudica*, *Phyllanthus niruri*, *Urena lobata*, *Ipomoea tiliacea*, and *Vigna vexillata*. These last two were vine species, which grew over other established vegetation but were not rooting in the wetland plots. Grasses appeared to dominate the sections with deeper water, whereas *C. diffusa* was dominant in the shallower areas.

Prior to the study the Shannon–Weaver–Wiener diversity index for the site was 2.37 bits per individual. Diversity over time (Fig. 3), measured by number of species and by the Shannon–Weaver–Wiener Index, increased initially but decreased as the test plots became nearly totally dominated by *C. diffusa*. By that point species of minor importance were almost completely excluded. Diversity was higher in the control plots than in the waste plots and tended to increase throughout most of the study period, with little change at the end.

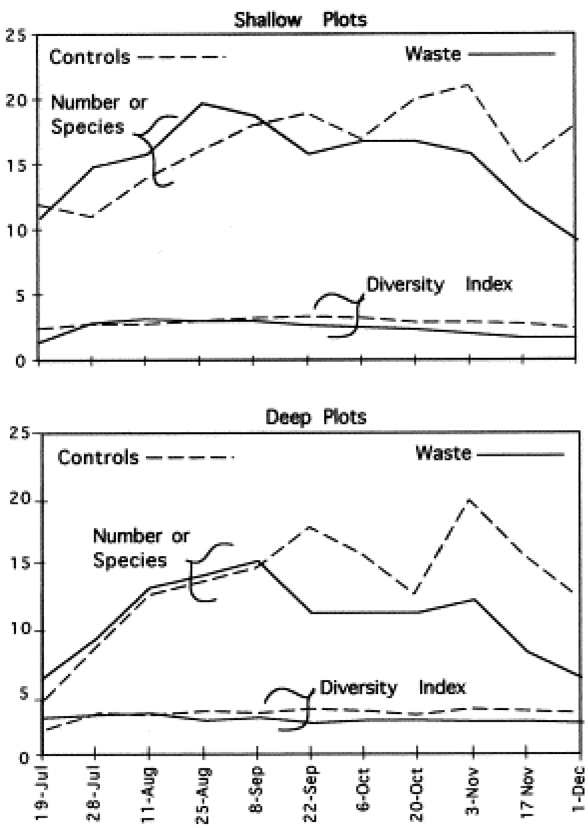


Fig. 3. Record of number of species and Shannon–Weaver–Wiener Diversity Index in control and waste plots.

The mortality of planted seedlings was high. Of 360 trees initially planted, only 75, or 21% of the seedlings, remained alive after 5 months. More survived in the clean water control plots, including all ten *C. calaba*, 12 of 14 *S. jambos*, and all five of the *P. officinalis*.

Surviving at the end of the study period were: *C. racemiflora* (19 live individuals for 53% survival), *A. inermis* (15, 42%), *S. jambos* (14, 39%), *S. berteriana* (ten, 28%), *C. calaba* (nine, 25%), *P. officinalis* (six, 17%), *O. pyramidale* (two, 6%), *P. montana* (one, 3%), and for *C. peltata* and *D. excelsa* none survived.

There was little growth in height, stem diameter, or leaf number among the survivors. Neither early successional species (*Cecropia*, *Ochroma*), nor native wet soil species (*Pterocarpus*, *Cyrilla*), nor climax species (*Dacryodes*, *Sloanea*) grew in competition with the invading vegetation.

When visited October 6, 1998, 34 months after the experiment ended, the entire area was completely covered with a dense, 0.5 m tall, matte of grasses, vines, and a few herbs. The pig farm was not operating. There were no visible differences between treatment plots or between plots and the surrounding areas. None of the planted seedlings were present and no other woody vegetation was observed in or adjacent to the experimental plots. Moreover, the vegetation in the area of the plots and surrounding the waste pond was similar to that observed prior to the experiment.

3.4. Results of the survey of eutrophic wetlands in the Luquillo region

Table 2 lists the other sites found in the Luquillo Forest region in which self-organization of eutrophic wetland vegetation was observed. A measurement of dissolved solids is included. In 65% of the sites, vegetation associations grew in bands oriented according to topography and were classified as zoned. Six sites had a patchy distribution of vegetation and were covered nearly exclusively by a single species.

