Development and Production of Cupuaçu Plants (*Theobroma grandiflorum*) on Degraded Areas: Implications of Water Relations

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Abstract

The high market value of the fruit pulp and the potential use of the seeds for the production of chocolate-like wares make the cultivation of cupuaçu-trees (*Theobroma grandiflorum*) very attractive. There is little knowledge concerning the suitability of cupuaçu as a crop-plant in agroforestry systems designed for the recultivation of degraded areas. In this context it needs to be known which factors determine the development and productivity of this plant.

We studied the development of 750 cupuaçu-plants grown in a monoculture and three mixed cultivation systems on a degraded area, a terra firme rain forest site near Manaus. The influence of various ecological variables on the development and fruit production has been analyzed, with special focus on water uptake and stomatal resistance.

It became evident that all mixed cultivation systems provide better conditions for the development and productivity of cupuaçu-trees than the monoculture. Comparing the mixed cultivation systems the development and productivity after the first 3 years was more advanced in the system with the highest planting density. Neither different fertilization treatments (30% and 100% of recommended dose) nor the topographiy were significantly related to the development of cupuaçu-plants.

An evident influence of the adjacent forest on the development and productivity of cupuaçu-plants was observed. The development of cupuaçu-plants was advanced towards the border of the experimental site. This influence of the adjacent forest became also very obvious through the "El niño"-phenomenon. A gradient of fruit productivity was observed declining from the border to the central part of the plantation. The positive influence of the forest's neighborhood was effective up to a distance of about 40 m. Climatic measurements revealed an evident gradient in the same spatial range concerning the potential evaporation, water vapor deficit and air temperature as a function of the distance to the primary forest. Thus, it is assumed that the observed effect on plant development and productivity bases on a positive influence of the forest's microclimate, especially concerning the water balance of the cupuaçu-plants.

In a drought experiment the root area of a five years old cupuaçu tree was cut off from water supply. It could be shown, that the zone of water uptake of the cupuaçu-tree is almost completely restricted to the upper 10 cm of the top soil. The reaction pattern of the stomata was altered evidently as the volumetric water content of the upper soil approximated 20% to 15% - a soil drought which occurred at different cupuaçu stands in the field after three days without rain. The magnitudes of increased diffusion resistances indicate the incidence of stomatal limitation to photosynthetic capacity during dry periods. Models of stomatal reaction reveal that the degree of photosynthetic limitation strongly depends on air humidity. Basing on this models it was calculated that in the microclimatic sphere of the forest the potential primary production of cupuaçu-plants could have been 10% higher than in the dryer microclimate in the central parts of the field.

We conclude that - despite the vast precipitation in the Central Amazon - water supply is a limiting factor for the cultivation of cupuaçu-trees. Plants grown solitary on degraded areas suffer frequently from drought. Thus, designs of plantations for the recultivation of degraded areas must consider the water balance of the system. Species composition and planting schemes should result in dense and storied structures of the plant community. Such structures reduce the vertical mass transfer and consequently counteract the water loss of the planting system leading to a higher buffer capacity against climatic extremes.

Keywords

1   Introduction

Terra-firme rainforest areas cleared and used in a conventional agricultural manner are productive only for a short time span and tend to degrade rapidly, leading to an unrelieved incentive of clearing primary forests for arable land. It would be a feasible approach to reduce human impacts on primary forests by bringing forward the long term utilization of abandoned areas through self stabilizing cultivation systems. The ecological stabilizing capacity of

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cultivation system, e.g. of an agroforestry system, depends on the relation between the plants and the pedoclimatic conditions. The extent to which pedoclimatic conditions are affected by the cultivated plants depends on the functional coherence of their above- and below-ground structures. Conversely, the functional coherence depends on the degree to which the cultivated plants are adapted to the local pedoclimatic conditions. Thus, studying plantation systems with regard to their ecological stability, it is necessary to consider integratively both the ecological profile of a particular crop species, and how this profile fits into the ecological functionality of the entire system.

In 1993 a field trial on an Amazonian terra-firme site was designed for a comparative study of different agroforestry systems with regard to their self stabilizing capacity. There are various scientific activities of different cooperational projects at the study site aimed at an integrative understanding of particular pedological, climatic and biological components of the exemplified agro-ecosystems containing the crop tree *Theobroma grandiflorum* (in Brazil named "cupuaçu").

