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A.S. Devakumar · P. Gawai Prakash · M.B.M. Sathik
James Jacob

Drought alters the canopy architecture and micro-climate of *Hevea brasiliensis* trees

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Abstract In this study a comparison of the canopy architecture and the growth and distribution of roots was made in 10-year-old trees of *Hevea brasiliensis* grown in a severely drought-prone area on the west coast of India under rainfed and irrigated conditions. LAI and light interception increased significantly in the irrigated compared to the rainfed trees. Girth and height of the tree were 29 and 19% more while width and height of the canopy were 19 and 20% more in the irrigated than rainfed trees. There were 22% more primary branches which had 26% more diameter in the irrigated trees than rainfed trees. The branches were inserted on the main trunk at an angle of 58.36° in the irrigated and 44.22° in rainfed trees. The above changes led to more light penetration which altered the light distribution inside the rainfed trees during summer and inhibited leaf photosynthesis particularly in the top canopy leaves. In the rainfed trees most of the growth occurred during the short favorable season immediately after the monsoon between June and October and no growth or even shrinking of the trunk was seen during summer. In the irrigated trees a higher growth was seen throughout the year and summer had no adverse effect. Although there was some difference in the root distribution pattern, the total root density per unit soil volume did not vary between the irrigated and rainfed trees.

Key words *Hevea brasiliensis* · Drought · Crown architecture · Micro-climate · Root growth

A.S. Devakumar (✉), M.B.M. Sathik, J. Jacob
Plant Physiology Division, Rubber Research Institute of India, Kottayam-686 009, India
Fax: +0481 578317

P. G. Prakash
Regional Research Station, Thane District, Dapchari, Maharastra, India

Introduction

Biomass production by a crop or native ecosystem is directly related to the total amount of solar radiation intercepted by the canopy (Halle et al. 1978). The total amount of leaf area present per unit land area (LAI), the architecture of the crown and the orientation of the leaves within the canopy determine the total amount of solar energy intercepted by plants (Fisher and Honda 1979; Halle et al. 1978). Canopy architecture, particularly the angle of leaf orientation, has been very successfully made use of in crop improvement programs in cereals (Gifford et al. 1984; Matsushima 1976). The ability of many modern high yielding varieties of rice and wheat to accommodate large LAIs is due to their near vertical leaf orientation which favors more light penetration and minimum mutual shading of lower leaves (Gifford et al. 1984; Matsushima 1976). Light penetrating through the canopy and falling on the ground surface will change the soil temperature and vapour pressure deficit leading to evapotranspirative loss of soil moisture and alters the micro-climate. Environmental extremes like drought would leave its impact on the growth and architecture of the canopy of tree crops because of their perennial nature (Takenaka 1994; Barthelemy et al. 1991).

From an evolutionary point of view plants are very specific in their allocation of resources to various organs (Givinish 1986; Sibly and Calow 1987), and this is applicable to trees in their distribution of resources to achieve an optimum canopy architecture (Barthelemy et al. 1991; Ceulemans and Saugier 1991) and root distribution for effective sunlight interception and absorption of water and minerals, respectively. Unlike annuals, there have been very few studies on the structural and functional organization of the canopy of tree crops such as *Hevea*. A mature *Hevea* plantation can have an LAI as large as 6 or 7 and the majority of the leaves will be exposed to very low PFD in the range of 150 to 300 $\mu mol m^{-2} s^{-1}$ for most part of the day except for occasional sun flecks. Only the outer leaves present in the top of the canopy are exposed to saturating PFD.

If the architecture of the above-ground organs of a crop is organized to maximize light interception, the root system is also distributed in such a way that there is maximum mining and absorption of water and minerals. Like canopy architecture, it has been shown that root biomass production and distribution are altered when plants are subjected to environmental stresses and such reports are common in annuals, but little is known about tree crops (Vartanin 1996).

In the present investigation, *H. brasiliensis* plants were grown in a severely drought prone region of India for 10 years under irrigated and rainfed conditions. In these trees we have examined the effects of drought and irrigation on the growth, canopy structure and root distribution.