Table 2. Eutrophic sites in the regional survey[a]

Sites receiving discharges of partially treated sewage
Mameyes R., Palmer, at sewage plant, 10 m, TDS 80 ppm, 12 spp, riffles with *Hydrilla verticillata*
Sabana R. sewage outfall at Luquillo: 430 m, TDS 10 ppm, 10 spp, *Eichornia crassipes*, *Pennisetum geniculatum* replacing *P. purpureum*
Humacao, 2 stage constructed wetland designed for non-discharge, 40 m: Stage 1, TDS 490 ppm, 15 spp; Stage 2, TDS 400 ppm, 3 spp; and Stage 3, holding pond, TDS 280 ppm, 5 spp
Humacao River at sewage plant, 10 m, TDS 180 ppm, 9 spp, *Eichornia crassipes*, *Eleocharis interstincta*, *Psychotria* replacing *Polygonum*
Sites receiving domestic gray water
Sabana residence 250 m, steep slope, 4 spp, *Xanthosoma* dominant
Savana, water culvert from two houses, 200 m, TDS 180 ppm, 6 spp, sparse vegetation, bananas
Sites receiving stormwater
Luquillo, stormwater ditch, 5 m, TDS 320, 6 spp: grasses in sun, *Colocasia esculenta* in shade
Saco River distributary, residences and cattle runoff, 5 m, TDS 220 ppm, 4 spp, *Pennisetum geniculatum*, *C. esculenta*, *P. purpureum* in sun
Rio Piedras, botanical garden retention pools, 25 m: Upper pool, TDS 270 ppm, 6 spp, *C. esculenta*, *P. geniculatum*; and Lower Pool, TDS 240 ppm, 5 spp, *Eichornia crassipes*
Lago Carraizo (Leiza), TDS 120 ppm, 10 spp, *Eichornia crassipes*
Sites receiving livestock wastes
Diaz Pig Farm waste pond (site of experimental plots), 150 m, TDS 850 ppm, lush zoned vegetation surrounding the pond, 5 spp
Morales Pig farm pond, herbicide treated, low ground cover, patchy, 50 m, TDS 790 ppm, 6 spp
Chiquito River, pig farm seepage into creek, 225 m, TDS 40 ppm, 8 spp, large leafed *M. accifolia*
El Verde, cattle ranch, 50 m, Runoff slough, TDS 280 ppm, 9 spp, *Polygonum. portoricense*; and Sluggish stream, TDS 380 ppm, 5 spp, *Nymphaea* sp.
Upper Sabana, damp depressions with cattle waste, 225 m, 6 spp *C. esculenta*
Lower Sabana, runoff from cattle ranch, 200 m, TDS 50 ppm, 12 spp, *Andira* and *Syzygium* in canopy; *Dieffenbachia sequine* prevalent
Sites receiving golf course runoff
Rio Mar golf course, coastal wetland, slightly saline, 5 m, TDS 1190 ppm, 7 spp, white mangrove, *L. racemosa*
Humacao, Palmas del Mar, swampy area next to complex forest, 5 m, TDS 400 ppm, 11 spp, *L. racemosa*
El Conquistador golf course and septic tank seepage, 5 m, TDS 890 ppm, 5 spp
Wetlands receiving little or no eutrophic influences
Sabana, stream at national forest entrance, 200 m, TDS 70 ppm, 8 spp, fern: *Thelypteris deltoidea*, *Vigna* sp., *Commelina*, *Colocassia*
Punta Santiago, coastal lagoon, near sea level, TDS 2000 ppm, 5 spp
Anton Ruiz Pterocarp Forest, near sea level, shaded site in center of mature forest, 3 spp
Pico del Este, high mountain quarry pond, 950 m, TDS 10 ppm, 7 spp, *Hilla paracitica*, *Hyptis astrorubns*, and *Fuirena umbellata*

The floating water hyacinth, *Eichornia crassipes*, was important at sewage treatment plant outfalls (sites 04 and 21), which agrees with the findings of Lugo (1976) and Osborne and Totome (1994). Hyacinths covered about half of the lake surface at site 19, the major reservoir supplying water to the city of San Juan.