The FAO (1986) considered cupuaçu as plant of great potential for agro-forestry in the Amazon for two reasons: The cupuaçu tree, a close relative of the cocoa tree, is native in the Amazon. And the high market value of the aromatic fruit flesh as well as the potential use of the seeds for chocolate-like products makes its cultivation economically very attractive, especially for small holders. Since the commercial cultivation of cupuaçu trees is not yet very prevalent in the Amazon there is still a need of knowledge concerning optimal agro-environmental conditions for its growth and production. The investigations presented here deal with the question, what pedoclimatic limitations could play an important role for the cultivation of cupuaçu plants on central Amazonian degraded terra firme sites, and to which extent these limitations could be compensated by appropriate cultivation systems.

2   Material and Methods

The field trial was conducted on an abandoned area of 19 ha, a former rubber plantation situated within intact primary and secondary forest. After slash and burn the field was divided into plots of 48 m x 32 m. On these plots four agroforestry systems containing *T. grandiflorum* were implanted randomly: A monoculture (which has been designed according to common practice) and three mixed cultivation systems differing in spacing and species composition (cf. Fig. 1). As additional variant each of these

cultivation systems was fertilized by 30% or 100% of the recommended dose of NPK-fertilizers (FELDMANN et al., 1995). Since the experimental site was surrounded by primary and dense secondary forest the distance of each plant to the forest border was also taken into consideration as ecological variable. The development and production of the 750 cupuaçu trees have been monitored from the third to the fifth year and the data were analyzed in relation to the particular treatments and agro-environments.

Since installation of the experiment the climatic parameters were recorded continuously by a climate station located in the center of the experimental field. The microclimatic gradient from the forest border into the plantation was measured in march 1999 with PICHE-evaporimeters and with an ASSMANN psychrometer.

Studies on plant water relations have been carried out on single plants. The root area of a five years old cupuaçu tree was cut off from water supply by tent squares installed at ca. 30 cm above the ground. The plant's uptake of the water stored in the soil was monitored indirectly by measuring the volumetric water content of the soil via time-domain-reflectometry (TDR). The TDR-probes were installed near the trunk, in 1 m and in 2 m distance to the plant, at depths of 10 cm, 50 cm and 100 cm. The soil humidity of an adjacent untreated cupuaçu tree was recorded in the same manner.

Preferably on days without rain the time course of leaf transpiration resistance of the treated plant and the control tree was measured using a Delta-T diffusion-porometer. Air temperature and humidity were measured at about 3 m distance to the plants' crowns with an ASSMANN psychrometer, the global irradiance in the range from 400 nm to 1400 nm was recorded via a Delta-T tube-solarimeter.

Empirical models of stomatal resistance of cupuaçu plants have been computed by multivariate regression terms which were approximated to the raw data with the quasi-Newton-method (StatSoft 1997). These models have been developed separately for the treated plant (low water availability) and the control plant. Data of the climate station were feed into these models in order to simulate the stomatal conductance. In order to estimate the potential influence of higher air humidity, the models were feed additionally with modified values of vapor pressure deficit (VPD), which have been reduced to a magnitude characteristic for the microclimatic sphere of the forest. The mathematical model of photosynthesis developed by FARQUHAR & VON CAEMMERER (1982) has been used to calculate roughly the potential stomatal limitation to CO_2 fixation. The ribulose-1,6-bis-phosphate