Materials and methods

This study was conducted at the Regional Research Station of the Rubber Research Institute of India situated in Dapchari, Maharastra, India (20° 04′ N, 72° 04′ E, 48 m MSL) where land has an even topography. Soil is oxisol, with pH 6.3, bulk density 1.4 mg m^{-3}, field capacity of 30% and permanent wilting point 17% (Mohana Krishna et al. 1991). The annual rainfall is 2430 mm. Most of the rainfall occurs between June and September and practically no rain fall between January and May (Chandrashaker et al. 1990). The total sunshine hours received between January and May (summer period) is approximately 1620 h when compared to 1291 h for the rest of the year. Soil moisture during severe summer reaches very close to permanent wilting point (Devakumar et al. 1998). Leaf water potential is as low as –21 bars during summer and –11 bars during post monsoon. Atmospheric relative humidity ranges from 26 to 100% (at 0740 hours) and 10 to 100% (at 1440 hours) in the summer months. During summer, high solar radiation associated with high temperature (Chandrashaker 1996) and low relative humidity lead to high vapor pressure deficit, increasing the evapotranspirative demand of the atmosphere. Rubber trees in this region are every year subjected to prolonged periods of both soil and atmospheric drought stress during summer seasons (January to May).

Five hundred budded plants of *H. brasiliensis*, clone RRIM 600 were grown in the nursery for a period of one year and transplanted to the field in 1987 at a spacing of 4.9×4.9 m. All the recommended cultural practices were followed (Anonymous 1997). During the initial 2 years after planting in the field (summer of 1987 and 1988) uniform life saving irrigation was given for all the 500 plants throughout the dry season. From the summer of 1989 onwards, 250 plants were maintained under rainfed condition without any summer irrigation while another 250 trees were given irrigation in summer. Potential evapo-transpiration of rubber was worked out using a modified Penman equation for Indian conditions (Rao et al. 1971) and the quantity and frequency of irrigation for different growth stages and seasons was worked out to provide a one crop evapo-transpiration (ET_c). For more details on irrigation see (Vijayakumar et al. 1998).

Trunk girth of individual trees was measured at 1.5 m above the bud union from 1990 on wards at monthly interval. The determinants of canopy architecture such as height and diameter of the crown, height and girth of the primary trunk, angle and diameter of the primary branches each were measured on 15 trees, selected randomly from the irrigated and rainfed plantations. Girth was used to compute the standing shoot dry biomass (Shorrocks et al. 1965). Stem volume was computed from girth and trunk height since the trunk of the budded trees are mostly uniform and cylindrical in shape (Webster 1989). Leaf area index was measured in ten trees each of irrigated and rainfed trees using Plant Canopy Analyzer (model LAI-2000, LI-Cor, USA) and light interception was worked out using Ceptometer with an 80 cm long line sensor at 50 random points each in irrigated and rainfed plantations (Analytical Development Corporation, UK). Photosynthetic rates of leaves present at top and bottom layers of the canopy were measured at steady state conditions using Photosynthesis System (model LI-6200, LI-Cor, USA). The conditions in the measurement cuvette were 30°C and 75% RH for the top canopy leaves and 27°C and 78% RH for the bottom canopy leaves. All the measurements were made in the morning between 0900 and 1000 hours. Measurements were made on five randomly selected trees of each treatment on a minimum of 15 leaves in each tree in the top and bottom canopies. Measurements were made during severe summer and post-monsoon seasons for 2 consecutive years.

Root density was estimated by collecting soil samples using a core sampler of 169 ml volume. Random samples of six trees each from irrigated and rainfed trees were selected and soil cores were collected at 0–15, 15–30 and 30–45 cm depths, at 50, 100 and 150 cm away from the tree basin. Sampling was done in north, south, east and west directions of a tree. After collecting the soil sample it was washed in running water and passed through a series of sieves to collect all the fine roots present in the soil core and dried at 120°C and weights were recorded. Measurements recorded on rainfed and irrigated trees were statistically compared using independent *t*-test.

