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The effects of the rainy season and irrigation on soil water and oxygen in a seasonal forest in Panama

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ABSTRACT. The effects of irrigation and the rainy season on soil gases, water and physical properties were studied in a lowland moist forest in Panama. Two control plots experienced a normal four-month dry season and two experimental plots were irrigated during the dry season.

The forest soils were well aerated. The average soil oxygen content at 20 cm never dropped below 15%. Irrigation in the dry season resulted in treatment effects on soil oxygen and water that persisted throughout the rainy season. The late rainy season soil oxygen content at 20 cm was 18.2% in the control plots and 16.8% in the irrigated plots. The late rainy season soil water content at 0–10 cm was 0.34 $m^3 m^{-3}$ in the control plots and 0.36–0.37 $m^3 m^{-3}$ in the irrigated plots. In the control plots, in the absence of any experimental manipulation, the soil physical properties changed within a single rainy season. Specifically, soil oxygen dropped and soil water increased during the eight-month rainy season.

The observed alterations in soil physical properties probably resulted from changes in soil structure and the abundance of large pores. The rainy season or irrigation may decrease soil porosity by dispersing aggregates of soil particles, whereas soil desiccation during the dry season may enhance the formation of aggregates and large pores. As a result, the irrigated soils held more water and were less permeable to gas and water than soils experiencing a normal dry season. We conclude that the dry season may play an important role in maintaining soil structure.

KEY WORDS: dry season, rainforest, soil atmosphere, soil infiltration rate, soil oxygen, soil structure, soil water content.

INTRODUCTION

In the tropics, as well as in most other climatic regions, plant community composition and soil genesis are affected in a fundamental way by the seasonality and amount of rainfall. Seasonality is important in any comparison of tropical forests since these forests differ considerably in the length of the dry season. Tropical dry forests have a long dry season of about six months, tropical moist forests have a moderate dry season of about three months, whereas tropical wet forests lack a pronounced dry season. All of these forest types have

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distinctive plant communities and soils (Holdridge 1967, Sanchez 1976). The plant community is affected not just by the severity of the dry season but also by the effects of rainfall on soil development. The seasonality of rainfall may also play a critical role in soil genesis but such effects are not well understood. In this study we focus on the effects of the normal dry season–wet season regime and of an experimental manipulation, dry season irrigation, on soil physical properties and their interaction with soil oxygen.

The relationship between soil structure and soil porosity is well studied (Russell 1974). In clayey soils of the humid tropics the extent of aggregation of primary soil particles (mostly clay) determines soil structure. The formation of small aggregates results in low porosity and slows water movement and gas exchange, whereas larger aggregates and higher porosity improve soil quality (Marshall & Holmes 1988). In soils of the humid tropics that are composed predominantly of clay, clay particles are cemented into large aggregates that are equal in size to silt and sand (El-Swaify 1980; Lal 1979, 1980; Warkentin 1982). Thus, though clayey, such soils behave as sandy soils in relation to aeration, infiltration and drainage (Radulovich *et al.* 1992, Sollins & Radulovich 1988). Even though the structure of tropical soils has been extensively characterized, seasonality as a determinant of soil structure has been little studied.

The oxygen content of soil air can vary between 20.8% and zero due to the effects of soil porosity and water content. In soils that are poorly structured or flooded, the soil atmosphere may contain 2% or less of oxygen, levels that stress typical plants of well-aerated soils (Stolzy 1974). Soil chemical processes also consume oxygen, and low soil oxygen radically alters soil chemistry (Gambrell & Patrick 1978). Hence, soils that are seasonally flooded and oxygen stressed support a characteristic plant community (Bedinger 1978, Junk 1989).

Soil oxygen availability is often inferred from soil structure and porosity. Well-structured, porous soils are assumed to be well oxygenated. However, soil oxygen availability must be measured directly in order to be certain how oxygen will affect soil organisms and chemistry. The effects of soil structure and water availability on oxygen supply are well understood in many temperate soils (Gliński & Stępniewski 1985). Even though tropical forest soils are considered to be well structured and well aerated (Sanchez 1976), the exact relationship between soil structure and soil oxygen in these soils is poorly understood. While seasonality and rainfall are known to modulate both drought stress and nutrient availability, the effects of seasonality on soil oxygen and soil structure are poorly documented.

To address this, we studied the effects of seasonality at a site that normally experiences a four-month dry season. The seasonality of soil water availability was manipulated by irrigating two 2.25 ha plots throughout the dry season. Here we report on the responses of soil physical parameters and soil oxygen to the normal rainy season and to the first three years of the experimental irrigation treatment in which soil moisture was maintained at a high level (above −0.04 MPa).

METHODS

Study site

The study was carried out on Barro Colorado Island (BCI), Panama (9° 09′N, 79° 51′W). BCI supports tropical moist forest (Holdridge Life Zone System, Holdridge & Budowski 1956). Mean annual rainfall is 2600 mm (Windsor 1990). A dry season begins in December and ends in April or May. Median rainfall for the first 13 weeks of the calendar year is just 88 mm (Windsor 1990). As the dry season progresses, soil water content falls from about 0.42 g g^{-1} to about 0.28 g g^{-1} (Windsor 1990) and soil water potentials can fall to −2.0 MPa (Becker *et al.* 1988). The soils are Alfisols that are derived from marine sedimentary bedrock (Johnsson & Stallard 1989). The mineral soil is rich in Ca, Mg and S, poor in P and K. N availability is high (Yavitt *et al.* 1993).

Irrigation and water availability

Two 2.25 ha plots were irrigated by sprinklers throughout the dry seasons of 1986 to 1990 and two similar plots served as controls. During the dry season, water was added to the manipulated plots. Eight randomly located monitoring stations were established in each plot. Soil water status was measured using tensiometers (Model 2725A, Soil Moisture Equipment Corp., Santa Barbara, CA) at depths of 25 and 45 cm and a hydroprobe (Model 503, Campbell Nuclear Pacific, Pacheco, CA) at depths of 25, 50 and 100 cm. Irrigation and the measurement of water availability are described in full in Wright & Cornejo (1990).

Soil gravimetric moisture content was determined from surface soil samples (0–10 cm depth) collected at each station every two weeks for 26 months (November 1986 to December 1988). Samples were dried to constant mass at 105°C. The data were converted to volumetric soil water content using the measured soil bulk density of 0.854 Mg m^{-3}.

Soil water content data were analysed by repeated measures analysis of variance. The response variable was mean volumetric soil water content for each month and the 32 stations were replicates. Treatment was a grouping factor, plots were nested within treatments and year and month were repeated measures factors. Winer (1971, pp. 539–558) discusses repeated measures ANOVA with one grouping and two repeated measures factors. Repeated measures analyses make restrictive assumptions on the form of the variance–covariance matrix and the conservative Greenhouse–Geisser correction to the F-test was used to adjust the degrees of freedom downward to protect against violations of these assumptions (Huynh & Feldt 1976).