Patchy sites had less total dissolved solids, averaging 273 ppm (S.D.=192). Zoned distribution pattern sites had an average total dissolved solids concentration of 508 ppm (S.D.=487).

Table 3 lists the plant species found in the wetland sites. Eighty-five different plant species were prominent in one or more of the 24 wetland survey sites. However, more than half of these (44 species) occurred in only a single site.

Table 3
Plant species found in eutrophic wetlands in the regi survey

Achrosticum aureum
Alternanthera sessiles
Amaranthus dubius
Andira inermis
Bambusa vulgaris
Calophyllum calaba
Casearia guianensis
Cinderia cruetasia
Cissus sicyoides
Cleome viscosa
Clidemia hirta
Cocos nucifera
Colocassia esculenta
Commelina diffusa
Costus spicatus
Crotalaria striata
Cyclopetis semicordata
Cynodon dactylon
Cyperus alternifolius
Cyperus odoratus
Dalbergia ecastophyllum
Dieffenbachia seguine
Digitaria sanguinalis
Eichornia crassipes
Eleocharis interstincta
Eleusine leucephala
Eriochloa polystachyart
Euphorbia heterophylla
Fimbristylus spathacea
Fuirena umbellata
Gliricidia sepium
Heteranthera reniformis
Heterocarpus offinalis
Hilla paracitica
Hura crepitans L.
Hydrilla verticillata
Hyptis astrorubens
Indigofera suffruticosa
Inga cuaternata
Ipomoea tiliacea
Kullinga pungan
Languncularia racemosa
Lemna sp.
Leptochloa filiformis
Ludwigia octavalvis
Lycopodium cernuum
Machaerium lunatum
Malachra aceifolia
Mangifera indica L.
Miconia spp.
Mimosa pudica
Momordica charantia
Musa sp.

Table 3 (*Continued*)

Nymphaea sp.
Panicum spp.
Paspalum paniculatum
Paspalum virgatum
Paullinia pinnata
Peltophorum pterocarpum
Pennisetum geniculatum
Pennisetum purpureum
Phyllanthus niruri
Pistia stratiotes
Polygonum portoricense
Portulaca oleracea
Psychotria sp.
Pterocarpus officinalis
Randia aculeata
Senna siamea
Sida stipulares
Sinedrella nodiflora
Solanum americanum
Solanum tortum
Spermacoce ocynifolia
Swietenia dominicana
Syngonium padophyllum
Syzygium jambos
Terminalia catappa
Thelypteris deltoidea
Thelypteris reticulata
Urena lobata
Vernonia cinerea
Vigna sp.
Wedelia trilobata
Xanthosoma violaceum

4. Discussion

In the experimental plots, high production rates were accompanied by explosive growth of a few species. Excess nutrients and light caused low diversity overgrowth.

4.1. Adaptation of tree species

Although each of the ten tree species selected for planting in the experimental wetland plots was a common component of some rainforest area and several were dominant in oligotrophic wetlands in the Luquillo Experimental Forest, none were successful in competing with the invading vegetation in these plots. The seedlings had to recover from transplant stresses. Soil oxygen was low, especially in the waste plots (1.2 ppm or less). Under these conditions the species presently available for self-organization were not adapted. Nor are these climax species adapted to grow in full daylight as seedlings. Although dominant in forest zones with water saturated soils, the palm *Prestoea* and the *Pterocarpus* did not survive in the experimental plots.

The experiments confirmed the previous observations that tree species capable of rapid growth in freshwater eutrophic wetlands of Puerto

Rico were not known. Only the seedlings of *A. inermis* survived the competition of invading plants.

The species was observed in seven of the 24 wetland sites in the regional survey.

4.2. Other eutrophic sites

The survey of other eutrophic sites also found low diversity with extensive overgrowths by a few species. However, the dominant species varied by site. Clearly productivity was high but channeled into vegetation of limited variety. The observed zonating of vegetation indicated gradients (Mitsch and Gosselink, 1993). In the regional survey of wetland sites, 20 different tree species were found. Those that occurred in two or more sites included *Terminalia cattapa* (three sites), *Senna siamea* (three sites), and *A. inermis* (seven sites).