Results

Leaf area index during summer season (April 1996) was significantly higher in irrigated trees than rainfed trees (Fig. 1 A), but during the post-monsoon season (October 1996) there was no difference in the LAI between the ir-

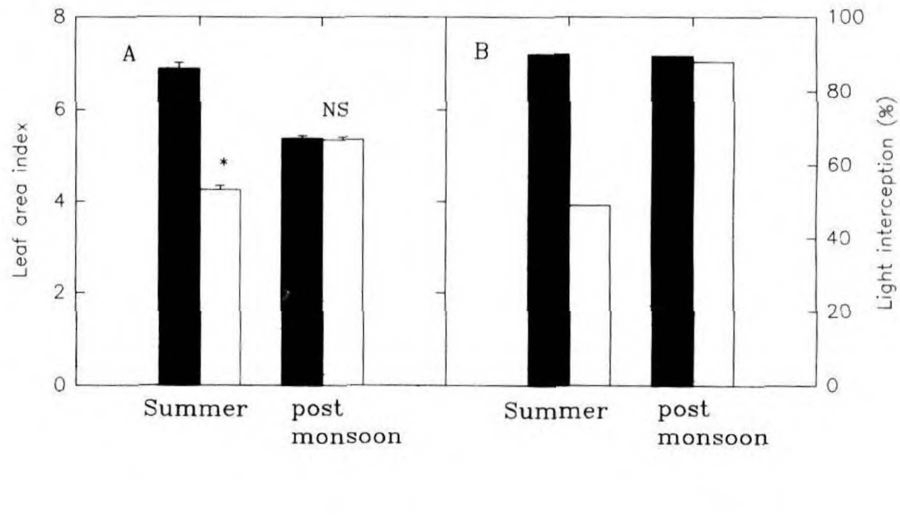

Fig. 1 Seasonal changes in leaf area index (**A**) and light interception (**B**) by the canopies of irrigated (■) and rainfed (□) trees measured during summer and post monsoon seasons

