Plant and Soil 65, 193–201 (1982). 0032-079X/82/0652-0193$01.35. Ms. 4837

Fine-root growth dynamics in cacao (*Theobroma cacao*)

J. KUMMEROW, M. KUMMEROW and W. SOUZA DA SILVA
Botany Department, San Diego State University, CA 92182, USA and Centro de Pesquisas do Cacau, C.P. 7, 45.600, Itabuna, Bahia Brasil

Key words Alfisol Fine root Humid tropics Precipitation Root growth Root tip Shoot flush *Theobroma cacao*

Summary Fine-root density in a mature cacao plantation in Bahia/Brazil was monitored at weekly intervals from October, 1980 until March, 1981. About 40 g m^{-2} of fine roots (diameter < 1 mm) were found during this period. The relative stability of this value over the six months period contrasted with significant changes in the number of growing root tips per unit of soil volume. These changes were not conditioned by the rainfall pattern although low root tip values were counted at the end of a minor drought period. A significant negative correlation was found between a shoot growth flush in January and the activity of the fine-root system as measured by the number of new root tips.

Introduction

Theobroma cacao is a representative of the understory tree vegetation of the Amazon rain forest[9] but is also an important tree crop. The growth of cacao trees is characterized by 2–3 flushes per year. During a flush young shoots and leaves expand rapidly for a period of 10–20 days, then growth ceases until the next flush begins. These flushes occur in an environment favorable for growth all year round, although it appears that minor drought periods of several days and subsequent heavy rain may contribute to stronger synchronization of the flushing between the trees in plantations[3]. Nevertheless, these flushes occur even under controlled uniform environmental conditions[11]. Full agreement regarding the endogenous or environmentally induced character of these growth flushes has not been reached[1,5].

The horizontal and vertical extension of the larger woody roots in cacao has been described for a variety of soil types[6,12]. Cacao trees possess a strong conical tap root growing downwards 1.0–1.5 m. Actual depth depends on prevailing soil conditions. The laterals are mainly horizontal and are concentrated in the uppermost 30 cm of the soil. In mature plantations, about six years and older, the lateral roots extend for several meters. Since cacao is planted commercially in a 3 × 3 m pattern, only excavations can trace a larger horizontal root to its originating tree. Fine root biomass (for a definition of this root class see[17]) and distribution with depth in an 11-yr cacao plantation in Bahia/Brazil showed that the non-woody fine root population was concentrated in the litter layer and to 5 cm depth[15].

It may be assumed that fine roots account for most of the nutrient uptake because the larger and less branched roots of 1–2 mm diameter were always strongly suberized. Therefore it was of interest to determine whether fine roots of tropical trees also show fluctuations in their growth activity. This would contribute to a better understanding of episodic growth in the moist tropics. If fine root growth activity occurs in an episodic fashion the application of mineral fertilizers should take this into account. Fertilizing at times of relative root quiescence would result in fertilizer losses due to surface run-off, percolation, and denitrification particularly in tropical areas where the annual rainfall is 1600–2000 mm. If fine-root growth is episodic and the growth flushes were correlated with shoot growth flushes, simple phenological observations of the cacao trees could determine the correct timing for fertilizer application. It is understood that nutrient uptake is not only a function of root surface. Demand is another controlling factor. However, data for mineral uptake rates of suberized roots in a tropical environment are not available. There is also the possibility of nutrient accumulation in non actively growing shoots, in which case flushing could occur without increased demand from the root system.

It was the purpose of the study to test the hypothesis that fine roots in a mature cacao plantation show changes in their growth activity and that these changes are correlated with shoot flush periods.

Methods

Research area

The research was conducted in an 11-yr cacao plantation of the 'Centro de Pesquisas do Cacau', situated 22 km west of the port of Ilheus in the state of Bahia/Brazil (lat. 14° 47′ S, long. 39° 16′ W, 86 m a.s.l.). The plantation was in production although the 1980/81 fruit load was unusually low. The closed canopy of the 4–5 m tall trees, planted according to local farming technique in a 3 × 3 m pattern, had a leaf area index of 3.5–4.0 (P. Alvim, pers. communic.). The cacao trees were shaded by ca. 15 m tall *Erythrina glauca*, planted 24 m distant from each other. The ground was covered by a 3–6 cm litter layer. Weeds were virtually absent with the exception of some *Tradescantia* sp. and a few epiphytic orchids and bromeliads. All observations were concentrated in a central 40 × 40 m area of this 10 ha orchard.