Some coastal sites had salinity from marine sources (high total dissolved solids) with mangroves (two sites) and decreased diversity. *Languncularia racemos* which is generally the most shoreward of the mangrove trees, was regenerating vigorously, and might be adapted to compete in systems where there is fluctuation in soil salinities and/or nutrients (McKee, 1995).

Naturalized in Puerto Rico, *T. cattapa* and *S. siamea* (a legume) are tolerant to salt spray and abundant along river banks near the coast in disturbed areas, with the base of the trunk above the water line (Francis and Parrotta).

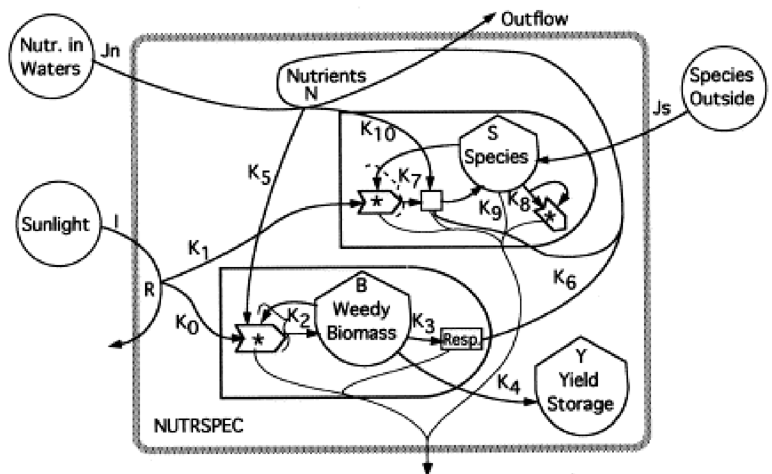
An apparent exception to the low diversity-eutrophic relationship is the high diversity of 15 species found in a wastewater wetland constructed at Humacao by Gregory Morris for school wastes designed to have no outflow. Nelson (1998) developed very high diversity in a similar system in Mexico. In both systems the waters entering were eutrophic, but allowed to flow below the surface slowly. The nutrient absorption on limestone gravels, plant uptake, and transpiration may have eliminated the excess of available nutrients, allowing the self-organizational process to switch to its high diversity mode.

The low diversity in coastal Pterocarp forests appears to be caused by salinity incursion of marine tides. The wetland Pterocarp forest at 400 m in the rain forest has 13 or more tree species (Alvarez-Lopez, 1990).

4.3. Simulation of self-organization with the model NUTRISPEC

Like controlled experiments, minimodels that contain components and mechanisms under study (while aggregating the less affected parts of an ecosystem) are useful for understanding the quantitative consequence of changes. Fig. 4a contains the simplified minimodel NUTRISPEC developed to represent the main factors in the eutrophic plot experiments. Differential equations are included as derived from the energy systems diagram. Fig. 4b has flows and storage values used for calibrating the model for the study plots.

Relationships in the model are stated in words as follows: The nutrient dependent, weedy biomass B, representing the species best adapted to overgrow others, is shown competing for energy with a high diversity alternative vegetation S. With high nutrients, the weedy biomass prevails by capture of the light energy with large net production (yield) and small respiration and recycle. The complex producer unit in the model (S in Fig. 4) is not sensitive to outside nutrients because of its tight recycle and efficiency facilitated by higher diversity and respiration equal to photosynthesis. Table 4 is the BASIC language listing of the program.



$R = I - K_1*R*S - K_0*R*N*B$

$R = I/(1 + K_1*S + K_0*N*B)$

$dB/dT = K_2*R*N*B - K_3*B - K_4*B$

$dS/dT = Js + K_7*R*S - K_9*S - K_8*S^2$

$dY/dT = + K_4*B$

$N = Jn + K_6*B - K_5*R*N*B - k10*R*S$

$N = (Jn + K6*B)/(1 + K5*R*B + k10*R*S)$

Calibration:

Sources: I=100%; R=5%;

Steady States: N=1.0 Kg/ha; B=20,000 Kg/ha; S=100 species; y=1 Kg/ha.