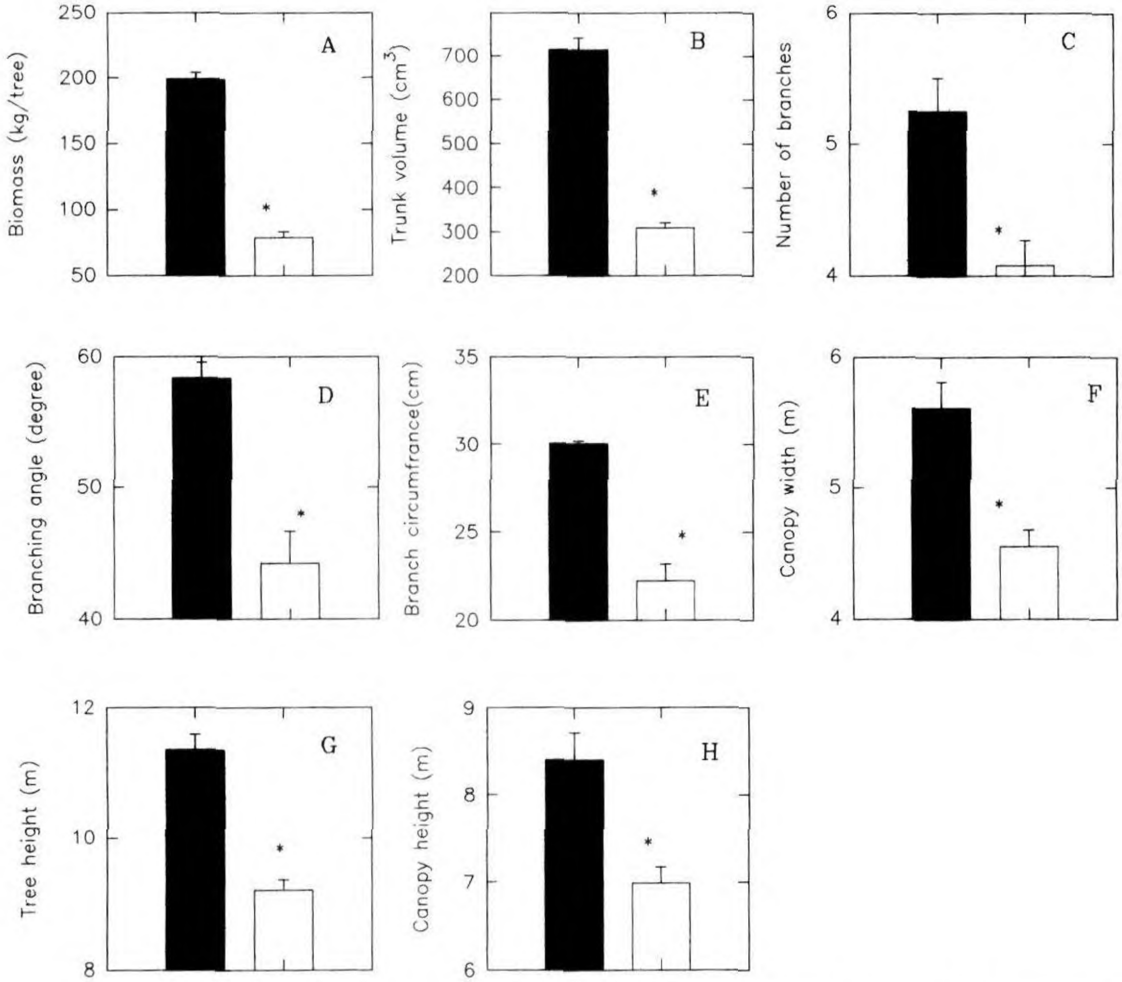

Fig. 2 Canopy architectural characters of irrigated (■) and rainfed trees (□) measured in summer 1996

rigated and rainfed trees. Irrigated trees intercepted nearly 88 and 90% of the solar radiation while rainfed trees intercepted 49 and 88% during summer and post-monsoon seasons respectively (Fig. 1B). Biomass produced by irrigated trees was significantly higher (60%) than the rainfed trees (Fig. 2A). Trunk volume was 57% more in the irrigated than rainfed trees (Fig. 2B).

The canopy components that altered its architecture showed wide variations in rainfed and irrigated trees. Irrigated trees produced significantly more branches than the rainfed trees (Fig. 2C). Not only the number of branches but their orientation of the branches was also different. Irrigated trees had branches inserted on the main trunk with a wide angle which was significantly more than the rainfed trees (Fig. 2D). Because of the wide branching angle and bigger size (Fig. 2E) of the branches canopy width was significantly greater in irrigated trees than rainfed trees (Fig. 2F). Irrigated trees were 2.14 m (19%) taller than the rainfed trees (Fig. 2G). Trunk height was 14% more and canopy height was 17% (Fig. 2H) higher than the rainfed trees.

Trunk girth was 29% more in the irrigated trees at the end of 10 years of growth (Fig. 3A). Girth was always higher in the irrigated trees when compared to rainfed trees from the time of initiation of irrigation treatment, but the annual mean girth increment started decreasing in the irrigated trees from 1993 (Fig. 3B). From 1990 monthly girth increment was higher in the irrigated than the rainfed trees between January and May, but June onwards growth rates were similar in both irrigated and rainfed trees (Fig. 4). Such a trend in the growth was seen up to 1993. From 1994 onwards growth rates gradually reduced in the irrigated trees. In the rainfed trees growth was negligible between January and May, and from June to October it was similar to irrigated trees and decreased from November onwards.

The light intensity received at the soil surface under the canopies of irrigated and rainfed trees was, respectively, 90 and 50% less than in the open field (Fig. 6). Consequently, the temperature on the surface of the soil was, respectively, 5.3°C and 2.02°C less in the irrigated and rainfed plantations than in the open soil. Temperatures 10 cm below the soil surface showed larger variation in the irrigated and rainfed treatments than in the open field. In the open field it was 2.07°C hotter 10 cm below the soil surface than at the soil surface. However, inside the plantation, it was nearly 10°C cooler 10 cm below the soil surface than at the soil surface in both irrigated and rainfed treatments.