Climate

Climatic data were available from a meteorological station 1 km away. Data covering the years from 1965–1978 have been published recently [7] and show a mean annual temperature of 23.3°C with annual mean minima and maxima of 19.4 and 28.6°C, respectively. Rainfall over this 13-year period averaged 1681 mm, with relatively even distribution throughout the year. In August, the driest month, 93 mm fell and December, with its 177 mm of rainfall was the wettest month. In general, about 140 mm per month were recorded, yet drought spells with only 50 mm per month have been observed during the 13-year period. The humid character of the local climate is further emphasized by a mean annual relative humidity of 84% ranging from 83% in January to 87% in June.

Soil

The soil of the research site was an Alfisol, series São Miguel. These soils have an effective depth of 1.5 m; they are well drained with moderate permeability and are rich in primary minerals. The well formed A horizon is underlain by a deep B horizon. These yellowish clays are practically neutral, tending to become slightly acid with increasing depth[19]. The most productive cacao plantations of Bahia have been established on these soils.

Root collection

Soil cores were collected with a 5.5 cm diameter steel pipe equipped with a sharpened edge as described previously[15]. The results of these earlier studies had shown that 90% of the fine-root biomass appeared in the uppermost 10 cm of the soil. Therefore, all the data reported here refer to fine roots extracted from 120 cm^3 soil cylinders taken from the 0–5 cm and 5–10 cm soil layers. Core sites were randomly selected although coring was not done within a 40-cm radius of the cacao stems. This precaution was taken in order to reduce damage to woody laterals as much as possible. Usually four cores per day were collected and divided into 8 samples (4 samples from 0–5 cm and 4 from 5–10 cm). Sampling was repeated 4 times per week. As a rule, all cores were processed the same day of their collection because oxidation of the whitish root tips made their recognition as new root tips difficult after two days and impossible after three days.

Root processing

All the soil cores were gently handwashed by using 0.5 mm mesh soil sieves. The roots were transferred to petri dishes and special care was taken to minimize the fragmentation of fine root clusters. These clusters consisted in highly branched distal portions of slightly thicker (1.0–2.0 mm), suberized roots. They appeared typically in soil clumps of 1–8 cm^3 and root tip numbers of 250 per cluster were not rare. We estimate that in spite of all precautions about 10% of the fine root biomass was not recovered from the soil. All thicker roots were completely extracted.

The washed roots were separated into dead and living material. Criteria to recognize dead roots were a) their aspect, b) their fragile nature when bent with a pair of forceps, and c) their 'mushy' consistency when probed with a preparation needle. With respect to the fine roots this was somewhat arbitrary; not even with the aid of a dissection microscope could a clear cut decision be made in all cases. The next step consisted of counting all new fine root tips per sample using a dissecting microscope. Blind tests with different helpers showed that root tip counts were reproducible. Dry weights of the fine-root samples were measured, then their total length was calculated by using the fine-root length/dry weight ratio (1 g fine roots = 36.4 m[15]). Larger roots were not considered in this study.

Shoot flushing

In the same area of soil core collection 100 randomly selected shoots from 20 trees were labelled. Care was taken to select shoots from all levels of the canopy. New leaves which emerged from the terminal buds of these shoots were counted in weekly intervals.

Dendrometer readings

In order to monitor water stress periods, dendrometers were attached to 10 randomly chosen trees to measure daily stem diameter fluctuations[2]. Readings were made at 8:00 and 14:00, times coincident with the highest and lowest stem water potentials, during the period of Dec. 1980 to March 1981. Differences between morning and afternoon readings were calculated and means of these differences from a dry period and a wet period were compared with the respective root tip densities.

