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Limiting factors for the establishment of *Cordia dodecandra* A.DC. and *Bixa orellana* L. on semi-arid calcareous soils in Yucatan, Mexico

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D 98

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ABSTRACT

In Northern Yucatan, huge areas of abandoned sisal plantations, now assigned to the communities, require agroforestry management strategies that take into account the high spatial variability of soil, the lack of surface water, and the generation of income for farmers. To meet this challenge, an experimental plantation with the indigenous multi-purpose tree species *Cordia dodecandra* A.DC. (Siricote) for production of fruits and highly valuable timber and the food coloring crop *Bixa orellana* L. (Achiote) was established. The objective was to investigate the relationship between nutrient and water availability on the two dominant soils as limiting factors for growth of the two species and for nutrient uptake of *C. dodecandra*.

A total of 184 circles of four m diameter were planted with eight plants, each with four *C. dodecandra* and four *B. orellana* on red Cambisol and black Leptosol. Seven fertilizer treatments were applied in minus-one-trials (complete fertilizer minus N, P, K, Mn, and Zn), with three irrigation levels. An additional treatment consisted in the inoculation of seedlings with exotic VA mycorrhizae. The irrigation levels were defined as regular irrigation during the dry season, sporadic irrigation at the peak of dry season only, and a non-irrigated control. *C. dodecandra* trees from homegardens were used as a reference for the evaluation of foliar nutrient levels of *C. dodecandra* seedlings.

Results show that on calcareous semi-arid Yucatan soils, nutrient-water interactions and the availability of P, K, and Mn limited growth of *C. dodecandra*. Growth on Cambisol with adequate water supply was limited by low availability of P, K, and Mn. On Leptosol with adequate water supply, low K availability was a growth-limiting factor. When water was scarce, low P availability had a significant impact on growth on both soils. Our data indicate the importance of P-Zn interactions for nutrient uptake of *C. dodecandra*. The application of P fertilizer interfered with Zn uptake, while Zn applications had a negative impact on foliar P levels. Foliar nutrient concentrations of *C. dodecandra* trees in homegardens indicated a potential deficiency of P, Zn and Mn. On the experimental area, foliar Mn and Zn levels on both soils were at the lower limit for adequate growth. Nitrogen did not seem to be a growth-limiting element on none of the two soils. Inoculation of *C. dodecandra* with a mixture of *Glomus mosseae*, *Glomus intraradices* and *Glomus deserticola* reduced both survival as well as growth of seedlings. The dominant influence on survival and growth of *B. orellana* was water availability during the dry season. Although water availability had a major impact on growth of *C. dodecandra* as well, survival during the dry season of this species was high (between 93 and 96%) regardless of irrigation. *C. dodecandra* established and grew well on both soils with only sporadic irrigation during the dry season.

C. dodecandra seems to be suitable as a major component of agroforestry systems in Northern Yucatan, providing farmers a promising management option for degraded sisal plantation lands. The planting of *B. orellana* is recommended if regular irrigation during the first dry season is feasible. The inoculation of seedlings with exotic VA mycorrhizae is not advisable. The impact of low availability of P, K, and of the micronutrients Zn and Mn on plant growth and yields should be investigated further in order to develop measures for mitigation of low nutrient availability on Yucatan soils.

ZUSAMMENFASSUNG

Im Norden Yukatans befinden sich weitgehend unbewirtschaftete Flächen ehemaliger Sisalplantagen im Besitz der Gemeinden. Für diese sind Rekultivierungsstrategien gefragt, die die hohe räumliche Bodenvariabilität, das limitierte Wasserangebot und den Mangel an Einkommensmöglichkeiten für die Bauern berücksichtigen. Aufgrund dessen wurde eine Versuchsplantage mit der heimischen Baumart *Cordia dodecandra* A.DC. (Siricote) und dem Busch *Bixa orellana* L. (Achiote) angelegt. Während die Samen von *B. orellana* Lebensmittelfarbstoff liefern, produziert *C. dodecandra* Früchte und Wertholz. Das Ziel dieser Arbeit war die Erforschung der Bedeutung von Nährstoff-Wasser-Interaktionen für die Nährstoffaufnahme von *C. dodecandra* sowie für das Wachstum der beiden Spezies auf den zwei dominanten Bodentypen der Region.

Auf rotem Cambisol sowie auf schwarzem Leptosol wurden insgesamt 184 Kreise mit einem Durchmesser von vier m mit je vier Individuen von *C. dodecandra* und *B. orellana* bepflanzt. Sieben Düngervarianten wurden als substraktive Mischungen (Komplettdünger minus N, P, K, Mn und Zn) appliziert. Für die Dauer der Trockenzeit wurden drei Bewässerungsstufen definiert: Regelmäßige, sporadische sowie keine Bewässerung. Zusätzlich wurde eine Anzahl Setzlinge vor dem Pflanzen mit exotischen vesikular-arbuskulären (VA) Mykorrhizen inokuliert. *C. dodecandra* aus Hausgärten dienten als Referenz für die Bewertung der Blattnährstoffwerte der Versuchsplantage.

Die Ergebnisse zeigen, dass sich in Nord-Yukatan Nährstoff-Wasser-Interaktionen und die Verfügbarkeit von P, K und Mn je nach Bodentyp limitierend auf das Wachstum von *C. dodecandra* auswirken. Bei Bewässerung während der Trockenzeit wurde das Wachstum auf Cambisol durch die geringe Verfügbarkeit von P, K und Mn begrenzt, während sich auf Leptosol allein die geringe Verfügbarkeit von K wachstumslimitierend auswirkte. Bei fehlender Bewässerung hatte die geringe Phosphorverfügbarkeit auf beiden Böden eine limitierende Wirkung. Phosphor-Zink-Interaktionen beeinflussten die Nährstoffaufnahme dieser beiden Elemente. Blattnährstoffgehalte von *C. dodecandra* in Hausgärten wiesen auf einen potentiellen Mangel an P, Zn und Mn hin. Auch auf der Versuchsfläche waren die Mangan- und Zinkgehalte der Blätter auf beiden Böden gering. Die Stickstoffversorgung hatte auf keinem der beiden Böden eine wachstumslimitierende Wirkung. Die Wasserverfügbarkeit während der Trockenzeit war der Haupteinflussfaktor für das Überleben und das Wachstum von *B. orellana*. Im Gegensatz dazu wurde zwar das Wachstum der *C. dodecandra* Setzlinge, nicht aber ihre Überlebensrate während der Trockenzeit (zwischen 93 und 96%) von den Bewässerungsstufen beeinflusst. *C. dodecandra* erzielte mit geringem Bewässerungsaufwand auf beiden Böden hohe Wachstumsraten. Die Inokulation von *C. dodecandra* mit einer Mischung aus *Glomus mosseae*, *Glomus intraradices* und *Glomus deserticola* verringerte sowohl das Überleben als auch das Wachstum der Setzlinge.

Die in Yukatan heimische Baumart *C. dodecandra* bietet gute Voraussetzungen für den erfolgreichen Einsatz in Agroforstsystemen im Norden Yukatans. Der Anbau von *B. orellana* wird nur dann empfohlen, wenn ausreichende Bewässerung gewährleistet werden kann. Der Einsatz von exotischen VA Mykorrhiza ist nicht ratsam. Eine weitergehende Erforschung der Auswirkungen der geringen Verfügbarkeit von P, K, Zn und Mn sowohl auf das Pflanzenwachstum als auch auf die Erträge wird empfohlen. Zudem sollten nachhaltige Maßnahmen zur Verbesserung der Nährstoffversorgung auf den Böden der Region entwickelt werden.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABBREVIATIONS

AAS	Atomic absorption spectrometry
ANOVA	Analysis of variance
appl.	Application
CONABIO	Comisión Nacional para el Conocimiento y Uso de la Biodiversidad
CONAFOR	Comisión Nacional Forestal
contr.	Control treatment
dbh	Diameter at breast height
df	Degree of freedom
DFG	Deutsche Forschungsgemeinschaft
EEV	Equality of error variances
EM	Ectomycorrhizal
expl.	Explanations
FAO	World Food and Agriculture Organization of the United Nations
fert.	Complete fertilizer treatment
IAI	Inter-American Institute for Climate Change Research
IAT	Institute of Agronomy in the Tropics
ICP-AES	Inductively coupled plasma atomic emission spectrometry
ICRAF	World Agroforestry Centre
INIFAP	Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias
ITA	Instituto Tecnológico Agropecuario
L	Liter
max	Maximum
min	Minimum
NS	Non-significant
Protrópico	Departamento de Manejo y Conservación de Recursos Naturales Tropicales
SE	Standard error
seedl.	Seedling
SIRE	Sistema Nacional para la Reforestación en México
SPFEQROO	Sociedad de Productores Forestales Ejidales en Quintana Roo
sti	Stem length increment
UADY	Universidad Autónoma de Yucatán

UNAM	Universidad Nacional Autónoma de México
VA	Vesicular arbuscular
VAM	Vesicular arbuscular mycorrhizal
VAMF	Vesicular arbuscular mycorrhizal fungi
vdi	Virtual diameter increment
WHO	World Health Organization of the United Nations
YFML	Youngest fully matured leaves
ZEF	Center for Development Research

1 INTRODUCTION

Due to the predominance of sisal (*Agave fourcroydes* Lem.) plantations in Northern Yucatan during the past 150 years, the economic importance of trees outside of the traditional homegardens has largely been neglected in the region. Few farmers in Northern Yucatan realize or use the benefit of native trees as supplier for multiple services and goods such as shadow and shelter for animals, food, medicines, and timber for construction and furniture, outside their traditional homegardens. After the abandonment of sisal production in the 'Henequén area', plantation lands were assigned to the communities (Nickel, 1995). The present challenge is to develop, based on Mayan farmers' traditional experience, agroforestry systems for the recultivation of the plantation areas that improve livelihoods and are adapted to the climatic and soil conditions of Northern Yucatan.

A number of native tree species are promising candidates as tree components for such recultivation schemes. To guarantee survival and growth of seedlings, suitable species have to be adapted to the rough environmental conditions of the Northern Peninsula. The native multi-purpose tree *Cordia dodecandra* A.DC. (Siricote) (Boraginaceae) was reported to establish and grow well during the first years (Flachsenberg, 2002). *C. dodecandra* produces timber with higher export market value than Mahogany (*Swietenia macrophylla* King). Fruits of Siricote are sold for the traditional dessert 'Dulce de Siricote'. Leaves serve as a substitute for sandpaper, and the bark of trees is used for medicinal purposes. Due to the roughness of the leaves, goats do not harm the seedlings, and soon benefit from shade and shelter provided by the tree. *C. dodecandra* can be combined with corn or other annual or perennial crops as well as with small ruminants (Vlek et al., 2004).

Due to high value timber of *C. dodecandra*, it has been extracted to the limits of a sustainable forest management of the species during the last century. Siricote is nowadays classified as an endangered species, and adult species in Southern Yucatan are found only in remote parts of the area that is used for forest extraction by the villages.

Homegardens of Mayan small scale farmers in the Yucatan Peninsula show a high plant diversity that ranges between 23 and 387 species per homegarden (Ruenes Morales et al., 1999). Among the frequently planted tree species there are many fruit trees such as the local species *Manilkara zapota*, several *Citrus species* and crops for local and export markets such as the food colorant bush Achiote (*Bixa orellana* L.). *B. orellana* was planted successfully in agroforestry plots in Southern Quintana Roo by ICRAF (Haggar, 2002).