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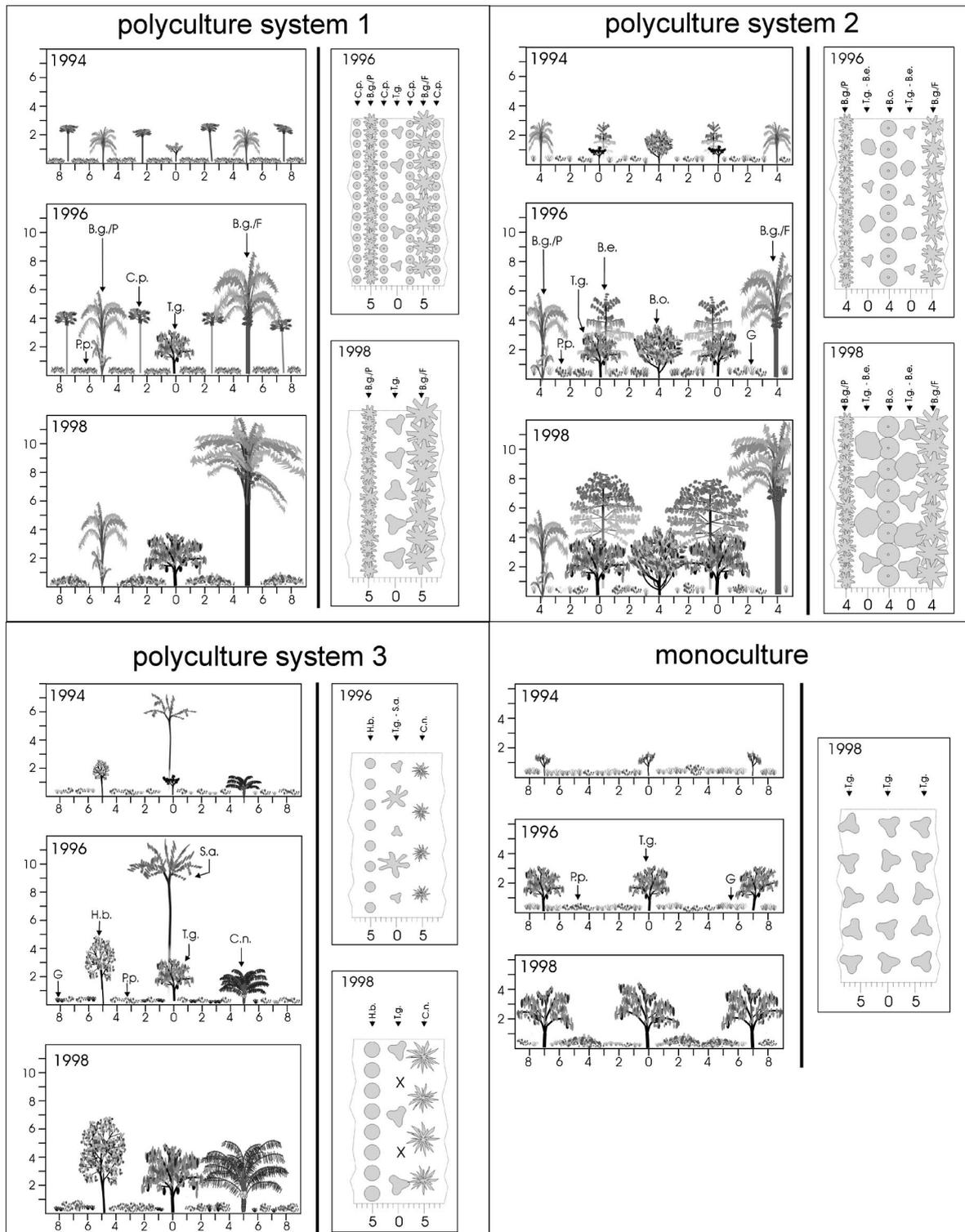
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Fig. 1: Idealized illustration of structural traits of the four cultivation systems in the second, fourth and sixth year since plantation: crown projection area and transverse view on plant rows of cupuaçu and neighbored species.

T.g. – *Theobroma grandiflorum*; B.e. – *Bertholletia excelsa*; B.g./P - *Bactris gasipaes* for palmito production; B.g./F – *B. gasipaes* for fruit production; B.o. – *Bixa orellana*; C.n. – *Cocos nucifera*; C.p. – *Carica papaya*; H.b. – *Hevea brasiliensis*; S.a. – *Schizolobium amazonicum*; P.p. – *Pueraria phaseoloides*; G – *gramineous* (mostly *Homolepis aturensis*). In system 3 *S. amazonicum* was replaced in 1996 by young trees of the timber species *Khaya ivorensis*, *Licaria canela* or *Calophyllum brasiliense* (symbolized by "X"). Scaling in meters. . (source: REISDORFF et al. unpublished)

(RuBP) saturated rate of photosynthesis (A{c}), where CO_2 is the minimum factor of carboxylation rate of RuBisCO (ribulose-1,6-bisphosphate carboxylase/oxygenase), and the RuBP limited rate of photosynthesis (A{j}), respectively, have been calculated by the equations

$$A_{\{c\}} = \frac{V_{c\max} \cdot (p_i - \Gamma^*)}{p_i + K_m)} - R_{day}$$

$$A_{\{j\}} = \frac{J \cdot (p_i - \Gamma^*)}{4 \cdot (p_i + 2 \cdot \Gamma^*)} - R_{day}$$

A is the assimilation rate, V_{cmax} is the rate of assimilation at saturating intercellular partial pressure of CO_2, p_i is the intercellular partial pressure of CO_2, Γ^* is the CO_2 compensation point in absence of dark respiration, K_m is the Michaelis-Menten constant for the carboxylation reaction (that takes into account competitive inhibition by O_2), J is the rate of electron transport, and R_{day} is the dark respiration during photosynthesis.