In experiments in which the cost of replication is excessive, it is recognized that full replication is impossible (Hulbert 1984). This experiment avoided pseudoreplication by including two control and two irrigated plots. The four plots, located in flat terrain and on apparently identical soils, were chosen to

avoid plot effects. Hence, our prior expectation was that plot effects would explain little of the variance in soil water content. The full ANOVA model was subjected to a preliminary test to determine if the data from the pairs of plots could be pooled. Winer (1971, pp. 378–384) discusses the procedure for determining whether the nested plot factors should be included in the final model. The significance levels associated with the nested plot effects were appropriately large ($P > 0.25$), and each nested plot effect was pooled within the appropriate error term. Consequently, in the repeated measures ANOVA described above, there were 16 replicates per treatment.

Soil gas sampling and oxygen, carbon dioxide and ethylene determinations

Soil gas samples were obtained as described previously (Kursar 1989) using plastic tubes inserted into the soil. All 32 stations had access holes at 20 cm and two sites in each plot had holes at 40 and 80 cm. Soil gas was sampled every two weeks for 36 months (January 1986–December 1988). Soil oxygen data were analysed as described above for soil water content.

Soil gas samples were withdrawn by syringe and passed over a galvanic oxygen sensor (Engineered Systems, Wilmington, Delaware). The sensor was calibrated with atmospheric air. The sample was stored in gas bags (Calibrated Instruments, Ardsley, New York) for laboratory determination of carbon dioxide and ethylene.

Carbon dioxide content was determined by injection of a 0.50 ml sample into the carbon dioxide free gas stream of an infrared gas analyser (ADC Series 225, Hoddesdon, UK) (Atkins & Pate 1977). Peak height was proportional to the carbon dioxide content. Ten per cent carbon dioxide (±0.02%) in nitrogen was used as a standard (Scott Environmental, Plumbsteadville, PA).

Ethylene was determined on a Carle Series 100 gas chromatograph with a flame ionization detector. The sample was analysed on an 80% Porapak Q/20% Porapak N column at 70°C. The flow rate of the carrier gas, nitrogen, was 30 ml min^{-1}. The samples were backflushed to vent. This stops any gases that were more strongly absorbed than ethylene from interfering with subsequent analyses. The system was calibrated using a 1.69 $\mu l\ l^{-1}$ ethylene sample prepared by dilution of a 16.9 $\mu l\ l^{-1}$ standard (Scott Environmental, Plumbsteadville, PA).

Water redistribution curves, soil infiltration rate, soil bulk density and drop test

All four of these physical parameters were evaluated during the wet season of 1990 after five years of irrigation. Water redistribution curves were measured on 19 June early in the rainy season as described by Cassel & Nielsen (1986) and modified for forest soils by Sollins & Radulovich (1988). Soil infiltration rates were measured on 16–19 June and 29–30 October during early and late rainy season, respectively. Ponded inflitration rates were measured by the method of the double-ring infiltrometer (Bouwer 1986). The internal ring had a diameter of 30 cm and the external 45 cm. A head varying between 7.5 and

5.0 cm was maintained at all times. Values reported are steady-state infiltration rates. The bulk density of soil at 0–20 cm was measured in December, at the end of the rainy season. Between 26 October and 30 November 1990, late in the rainy season, a drop test was carried out as described by Marshall & Holmes (1988). Intact soil was dropped on a concrete floor from a height of 1 m. Soil pieces were passed through 25, 12.5, 4 and 1 mm meshes by shaking without further breaking the soil apart.

RESULTS

Rainfall and soil water potential

In 1986, 1987 and 1988, the three years of the study during which data on soil oxygen and water were collected, 2069, 2593 and 2602 mm of rain fell, respectively (Figure 1). Total rainfall was low in 1986 and close to the long-term average in 1987 and 1988. In a typical year less rain falls in the early wet season and more in late wet season. Monthly means are 273 mm for May, June and July, 349 mm for October and 423 mm for November (Windsor 1990). In 1987 this pattern was reversed with 489 mm for May, 334 mm for October and 282 mm for November (Figure 1).

Soil water potentials at 25 cm in the two control plots fell to −0.5 to −1.5 MPa during the dry season (Figure 1). In the manipulated treatment, average soil water potentials at 25 cm were always above −0.04 MPa (Figure 1). Following the beginning of the rainy season, the soil water potential increased and reached zero by the end of May. During the rest of the rainy season variations in soil water potential were undetectable by tensiometers. However, three relatively dry periods during the 1986 rainy season caused soil water potential to drop to −0.02 to −0.04 MPa (Figure 1).

Soil water content

Soil water content remained high year-round in the manipulated plots, 0.30–0.38 $m^3\ m^{-3}$, but dropped to low levels each dry season only in the control plots, 0.21–0.26 $m^3\ m^{-3}$ (Figure 2). This pattern would contribute to the significant treatment and month effects and month by treatment interaction found in the analysis of soil water content (Table 1). A second pattern contributing to the month effect was the increase in soil water content throughout the rainy season. The seasonal increase was most pronounced in the control plots where soil water increased from 0.295 $m^3\ m^{-3}$ in June to 0.340 $m^3\ m^{-3}$ in November (Figure 3A).

To eliminate the effect of the dry season and to investigate treatment effects that were manifested only during the rainy season, the analysis of soil water content was repeated using just three months from the late wet season for each year (Table 1). The month, treatment and year effects still were significant. The month effect originated from the drop in the soil water content that occurred in the 'veranillo' or little dry season in August or September (Rand & Rand 1982) followed by increasing soil water during October and November (Figure 2).