Results

Fine root distribution

In order to complement the existing information on the depth distribution of

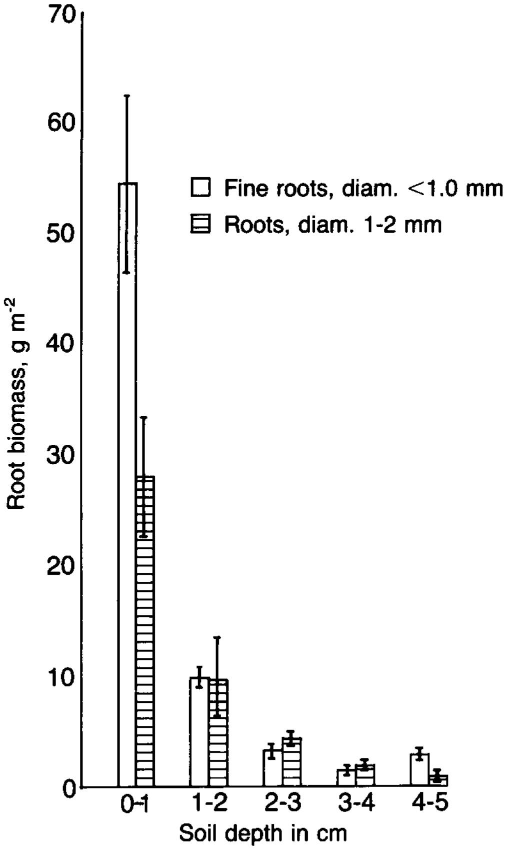

Fig. 1. Fine-root and 1 to 2-mm root distribution as a function of soil depth. Values are averages obtained from four soil blocks 1 cm deep and 5 cm on a side. Vertical bars indicate standard errors.

the cacao fine roots, five cubes of 5-cm sides were cut with a sharp knife from the soil beneath the litter layer. The sites were randomly selected from outside a 1-m radius of any cacao stem. These soil blocks were carefully cut into slices 1 cm in thickness and from each slice the fine roots were removed. Most of the fine roots were found in the uppermost centimeter of the soil (Fig. 1). It became evident that the fine root fraction (mean diam. $=0.22$ mm, ± 0.014, $n = 100^{15}$) predominated in the surface layer, while in the deeper layers (1–5 cm) fine roots and roots with diameters of 1–2 mm were represented about equally.

Fine-root biomass

The fine-root biomass (roots with < 1.0 mm diameter), recorded in weekly intervals for six months, did not show significant seasonal variations. The mean dry weight obtained from about 600 core extractions over six month each for the 0–5 cm and 5–10 cm soil depth, measured 30.3 ± 1.2 g m^{-2} and 8.4 ± 0.7 g m^{-2},

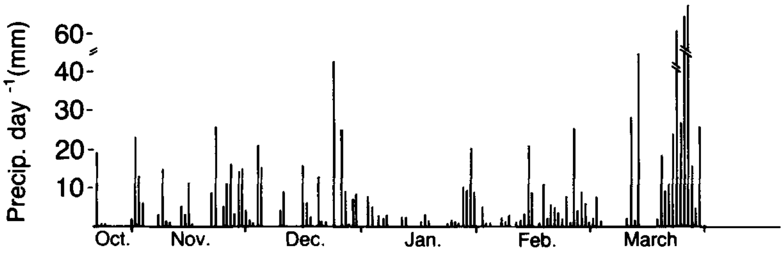

Fig. 2. Daily precipitations in mm measured at the meteorological station of the Centro de Pesquisas do Cacau, Itabuna, 1 km distance removed from the research site. The off-scale values in March are 65.1 mm (3/23), 132.2 mm (3/25), and 68.8 mm (3/26).

respectively. This means that a total of about 40 $g\,m^{-2}$ represents the standing crop of living fine roots. About 3/4 of these were concentrated in the uppermost 5 cm of the soil. The dead fine root biomass amounted to approximately 10 $g\,m^{-2}$. Some exploratory tests on fine root densities in deeper soil layers indicated that at least 90% of the fine roots were located in the upper 10 cm of the soil.