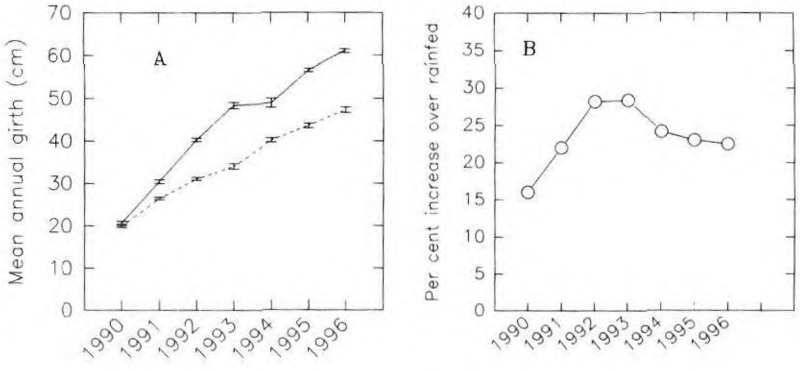

Fig. 3 Annual girth increment of irrigated (*solid line*) and rainfed (*broken line*) trees (**A**) and the percent increase in the annual girth (**B**) of irrigated trees over rainfed trees

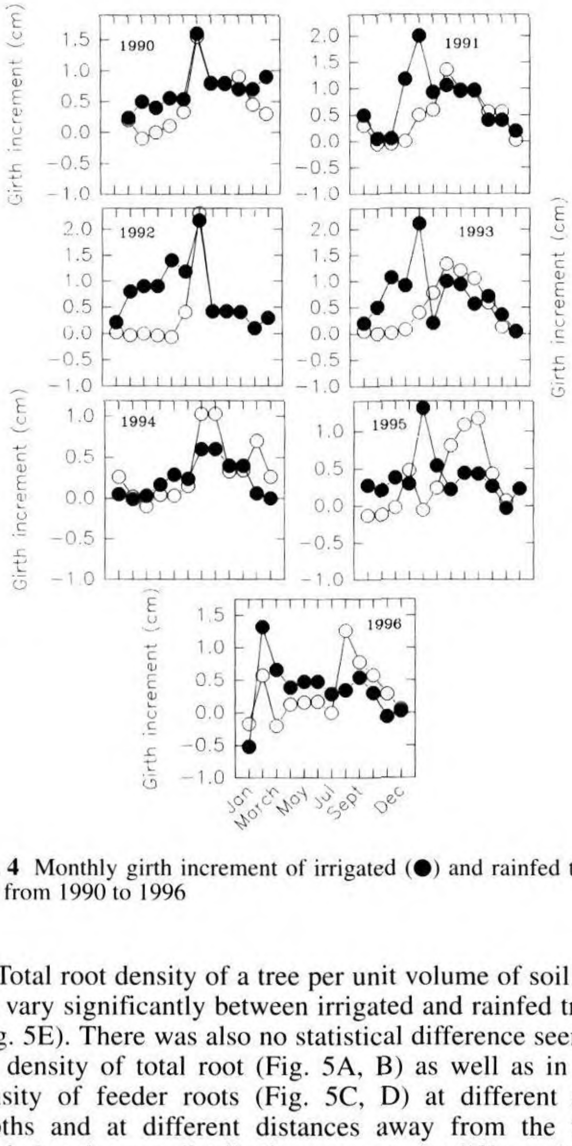

Fig. 4 Monthly girth increment of irrigated (●) and rainfed trees (○) from 1990 to 1996

Total root density of a tree per unit volume of soil did not vary significantly between irrigated and rainfed trees (Fig. 5E). There was also no statistical difference seen in the density of total root (Fig. 5A, B) as well as in the density of feeder roots (Fig. 5C, D) at different soil depths and at different distances away from the tree trunk, but the root distribution seems to be different in irrigated and rainfed trees. Most of the feeder roots were found to be present in the top 15 cm of the soil in both treatments.

The rate of photosynthesis of the exposed top canopy leaves of the irrigated trees was very high (Fig. 6), but the top canopy leaves of rainfed trees were respiring under saturating light during summer. In the rainfed trees the shaded lower canopy leaves alone contribute to the canopy carbon assimilation in the summer. At any given light and canopy level, leaf photosynthesis rates were comparable in the irrigated and rainfed trees during the post-monsoon season.