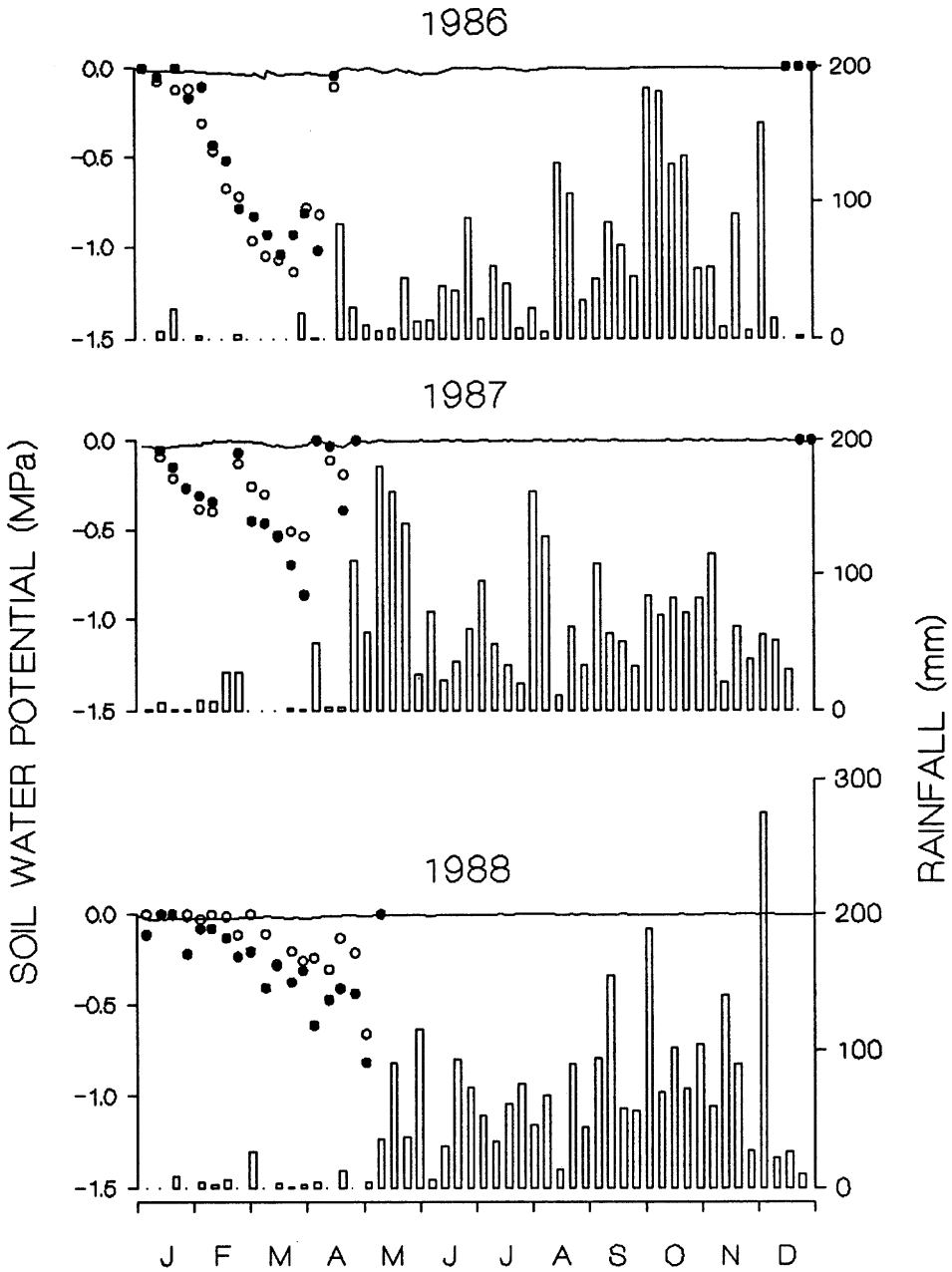

Figure 1. Variation in the weekly rainfall and soil water potential in control and irrigated plots in Panama. The open and closed circles represent the dry season soil water potentials in the two control plots. The solid line at the top of each figure represents the soil water potentials in the irrigated treatment. The soil water potentials from a depth of 25 cm are reported.

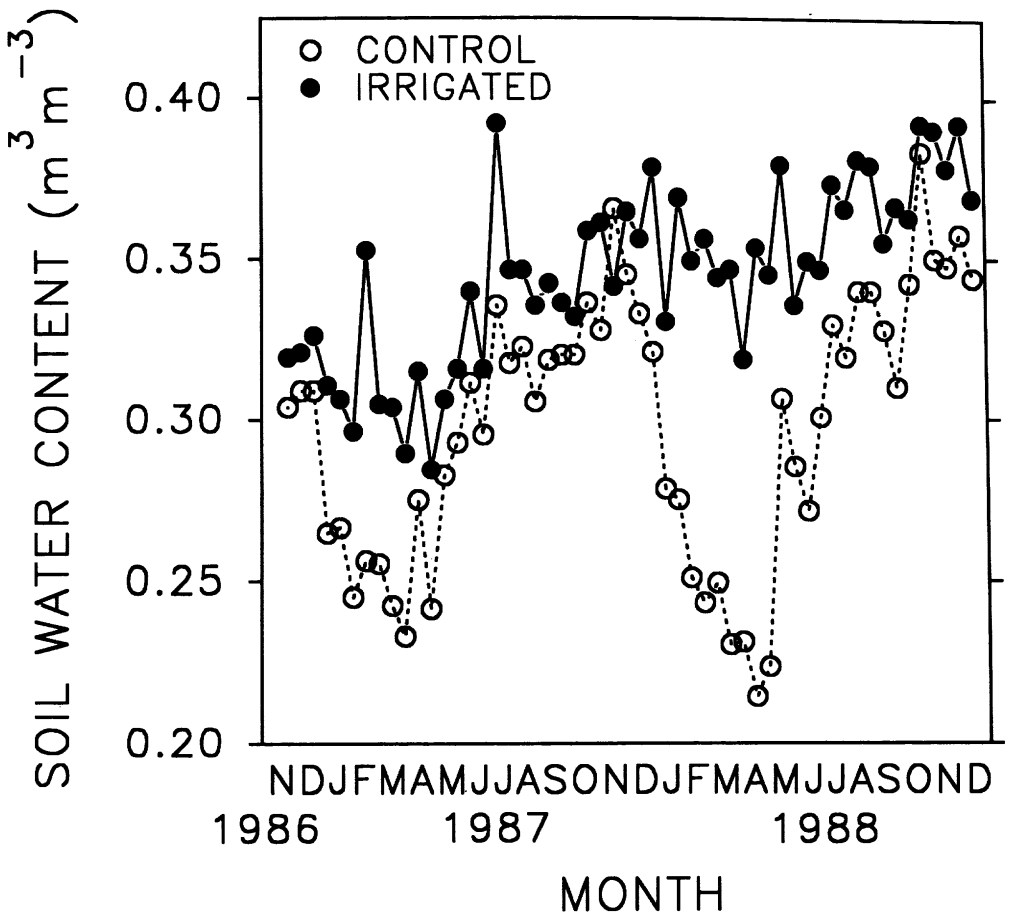

Figure 2. Changes in volumetric soil water content with time in the control and irrigated plots (two-week intervals).

The treatment and year effects originated from a yearly increase in the difference between the treatment and control. In 1985, prior to the irrigation treatment, the soil water content of the plots did not differ. The difference between the two treatments in soil water during the late rainy season rose from 0.014 $m^3 m^{-3}$ in 1986 to 0.023 $m^3 m^{-3}$ in 1987 and 0.039 $m^3 m^{-3}$ in 1988 (Figure 4A). This surprising result suggests that irrigation only during the dry season altered the soil water content during the rainy season. This effect took place slowly, requiring at least three years. To confirm that the irrigated soils held more water, we also determined the soil field capacity. In June of 1990, early in the rainy season that followed irrigation for five dry seasons, field capacity was determined from soil water redistribution curves (not shown). Field capacity in the control plots

Table 1. Analysis of variance tables for volumetric soil water content and soil oxygen content. The analysis of soil water labelled 'All data' includes 24 months of data, from January 1987 to December 1988. The late rainy season analysis for soil water includes data from September, October and November of 1987 and 1988. The analysis of soil oxygen labelled 'All data' includes 36 months of data, from January 1986 through December 1988. The late rainy season analysis for soil oxygen includes data from September, October and November of 1986, 1987 and 1988.