New root tips

The activity of the fine root system was estimated by the number of growing root tips. In contrast to the stability of the fine root biomass, the number of growing root tips showed a definite episodic pattern (Fig. 3). Maximum growth activity recorded in November was followed by a steady decline through mid-December. From mid-December through February the values remained low, then increased in March. Statistical evaluation (Anova, Newman-Keul[23])

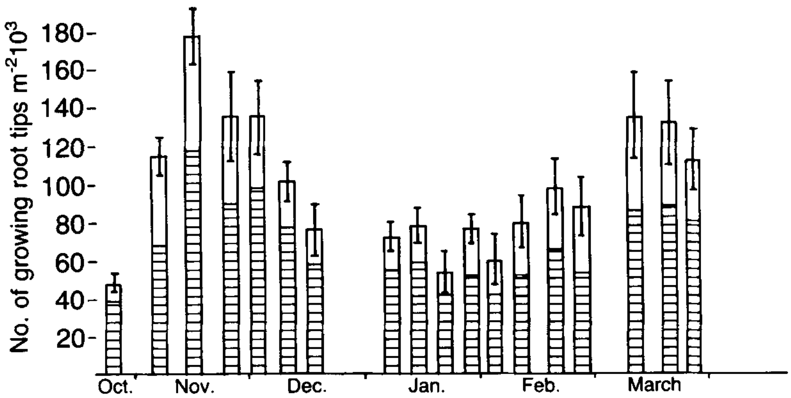

Fig. 3. Number of growing root tips per m^2. The top of each bar indicates root tips in 0–10 cm depth. Hatched bars give the values for the 0–5 cm depth. Vertical lines indicate standard errors. For each column n = 16 or more.

showed that the maximal values obtained in November and the January-February low values were significantly different. The January-February root tip numbers are also different from the March values ($P < 0.005$).

When the fine-root tip densities shown in Figure 3 are compared with the time course of precipitations (Fig. 2), we can see that the relatively small number of root tips in January is coincident with a very dry January (83.4 mm of precipitation). In February, however, there was a normal amount of rainfall (134.1 mm), yet the root tip density remained fairly low. The March root tip densities were high and this coincides with abundant rainfall (484.8 mm). However, the steep increase in new root tips in November and the following decline in the first half of December appear unrelated to the rainfall pattern.

Dendrometer observations

From January 7 to 15, only 6.5 mm of rain fell in three small showers. The mean daily morning and afternoon dendrometer difference was 4.65 ± 0.26 mm. A comparable period in March (3/10–3/18) which had abundant rainfall (73.4 mm) from two major storms and three showers, gave a mean dendrometer difference of 3.20 ± 0.51 mm. Thus, the low root tip density in January is coincident with high diurnal stem diameter fluctuations caused by water stress. The corresponding March dendrometer value at a time of abundant rainfall, was significantly smaller ($P < 0.005$, t-test) and the root tip densities were higher. It is unfortunate that dendrometer values were not available for the second half of November, the period of the steepest decline in root tip density, although we may speculate that morning-afternoon stem diameter differences would have been small considering the abundant and well distributed rainfall during this period.

New leaf formation

Beginning at the end of November, shoot growth intensity was assessed by counting the formation of new leaves on 100 randomly labelled branches from 10 trees. The results (Fig. 4) show a flushing period in January which was a period of

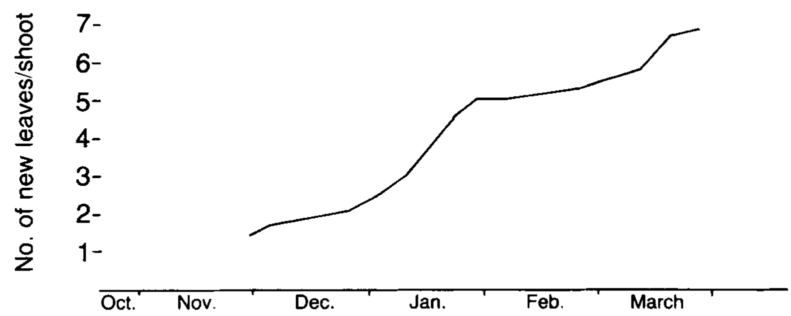

Fig. 4. Cumulative curve of the number of newly developed leaves per shoot. Data are means from 100 labelled shoots.

scarce precipitation and low root tip densities. A correlation over time between the number of new leaves per shoot and the number of growing root tips per m^2 produced a significant negative correlation coefficient ($r = -0.767$, $P < 0.005$).