3   Results/Discussion/Conclusions

The four agroforestry systems developed very different structural features, which is illustrated in Fig. 1. The depictions of the crown projection areas demonstrate the decreasing density from system 1 to system 3. The lowest density was observed in the monoculture. During the first four years none of the cupuaçu trees was shaded to a relevant extent by the neighbored plants either in the most dense system. Regarding the lack of direct interaction between the neighbored plants we expected no remarkable differences of plant development between the systems. But we observed significant differences of the vegetative development of the cupuaçu-plants, being advanced in system 1, intermediate in system 2 and minor in system 3. In the monoculture the development of the plants was most retarded. The fruit production in the third, fourth and fifth year of growth showed the same pattern: the highest productivity was observed in system 1, followed by system 2 and system 3. In the monoculture only very few plants developed fruits. Not only the production, but also the rise of productivity had the same order, which was highest in system 1 and lowest in the monoculture (Fig. 2).

The plant development and production corresponded with the density of the cultivation systems. This could be due to a higher quantity of fertilizer per area in the dense plantation systems. This hypothesis would be proof, if higher doses of fertilization would at least partially compensate the
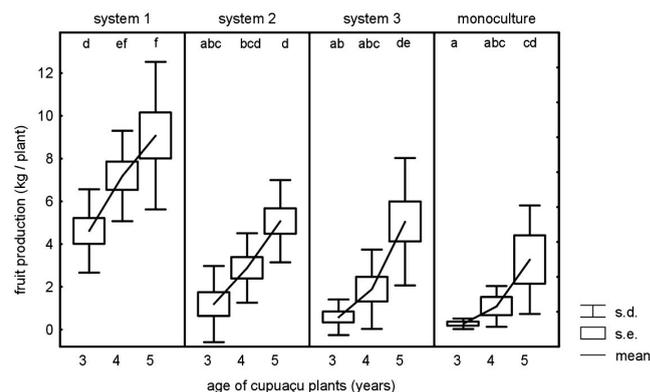

Fig. 2: Fruit production of cupuaçu trees in the four agroforestry systems after 3, 4 and 5 years. The mean values per plot of fruit production in kg per tree in the years 1996, 1997 and 1998 were analyzed by ANOVA (n=10 for system 1, 2 and 3, n=5 for the monoculture. Different letters at the top of the graph indicate significant differences at p<0.05 (Tukey's HSD test for unequal N). . (source: REISDORFF et al. unpublished)

observed "system effect". As mentioned before, every cultivation system existed in two variants. We observed only a slight tendency of higher productivity in the 100%-variants compared to the 30%-variants, which was not significant. Hence, the system effect was considerably stronger: Comparing for instance the 100-%-variant of system 3 with the 30-%-variant of system 1, we observed that the plants in system 1 were developed better and produced more fruits than the plants which received the threefold quantity of fertilizer in system 3 (Fig. 3). Thus, it seems not probable,
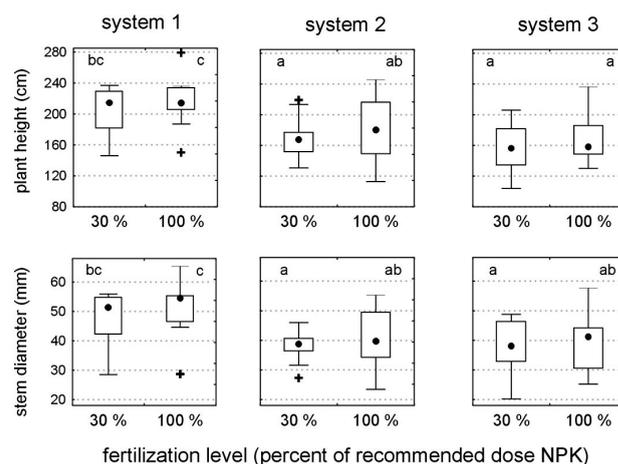

Fig. 3: Vegetative development of 3 years old cupuaçu plants in the three agroforestry systems at two fertilization levels.
Median, 25-75-percentile and range ("+" indicate outliers) of plant height and stem diameter. The mean values per plot were analyzed by ANOVA (n=10). Different letters at the top of the graph indicate significant differences at p<0.05 (LSD test).
(source: REISDORFF et al. unpublished)

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that the "system effect" is uniquely a result of an improved nutrient supply by fertilization in the dense systems.