It is difficult to give recommendations for successful management of tree and crop plantations in Northern Yucatan, because of the high spatial variability of soils, generally black Leptosols (Tsekel) and red Cambisols (Kankab). The predominant soils of the Northern Peninsula are stony and shallow; with depths of less than 20 cm. Soil fertility is highest in the shallow topsoil. According to Weisbach et al. (2002), in red and black soils nutrient availability and soil moisture seem to be closely interconnected. Forest trees in central Yucatan showed deficiencies in N, P, Zn and Mn (Zech et al. 1991). With predominantly high evaporation and a five-month drought period, water availability is important for growth and survival of plants. Hurricane occurrence presents a threat to planted seedlings and trees.

In September 2002 hurricane Isidore reduced tree cover in some communities by up to 70%, and farmers are now becoming interested in re-establishing lost tree cover and hence in using the potential of native tree species. So far, farmers in the Northern Peninsula have rarely established small-scale plantations of indigenous multi-purpose trees to obtain additional income. In contrast communities in Southern Yucatan, where climatic and soil conditions are more favorable, are well aware of the commercial value of timber of indigenous species. Southern farmers have established agroforestry plots and small-scale plantations with species such as *C. dodecandra* on their own account.

Farmers in Northern Yucatan still need detailed information on the adaptability and successful management of potential indigenous species in order to recultivate abandoned sisal plantations most effectively. Gaining experience with the establishment of native tree species is the first step to create economically and ecologically sustainable agroforestry systems on the abandoned plantation land. The present lack of knowledge on how these indigenous tree species develop on the dominant soil types of Northern Yucatan has to be addressed (CONAFOR, 2004a).

The objective of the present study was to determine the suitability of *C. dodecandra* and *B. orellana* for the establishment of agroforestry schemes on stony soils with limiting precipitation, and hence to identify the major factors influencing survival and growth of seedlings, considering nutrient and water availability, different soils and the impact of exotic VA mycorrhizae.

The specific objectives were

1. to evaluate the interrelation between irrigation and nutrient availability on calcareous semi-arid soils in Yucatan, and its impact on survival and growth of tree seedlings of *C. dodecandra* and *B. orellana*.
2. to determine the importance of the macro- and micro-nutrients N, P, K, Zn, and Mn for growth and nutrient uptake of tree seedlings of *C. dodecandra* on calcareous semi-arid soils in Yucatan.
3. to assess the effect of exotic vascular arbuscular (VA) mycorrhizae on survival and growth of tree seedlings of *C. dodecandra* on calcareous semi-arid soils.

Hypotheses

1. Under the soil and site conditions in Yucatan, low water availability limits growth and survival of tree seedlings of *C. dodecandra* and *B. orellana*.
2. On the calcareous semi-arid soils of Yucatan, low availability of N, P, K, Zn, and Mn, in combination with low water availability limits seedling growth and nutrient uptake of *C. dodecandra*.
3. The inoculation with exotic strains of vascular arbuscular (VA) mycorrhizae enhances survival and growth of *C. dodecandra* on calcareous semi-arid Yucatan soils.

2 BACKGROUND INFORMATION AND STATE OF KNOWLEDGE

2.1 Study area

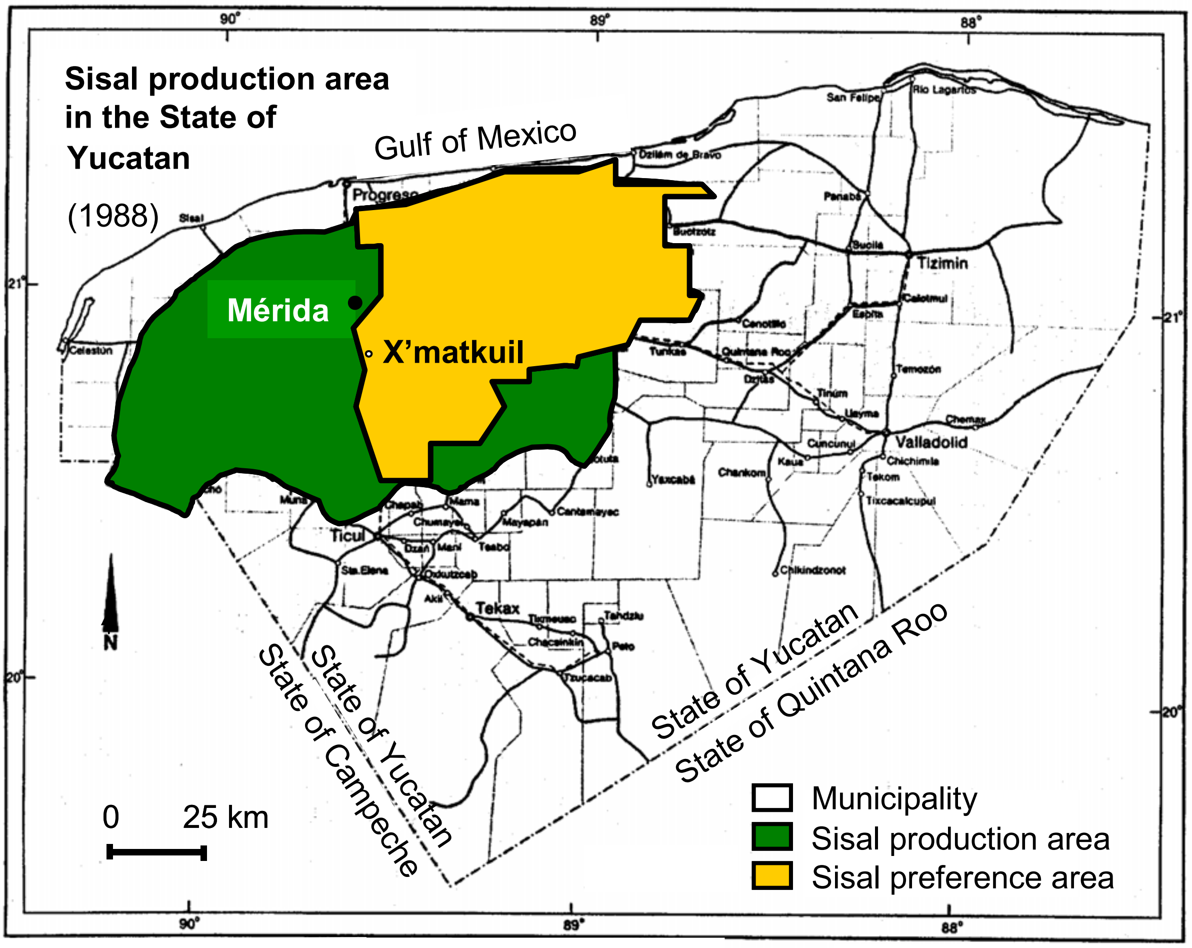

Figure 1: Sisal production area in the State of Yucatan, Mexico (Nickel, 1995, modified)

The Yucatan Peninsula is located in southern Mexico, comprising the States of Yucatan, Quintana Roo and Campeche. The area of abandoned *A. fourcroydes* plantations for sisal production is situated in the northern part of the Peninsula, in the State of Yucatan (Nickel, 1995) (Figure 1). The high percentage of stones and rock fragments of Yucatan soils combined with the absence of aboveground rivers and creeks present a challenge for agricultural land use.

2.2 Climatic conditions

The climate of the Peninsula is characterized by a humidity gradient ranging from semi-arid climate in the North part to sub-humid climate in the South (Balam Ku et al., 1999; Duch, 1988; Escobar, 1986). There is a pronounced dry period from January to May/June, with highest temperatures in April and May that is an important factor in crop production of the Maya. The dependence of farmers on erratic precipitation events and the occurrence of tropical cyclones pose a risk to farming activities (Hernández

Xolocotzi et al., 1995). Hurricanes and storms occur in Yucatan in regular intervals, typically in September and October during rainy season. During this study, hurricane Isidore destroyed great part of infrastructure, trees and crops in Northern and central Yucatan in September 2002. It was accompanied by strong rainfall and winds with velocities of up to 220 km/h.

2.3 Land use in Northern Yucatan

The decades of *A. fourcroydes* plantations in Northern Yucatan had a detrimental effect on soils regarding further agricultural production, as the removal of the vegetation cover and the exposure of the soil fostered erosion of the surface soil and an increase in stoniness (Duch, 1995). The traditional land use practice is corn production (so-called milpa), a slash-and-burn cultivation cycle with fallow intercalated by corn. *Zea mays* (corn) is combined with other crops such as pumpkin (*Cucurbita species*), beans (*Phaseolus species*), and tropical chickpea (*Vigna unguiculata* L.) (Hernández Xolocotzi et al., 1995). At least 17 years of fallow are necessary for regeneration of the soil after one to tree years of crop production. Due to increasing pressure on the land, the fallow period is shortened. This leads to a decline in productivity, in addition to the loss of organic material and the volatilization due to burning. In the former sisal production zone, corn yields of 700 and 500 kg/ha for the first and second year after burning were reported. The stoniness of the soil makes the use of conventional agricultural machinery impossible (Arias, 1995).

Red Cambisol and black Leptosol represent different challenges to farmers. On shallow red Cambisol, corn plants easily bend. On deeper Cambisol, weeds tend to develop very fast. Seed germination rate is higher on red soils than on black soils on terrain elevations. Black Leptosols only provide a limited area for planting, due to their high rocky- and stoniness. Different soils are preferred for specific crops. On black Leptosol and shallow red Cambisol, typical crops are *Zea mays*, *Phaseolus species*, and *Cucurbita species*. Due to the absence of rocks and stones, deeper Cambisols are chosen for a variety of other crops such as Yucca (*Manihot esculenta*) (Estrada Medina, 2000). There is little knowledge on preferred tree species for different soil types, as there is not much practice of tree planting in the Northern Peninsula. Farmers from the community Hocaba mentioned *Bursera simarouba* and *Piscidia piscipula* as tree species that grow fast on Cambisol (Estrada Medina, 2000). Latin-American Cedar (*Cedrela odorata)* was recommended by foresters of the State of Yucatan as a species apt for establishment on stony Leptosol (CONAFOR, 2003; Reuter et al., 1998).

2.4 Dominant native tree species in Yucatan forests

The forest cover of the Yucatan Peninsula is dominated by forests with dominant trees of the upper stratum of more than 15 m of height (“selva mediana”). In the Northern part of the Peninsula, deciduous forests of 10 to 15 m height are primarily found, with dominant native tree species such as Kitamche (*Caesalpinia gaumeri*) and Jabin (*P. piscipula*) (Pennington and Sarukhan, 1998; Flores and Gerez, 1994). In the Northern part of the State of Yucatan, in areas of low precipitation, low deciduous thorny tropical forests with Cactaceae (*Nopalea cohenellifera*) and Leguminosae families (*Acacia pennatula, Acacia cornigera*) are found (forest classification according Miranda, 1958; Flores and Gerez, 1994). A major commercial tree species known to be adapted to the climate and soil conditions is Latin-American Cedar (*C. odorata*). In a 12-year-old stand in dry tropical secondary vegetation on abandoned Henequén plantations, fast-growing *Cordia alliodora* had the highest seedling density (Mizrahi Perkulis et al., 1997). The well-known tree species of high commercial value of the medium sub-evergreen forests of the Southern Peninsula is Mahogany (*S. macrophylla*). A wide range of lesser-known tree species with valuable timber such as *C. dodecandra* accompanies it (Pennington and Sarukhan, 1998; Reuter et al., 1998; Flores and Gerez, 1994).