Coefficients:	K0*R*N*B=95	K0=9.5E-3
	K1*R*S=95	K1=0.19
	K2*R*N*B=100	K2=0.01
	K3*B=10	K3=0.005
	K4*B=40	K4=0.02
	K5*R*N*B=1.0	K5=1E-4
	K6*B=0.2	K6=1E-5
	K7*R*S=0.1	K7=0.0002
	K8*S*S=0.1	K8=1E-5
	K9*S=0.05	K9=5E-4
	K10*R*S=0.1	K10=2E-4

Fig. 4. Energy systems diagram, differential equations, and coefficient calibrations for the minimodel NUTRSPEC.

Table 4. Simulation program of the NUTRSPEC model in BASIC

```
10 REM NUTRSPEC (nutrients & diversity)
20 LINE (0,0)-(320,180),3,B
25 LINE (0,90)-(320,90),3
30 REM Starting Values
40 B=200
45 S=1
47 G=2
50 N=0.1
52 REM Coefficients
55 K0=0,0095
57 K1=0.19
58 K2=0.01
60 K3=0,005
63 K4=0.02
67 K5=0,0001
70 K6=0,00001
73 K7=0,0002
77 K8=0.00001
80 K9=0,0005
84 K10=0,0002
87 REM Scaling
90 DT=1
100 T0=6
110 N0=0.03
120 S0=1
130 B0=55.5
140 Y0=5555
145 REM Sources
150 I=100
170 Jn=0,1: REM low nutr RUN=0,1; High nutr RUN=3.
180 Js=0.001
200 REM Plotting and Equations
210 PSET(T/T0, 90−n/N0)
220 PSET (T/T0, 90−S/S0)
230 PSET (T/T0, 180−B/B0)
240 PSET (T/T0, 180−Y/Y0)
250 R=I/(1+K0*n*B+K1*S)
260 N=(Jn+K6*B−K10*R*S)/(1+K5*R*B)
270 dY=K4*B
280 dB=K2*R*n*B−K3*B−K4*B
290 dS=Js+K7*R*S−K9*S−K8*S*S
305 IF n<0,00001 THEN N=0,00001
310 Y=Y+dY*dt
320 B=B+dB*dt
330 S=S+dS*dt
350 T=T+dt
360 IF T/T0<320 GOTO 100
```

Fig. 5(a) has the result of model simulation with high nutrient inflow. In this kind of eutrophy the weedy biomass prevailed, taking the light energy away from the diversity production in arrested succession, with a net yield of organic storage. But when the inflow of nutrients to the model (J_n) was greatly reduced, Fig. 5(b) resulted, with diversity production prevailing because of its greater efficiency (not dependent on inflow of high nutrients, and without storage of net yield). The model is a quantitative expression of the two modes of achieving maximum production, depending on the presence or absence of unused sunlight and nutrients.

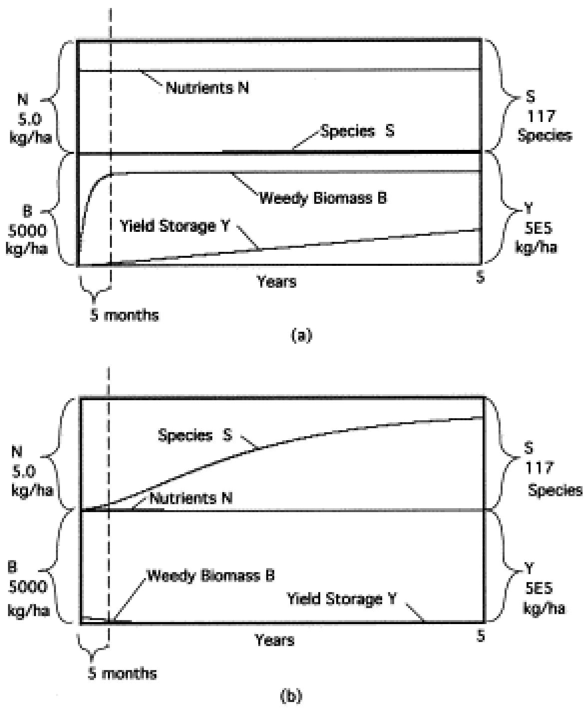


Fig. 5. Simulation results of the model NUTRSPEC in Fig. 4. (a) High nutrient inflow (J_n=3); (b) low nutrient inflow (J_n=0.1).