Discussion

H. brasiliensis, the only commercially viable source of natural rubber, is a deciduous tree which sheds all its leaves in winter (December/January) and puts forth new flushes within a period of 2–3 weeks (Webster 1989). There is practically no rainfall between January and May (Chandrashaker et al. 1990) and therefore, the newly formed leaves in the rainfed trees experienced progressive drought stress. Because of the poor growth of the drought-stressed plants (Fig. 3), they have limited resources to remobilize for the production of large number of leaves as compared to the irrigated trees. As summer advances, there is progressive leaf drying and leaf shedding in the rainfed trees. Because of these reasons, the LAI was significantly less in the rainfed than irrigated trees during summer (Fig. 1A).

The total light interception was significantly low in the rainfed than the irrigated trees because of the small size of the canopy (Fig. 1B). This resulted in more light reaching the lower canopy leaves and the soil surface in the rainfed trees. High light was found to be inhibitory to leaf photosynthesis in water stressed leaves (Fig. 6). The sparse canopy in the rainfed trees led to more light penetrating to the deeper layers of the canopy. Photoinhibitory damage to green leaves leads to senescence and loss of leaves (Powels 1984). While the winter leaf shedding is common for both irrigated and rainfed trees (Kozlowski 1976; Orshan 1972), the latter suffer from a second loss of functional leaves during summer which affects its total photosynthetic productivity and thus carbohydrate reserves for new growth in the following seasons.

In addition to the photoinhibitory damages to the leaves the microclimate inside the canopy is altered, (e.g. increased temperature) due to more light penetrating through the canopy and reaching the soil (Fig. 6) which resulted in increased evaporational loss in the rainfed