Could favorable micro-climatic conditions in the dense plantation systems be responsible for the improved plant development? If the cupuaçu plants would be sensitive to slight differences of air humidity, then even micro-climatic gradients across the field should lead to measurable gradients of plant development. The experimental field is surrounded by primary and secondary forests. We measured a continuos gradient of decreasing humidity and increasing temperature from the forest border to the inner parts of the field, resulting in a twofold to threefold increase of vapor pressure deficit over a distance of about 50 meters (Fig. 4). The development of cupuaçu-plants showed a clear and significant gradient parallel to this climatic gradient, with best development in the most humid sphere near the forest (Fig 5). Hence, the micro-climatic influence on fruit production was less pronounced in humid years, and more pronounced in dry years, especially during the El Niño-phenomenon which was marked by extreme drought in the Central Amazon. Thus, we came to the conclusion, that the micro-climatic gradient must have influenced the water balance of cupuaçu plants, leading to less incidence of stress or at least leading to less water limitation of primary production in the micro-climatic sphere of the adjacent forest.

The effect of the microclimatic gradient was stronger in the open cultivation systems, whilst there was nearly no effect in the most dense system (Fig. 5). Hence, near the forest the

vegetative development of the cupuaçu plants in all systems was nearly equal. But with increasing distance to the forest the plants in the systems 2 and especially in system 3 were developed worse. These observations give evidence to the hypothesis, that in systems with higher planting densities the development and productivity of cupuaçu plants was favored by the stabilization of micro-climatic conditions which counteract rapid water losses during dry periods.

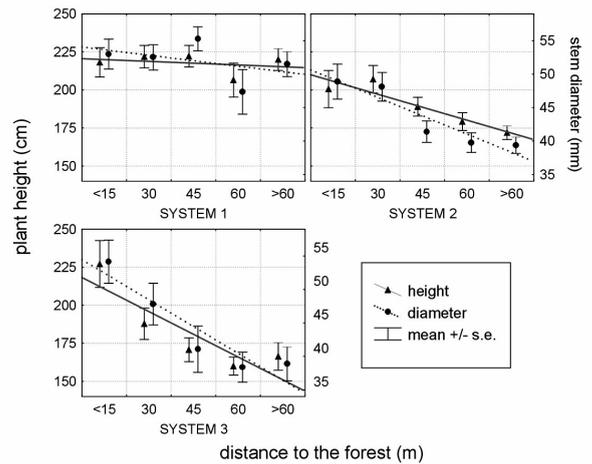This hypothesis rose the question, to which extent water

Fig. 5: The influence of the microclimatic gradient on the vegetative development of cupuaçu plants in agroforestry systems of different plant densities (relative densities: system 1 > system 2 > system 3). Plant height and stem diameter of 3 years old cupuaçu plants at increasing distances to the adjacent forest. Plot of mean values, standard error and linear regressions. Number of analyzed plants: 160 in system 1, 240 in system 2 and 80 in system 3. (source: REISDORFF et al. unpublished)

availability could be a limiting factor in the Central Amazon. The climate at the study site reveals, that in spite of the vast precipitation, relative dry periods of at least 6 to 20 days per month are common from June to September. Beside this seasonal dry periods, series of 3 to 5 days without precipitation occur nearly every month during the observed five years. Measurements of the water content of the top soil at different cupuaçu-stands showed that after only 4 days without rain the water potential especially near the cupuaçu trunk can fall rapidly towards critical values (data not shown).

In a drought experiment a five years old cupuaçu-tree was cut off from above ground water supply by sheltering its rooting area against rain. The water uptake of the tree could be followed by measuring the decrease of soil humidity. It became evident, that the water uptake was most intense in the upper soil layer, and the use of the water resources of deeper soil regions was very limited.