2.5 Mayan homegarden tree and crop species

Mayan farmers cultivate homegardens (so-called solares) with a high variety of tree and crop species of socio-economic importance. Some of the structural homegarden species are native fruit trees such as Tropical Cherry (*Spondias purpurea*), Nance (*Byrsonina crassifolia*), and Mamey (*Pouteria mammosa*), and fodder providing species such as Ramón (*Brosimum alicastrum* Sw.). Multi-purpose species such as Siricote (*C. dodecandra*) and *M. zapota* provide both valuable timber and a variety of other products (Ruenes Morales et al., 1999; Vara Morán, 1995). Local crops include Papaya (*Carica papaya* L.) for fruit and Achiote (*B. orellana*) for food colorant production.

Tree species have to be adapted to the rough environmental conditions to guarantee survival and growth of seedlings. The valuable timber tree species *Cedrela odorata* qualifies for plantations on poor soils because of its ability to grow on shallow soils with a low nutrient content. Latin-American Cedar plantations, though, are susceptible to damages by the shoot borer *Hypsipyla grandella*. The fodder tree species *Brosimum alicastrum* is reported to be tolerant to drought, and seems superior on stony shallow sites (Gillespie et al., 2004; Snook, 1993; Evans, 1992; Lamprecht, 1986; National Academy of Science, 1976; Pennington and Sarukhan, 1998).

2.5.1 *Cordia dodecandra*

The native multi-purpose tree *C. dodecandra* A.DC. (Siricote) from the family Boraginaceae was reported to establish and grow well during the first years (Flachsenberg, 2002). *C. dodecandra* produces timber with higher export market value than mahogany (*S. macrophylla*). In 2002, the price for *C. dodecandra* roundwood on the national market was more than twice as high as the price for *S. macrophylla* roundwood (Ferral, 2002). Fruits of *C. dodecandra* are sold for the traditional dessert “Dulce de Siricote”. Leaves serve as substitute for sandpaper, and the bark of trees is used for medicinal purposes. Due to the roughness of its leaves, goats do not harm the seedlings, and soon benefit from shade and shelter provided by the tree (Vlek et al., 2004). Synonyms are *Cordia angiocarpa* A.Rich., *Cordia heccaidecandra* Loesener, *Cordia dodecandria* S. and M. and *Plethostephia angiocarpa* (A.Rich.) Miers.. Common names for *C. dodecandra* include Ciricote or Siricote (on the Yucatan Peninsula), Trompillo (Veracruz), Cupapé (Chiapas), Palo de Asta (Guatemala) and the Mayan name K’opté. The name K’opté contains the Mayan word “té” meaning very hard wood (Pennington and Sarukhan, 1998; Ucán Ek, 1983).

In Northern Yuacatan, *C. dodecandra* is found in Mayan homegardens, where it is part of the upper canopy stratum. *C. dodecandra* is listed as one of the species in danger of extinction (Flores and Gerez, 1994). It was registered in Mexico in the Southern States of Veracruz, Chiapas, Campeche, Quintana Roo and Yucatan, as well as in Belize and Eastern Guatemala. *C. dodecandra* grows up to a height of 30 m, with diameters of up to 70 cm and a straight bole. The ascending branches form a dense crown with a rounded or pyramidal shape (Pennington and Sarukhan, 1998). The tree has a strong taproot (Jankiewicz et al., 1986). The bark is ash-gray, 10 to 20 mm thick. It is used as a dying agent for sisal fibers, and for the preparation of a remedy against coughs. The softwood is light yellow, while the heartwood is greenish brown to dark brown with large vessels, short and conspicuous rays, vasicentric parenchyma, aliforme, and some paratracheal bands. The decorative pattern of the heartwood, with blackish brown streaks on olive-brown background, and its high durability made it a highly appreciated timber for high-quality veneer, as well as decorative furniture and ornamental pillars. It has been widely used for construction, for doors, windows, beams and railroad ties. Small parts of heartwood were used for handicraft and small wooden sculptures. The high price of the timber resulted in over-exploitation for the national and international market during the past decades, and led to regulations restricting the harvesting of this species. At present, special permits are required before harvesting Siricote, in order to prevent extinction of this valuable timber species (Ferral, 2002; Pennington and Sarukhan, 1998; Ucán Ek, 1983).

C. dodecandra flowers and bears fruits in the dry season. Flowers have a green-yellow calyx of 1.5 to 2 cm length and a 4 to 6 cm long corolla of intense orange color, with 12 to 13 stamens of varying length, the longest as long as the corolla (Pennington and Sarukhan, 1998). Potential pollinators probably include insects similar to those pollinating *Cordia alliodora*: in humid as well a in dry areas of Costa Rica, bees, wasps, butterflies, beetles and flies (of the orders of Coleoptera, Diptera, Hymenoptera and Lepidoptera) visit its flowers (Boshier and Lamb, 1997). *C. dodecandra* is used for apiculture (Villanueva, 1989). Fruits of *C. dodecandra* are conic drupes of up to 5 cm diameter. They are yellowish-green, have a thick skin and a highly lignified stone with one to two seeds. The fruit is cooked in sugar, consumed or sold as a traditional Yucatan dessert ("Dulce de Siricote"). It tastes similar to potted fig. At room temperature, fresh fruits can be stored for a week. Seeds are also edible (Pennington and Sarukhan, 1998; Jankiewicz et al., 1986; Ucán Ek, 1983). Leaves are dark green on the upper side and light green on the reverse, oval to elliptic, with a surface of 5.5 by 4 to 12 by 9 cm, and petioles of 10.8 to 3 cm. Their surface is hairy and rough (Pennington and Sarukhan, 1998). Therefore, Mayan carpenters use them to soften timber, and by Mayan farmers they are traditionally used to clean dishes, especially bowls made out of the fruits of *Crescentia cujete*. In some villages this is still a common practice (Rojas Lara, 2004). Leaves may be stored dry and wetted again before use (Ucán Ek, 1983). The tree bears fruits from the age of 3 to 4 years on, and produces timber after 25 to 30 years (Montañez, 2002). The fruit yield from 5- to 8-year-old trees is 10 to 15 kg/tree (Jankiewicz et al., 1986).

2.5.2 *Carica papaya*

Carica papaya L. (*Caricaceae*) is native to southern Mexico and neighboring Central America. It is now cultivated in tropical and subtropical countries on a worldwide scale. It is a short-lived, fast-growing crop that attains heights of up to 8 m. Papaya is propagated by seeds. It flowers 5 months after sowing. Five months later, the fruit matures. The fruit is between 10 and 50 cm long, and has a weight of up to 7 kg. Fruits that are produced for commercialization have a weight of 0.5 to 2 kg, and a length of 10 to 20 cm. (Wichmann, 2001; California Rare Fruit Growers, 1997; Samson, 1991; Aguirre and Amo, 1983).

Apart from the traditionally cultivated varieties, Papaya 'Maradol' was planted by an increasing number of farmers in Yucatan from 1996 on. In 2001, due to its high commercial value in comparison to citrus and sisal production, the annual production had reached 61,000 t in Northern Yucatan. But since 1999 virus infection – known as "mosaico" - started to severely damage Papaya plantations, reducing the plantation area in parts by 95%, and increasing the risk for farmer's plantations in Northern Yucatan (Anonymous, 2002; Samson, 1991; Aguirre and Amo, 1983).

2.5.3 *Bixa orellana*

Bixa orellana L. (Achiote) is another structural species of Mayan homegardens. An established local and export market for seeds of *B. orellana* exists in Yucatan, due to the use of seeds for the production of food colorant (Godoy Hernandez, 2002). Common names of *B. orellana* include Achiote, Bija (Spanish), Urucú (Portuguese), Kesumba (Indonesian) and Annatto (English and French). *B. orellana* from the family Bixaceae originated from the Amazon region, and was distributed to Argentina and up to Southern Mexico in pre-Columbian times. Nowadays, it is used in agroforestry schemes on a worldwide scale. Main producing countries include Bolivia, Brazil, the Dominican Republic, Guatemala, Kenya and the Ivory Coast. There is an increasing demand for *B. orellana* seeds in Northern America and the European Union. The extract from pigment coating the seed called bixina is used as a yellow-reddish food colorant, especially for dairy products. The dye is also used for manufacturing cosmetics. In Mexico, Spain and the Philippines, it is added as a condiment to traditional dishes such as "Pollo Pibil" in Yucatan. Relative to standards of the World Health Organization (WHO), *B. orellana* has a high protein content, and was found to be rich in iron (Glew et al., 1997). It is an ingredient of poultry fodder, increasing the yellow color of the yolk of eggs. Leaves and roots have medicinal uses. The species is meliferous.

B. orellana is an evergreen shrub or small tree of generally less than 4 m height, but occasionally reaching up to 8 m. Leaves are 8 to 20 cm long. The fruit is a capsule, opening in two, that contains numerous seeds of 4.5 mm length, with bright orange-red coats. Fruit production under favorable conditions starts after 18 months or earlier and full crops of seeds can be expected after 3 to 4 years (Geilfus, 1994; ICRAF, 2005; Godoy Hernandez, 2000). Achiote prefers well-drained, slightly alkaline soils (ICRAF, 2005). It requires a minimum annual precipitation of 1000 mm, and grows best at 2000 mm (Geilfus, 1994). *B. orellana* was found to develop an extensive rooting system, especially close to the soil surface (Voß et al., 1998).

2.6 Soils of Yucatan

The Peninsula is described as a flat calcareous plain. It is a karstic region with an altitude of 0 to 20 m above sea level in the northern part (Seele, 2001). The predominantly tertiary limestone is of marine origin. It is slightly undulated, with scattered convex mounds with gentle slopes of often less than 3 m height. Shallowness and areas where bare limestone is exposed characterize the highly heterogeneous soils of the region (Duch, 1995 and 1988). Typically, soil organic matter content is high (Reuter et al., 1998).

Characteristic for the soils of Yucatan is their high spatial variability. On a small plot of 20 m x 20 m, the occurrence of two completely different soils – such as the stony shallow black Leptosol, and red Cambisol – is very likely. According to the World Reference Base for Soil Resources (FAO, 1998), there are Rendzinas, Leptosols, Cambisols, and Vertisols. The Mayan soil classification of the Yucatan Peninsula is based on Mayan farmers' knowledge about the soils of the Peninsula. They distinguish between two major soil classes according to their position in the micro relief and their color. Boxlu'um are black soils on top of mounds, with its variant Tsekel describing black soil between stones, while Kankab is defined as red soils on flat areas (plains). Each of the two soil classes is divided into sub-classes, considering differences in color, depth, as well as in stoniness, rockiness, type of rocks, and other characteristics (Estrada Medina, 2000).