	Soil water						Soil oxygen					
	All data			Late rainy season			All data			Late rainy season		
Source	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Between subjects												
Treatment	1	0.5949	79.3*	1	0.0536	23.0*	1	224.4	15.5*	1	105.2	10.3
Error	30	0.0074		30	0.0023		30	14.4		30	10.1	
Within subjects												
Year	1	0.1116	162.4*	1	0.0328	126.4*	2	74.4	40.8*	2	44.5	15.9*
Year × treatment	1	0.0380	55.2*	1	0.0014	5.3	2	14.8	8.1	2	8.2	2.9
Error	30	0.0007		30	0.0003		60	1.8		60	2.8	
Month	11	0.0612	130.1*	2	0.0121	29.0*	11	75.3	67.9*	2	16.5	8.2*
Month × treatment	11	0.0147	31.3*	2	0.0007	1.7	11	1.7	1.5	2	1.7	0.8
Error	330	0.0004		60	0.0004		330	1.1		60	2.0	
Year × month	11	0.0053	12.9*	2	0.0023	3.9	22	6.0	9.6*	4	2.5	2.4
Year × month × treatment	11	0.0043	10.4*	2	0.0018	3.0	22	1.7	2.6	4	0.8	0.8
Error	330	0.0004		60	0.0006		660	0.6		120	1.0	

* Indicates $P < 0.05/28$.

Figure 5. Variation in the mean soil oxygen content at three depths matched against the patterns in rainfall (two-week intervals).

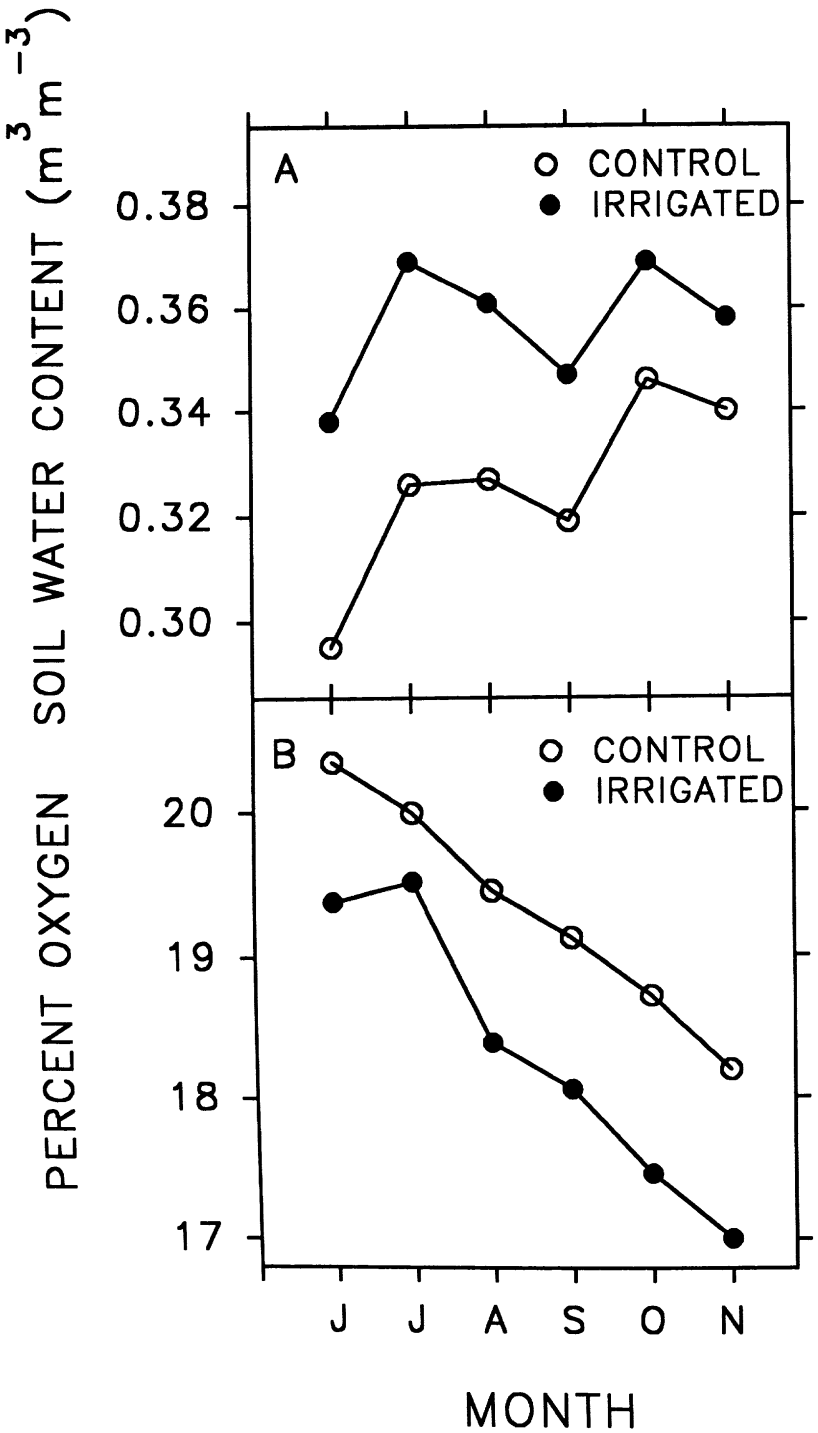

Figure 3. Monthly volumetric soil water content and oxygen content during the rainy season. Data from 1986 to 1988 are averaged for each month. The soil water content data from June to October include only 1987 and 1988 data.