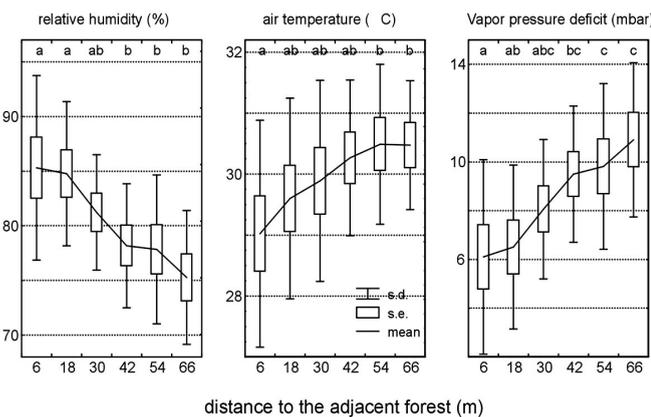The measurements of transpiration resistance during the

Fig. 4: Microclimatic gradient from the adjacent forest into the plantation. Data basing on measurements of wet and dry bulb temperatures with an aspirated Assmann psychrometer 1 m above ground at different days in march 1999 between 11 a.m. and 3 p.m. Different letters at the top of the graph indicate significant differences at p<0.05 (n=9, LSD test). (source: REISDORFF et al. unpublished)

drought experiment revealed, that decreasing water availability of the soil led to an increased reactivity of the stomata on vapor pressure deficit (VPD). A tendency of stomatal closure around midday has not been observed in any of the diurnal measurements. But the stomatal reaction on VPD becomes stronger in the course of a day indicating a progressive impairment of the water status of the plant. This is illustrated by Fig. 6 which compares graphically the models for stomatal resistance which have been developed on the basis of the diurnal transpiration resistances of the control plant and of the plant which suffered reduced water availability.

Could the observed range of stomatal resistance limit the CO_2 flux and, thus, the assimilation of cupuaçu leaves? The
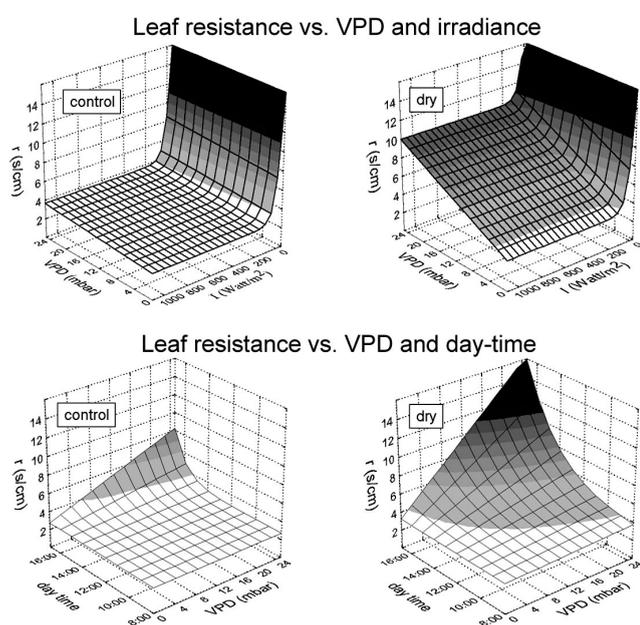
Fig. 6: Regression models of the stomatal reaction of cupuaçu plants on irradiance and on vapor pressure deficit in a day course. Regressions have been conducted on the basis of day courses of transpiration resistance of neighbored plants, from which one has been cut off from rain and above ground water flux ("dry" variant). The volumetric water content of the soil in the roots' catchment area was between 34% and 38% in the control and between 18% and 27% in the dry variant. The regression terms are:
control
$r=(8,8+0,14*VPD*e^{(-14,67+23,33*t)}+0,15*e^{(4,7-25,5*I\ 10\ ^{-3})})*0,31$ R=0,83; proportion of variance explained: 69,5%
dry
$r=(6,8+0,27*VPD*e^{(-4,84+8,91*t)}+0,15*e^{(4,7-25,5*I\ 10\ ^{-3})})*0,48$
R=0,86; proportion of variance explained: 73,1%
r: stomatal transpiration resistance (s/cm); VPD: vapor pressure deficit (mbar); t: day time (h);
I: global irradiance (Watt/m^2), e: Euler's e.
(source: REISDORFF et al. unpublished)