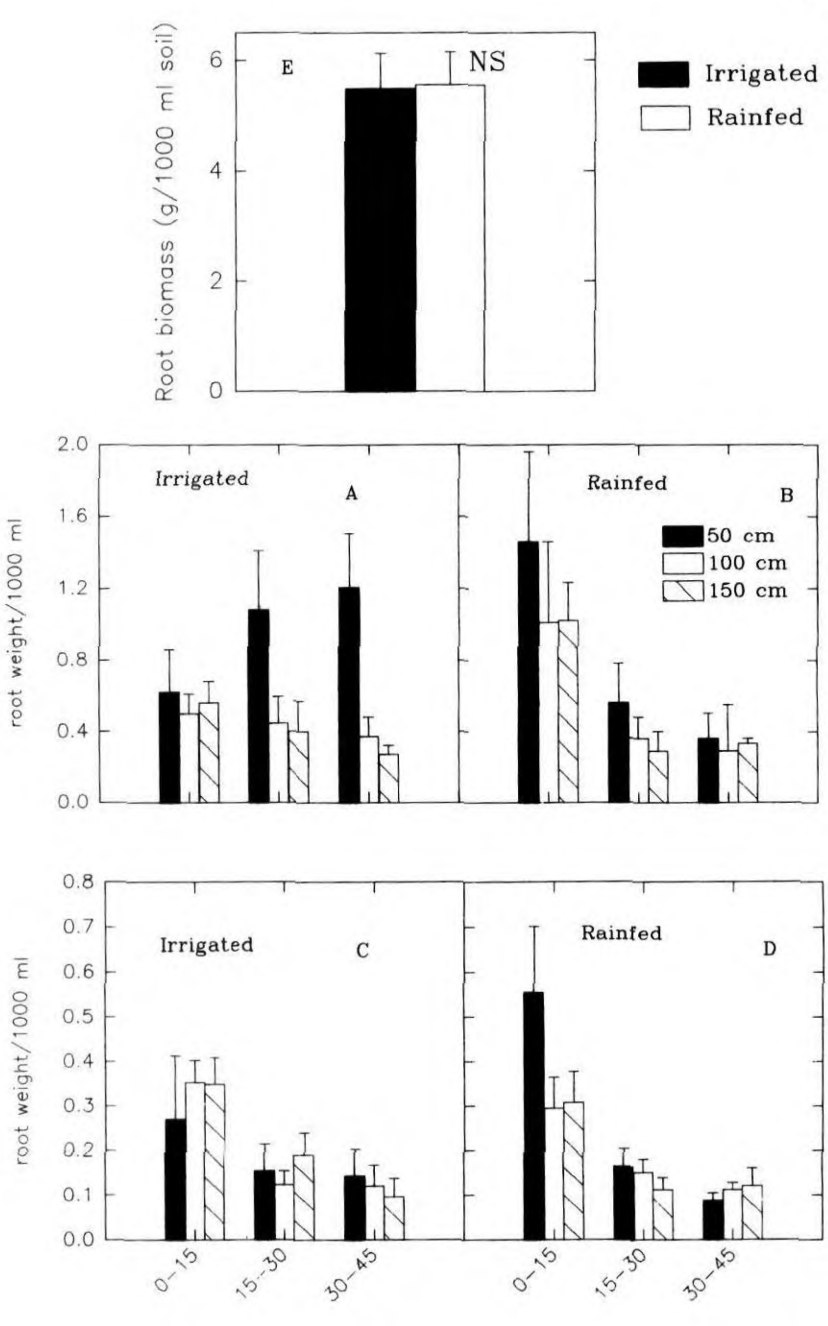

Fig. 5 Root density (**A**) and distribution of lateral (**B**, **C**) and feeder roots (**D**, **E**) of irrigated and rainfed trees

crop during summer. This aggravates the drought condition further. In the irrigated crop, since the canopy was closed there was less evaporation from the soil surface during summer. The microclimate within the canopy will also affect weed growth. For example, more weed growth was noticed inside the rainfed crop (Fig. 6) than in the irrigated crop, possibly because of better light availability in the former. These weeds also compete for the limited moisture during summer.

After the monsoon rains are over and the drought stress is fully alleviated, the LAI and light interception are comparable in both the treatments (Fig. 1A). This indicates that the rainfed trees have put forth new flushes after the rains which is an additional investment on its already limited resources. Irrigated trees had high LAI in summer but during summer a portion of these leaves due to normal senescence of the older leaves in the bottom canopy, there was a small drop in the LAI during the post-monsoon. The photosynthetic rates of the leaves are comparable during the post-monsoon season in the two treatments (Fig. 6). The rate of growth was also comparable in the two treatments during the post-monsoon season. It may be noted that most of the growth in the rainfed trees occurred during this stress-free period and that during summer they even showed shrinking (Fig. 4) of the trunk due to extreme negative water balance in the trees (Winget and Kozlowski 1964; Chandrashaker 1996).