Considering the water budget of calcareous soils of Yucatan, drainage is the main factor for water losses. Free drainage is characteristic for calcareous soils (Jeffrey, 1987). Soil evaporation accounts for water losses to some extent. It takes place at shallow soil depths, typically below 15 cm, and varies considerably over time due to soil temperature changes (Ben-Asher et al., 1983). In calcareous Yucatan soil, the first rock layer or rock fragment is often found at less than 15 cm. The calorific values of the rock fragments tend to increase soil temperature and hence contribute to high evaporation. Because of the characteristic features of the micro relief, runoff is very low. Infiltration may have a high spatial variation due to the different types of rocks typical for the soil series (Estrada Medina, 2000).

Soil permeability increases with the porosity of the soil or rock layer, and is further influenced by texture and aggregate structure. Soils with higher sand content generally have higher infiltration rates (Dingman, 1994). Sandy soils have very low water content in comparison to clayey soils (Rowell, 1994). Tsekel soil (Leptosol), in comparison to Kankab soil (Cambisol), has a very high infiltration rate, due to its coarser texture, high porosity of the rock sediment underneath and higher solubility of rock layers (Reuter et al., 1998; Estrada Medina, 2000). Therefore, with sporadic irrigation, water infiltrates more rapidly in black soil, while in red Cambisol, it is retained in upper soil layers by the finer texture. This water is then directly available to roots, and contributes to the availability of soil nutrients.

2.7 Hydrological conditions

The rivers and creeks of the Yucatan Peninsula are subterranean and interconnected. In Northern Yucatan, the ground water table is at a depth of 8 m. The karstic landscape with gentle terrain elevations and the calcareous soil substrate favour fast infiltration of rainfall. This led to the formation of sinkholes temporarily filled with water (so-called sartenejas) and natural ponds of over 80 m depth (so-called cenotes), as well as grottos and underground rivers. The local population has used these water reservoirs since the time of the Ancient Maya, when they had a religious connotation (Escobar, 1986; Reuter et al., 1998; Duch, 1995 and 1988). Drought may have caused the collapse of Maya Civilization in the Terminal Classic Period (Haug et al., 2003). Drought stress has a strong impact on plant growth, because of its effects on carbohydrate metabolism, photosynthetic efficiency, and plant water status (Escobar Guti et al., 1998; Epron, 1997; Massaci et al., 1996; Paakkonen et al., 1998). In semi-arid regions in the subtropics, water deficit is combined with high temperatures that may aggravate the negative effect on plant growth.

2.8 Nutrient availability

Though nutrient stocks in the dry tropics are high, their availability is low and the melioration of these soils difficult. Major limits to nutrient availability for plants are drought and – on calcareous substrate – sorption of essential nutrients (Becker and Asch, 2004). Calcareous soils may possess low absolute quantities of macronutrients, especially phosphate, potassium and nitrogen. At pH values above 7.5, the availability of phosphate, manganese, zinc, copper and iron is less than optimum (Jeffrey, 1987).

Decreased availability of N, P, K, Mg, Mn, Zn and Fe to citrus was found in Southern Florida on calcareous soils with pH between 7.6 and 8.3 (Obreza et al., 2003).

Foliar nutrient content of plants gives information about their growth capacity (Cornelissen et al., 1997; Thompson et al., 1997). The comparison of foliar nutrient concentrations was found to be a successful tool for detecting nutritional disorder in trees (Bowen and Nambiar, 1984). Low nutrient contents of trees have been related to nutritional stress with symptoms such as stunted growth (Drechsel and Zech, 1991). In addition to foliar nutrient ranges, foliar nutrient ratios are a useful tool to detect nutrient deficiencies. Due to the uptake competition between basic cations, ratios between K, Mg and Ca may provide information on deficiencies in trees e.g. the K/Mg ratio (Bergmann et al., 1994). As the uptake of Zn and P were found to be closely related, the P-Zn ratio is an important indicator for the nutritional status of the plant (Bergmann, 1993).

The knowledge on nutrient requirements of native tropical tree seedlings is still scarce. Webb et al. (2000) analyzed the growth response of four plantation timber species (including *Cedrela odorata*) during plantation establishment to increasing phosphorus supply in north Queensland, Australia. Their results showed that under the same edaphic and climatic conditions, there is a wide diversity in the ability of tropical tree species to acquire and use phosphorus. In a study on limitations in mineral supply of forest trees in central Yucatan, Zech et al. (1991) stated that deficiencies in N, P, Zn and Mn were responsible for reduced vitality and growth of trees. Retarded growth is a typical symptom for N and P deficiency (Bergmann, 1993). Deficiency in available phosphorus had a negative impact on growth of seedlings of *C. dodecandra* (Flachsenberg, 2002). Though the analysis of available P and organic matter content of the dominant soil groups of Northern Yucatan, red Cambisol and black Leptosol, did not explain the relative productivity attributed to these soils, it indicated that nutrient availability and soil moisture were closely interrelated (Weisbach et al., 2002). Foliar nutrient contents of N, P, and base cations can show the availability of these nutrients across different sites (Foulds, 1993; Thompson et al., 1997).

2.9 Plant tissue analysis

Plants require different relative amounts of nutrients during the various stages of their growth. When evaluating the nutritional requirements of a tree seedling, its age and current stage of growth has to be considered. For many tropical trees such as *C. dodecandra*, plant analyses at different stages of growth have not yet been carried out. If high calcium content of the leaves is to be expected, the suitability of the selected digestion procedure for tissue analysis has to be ascertained first. Plant analysis allows detecting nutrient deficiency disorders of trees as soon as a data set of tissue analyses of the respective tree species is available (Mills and Jones, 1996; Jones, 2001).

The objective of a laboratory analysis of collected plant tissue is to determine the foliar nutrient concentration of a certain plant. The results of the analysis are compared with existing data on sufficiency ranges or standard values of the plant to evaluate the nutritional status of the plant. Then, it can be detected whether soil fertility level and additional fertilizers are able to provide sufficient nutrients to the plant to foster its growth (Mills and Jones, 1996).

2.10 Exotic vesicular arbuscular (VA) mycorrhizae

VA mycorrhizae are the most widespread type of mycorrhizae in tropical forest ecosystems (Smith et al., 1998). While tropical mycorrhizae have been studied in tropical rainforests, the relevance of mycorrhizae to water and nutrient dynamics under conditions of seasonal water scarcity in the tropics remains poorly investigated (Huante et al., 1993). Hyphae of VA mycorrhizae may extend the zone for nutrient uptake by several centimetres. They have the capacity to deliver a high proportion of the plants demand of P, as well as Zn and Cu (Marschner, 1992). For many economically important tropical plants, especially trees, the mycorrhizal status has not yet been revealed (Smith et al., 1998). Forests of the Yucatan Peninsula were predominantly classified as VAM systems, with some ectomycorrhizal (EM) forests in the Southern Peninsula (Allen et al., 1995; Moser, 1967). As VA mycorrhizal (VAM) dependency was found for *Cordia alliodora*, *Cordia* has to be classified as a VAM genus (in contrast to the EM status of forest trees such as *Eucalyptus*) (Huante et al., 1993).

The adaptation of species that grow well in calcareous environments is still poorly understood. More work is necessary to investigate the role of mycorrhizae on these soils (Jeffrey, 1987). In the greenhouse, positive growth results were obtained for *Chromolaena odorataon* on sterilized red Cambisol and sterilized black Leptosol from the experimental area in Yucatan after inoculation with *Glomus manihotis* (Dittschar, 2005). For several tree species of the Yucatan Peninsula such as *Ceiba pentandra* and *Brosimum alicastrum*, the application of inoculum collected from 2 to 3 years old burned Acahual sites resulted in an enhancement of growth. The comparative growth advantage of inoculated trees was still visible after 4 years (Allen et al., 2001).

2.11 Insect damage on native tree plantations in Yucatan

Major factors that limit plant growth in natural and agricultural systems worldwide, apart from water and nutrients are diseases and pests. So far, with few notable exceptions, the entomofauna of agroforestry species has not been part of the investigations on the respective agroforestry schemes (Rao et al., 2000; Schroth et al., 2000). Leaf nutrient concentrations influence damage by herbivores and pathogens (Coley et al., 1985). On the Yucatan Peninsula, *Hypsipyla grandella* and *Chrysobothris yucatanensis* caused major damages on plantations of *C. odorata* and *S. macrophylla* (Diaz Maldonado, 2002). Hence, the risk of the incidence of damaging insects on plantations of multi-purpose trees such as *C. dodecandra* has to be assessed before recommending them as useful species to farmers. No severe insect incidence on *C. dodecandra* trees was reported to date. Nevertheless, the occurrence of phytophagous insects in association with the species on the Peninsula was documented by ICRAF (1999).

3 MATERIALS AND METHODS

3.1 Study sites

3.1.1 Location of study sites

The experimental plots were situated in the center of the “Henequén area”, on three research sites in X’matkuil, located 15.5 km South from Mérida. The area of abandoned plantations of *Agave fourcroydes*, the “Henequén area”, is situated in the northern part of the Yucatan Peninsula, in the State of Yucatan, Southern Mexico (Figure 1). Study sites were selected according to water availability for irrigation, presence of both red Cambisol and black Leptosol, distance of the sites to one another and to the Faculty of Veterinary Sciences of the Autonomous University of Yucatan, and type of land ownership to guarantee the maintenance of the established plots during the research.

The three sites were located in a radius of approximately 5 km in the neighborhood of the village X'matkuil (20° 45' N, 89° 45' W) where the Veterinary Faculty is situated. Faculty members were the owners of the sites 2 and 3. Site 1 belonged to the Veterinary Faculty and had been handed over to the Department Protrópico for study purposes in 2000. On all three sites, red Kankab soil (Cambisol) and black Tsekel soil (Leptosol) were present in about equal proportions. On all sites, wells guaranteed the availability of water. The established pump systems on site 1+2 accounted for the irrigation during dry season on these two sites.

3.1.2 History of study sites

The Faculty of Veterinary Sciences assigned the experimental site 1 to the Department Protrópico in 1999. In the same year, a major part of the site (located north of the well) was cleared from the 40-year-old fallow vegetation by the traditional slash-and-burn-practices (“roza-tumba-quema”), burned in May and sown in June. On some patches of red Cambisol, Leguminosae (*Vigna unguiculata*) were planted in the first year, followed by corn and Leguminosae (*Vigna* and *Mucuna species*) in 2000 and 2001. The so-called “sub site” south from the well was covered with 50-year-old secondary vegetation until 2001, when it was burned and planted with 8 varieties of *Mucuna*. The “sub site” was dominated by red Cambisol, surrounded on three sides by mounds that were covered with secondary vegetation.

Historically, site 2 owned by Dr. J. J. Jiménez-Osornio was used as a sisal plantation. For about 10 years, it was covered by secondary vegetation of about 5 to 8 m of height. In 1998, part of the site was subject to the traditional slash-burning (“roza-tumba-quema”) practices (west of the access path). Another part of the area was cleared from secondary vegetation (“roza-tumba”), but not burnt, and part of it was used for an experimental trial on corn in 2001 (east of the access path). A detailed history of site 3 owned by José Castillo was not available. Considering the good accessibility and the location close to the village of X'matkuil and current remaining patches of low thorny secondary vegetation, it may be assumed that the site was formerly part of a sisal plantation, with an interim period of fallow, and subsequent slash-and-burn practices.