photosynthesis model developed by FARQUHAR & VON CAEMMERER (1982) was applied assuming a maximum rate of carboxylation at saturating intercellular partial pressure of CO_2 (V_{cmax}) of 100 and 50 $\mu mol*m^{-2}*s^{-1}$ respectively, and a rate of electron transport (J) of 140 and 70 $\mu mol * m^{-2} * s^{-1}$. These values cover the range which is referred in the literature for C_3-plants. The other parameters which are reported to be remarkably similar among higher plants (LAMBERS et al. 1998, JONES 1992) have been calculated according to FARQUHAR and WONG (1984) as follows: $\Gamma* = 41$ µbar, K_m=691 µbar, R_{day}=0,011*V_{cmax}. The resulting CO_2 demand functions are shown in Fig. 7. In the same graph two stomatal conductances for CO_2 are diagrammed as supply functions, indicating the operational range of the stomatal conductance of the examined cupuaçu plants (maximum at about g = 90 mmol m^{-2}*s^{-1} and minimum at about g = 30 mmol m^{-2}*s^{-1} ; hourly averages). The deduced relationship between the leaf conductance for CO_2 and the assimilation rates shows, that the actual rate of CO_2 assimilation could be lowered up to 50% or 60% respectively of the maximum rate by stomatal limitation of the CO_2 flux.

Thus, on the basis of diurnal courses of transpiration resistance it can be estimated to which extent the stomatal limitation potentially affect the carbon balance. In Fig. 8 this analysis is exemplified for a day in April 1999. The stomatal limitation of assimilation has been calculated on the basis of measured leaf resistances of the control plant and of the cupuaçu tree under reduced soil water availability. These calculations have been conducted using the demand functions assuming a carboxylation maximum V_{max} of 100 and 50 µmol * m^{-2} * s^{-1} respectively (values for the latter assumption in brackets). In addition it has been calculated to which extent a reduced vapor pressure deficit of the surrounding air could result in an attenuation of stomatal reaction and, thus, in a mitigation of stomatal limitation. For this purpose the recorded climate parameters for this day were fed in the model of transpiration resistance assuming a reduced VPD as in the microclimatic sphere of the forest. In the sum of the day the potential assimilation of the stressed plant was reduced to 73,2% (78,9%) in comparison to the control plant. This limitation was attenuated to 84,7% (88,8%) when the stomatal reaction was modeled assuming lower VPD (reduced to a magnitude that was observed to be characteristic for the microclimatic sphere of the forest). This means that under low water availability the potential primary production of cupuaçu plants in the microclimatic sphere of the forest could have been around 10 % higher than in the unmodified microclimate in the central parts of the field.
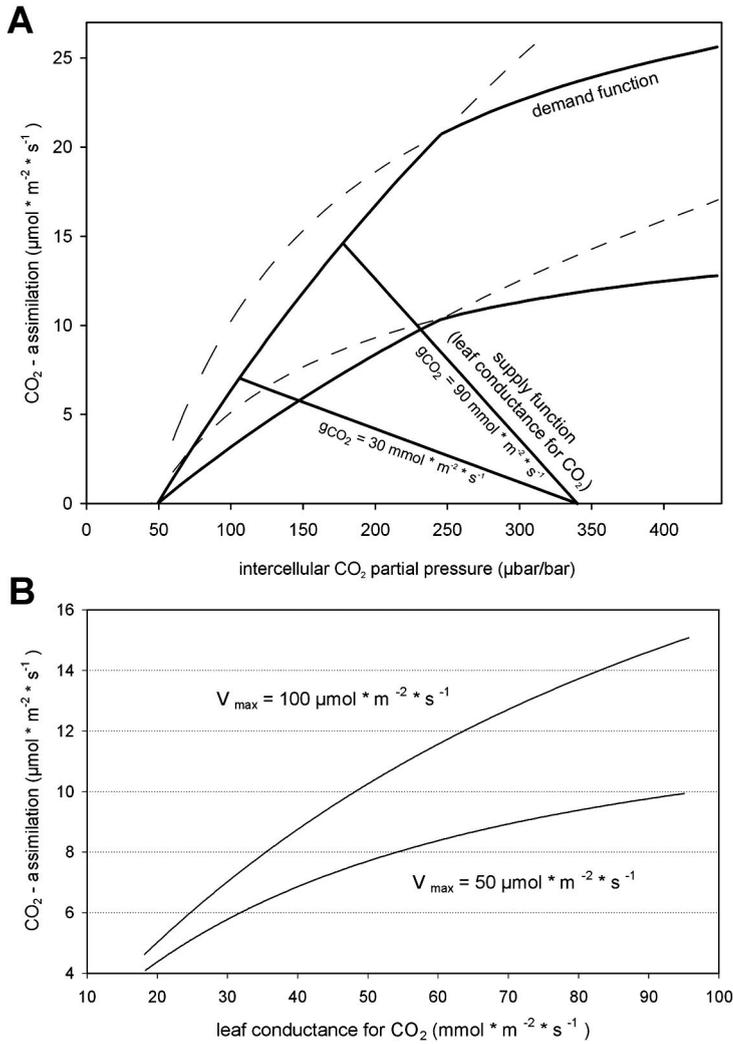
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A

B

Fig. 7: A) Relationship between the assimilation rate and the intercellular partial pressure of CO_2 for a model leaf of a C3 plant (demand functions), and the rate of diffusion of CO_2 from the atmosphere to the intercellular space limited by the leaf conductance (supply functions). B) Rate of assimilation versus the conductance for the metabolic characteristics shown in Fig. A. Graphical presentations according to the model proposed by FARQUHAR & SHARKEY (1982).