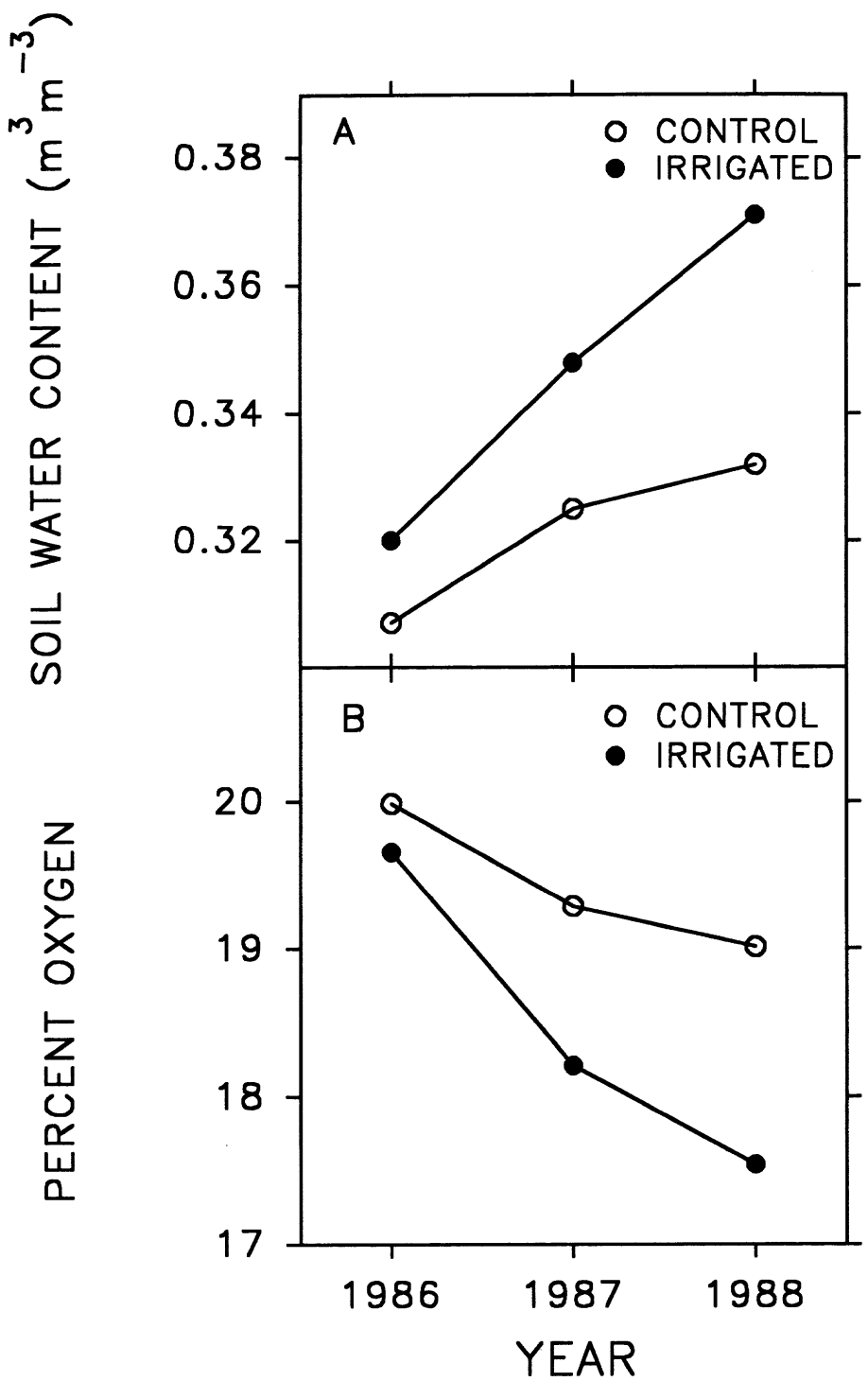

Figure 4. Annual volumetric soil water content and oxygen content during the rainy season. Data from June to November were averaged for each year. The 1986 soil water content data include only two sampling periods in November.

was 0.320 $m^3 m^{-3}$ (SE = 0.018) and in the irrigated plots was 0.354 $m^3 m^{-3}$ (SE = 0.027). The difference between the two treatments in field capacity, 0.034 $m^3 m^{-3}$, was similar to the 1988 difference in volumetric soil water content, 0.039 $m^3 m^{-3}$.

Soil atmosphere

In the rainy season the soil atmosphere at 20 cm contained 17.5% to 20% oxygen in the control plots and 15% to 20% in the irrigated plots (Figure 5). In the dry season the soil oxygen at 20 cm approached atmospheric, 20.8%, in the control plots and was 19.5% to 20.5% in the irrigated plots. Irrigation lowered soil oxygen during the dry season, though not to rainy season levels. This pattern caused the significant treatment effect and contributed to the month effect found in the analysis of soil oxygen (Table 1).

As just described for soil water content, the analysis of soil oxygen was conducted using only three months of late wet season data from each year (Table 1). Only the year effect was significant. Analogous to the results for soil water, this effect probably resulted from a progressive, year-to-year decline in the late rainy season soil oxygen content. The decrease in soil oxygen in the irrigated plots exceeded the decrease in oxygen found in the control soils (Figure 4B). As a result, the soil oxygen content differed between the two treatments by 0.33% in 1986, 1.07% in 1987 and 1.47% in 1988.

As described previously for soil water, the effect of month on the soil oxygen content during the late rainy season (Table 1) can be related to the time elapsed since the beginning of the rainy season. In the control plots, the soil oxygen content dropped steadily throughout the wet season, from 20.3% in June to 18.2% in November (Figure 3B). Effects of the 'veranillo' were not observed for soil oxygen.

Others have found that the rate of diffusion of gases decreases, sometimes non-linearly, when the soil water content exceeds 0.20–0.30 $m^3 m^{-3}$ (Black 1968, Gliński & Stępniewski 1985). This result suggests that soil oxygen might drop when the water content exceeds 0.25 $m^3 m^{-3}$, a response that we observed (Figure 6). The soil atmosphere at 20 cm contained 20.6% oxygen when the soil water content at 10 cm was 0.26 $m^3 m^{-3}$ or less. When the soil water content exceeded 0.30 $m^3 m^{-3}$, the average soil oxygen content dropped to 19% and varied more.

Soil gas samples also were analysed for the presence of ethylene eight times during the dry and rainy seasons of 1986. Samples were taken from 20, 40 and 80 cm at four sites in the control plots and an equal number in the irrigated plots. No samples contained ethylene above 0.10 $\mu l\ l^{-1}$, the detection limit of the system. The soil carbon dioxide content was negatively correlated with the soil oxygen content and the relationship had a slope of −1.09 and an intercept at 20.8% oxygen (R^2 = 0.48) (Figure 7).