3.2 Climatic conditions

The climate in Mérida, Yucatan, at 15 km from our experimental sites, was classified as hot sub humid with precipitation of average frequency in summer. Mean annual temperature was 26.8°C, with the lowest mean monthly temperatures in January. The peak of the dry season in the Northern Yucatan Peninsula is from April to May, with long-term mean maximum monthly temperatures of up to 40°C in May recorded for Mérida.

Mean annual precipitation in State of Yucatan is 983 mm, with a precipitation gradient from the coastal zones in the north (Progreso: 444 mm) towards the Center of the Peninsula (Oxcutzcab: 1227 mm). Mean annual precipitation in Mérida, close to the experimental site, was 984.4 mm. Long-term mean maximum monthly precipitation in Mérida was 187 mm in September, equivalent to 19% of the total annual precipitation. More than 80% of the annual precipitation was measured between May and October. Minimum precipitation was recorded in Mérida between January and May. In November/December, rains accompany the winds called "nortes" (Orellana, 1997; Duch, 1988). Hurricane season is from September to October.

3.3 Selection of Mayan homegarden tree and crop species

Figure 2: *B. orellana* and *C. dodecandra* at the age of 15 months on experimental plots (left), *C. dodecandra* tree in Mayan homegarden, Hocabá, Yucatan, Mexico (right)

The selection criteria for the tree and crop species were the following:

• Mayan homegarden species, knowledge of farmers, in order to facilitate the acceptance and use by farmers

- Economic benefit derivable from the species, either for auto-consumption, or on regional and export markets
- Tree with preference multi-purpose tree
- Availability of seedlings at local tree nurseries
- Native species, adapted to the climatic and soil conditions of Northern Yucatan
- Native species without record of pest or insect damage

As tree species, we chose the multi-purpose tree *C. dodecandra*, a commercial timber and fruit tree species that is planted in common in homegardens in Northern Yucatan (Figure 2). As crop species, we selected *C. papaya*, a species sensitive to changes in nutrient availability. After the incidence of hurricane Isidore most of the *C. papaya* seedlings were destroyed. As *C. papaya* seedlings in the regional nurseries were no more available, we had to choose a different species for replanting. Due to the destruction of seedlings in the nurseries, both seedling availability and the adaptation of the species to climatic and soil conditions of the region became essential criteria for the selection. As a substitute for *C. papaya*, we planted *B. orellana* (Figure 2), a Mayan homegarden species of commercial importance that has been successfully used in agroforestry schemes.

3.4 Soil and site conditions: stony calcareous Yucatan soils

To analyze the impact of the dominant Mayan soil series on tree growth, seedlings were planted on two soil classes differentiated by color, stoniness, and position on micro relief (Figure 3). On all three sites, soils were a small-scale mosaic of red, less stony Cambisol (Kankab), often with a terminal calcareous layer at varying depths, and black stony Leptosol (Tsekel) with a high percentage of rock fragments and stones (up to 80%). If the depth of the calcareous layer at planting sites for the individual seedlings was less than 40 cm, the planting spot was moved in order to comply with the required depth of the planting hole. Cambisol was found in the depressions of the micro relief, while Leptosol was characteristic for the terrain elevations. Elevations were between 1 and 1.5 m high, with mostly gentle slopes.

Figure 3: Planting on black Leptosol (above) and red Cambisol (below) on study sites at X’matkuil, Yucatan, Mexico

Soil classes according to Mayan classification:

- Red Kankab (Cambisol) (Figure 3)
- Black Tsekel (Leptosol) (Figure 3)

Red Kankab soils on plains were classified as Cambisol or Luvisol. Black Tsekel soils on mounds corresponded to Leptosol (formerly denominated Litosol) or Rendzina. Black Tsekels form in situ on elevations of the terrain. They are very shallow. Tsekel soils have a high percentage of rock outcrops and stones and low water retention capacity. On plain terrain, red-colored less stony Kankabs (high in Fe_2O_3) with medium organic matter content are found. Described as clay with limestone fragments, their subsoil consists of limestone powder, forming a hard layer that may inhibit taproot development. Their depth varies between 20 and 100 cm. Kankab soils have a moderate water retention capacity. Kaakabs are located on moderate slopes. Tsekel (black Leptosols), Kaakab (litic Cambisol) and Kankab (cromic Cambisol) are the dominating soil series of the “Henequén area” (Estrada Medina, 2000; Peniche, 1994; Dunning, 1992; Duch, 1995 and 1988).

Higher organic matter content and higher nutrient availability was measured in black soils in comparison to red soils. Nevertheless, chemically extractable nutrient amounts did not explain differences in fertility of these soils (Weisbach et al., 2002). Various layers of calcareous rock, all of them water permeable, limit the shallow black Tsekel soils. Typically the lowest rock layer for soils is formed by white calcareous powder, called Saskab, which is highly susceptible to weathering. It is up to several meters deep and reaches the ground water table (Estrada Medina, 2000). Kankab soils are of red or brown-reddish color. They are divided into the sub-classes Kankab (with a depth of more than 10 cm) and Haylu'um (with a depth of less than 10 cm) (Estrada Medina, 2000). In the following text, the term Kankab will be used to refer to the soil class, i.e. the red or brown-reddish soils of the areas in between terrain elevations. As the Kankab soil in the study area showed a relatively high percentage of stones, it was classified as stony Kankab soil.

Soils on top of mounds, Boxlu'um, are differentiated considering their stoniness, rockiness, type of rocks and stones, color, and depth. Boxlu'um soils are generally black in color. Black soil between stones is called Tsekel. Soil delimited by rocks (on top of a calcareous layer named laja) is called Chaltun. In the following text, we will refer to black soil on terrain elevations with high stony- and/or rockiness as Tsekel soil. Soil moisture in the upper layer of Kankab soil is generally higher than in the upper layer of Tsekel soil (Estrada Medina, 2005).

3.5 Assessment of soil characteristics

Soil color and rocky- and stoniness were assessed for red Kankab (Cambisol) and black Tsekel (Leptosol) on all three experimental locations. At each location, three representative sites were selected for each soil type, with three micro-sites within a circle of 10 m diameter. The assessment took place on dry days (precipitation of the previous day of 0 to 1 mm) of November 2002.

Soil color was recorded using Munsell Color Chart. Rockiness and stoniness were estimated according to the percentage of rock and stone cover on the surface in a circle of 3 m radius. The spatial distribution and elevation of terrain elevations (mounds) was recorded using a clinometer, a measuring tape and a measuring stick of 1.65 m height (eye height of the author). Excavations were carried out to a depth of 30 cm on black Tsekel soils for soil sampling on 30 randomly distributed spots at our experimental sites, and a soil profile on black Tsekel was dug to a depth of about 80 cm. Excavations to a depth of 20 cm on red Kankab soil were carried out for soil sampling on 30 randomly distributed spots at our experimental sites. The pH of each sample was measured in H_2O and in 0.01 M calcium ($CaCl_2$) solution (Rowell, 1994; Scheffer and Schachtschabel, 1992).

3.6 Hydrological conditions: water availability and growth

Characteristic for the Peninsula are subterranean rivers and creeks, and natural ponds with depths of up to 80 m (so-called cenotes). In order to successfully carry out the experiments, plots were located in an area with sufficient water availability during the dry season. On two of the three experimental sites, an irrigation system was installed. It consisted in tubes of 5 cm diameter leading from the pump at the well (Figure 4) to each plot under irrigation, where eight smaller tubes delivered the irrigation water to the planting spots of seedlings (Figure 4). During the first two to three months after transplantation to the field, seedlings were irrigated with eight liters per seedling if there was no rain for more than two to three consecutive days, but no longer than until end of November 2002.


Figure 4: Well at the experimental site 1 of the Faculty for Veterinary Sciences, and irrigation system installed on plots at experimental site 1, X'matkuil, Yucatan

To evaluate the influence of water availability, three watering regimes were defined for irrigation during dry season (from January to June):

- Regular irrigation, twice a week during dry season (Figures 9 and 10)
- Sporadic irrigation at the peak of dry season only (Figures 5, 6 and 7)
- Tree seedlings without irrigation during dry season (Figure 8)

On plots with regular irrigation, seedlings received 16 liters of water twice per week during the entire dry season. Seedlings with sporadic irrigation were irrigated with approx. eight liters (half a bucket) of water twice a week for five weeks during the peak of the dry season from April to May. Hence, seedlings with regular irrigation received 9.6 times as much irrigation water (in total 768 liters) compared to seedlings with sporadic irrigation that received a total of 80 liters of water. Seedlings without irrigation were not irrigated during dry season.

Figure 5: 15-month-old *C. dodecandra* on sporadically irrigated black Leptosol at the study site 2, X'matkuil, Yucatan, Mexico

Figure 6: 15-month-old *C. dodecandra* on sporadically irrigated red Cambisol at the study site 2, X'matkuil, Yucatan, Mexico

Figure 7: Sporadically irrigated 15-month-old *C. dodecandra* on red Cambisol (in the back) and on black Leptosol (in the front) on experimental site 2

Figure 8: Non-irrigated 15-month-old *C. dodecandra* on black Leptosol on study site 3

Figure 9: Regularly irrigated 15-month-old *C. dodecandra* and *B. orellana* on black Leptosol on study site 2

Figure 10: Regularly irrigated 15-month-old *C. dodecandra* and *B. orellana* on red Cambisol on study site 2

On site 3, eight plots with different subtractive fertilizer treatments, irrigation for the first four months of dry season was effectuated about four times a week, for half an hour (16 liters per seedling), resulting in 1.3 times the amount of additional water (1024 liters) than for “regular irrigation”. These plots were all located on red Cambisol. In the following text, their irrigation level was denominated “highly irrigated”.

3.7 Fertilizer treatments and application rates

To analyze the impact of nutrients on tree growth, we carried out subtractive experiments (minus-one-trials) with different fertilizer treatments, planting seedlings of two species (*C. dodecandra* and *B. orellana*) on two different soil types (red Cambisol and black Leptosol).

We applied seven subtractive fertilizer treatments (leaf-applied complete fertilizer minus N, P, K, Mn, and Zn) including the non-fertilized control treatment (Tables 1 – 5).

Fertilizer treatments:

- Complete fertilizer minus N
- Complete fertilizer minus P
- Complete fertilizer minus K
- Complete fertilizer minus Zn
- Complete fertilizer minus Mn
- Complete fertilizer
- Control without fertilizer additions

Figure 11: Application of foliar fertilizer on experimental plots in August 2003

Several successive fertilizer applications during the rainy season with foliar spray were selected as the type of application to improve macro- and micronutrient uptake from the applied mixture by seedlings (Figure 11). When applying ammonium-N or urea containing fertilizers, ammonia volatilization occurs, especially in calcareous soil. This can be avoided if N is moved into the grove floor either by irrigation or by rainfall. Applied phosphate becomes unavailable due to fixation in calcareous soils. Regular P applications enhance continuous plant supply. Foliar applications of Mg and K fertilizer as well as foliar sprays containing Zn and Mn are recommended to correct deficiencies for citrus on high pH soils. Fe is best applied in its organically chelated form. To prevent micronutrient deficiencies in crops and fruit trees on calcareous soils, foliar sprays are recommended (Rowell, 1994; Obreza et al., 2003).