The demand functions in fig. A have been generated by the equations described in the materials and methods section, assuming a V_{cmax} of 100 (upper graph) and 50 $\mu mol*m^{-2}*s^{-1}$ respectively, a rate of electron transport (J) of 140 (upper graph) and 70 $\mu mol*m^{-2}*s^{-1}$, $\Gamma* = 41$ μbar, $K_m = 691$ μbar, $R_{day} = 0,011*V_{cmax}$. The two curves define a probable operation range of photosynthesis of C_3 plants like cupuaçu. The supply functions mark the operational range of leaf conductance for CO_2 of the examined cupuaçu plants. The intersections of the demand functions with the supply functions indicate the maximum of possible assimilation rates at the particular stomatal aperture. This is shown in Fig. B which depicts the relationship generated by varying the "supply function". (source: REISDORFF et al. unpublished)
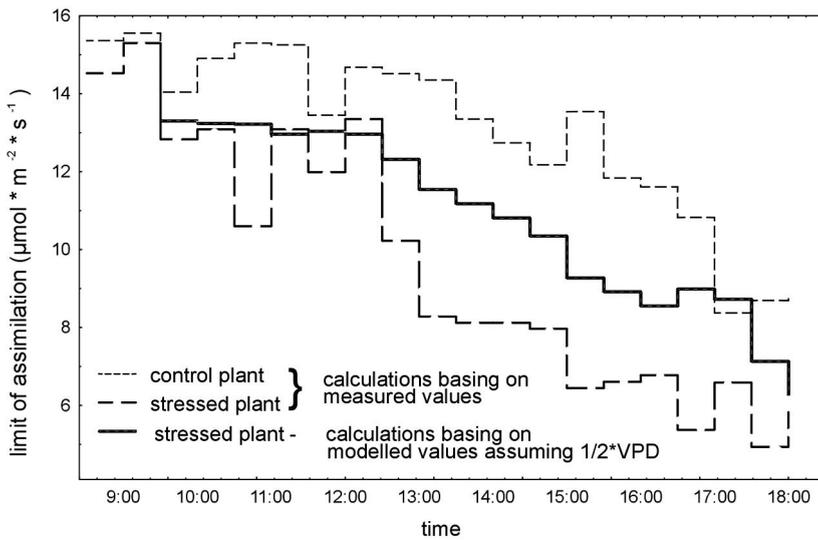

Fig. 8: Example for potential stomatal limitation to assimilation in a day course. The stomatal limitation to the potential assimilation has been calculated on the bases of measured transpiration resistances of the leaves of the control plant and under reduced soil water availability, assuming a carboxylation maximum V_{max} of 100 $\mu mol * m^{-2} * s^{-1}$. In addition it has been calculated to which extent a reduced vapor pressure deficit could result in an attenuation of stomatal reaction and, thus, in a mitigation of stomatal limitation. For this purpose a day course of transpiration resistance was simulated by the stomatal model described in Fig. 6 using the recorded climate parameters of the respective day assuming halved values of the measured VPD. The CO_2-flux limited assimilation was calculated as described above. (source: REISDORFF et al. unpublished)

Since cupuaçu plants are characterized by a very slow increase of both above ground and below-ground biomass during the first two to three years (Voß et al., 1998), the soil volume colonized by fine roots and, thus, used for water uptake is comparatively small in this phase. Thus, a considerable incidence of water stress especially during the initial phase of the cultivation experiment has to be assumed. In the microclimatic sphere of the adjacent forest as well as in more dense cultivation systems the water stress was likely to be less pronounced. The data indicate that two additive factors could have led to the very effective mitigation of water stress in the more humid microclimates: A prolonged and stabilized water availability in the major catchment area of the cupuaçu roots and a lower incidence of stomatal limitation to assimilation.

4   References

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5   Acknowledgement

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