Discussion

Fine roots of trees in humid, tropical forests grow frequently at the litter-soil interphase and in the uppermost centimeters of the soil[13,21,20]. The cacao plantation in our research area in southern Bahia was no exception. More than 90% of the fine-root growth occurred in the upper 10 cm of the soil with a high concentration of the finest rootlets just beneath or occasionally in the decomposing litter. The fine-root biomass values found in this study, 40 g m^{-2} (= 400 kg ha^{-1}), were in the same order of magnitude as those reported from other ecosystems, such as the Scots pine forest in Central Sweden[18] and the summer-dry chaparral in southern California[16]. It is significant that the biomass did not change significantly in the six months of our observations. This is in contrast to the two above-mentioned studies and others[8,10] which all showed considerable fine-root biomass variation in the course of a year. However, all these studies were made under conditions of more or less severe seasonal variations in climatic conditions. The climate in our research area was by no means uniform[7], but growth conditions are generally favorable during the whole year. Thus, it appears that fine-root growth of cacao is indeed continuous.

A more sensitive indicator for changes in fine-root activity appeared to be the number of growing root tips per unit of soil volume[4,14,18]. Significant changes in the number of living-root tips with time were found for the cacao trees. This seems somewhat contradictory with the observed stability of the fine-root biomass, as a significant increase in growing root tips should result in a higher fine-root biomass. We can only speculate that fine-root turnover under the warm and moist conditions of the research site is too fast to allow for the accumulation of a large fine-root biomass. Repeated observations of individual rootlets on the soil surface indicated that these did not survive more than six days, even when surface moisture conditions would have favored continued rootlet growth. It is possible that in the soil the life span of rootlets is longer, but no data are available. Thus, rapid increases in growing root tips may not be reflected in larger fine-root biomass because of concurrent increases in the rates of rootlet death and decomposition.

From these data the question arose: Are changes in the growth activity of fine roots correlated with alterations in the current environmental conditions? The answer appears to be 'No'. It is true that a low fine root activity was coincident with a drought period in January. However, in the last two weeks of November when there was abundant rainfall, a sharp decrease in the number of growing root tips occurred. Dendrometer values, an indication of the water status of the trees, showed that short drought spells produced morning: afternoon stem diameter fluctuations, which were significantly larger than those taken during the more rainy periods. However, it is improbable that the trees of the research site experienced any growth-inhibiting water stress during the observation period. In January, the month with the lowest rainfall, the trees flushed and produced a set of new leaves (Fig. 4).

A negative correlation between the decrease of fine-root activity and flushing was shown. This observation is supported by data from Vogel[22] who found that flushing of individual cacao trees grown in containers with slanted observation windows was preceded by intensive root growth. $^{14}CO_2$ applied to the foliage of flushing cacao trees under greenhouse conditions indicated that during the period of rapid leaf area expansion and shoot elongation, carbohydrate transfer to roots was negligible (Hardwick, pers. communic.). The developing shoots functioned as strong carbohydrate sinks. Thus, root growth would be limited by the lack of sufficient carbohydrate. These results were obtained with individual trees; the situation in a mature plantation is more complex. Roots extend beyond the canopy projection of the trees and consequently, correlations between growth activity of fine-root samples extracted from soil cores and the phenophase of specific trees becomes dubious since it is unclear to which tree the fine roots in this soil core belong. We have to expect that growth curves for roots and shoots from a larger number of trees have a more flattened shape when compared to those from individual trees. Nevertheless, it would be interesting to pursue the relationship of shoot and fine root flushing over an entire year.

The information collected in this study supports our initial hypothesis: In a mature cacao plantation fine roots display an episodic growth pattern. Precipitations, and consequently, soil moisture may influence the intensity of fine root growth. Shoot flushing occurred when fine-root growth activity was at its lowest level.

Acknowledgements The authors are grateful to Dr. Paulo de T. Alvim who made this study possible. Thanks are due to Cecilio Aranjo Afonso and Katia Mendonça Teles for the help with the sample processing. Dr. Ken Johnson's help with the manuscript preparation is gratefully acknowledged. The study was supported by the Comissão Executiva do Plano da Lavoura Cacaueira and by the National Science Foundation of the USA, Grant No. INT80–06385.