Macronutrients N, P and K were applied at equal proportions, with few exceptions for P and K application rates due to the nutrient ratios of the fertilizer mix components (Tables 1, 2, and 3). To attain an even composition of the nutrient mixtures, the element concentrations of the different commercial products were calculated. As foliar K fertilizer was not available in the project region at the time of fertilizer applications, fertilizer minus P was mixed with Lobi 44 and imported granular NKS. In 2002, micronutrient fertilizer mix was used as foliar spray ("Poliquel Multi"), and complemented with selected micronutrients; in 2003, the complete micronutrient spray was prepared from chemicals (Tables 4, 5a+b). In 2002, fertilizer mix was diluted in 0.5 L water per plot, as seedlings were still smaller. In 2003, fertilizer mix was diluted in 1 L water per plot to cover the more extensive crowns entirely with fertilizer spray (Figure 12). In the afternoon after fertilizer applications, rainfall events occurred and probably washed part of the applied fertilizer into the soil below the seedling. Despite high solar radiation, no leaf burn was observed after foliar fertilizer applications.

Figure 12: Field laboratory for the dilution of micro- and macronutrient mixtures for foliar application

Leaf fertilizer was applied four times, once initially in November 2002, 1 month after planting *B. orellana* (Achiote) and about 4 months after planting *C. dodecandra* (Siricote) seedlings. In 2003, liquid fertilizer was applied three times between August and November 2003.

According to treatments, the following products were used to produce adequate mixtures:

Table 1: Macronutrient sources: element ratios of commercial macronutrient fertilizers used for foliar application

Element	**Source**	**NPK - fertilizer – ratio**	**% of element**
Nitrogen	Lobi 44 (urea)	44 – 0 – 0	44
Nitrogen	Velfoliar	15 – 60 – 0	15
Nitrogen	Superfos	12 – 60 – 0	12
Nitrogen	NKS de Chile	12 – 0 – 45	12
Phosphorus	Velfoliar	15 – 60 – 0	26
Phosphorus	Superfos	12 – 60 – 0	26
Phosphorus	Potasio liquido	0 – 32 – 53	14
Potassium	NKS de Chile	12 – 0 – 45	37
Potassium	Potasio liquido	0 – 32 – 53	44

Fruit growers use foliar sprays worldwide due to their reliability and the immediate tree response. Still, literature on foliar applications on multi-purpose indigenous trees in the tropics is scarce. There are a high number of commercial foliar sprays, but often there is not much information apart from the indications given by the manufacturer. The effects vary with tree species and concentrations. Tree species have different foliar absorption due to amount, distribution, and chemical composition of surface waxes on leaves (Swietlik and Faust, 1984). The crown volume also determines the adequate application rate per surface unit. For this study, the application rates were determined considering the literature on foliar fertilizer rates for fruit trees, advice of the technical manager of citrus plantations in Northern Yucatan owned by Coca Cola Inc., of wholesalers of foliar fertilizers in Mérida, Yucatan, of recommendations by manufacturers, and by Juanita Marin, at the research station of the National Institute for Forestry, Agriculture and Livestock Research (INIFAP), Mocochá, Yucatan.

Table 2: Macronutrient fertilizer composition and foliar application rates (Fert. = complete fertilizer treatment; -Mn, -Zn, -N, -P, -K = subtractive fertilizer treatments)

Treatments	**Elements**	**Fertilizer mix components**	**Appl. / 8 plots**
Fert., -Mn, -Zn	NPK	Potasio liquido (PK)	40 ml
		Velfoliar (NP)	45 g
		Lobi 44 (N)	35 g
-N	PK	Potasio liquido (PK)	40 ml
-P	NK	Lobi 44 (N)	35 g
		NKS de Chile (NK+S)	70 g
-K	NP	Velfoliar (NP)	45 g
		Lobi 44 (N)	35 g

Table 3: Total macronutrient application rates per hectare and per seedling, applied by foliar spray

	Macronutrient applications					
	Total 2002+2003 (4 appl.)			Total 2002+2003 (4 appl.)		
	1 ha = 200 plots			1 appl. (2002) with 1600 seedl./ha 3 appl. (2003) with 1200 seedl./ha		
Fertilizer treatments	**N**	**P_2O_5**	**K_2O**	**N**	**P_2O_5**	**K_2O**
		g/ha			**mg/seedl.**	
Fert., - Mn, - Zn	2.215	3.932	2.120	1.211	2.150	1.160
- N	0	1.273	2.120	0	696	1.160
- P	2.380	0	3.120	1.302	0	1.707
- K	2.215	2.659	0	1.211	1.454	0

Table 4: Micronutrient compositions of commercial foliar fertilizer "Poliquel Multi" and of micronutrients mix from chemicals (foliar spray)

Micronutrient applications		**2002**	**2002**	**2003**
Element	**Source**	**Poliquel multi micronutrient-mix**	**Chemical**	**Chemical**
		ml element/ha	**g element/ha**	
Mn	Mn-fertilizer	2,5	36,6	29,3
Zn	Zn-fertilizer	40,0	33,9	40,6
Mg	Mg-fertilizer	10,0	29,6	28,4
B	B-fertilizer	0,4	5,5	1,3
Cu	Cu-fertilizer	0,4	3,2	1,5
Mo	Mo-fertilizer	0,05	11,7	4,7
S	Zn, Cu, Mn-fertilizer	40,0	39,6	37,8
Cl	Mg-fertilizer		86,2	82,8
P	Mo-fertilizer		0,3	0,1
Fe (multi)		30		
Co (multi)		0,02		
			ml chelate/ha	
Fe-chelate	Poliquel fierro		40	240

Table 5a: Fertilizer for foliar micronutrient applications

Element	Fertilizer
Mn	$MnSO_4 \cdot H_2O$
Zn	$ZnSO_4 \cdot 7\ H_2O$
Mg	$MgCl_2 \cdot 6\ H_2O$
B	H_3BO_3 (18%)
Cu	$CuSO_4 \cdot 5\ H_2O$
Mo	$H_2\ (P(Mo_3O_{10})_4) \cdot H_2O$
Fe-chelate	Poliquel fierro
Micro-mix	Poliquel multi

Table 5b: Micronutrient application rates per hectare and per seedling, applied by foliar spray

	Micronutrient applications					
	2002	2003	Total	2002	2003	Total
	1 ha = 200 plots			1600 seedl. per ha	1200 seedl. per ha	
Element	**Fertilizer g/ha**	**Fertilizer g/ha**	**Fertilizer g/ha**	**Fertilizer mg/seedl.**	**Fertilizer mg/seedl.**	**Fertilizer mg/seedl.**
Mn	113	90	203	70	75	145
Zn	150	180	330	94	150	244
Mg	250	240	490	156	200	356
B	31	7,5	39	20	6	26
Cu	13	6	19	8	5	13
Mo	19	7,5	26	12	6	18
	ml/ha	**ml/ha**	**ml/ha**	**ml/seedl.**	**ml/seedl.**	**ml/seedl.**
Fe-chelate	500	3000	3500	0,3	2,5	2,8
Micro-mix	1000	0	1000	0,6	0,0	0,6

3.8 Inoculation of seedlings with exotic VA mycorrhizae

3.8.1 Inoculation in the nursery

On the experimental site, one of the treatments on both soils and with three irrigation levels consisted in the inoculation of *C. dodecandra* seedlings with exotic VA mycorrhizae before transplanting. In the tree nursery, mycorrhizal inoculum was added to 80 Siricote seedlings. After germinating in the seedbed, the small seedlings were separated into bags filled with local red Kankab soil. As the seedlings were transplanted into the bags at bare root, a spoon of VAM inoculum “BIORIZE” was added close to the root. The transplanted seedlings were irrigated and placed into shade, where they were stored until they were brought to the experimental sites. Four weeks after inoculation, seedlings were transplanted into the field. Survival of seedlings was recorded in September 2002, six weeks after transplanting into the field. Dead seedlings were replaced in November 2002, and survival was again recorded in December 2002, as well as after the first dry season, in July 2003. Height and diameter growth was measured in July 2003 and in January 2004.

3.8.2 Comparison of different mycorrhizal inoculums

In November 2003, three-month-old *C. dodecandra* seedlings (n = 40) were inoculated with three different VAM inoculums and transplanted into red and black soil at the nursery of the Department Protrópico. Seedlings were separated from the soil of their original bags, and potted bare-root in pots of about 20 cm diameter and 30 cm height filled with red or black soil. Red soil was a mixture of 50% non-sterilized red Kankab from plots of experimental site 2, and 50% sterilized red Kankab from the village nursery. Non-sterilized black soil originated from an experimental plantation of Protrópico at a limestone quarry in Southern Mérida. About 15 ml of mycorrhizal inoculum were added to the rhizosphere.

The mycorrhizal treatments were:

- The granular VAM mixture “Endorize Mix 4”, a combination of *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe, *Glomus intraradices* Schenck and Smith and *Glomus deserticola* (Trappe, Bloss. and Menge), recommended for fruit trees (BIORIZE, 2002) and tropical soils by the manufacturer BIORIZE, origin: tropical Africa (BIORIZE R&D, 8, Rue Sainte Anne, 21000 Dijon, France, French registration APV N° 9810002),
- *Glomus mosseae* inoculum, strain: GOE 85-1, origin: Zaire, from the Institute for Tropical Agriculture, Göttingen University,
- *Glomus manihot* inoculum, strain: GOE 78-1, origin: Columbia, from the Institute for Tropical Agriculture, Göttingen University, and
- The non-inoculated control treatment.

Survival and height of seedlings in the nursery was assessed 3 times, at intervals of 6 weeks: 2 weeks after transplanting in November 2003, 8 weeks after transplanting in January 2004 and 14 weeks after transplanting end of February 2004.

3.9 Establishment of the experimental plantation

Before planting, the research site was cleared manually from secondary vegetation, and glyphosate was applied once. The sites were not burned. Planting holes were dug manually to a depth of 40 cm and widths of 30 cm. Seedlings were planted including the soil from nursery bags covering the roots. During the establishment phase of the seedlings (the first two to four weeks after planting) all plots were irrigated, 50% of them manually with buckets.

Seedlings were germinated in four local nurseries from seeds of seed trees in local communities, and planted at the age of three to six months. At first, *C. dodecandra* was planted in July 2002. It was intercalated with *C. papaya*. After hurricane Isidore in September 2002, *C. dodecandra* seedlings were staked to stabilize them. Support stakes were removed in May 2003. *C. papaya* was nearly completely lost due to the hurricane. They were replaced by *B. orellana* in November 2002. Simultaneously, lost *C. dodecandra* were re-planted to complete the number of four seedlings per species per plot. Seedlings were replanted twice, in September 2002 before the hurricane, and in November 2002. When dead seedlings were replaced on red Kankab soil, soil depth in planting holes was evaluated.

Weeding was carried out manually every two to three months during rainy season, removing any grass and plant cover in a circle of about 200 cm diameter around individuals. In the inner and outer circle of research plots, vegetation was cut manually at about 5 cm above soil level every two to three months. Climbing weeds were removed every four to eight weeks during rainy season.

3.10 Assessment of seedling survival and growth

Survival of seedlings was assessed three times on the entire experimental area: two months after transplanting in September 2002, after the hurricane in October 2002, and after the first dry season in June 2003. *B. orellana* seedlings could not be planted before mid dry season on non-irrigated plots; therefore there was no data on survival without irrigation.