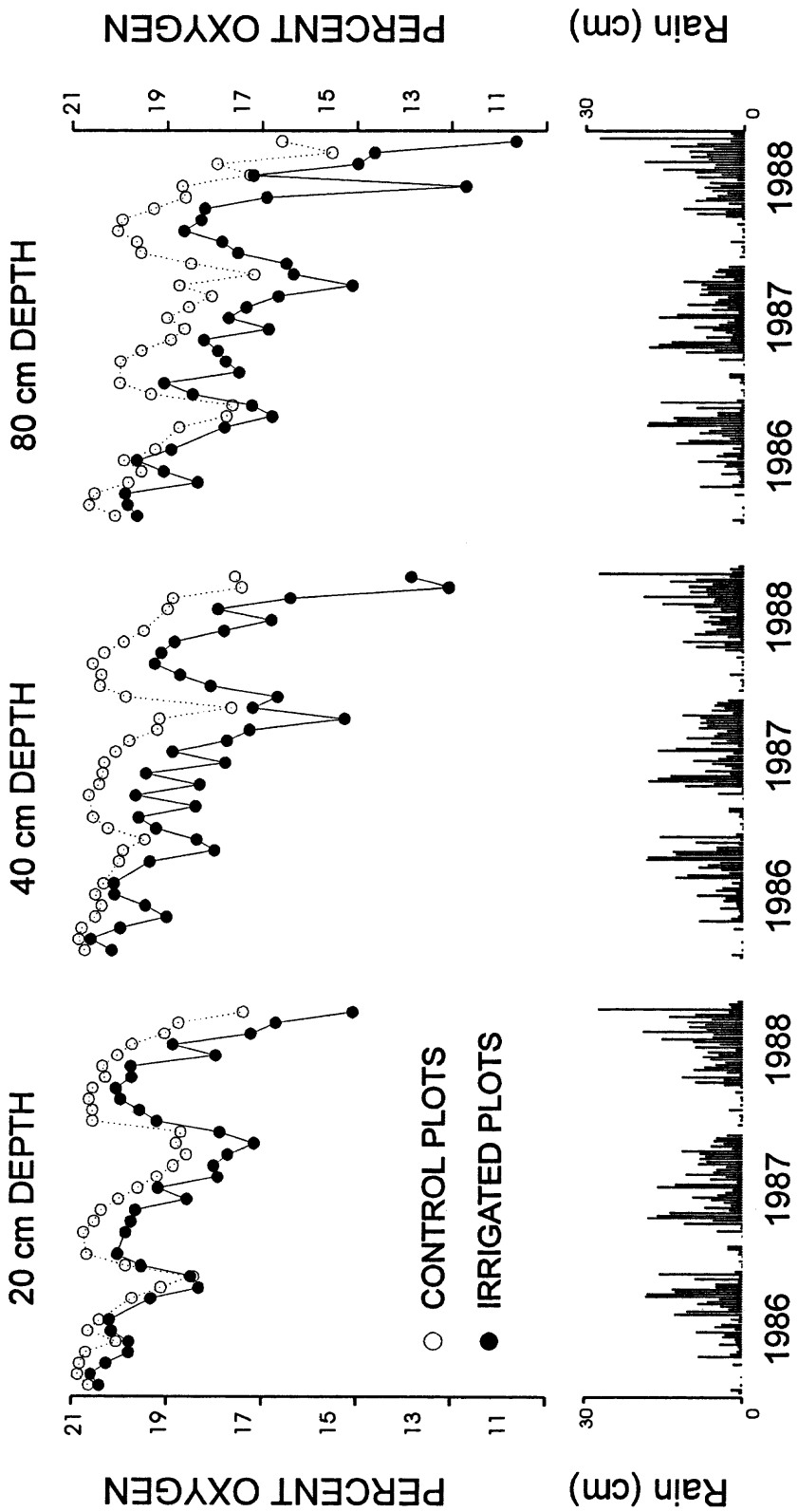

Figure 5. Variation in the mean soil oxygen content at three depths matched against the patterns in rainfall (two-week intervals).

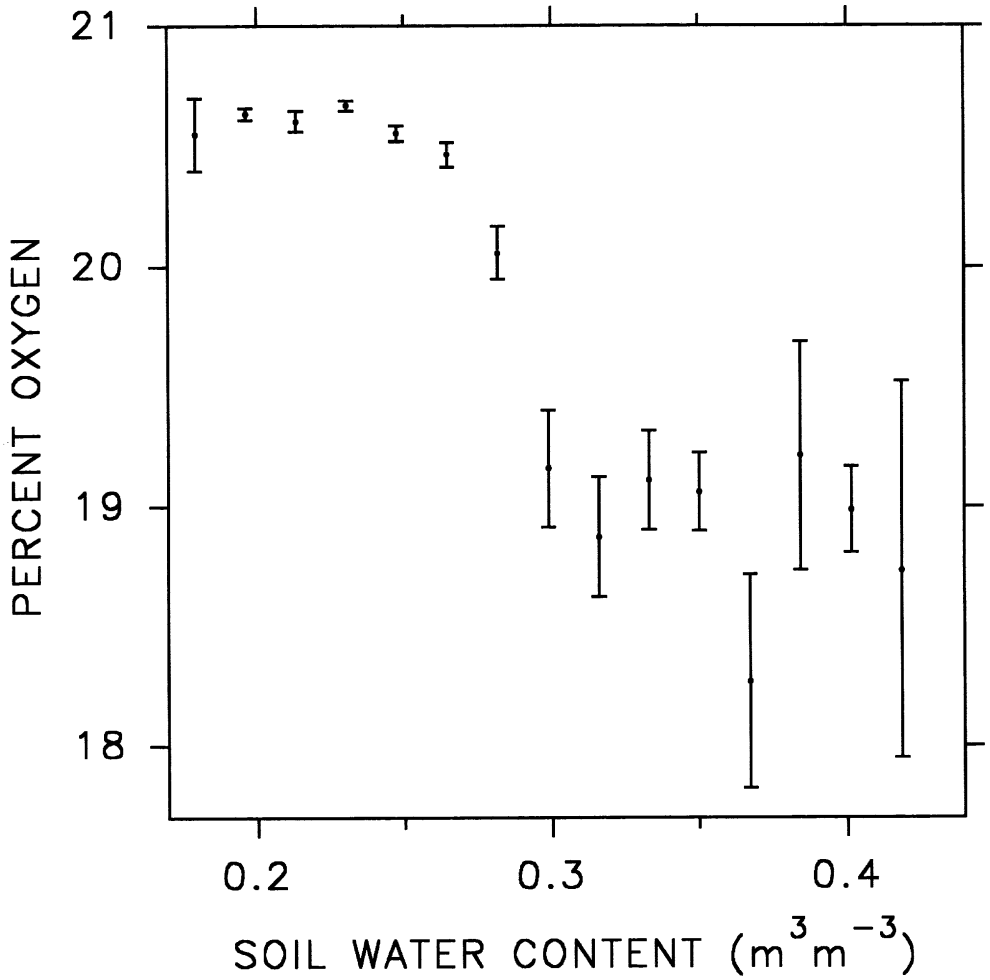

Figure 6. The relationship between soil oxygen content and volumetric soil water content in the control plots. The error bars indicate the standard deviation in the soil oxygen content values.

Soil physical properties

Soil physical properties were determined during the rainy season of 1990 following five years of dry season irrigation. Soil bulk density was 0.854 Mg m^{-3} (N = 12, SE = 0.029) in the control plots and 0.855 Mg m^{-3} (N = 12, SE = 0.034) in the irrigated plots. Soil infiltration rates were determined early in the rainy season and the experiment was repeated late in the rainy season. The soil infiltration rates on the control soils were about two-fold larger than on the irrigated soils on both dates ($F = 4.60$, df = 1, $P < 0.05$; Table 2). During the rainy season the infiltration rate dropped about 10-fold in both treatments ($F = 18.35$, df = 1, $P < 0.001$; Table 2).