Received 6 August 1981

References

1 Alvim P de T 1977 Ecophysiology of cacao. *In* Ecophysiology of tropical Crops. Eds. P de T Alvim and T T Kozlowski. Academic Press, New York, pp 279–313.

2 Alvim P de T 1975 A new dendrometer for monitoring cambium activity and changes in the internal water status of plants. Turrialba 25. 445–447.

3 Alvim P de T and Alvim R 1978 Relation of climate to growth periodicity in tropical trees. *In* Tropical Trees as living Systems. Eds. P B Tomlinson and M H Zimmermann. Cambridge University Press, pp 445–464.

4 Böhm W 1979 Methods of studying root systems. Ecological Studies 33, Springer-Verlag, Berlin.
5 Borchert R 1978 Feedback control and age-related changes of shoot growth in seasonal and nonseasonal climates. *In* Tropical Trees as living Systems. Eds. P B Tomlinson and M H Zimmermann, Cambridge University Press, pp 497–515.
6 Cadima Zevallos A 1970 Estudo do sistema radicular do cacaueiro em alguns tipos de solos da região cacaueira da Bahia. Publicação do Centro de Pesquisas do Cacau, Itabuna, Bahia, Brasil.
7 CEPEC Centro de Pesquisas do Cacau 1978 Informe Técnico 1977–1978, Divisão de Climatologia, Itabuna, Bahia, Brasil pp 221–238.
8 Cox T L, Harris W F, Ausmus B S and Edwards N T 1978 The role of roots in biogeochemical cycles in an eastern deciduous forest. Pedobiologia 18, 264–271.
9 Cuatrecasas J 1964 Cacao and its allies; a taxonomic revision of the genus Theobroma. Washington, Smithonian Institution.
10 Ford E D and Deans J D 1977 Growth of Sitka spruce plantation: spatial distribution and seasonal fluctuations of length, weight, and carbohydrate concentration of fine roots. Plant and Soil 47, 463–485.
11 Greathouse D C, Laetsch W M and Phinney B O 1971 The shoot-growth rhythm of a tropical tree, *Theobroma cacao*. Am. J. Bot. 58, 281–286.
12 Himme M van 1959 Etude du systeme radiculaire du cacaoyer. Bull. Agric. Congo Belge et du Ruanda-Urundi 50, 1541–1600.
13 Klinge H 1973 Root mass estimation in lowland tropical rainforests of Central Amazonia, Brazil. I. Fine root masses of a pale yellow latosol and a giant humus podzol. Trop. Ecol. 14, 29–38.
14 Kummerow J and Russell M 1980 Seasonal root growth in the arctic tundra. Oecologia 47, 196–199.
15 Kummerow J, Kummerow A and Alvim P de T 1981 Root biomass in a mature cacao (*Theobroma cacao* L.) plantation. Theobroma 11, 77–86.
16 Kummerow J, Krause D and Jow W 1978 Seasonal changes of fine root density in the southern Californian chaparral. Oecologia 37, 201–212.
17 Lyford W H 1975 Rhizography of non-woody roots of trees in the forest floor. *In* The Development and Function of Roots. Eds. J G Torrey and D T Clarkson Academic Press, London, pp 179–196.
18 Persson H 1980 Spatial distribution of fine-root growth, mortality and decomposition in a young Scots pine stand in Central Sweden. Oikos 34, 77–87.
19 Silva L F da e Melo A A O de 1970 Levantamento detalhado dos solos do Centro de Pesquisas do Cacau. Boletin Têcnico No. 1, Centro de Pesquisas do Cacau, Itabuna, Bahia, Brasil, pp 3–86.
20 Stark N M and Jordan C F 1978 Nutrient retention by the root mat of an Amazonia rain forest. Ecology 59, 434–437.
21 Stark N and Spratt M 1977 Root biomass and nutrient storage in rainforest oxysols near San Carlos de Rio Negro. Trop. Ecol. 18, 1–9.
22 Vogel M 1975 Recherche du terminisme du rhythme du croissance du cacoyer, Cafe, Cacao, The 19, 265–290.
23 Zar J H 1974 Biostatistical Analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J. pp 151–161.