Seedling growth parameters such as stem length, height, stem diameter at 10 cm above ground and crown diameter were measured in July 2003 and January 2004 (Figures 13 – 15). Crown measurements, tree height and diameter measurements were performed according to Briscoe (1990). The height of *B. orellana* was measured as height of the highest branch respectively stem. Stem and branches at 10 cm above ground were measured; in case of *B. orellana* all branches with diameters of more than 1 mm were assessed. The virtual diameter at 10 cm was calculated adding basal areas of stem and branches. To obtain the virtual diameter, the total area of stem and branches at 10 cm above ground of each seedling was considered the basal area of one single stem. The diameter of this virtual stem (the “virtual diameter”) was deduced from the total basal area of stem and branches (Schulz, 2003). Several 20-month-old *C. dodecandra* seedlings on the site of the Faculty were harvested including roots to observe the rooting pattern. At the end of November 2003, two 19-month-old *C. dodecandra* seedlings from sporadically irrigated Cambisol plots at experimental site of the Faculty were harvested and the roots excavated. One seedling was harvested on a complete fertilizer plot on the so-called sub site area, and another one on a plot with complete fertilizer minus Mn outside the “sub site” area. They were put into plastic bags and transported to the laboratory. Fresh weight was recorded the same day. Height of surrounding vegetation and mounds was measured with Suunto clinometer PM-5/1520.

Figure 13: Assessment of crown diameter and stem length of *C. dodecandra*

Figure 14: Assessment of crown diameter and height of *B. orellana*

Figure 15: Assessment of diameter of *C. dodecandra* (left) and *B. orellana* (right)

3.11 Assessment of insects associated with *C. dodecandra*

In cooperation with this project, the insects associated with *C. dodecandra* in Northern Yucatan were investigated. Insect sampling and identification as well as damage assessment in homegardens in the community of Hocabá and on experimental plots by Gabriel A. Tamayo Rivera started one year after establishment of the plantation in June 2003. Identification of insects from sampling on experimental plots by Gabriel A. Tamayo Rivera in cooperation with the Instituto Tecnológico Agropecuario (ITA) No. 2, Conkal, Yucatan, and the Department Protrópico, Autonomous University of Yucatan, is still under way. Field observations by the author on insect incidence and damage on experimental plots, and from several private agroforestry plantations with *C. dodecandra* in Southern Yucatan were compared with data from insect identification in Mayan homegardens.

3.12 Sampling methods for foliar analysis

3.12.1 Collection of leaf samples on experimental sites

Youngest fully matured leaves (YFML) – the first fully developed leaves at the twig or branch tip - were sampled from outer mid and upper crown of seedlings on the experimental plots. Leaf samples for the nutrient level comparison with the literature were collected from seedlings on unfertilized plots on red and black soil, with regular and sporadic irrigation during dry season. For the comparison of foliar nutrient concentrations, nutrient levels of leaf samples collected at mid-rainy season were used, because most of the relevant literature was based on samples collected at the beginning or in the middle of rainy season. Values refer to the dry weight of YFML.

Youngest fully matured leaves from *C. dodecandra* (Siricote) and *B. orellana* (Achiote) seedlings were sampled for nutrient analysis. Samples of Siricote and Achiote leaves were collected twice from all planted trees: in the rainy season in July-August 2003, and at the beginning of dry season in December-January 2003-2004, four weeks after the last application of leaf fertilizer. Leaf samples were collected in brown paper bags.

3.12.2 Foliar sampling in Mayan homegardens

As a reference for leaf nutrient levels from our own experiments, leaves from *C. dodecandra* grown in Mayan homegardens were sampled in October 2003 in cooperation with Gabriel A. Tamayo Rivera and M. Rocio Ruenes Morales, Department Protrópico, Autonomous University of Yucatan. Youngest fully matured leaves (YFML) were sampled from the outer mid crown of adult trees (n = 5). Homegardens were selected according to the presence of adult trees of *C. dodecandra*.

3.13 Laboratory methods for foliar analysis

3.13.1 Drying of leaf samples in Yucatan

Leaf samples were oven-dried at 60° C at Protrópico Department, Veterinary Faculty, Autonomous University of Yucatan. We collected and dried a total of about 2000 leaf samples from Siricote and Achiote seedlings. All dried samples were brought to Germany.

3.13.2 Sample selection for laboratory analysis

Each sample consisted of various leaves (YFML) from the same seedling. Due to time frame and budget considerations, the number of samples chosen for analysis was reduced to a total number of 272 samples (Table 6) according to the selection criteria presented in Table 7.

Table 6: Number of samples selected for analysis

<u>Collection after 4 fertilizer applications:</u>

8 fertilizer treatments including control x 2 irrigation levels x 2 soil types x

2 repetitions x 2 sites x 2 seedlings per plot

= 256 samples

- 16 samples (because non-irrigated black soil repetition on 1 site missing)

= 240 samples

<u>Collection at the beginning of rainy season, after 1 fertilizer application:</u>

2 fertilizer treatments (control and complete fertilizer) x 1 irrigation level x 2 soil types

x 2 repetitions x 2 sites x 2 seedlings per plot

= 32 samples

=> Total of 272 samples

Table 7: Criteria for the selection of leaf samples for analysis

Sampled	Selected for analysis	Selection criteria
3 sites at a distance of 5 km (Faculty, Dr. Jiménez, J. Castillo), 2 replications on each site	Only samples from 2 sites (Dr. Jiménez + Faculty) with sporadic and regular irrigation	To analyze a complete data set (all fertilizer treatments, with a statistically relevant no. of samples) on sporadic and regular irrigation rather than a reduced data set for all 3 irrigation levels
2 sampled species, *B. orellana* (Achiote) and *C. dodecandra* (Siricote)	Only samples of one species (the multi-purpose tree *C. dodecandra*)	Survival rate of *C. dodecandra* seedlings was higher than that of *B. orellana* seedlings, especially on non-irrigated plots; some treatments had no *B. orellana* left To compare samples from all treatments for one species rather than comparing only a reduced number of treatments for both species
2 times collection of samples: 1) At the beginning of rainy season in July 2003 (after 1x fertilizer application) 2) At the beginning of dry season in December 2003 (after 4x fertilizer application)	1) For the first sampling date only samples from control plots (without fertilizer) and plots with complete fertilizer 2) For the second sampling date samples from all plots / treatments	Considering the objective of the thesis, to correlate seedling growth with irrigation level, soil type, and fertilization treatments, the second sampling date (after 4x fertilizer application) was crucial.
3 to 4 seedlings per plot, according to seedling survival	2 seedlings per plot = a total of 8 seedlings per application	

3.13.3 Grinding of leaf samples

Leaf samples were ground using rotor speed mill Pulverisette 14 (Fritsch), equipped with a sieve of 0.2 mm. Due to the steel blades of the mill, Fe contamination had to be taken into account.

When analyzed using inductively coupled plasma atomic emission spectrometry (ICP-AES), three *C. dodecandra* leaf samples showed extremely high iron values. To evaluate whether extremely high Fe values resulted from Fe contamination by the mill, measurements of Ni and Cr were carried out on *C. dodecandra* leaf samples. Increased Fe values coincided with extremely high nickel and chrome values. This indicated that high Fe values resulted from steel of the mill. Hence, Fe values of these three samples were excluded from further analysis.

3.13.4 Comparison of digestion methods for foliar analysis

Wet acid digestion with sulfuric acid (H_2SO_4) with repeated additions of 30% H_2O_2 has been documented as a successful digestion method for the analysis of macro- and microelements in plant tissue and soil (Wolf, 1982; Mills and Jones, 1996). For the digestion of plant tissues rich in Ca (>10 g/kg), however, other digestion procedures are recommended (Mills and Jones, 1996; Jones, 2001). Calcium concentration for Siricote leaves grown on calcareous soils of the Peninsula of Yucatan was expected to exceed 10 g/kg.

To identify a suitable digestion procedure for *C. dodecandra* leaf samples grown on calcareous soils of the Peninsula of Yucatan - as well as for soil from the experimental plots in X'matkuil - we compared two established digestion methods:

- Wet acid digestion procedure using hot sulfuric acid (H_2SO_4) with repeated additions of 30% H_2O_2 in test tubes in digestion heater block at 360° C (Wolf, 1982; Mills and Jones, 1996), and
- Wet acid digestion using hot nitric acid (HNO_3) in Teflon vessels in drying chamber at 180° C (Heinrichs et al., 1986).

Each leaf and each soil sample was analyzed with 2 repetitions to compare the reproducibility of the digestion procedures. A coniferous leaf standard of the Institute of Forest Nutrition and Soil Science was used as standard reference material for plant samples. Blanks were compared to determine the accuracy of the two methods (Jones, 2001). Sample digests were analyzed with inductively coupled plasma atomic emission spectrometry (ICP-AES) at the Institute of Forest Nutrition and Soil Science.

Blank values with nitric acid digestion in comparison to sulfuric acid digestion were extremely low. Using the nitric acid for digestion, the extraction of Ca for *C. dodecandra* leaves was about 25% higher than with sulfuric acid and peroxide. With this method, Ca concentrations between 22.8 g/kg and 43.5 g/kg were found in test samples. Using HNO_3 for soil digestion, much higher amounts of Mg, Fe, and Al for both soils as well as higher amounts of manganese in red Kankab soil were extracted. Wet acid digestion using nitric acid was carried out at the Institute of Agronomy in the Tropics (IAT), University of Göttingen (Figure 16).

3.13.5 Nitrogen analysis with Dumas method

Total nitrogen content of leaves was analyzed with the Dumas method using Elemental Analyzer NA 1500 (Carlo Erba, Milan, Italy) (Figure 16). In a first step, 24 leaf samples from the total range of treatments were measured. Each leaf sample was analyzed twice (two repetitions) and the results were compared to detect the reproducibility of the method for our samples. Due to low variation between the two repetitions, it was decided to measure each leaf once. In contrast to Kjeldahl digestion, the Dumas method allows the quantitative determination of the amount of nitrogen in all forms (NH_4, NO_3, protein, and heterocyclic N) in plant tissues (Jones, 2001).

Figure 16: Preparation of wet acid digestion with nitric acid (left) and weighing of samples for elemental N analysis (right)

3.13.6 Elemental analysis using ICP-AES

The element content for P, K, Ca, Mg, S, Mn, Fe, and Al of the sample digests was determined with inductively coupled plasma atomic emission spectrometry (ICP-AES). Plasma excitation has the advantages of minimal matrix and spectral interference, excellent sensitivity (in general less than 0.1 mg/kg), and a linear usable concentration range of three to five decades (Mills and Jones, 1996; Jones, 2001). For this study, the fast analysis of a high number of elements at a relatively low price combined with high sensitivity was the most important reason for selecting this method.

3.13.7 Analysis of zinc using AAS

Zinc determination was not included in the ICP-AES at the Institute of Forest Nutrition and Soil Science. Therefore, zinc was determined using flame atomic absorption spectrometry (AAS), a method routinely used to detect Ca, Mg, Cu, Fe, Mn, and Zn in plant tissue digests (Mills and Jones, 1996), at the Institute of Agronomy in the Tropics.