In the drop test, large clods of soil were broken into smaller pieces that were separated by sieving. The drop test measures soil friability or hardness which depends, in turn, on the aggregation of soil particles and the network of large

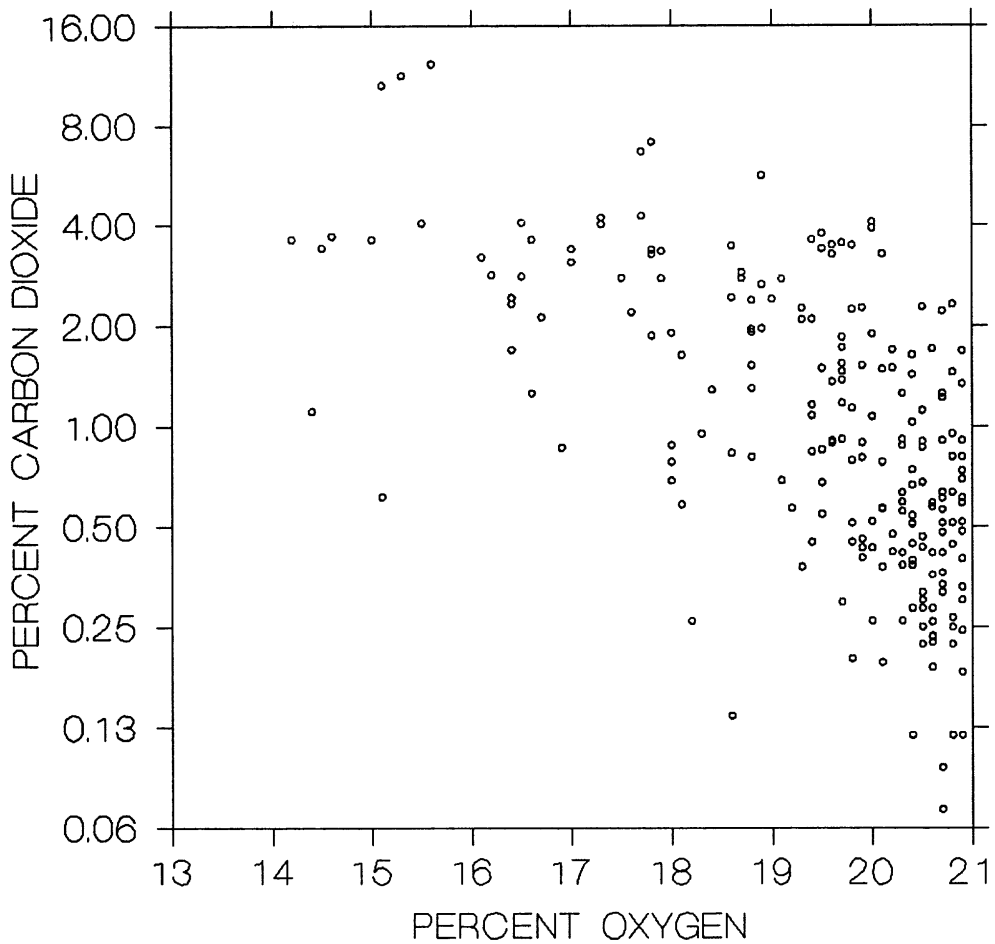

Figure 7. The relationship between soil carbon dioxide content and soil oxygen content. Each point represents data at one station, date and depth. Data from 20, 40 and 80 cm are combined.

Table 2. The effect of irrigation and season on the steady state infiltration rate. The units for infiltration rate are mm h^{-1}.

	June			October		
Treatment	Mean	SD	N	Mean	SD	N
Control	1840	1590	7	221	180	8
Irrigated	936	898	6	78.7	50.9	8

pores. A more friable soil will crumble into smaller pieces. Of the soil that passed through the 25 mm mesh about half was stopped by the 12.5 mm mesh and half by the 4 mm mesh for both control and irrigated soils (Table 3). In contrast, 21% of the control soil and 10% of the irrigated soil broke into pieces smaller than 25 mm indicating that the control soil was more friable and the

Table 3. Drop test results. The amount of soil stopped by each sieve after fracturing a soil sample by dropping (grams and percentage of the total in parenthesis).

	Amount stopped (g)	
Mesh (mm)	Control	Irrigated
25	60 (79)	65 (90)
12.5	7.8 (10.3)	3.2 (4.4)
4	6.5 (8.5)	3.2 (4.4)
1	1.7 (2.2)	1.0 (1.3)
0	0.08 (0.1)	0.15 (0.2)
Total	76.08	72.55

irrigated soil was more massive (within-subjects treatment × mesh interaction, $F = 5.54$, $df = 4$, $P < 0.001$; Table 3).

DISCUSSION

The permeability of the soil to air and water

Ethylene, if present, is too low to cause abnormal root responses (Feldman 1984). The effects of soil carbon dioxide, about 4% on BCI (Kursar 1989), on plant growth are poorly understood (Morison & Gifford 1984). Cultivated tropical soils contain about 8–21% oxygen (Garay 1966, Vine *et al.* 1942). In this study the average soil oxygen content at 20 cm exceeded 17.5% in the control plots and 15% in the irrigated plots. When censused immediately after a heavy rainfall (November 1988, Figure 5A), the average did not drop below 15% and no single measurement at any depth dropped below 5%. In general a soil atmosphere containing 1% or less of oxygen can stop growth, 5–15% oxgyen can decrease growth and higher oxygen usually results in maximal growth (Armstrong & Webb 1985, Drew 1990, Gliński & Stępniewski 1985; Patrick *et al.* 1969, 1973; Stolzy 1974). The slope of nearly −1.0 in the plot of carbon dioxide versus oxygen (Figure 7) indicates that aerobic respiration was not inhibited by low oxygen (Wood & Greenwood 1971). A high water table will greatly decrease the availability of oxygen but on BCI the water table rarely rises as high as 20 cm below the surface (Kursar 1989). The high oxygen level, moderate carbon dioxide level and the absence of ethylene or a high water table all indicate that the soil on BCI is conducive to plant growth.

The aeration results are consistent with observations on the structure of soils in the humid tropics. In contrast to clayey soils of the temperate zone, tropical clay soils, including those on BCI, are remarkably well structured (Lal 1979, Sollins & Radulovich 1988). We found that infiltration rates were high and the bulk density was low though both are probably typical of rainforest soils (Lal 1980, Sollins & Radulovich 1988). Field capacity was attained very rapidly, in three hours, in soil water redistribution experiments (data not shown). The

high oxygen content even at 80 cm indicates that the BCI soils are well structured down to 80 cm.

About 90% of all roots are found in the upper 40 cm of soil on BCI (Odum 1970). We conclude that BCI soils are well aerated and well drained throughout the year down to depths that include nearly all roots. Plants in the BCI forest are highly unlikely to be stressed by an imbalance in soil gases or waterlogging.