5. Systems overview and conclusions

The survey of eutrophic sites as well as the plot experiments support the overgrowth principle that early self organization has low diversity when there are excess resources. However, previous seeding and other factors may determine which weedy species predominate in eutrophic conditions. Since some of these may ultimately be useful for agriculture or ecological engineering management of disturbed areas, a list of these species is included as Table 3.

The systems diagram in Fig. 6 summarizes the eutrophic wetland ecosystem that developed after five months. The diagram is an overview hypothesis as to what is important to this microecosystem including the basic scientific relationships for any wetland. Inputs entering the system from outside the boundary (bermed edge of plots) include sunlight, wind, three different water inputs (rain, clear water from the hose, and the wastewater from the pond), wildlife feeding, and human management and service. The diagram shows the pathways from right to left by which products reinforce the basis for their own support, the mechanisms that reinforce empower production and use. The simulations of the simplified minimodel (Fig. 4 and Fig. 5) were consistent with the overgrowth-diversity hypothesis and the observed effect of excess nutrients.

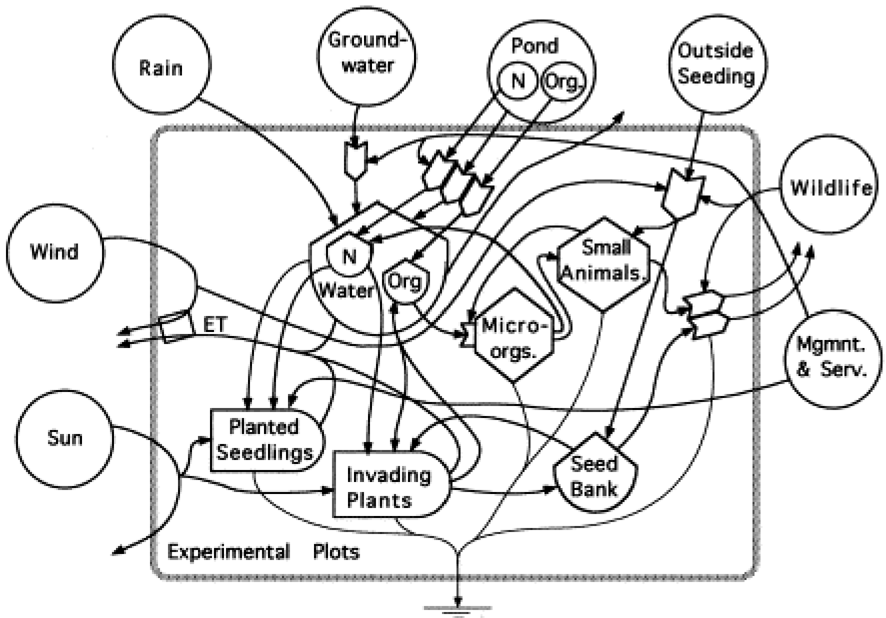


Fig. 6. Energy systems summary of the experimental plots. (Symbols from Odum and Odum.) ET, evapotranspiration; N, inorganic nutrients; Mgmnt. and Serv., management and service; Org, organic nutrients.

It appears that when fertile wastewaters are applied to rainforest lands, initially there is accelerated vegetative growth of a few species that absorb many inputs and cover the area. High nutrient waste plots fill in with colonizing vegetation much faster and with lower diversity than in control plots, demonstrating the maximum empower principle's first priority for maximizing intake of excess light and nutrients using low diversity competitors. Wetland tree species which can survive under these conditions were not found among the principal rain forest species in Puerto Rico with the possible exception of *A. inermis* and *S. jambos*.

Conversely, information on diversity and plant community composition for an area can be used as a rapid means of water quality bioassessment. As used for periphyton by Yount (1956), diversity indices integrate conditions over the time of growth, identifying excess nutrients in rainforest wetland waters.

For forest restoration in eutrophic wetlands of Puerto Rico and other areas where there may not now be any native or introduced tree species adapted to cultural eutrophy, exotic imports might be considered. An adapted, fast-growing tree species could help large areas of marshy wetlands of humid climates to emerge from arrested succession, ultimately helping restore the native wetland climaxes. However, care and experimental testing of alternatives is a prerequisite along the lines of the earlier success with exotics for upland reforestation.

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