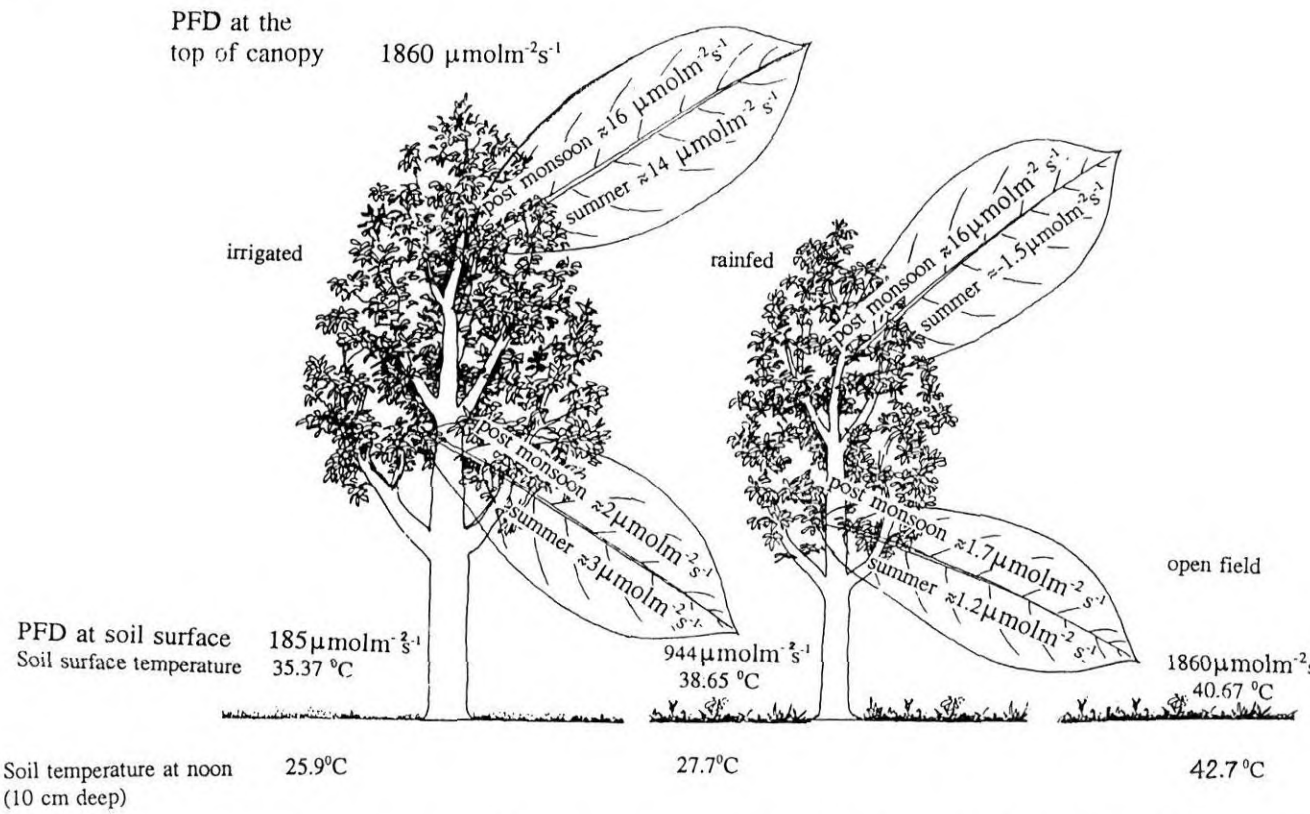

Fig. 6 Schematic model of the canopy structure (drawn to scale) of a typical 10 year-old rubber tree grown with and without summer irrigation showing the changes in the micro-climate under the trees. Leaf photosynthesis at different seasons in top and bottom canopy leaves

Irrigated trees maintained a large LAI and high light interception throughout the year and there was no photoinhibition of leaf photosynthates and therefore, their carbohydrate resources were adequate to produce more branches to accommodate the large leaf area (Fig. 1A). Branches were also bigger in size and they were inserted on the primary trunk at a wider angle in the irrigated trees (Fig. 2D). This led to a wider and taller crown in these trees (Fig. 2E, G) enabling them to harvest more sunlight. The wider angle of the primary branches gave adequate room for more secondary branches to be produced and thus accommodate more leaves in the irrigated trees. The branches were stronger in the irrigated trees as evident from their girth which was needed to sustain the weight of the large leaf area they were holding. The trunk of the irrigated tree was also proportionately large enough to hold the large canopy and the branches.

In rainfed trees canopy components and the overall tree size were smaller because of their poor biomass producing ability under drought. Reallocation of reserved resources to survive the prevailing adverse conditions would affect the canopy architecture. The most important consequence of such a change in the canopy architecture seems to be in the reduced leaf area index and enhanced light distribution inside the canopy which led to severe photoinhibition of photosynthesis during summer in the rainfed trees.

While the shoot growth and its structural organization were drastically altered in the irrigated and rainfed trees, there was little difference in the root density between the two treatments. However, some differences in the root distribution pattern were evident between the irrigated and rainfed trees. More roots were present in deeper layers of the soil in the irrigated trees (Fig. 5B, D) which is reported in many tree species including rubber (Kramer and Kozlowski 1979; Webster 1989). Nisbet and Mullins (1986) have shown that there will be more root elongation under well watered conditions. In the rainfed trees most of the roots were concentrated in the top layers (Fig. 5C, E) which could be mainly because of the production of short roots in response to drought (Gasteller and Vartanin 1995).

Drastic changes brought about to the canopy architecture of drought stressed *Hevea* trees and what that would mean to their microclimate and leaf photosynthesis is quite evident. Compactness of the canopy to prevent high light intensities (which can be photoinhibitory) from reaching the lower canopy leaves may be one phenotypic feature ideal for a drought tolerant clone. The functional components affecting the structural organization of the canopy are important traits for drought tolerance in *Hevea*.

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