Rainy season and irrigation effects on soil water, oxygen and physical properties

Following the beginning of the rainy season, soil water potential reached zero by the end of May and remained at zero nearly the entire rainy season (Figure 1). Even though soil water potential remained constant, the soil water content in the control plots increased from 0.295 $m^3 m^{-3}$ in June to 0.340 $m^3 m^{-3}$ in November (Figure 3A). At another site on BCI the 13-year average for the soil water content increased from 0.397 $g g^{-1}$ in June to 0.429 $g g^{-1}$ in November (Windsor 1990). The possibility that the seasonal distribution of rainfall could explain these results was rejected since the normal rainfall pattern was reversed in 1987, yet the same June to November trend in soil water was observed (see Results). In addition to a rainy season increase in soil water, the infiltration rate and soil oxygen decreased during the rainy season (Table 2, Figure 3B).

Irrigation also had substantial effects on infiltration rates and soil water and oxygen that persisted into the rainy season. The effect of irrigation on soil water and oxygen increased each year, resulting in a treatment by year interaction for soil water (Figure 4, Table 1). Evidently, the changes in the irrigated soil were slow to occur.

Our results clearly show that soil physical properties are changing within a single rainy season as well as in response to the irrigation treatment. Of all of the determinants of soil physical properties, soil structure is one of the most labile (Hamblin 1985). Soil structure can change because soil particle packing and aggregation are altered by cultivation, biological processes such as growth of fungal hyphae, wetting or drying, expansion and water flow (Marshall & Holmes 1988). In particular, wetting can disperse aggregates and decrease water movement and gas exchange (Emerson 1983, Marshall & Holmes 1988). Soils differ in the stability of aggregates; Oxisols are stable and Alfisols are liable to dispersion (El-Swaify 1980; Lal 1979, 1980; In our study of an Alfisol, the rainy season or the irrigation treatment appears to have caused the dispersion of soil aggregates.

Even though it has been suggested that seasonality could affect the structure of tropical soils (Heinonen 1986), little direct evidence has been presented. In our study, eliminating the annual drying cycle had effects even in the third year of the experiment and the long-term effects of irrigation remain to be determined.

Interactions between climate, soil structure and the plant community

Even though the dry season is a period of water deficit, the regeneration of soil structure during the dry season may be essential for maintenance of soil

quality. Aggregation may affect the formation of large soil pores which may, in turn, determine the rate of water flow and gas exchange in well-aggregated tropical soils (Radulovich *et al.* 1992). If the soil has a more massive structure, such as the drop test indicated for the irrigated soils, then there are fewer large pores and slower oxygen exchange and water drainage. Recently, it has been suggested that most rainwater flows through large pores, rather than micropores if the soil is well aggregated (Sollins & Radulovich 1988). Rapid water movement though large pores could alter the retention and transport of nutrients. The rapid movement of rainwater downward through large pores would decrease the leaching of nutrients trapped in micropores. In contrast, leaching of nutrients from the forest floor that are carried downward in rainwater via large pores might increase (Radulovich *et al.* 1992, Sollins & Radulovich 1988). Soil structure also affects the amount of water retained in the soil and the quantity of water that can be extracted by plants during a drought (Lal 1980, Marshall 1962). A severe drought occurred at our study site in 1982–1983 during which 121 mm of rain fell during a 24-week period in which the average rainfall is 787 mm (Leigh *et al.* 1990). This suggests that the quantity of water stored in the soil could be important for plant survival during drought years even though the forest may experience only moderate water stress during a typical dry season. In sites where soil structure is poor, a change in soil structure could have a big effect on soil aeration (Letey 1985). The soil at our study site (and probably most rainforest sites) was well aerated and the observed changes in soil structure and aeration did not lower oxygen availability to a stressful level. Mechanical resistance to root growth may occur in all soils (Hamblin 1985). Soil structure is an important determinant of mechanical impedance of the soil (Hamblin 1985, Simpson & Gumbs 1982, Tardieu 1989) but the extent of soil resistance to root growth is unknown for rainforest soils. Even though the soil parameters just mentioned represent important elements of the soil system that modify plant growth, we do not know how the changes in soil structure that we have observed might affect soil mechanical resistance and the availability of water and nutrients.

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Book review

JANSMA. 1994. *Ecology of some Northern Suriname Savannas.* 199 pages + 4 maps in cover. Koeltz Scientific Books, Koenigstein, Germany. ISBN 80-901699-1-0.

This book results from a one-year period of fieldwork in Northern Suriname in the late seventies. And although this may seem a rather late publication, it is a most welcome and valuable one because we have very little new information from the savanna areas on Northern Suriname since the basic studies of Heyligers (1963) and Van Donselaar (1965). Jansma deals with the same topic as those authors: the floristic and physiognomic characterization of the savanna vegetation and the vegetation – habitat relationships. He studied five savanna areas: the Zanderij, the Coesewijne – Wana, the Awara – Sapara, the Donderskamp, and the Copie areas.

The savanna ecosystems are not considered natural equilibrium systems, but rather appear relics from drier interpluvials, since then kept open by frequent fires. It is the Amerindians that

appear to keep the savannas open: they burn the savannas not for agricultural purposes but they prefer to live in the open landscape and have their slash-and-burn fields in the adjacent forest, where the soils are more fertile. Without their fires the Northern Suriname savannas would regenerate into forest within decades.

These Northern Suriname savannas roughly belong to one of three types: (1) the tall grass savannas of the Coesewijne type on yellowish loamy sands. Here the intrusion of woody species starts mainly by recruitment from bird-dispersed seeds; (2) the bushclump savannas of the Kasipora type on dry white sands; and (3) the bushclump savannas of the Zanderij type on wet white sands. In the bushclump savannas local termite heaps provide the initial sites for woody encroachment. In their wettest parts, along water courses, there are many *Mauritia flexusoa* palms in the savanna vegetation. Five other vegetation types in the savanna areas, considered to be fire-dependent successional stages, are also briefly described.

These and other general aspects are briefly discussed in Part I of the book (60 pages), together with an outline of Jansma's main results. He carried through a complete sampling of the floristic composition and physiognomic structure (17 characters) of the vegetation, together with a comprehensive inventory of soil profiles, in 246 field plots along transects through the savanna areas. The data were analysed by clustering techniques (mainly Ward's averaging) and grouped into 21 clusters, or eco-units, which are phytosociologically defined clusters described with their associated physiognomies and soils and hydrological features.

Part II of the book (75 pages) gives the results in great detail and compares the clusters with the phytosociological units described by Heyligers (1963) and Van Donselaar (1965). This part also contains chapters on the local climate (by L.C.P. Keizer), the geomorphology and geology, and the results of the physiognomic analysis and the soils inventory (based on the USDA Soil Taxonomy System).

The book further has summaries in English and Spanish, synoptic vegetation tables, soils profiles tables, a list of plant taxa of the savannas, an index, and four maps, loose in the cover (a base map, a phytosociological vegetation map, a physiognomic vegetation map, and a soils map, all of the Zanderij area).

This book is a detailed descriptive account; and experimental ecological approach is totally absent. That type of work still stands to be done. It is, nevertheless, impressive to see how much descriptive data the author collected in the one-year field period. And this book is certainly much welcomed by ecologists working in northern South America because of the extreme scarcity of information on the savannas of the Guianas since about two decades.

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