3.14 Experimental design

On 184 plots of 7 m x 7 m on black Leptosol (Tsekel) and red Cambisol (Kankab), four *C. dodecandra* and four *B. orellana* were planted. Seedlings of the two species were planted alternately, forming a circle with a diameter of four m in the center of the plot. The planting distance between *C. dodecandra* individuals was 2.8 m (Figure 17). The experimental plots covered a total area of 0.9 ha, planted with 736 seedlings per species. Due to the small-scale mosaic of different soils, plots were distributed in a scattered pattern over the experimental sites (Figures 18 – 20). The experimental plots were established in July 2002, plantation of seedlings of *C. dodecandra* was finished in August 2002. Due to hurricane Isidore in September 2002, plantation of seedlings of *B. orellana* was finished in November 2002.

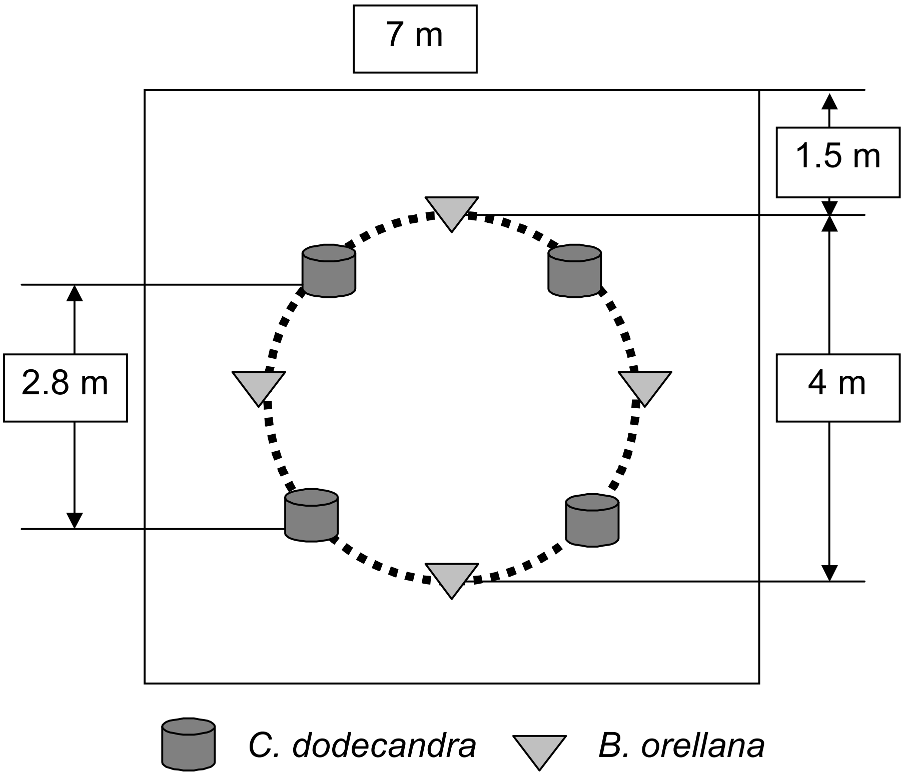

Figure 17: Experimental plot design with *C. dodecandra* and *B. orellana* seedlings

The experimental design was originally conceptualized as a plot design with six replications for two soils, two irrigation levels, and seven fertilizer treatments plus the mycorrhizal treatment (6 x 2 x 2 x (7 + 1) = 192 plots). On each plot, four seedlings of each species should be planted. The six plot replicates were allocated in equal proportions to the three available experimental sites. On each site, two plots of each soil

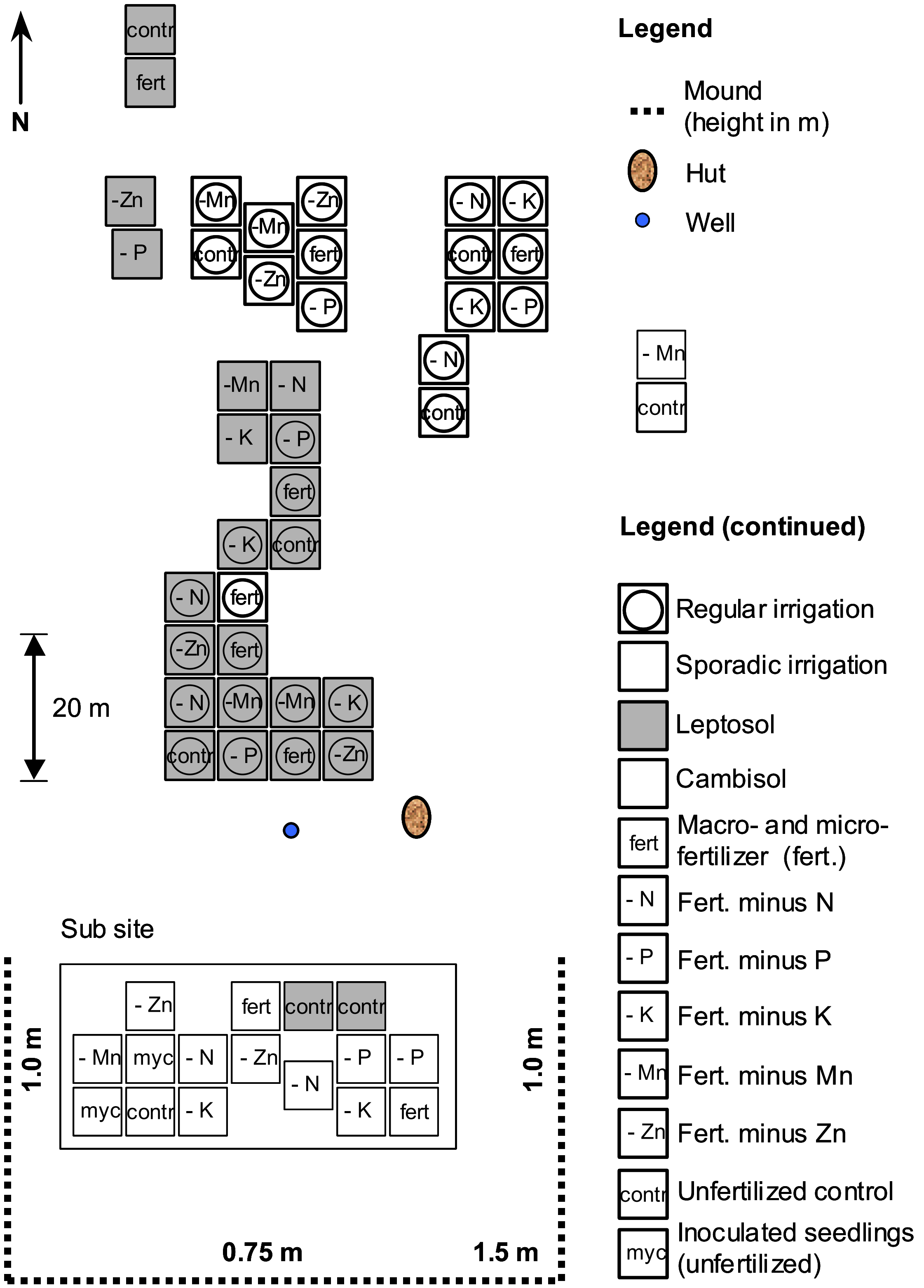

Figure 18: Experimental site 1 at X'matkuil, Mérida, Yucatan, Mexico, owned by the Veterinary Faculty of the Autonomous University of Yucatan

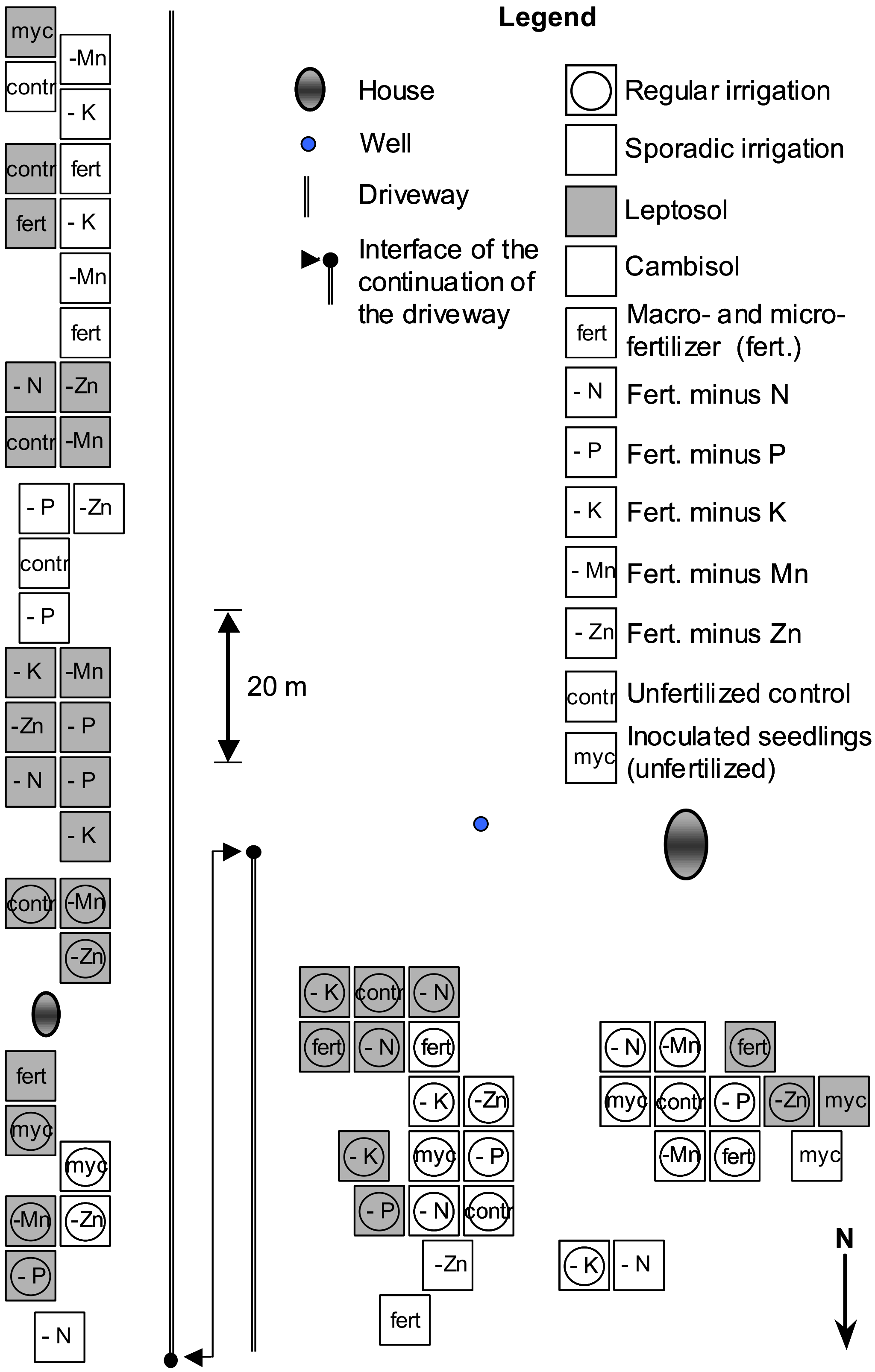

Figure 19: Experimental site 2 at X'matkuil, Mérida, Yucatan, Mexico, owned by Dr. J. J. Jiménez-Osornio, Director of Protrópico (UADY)

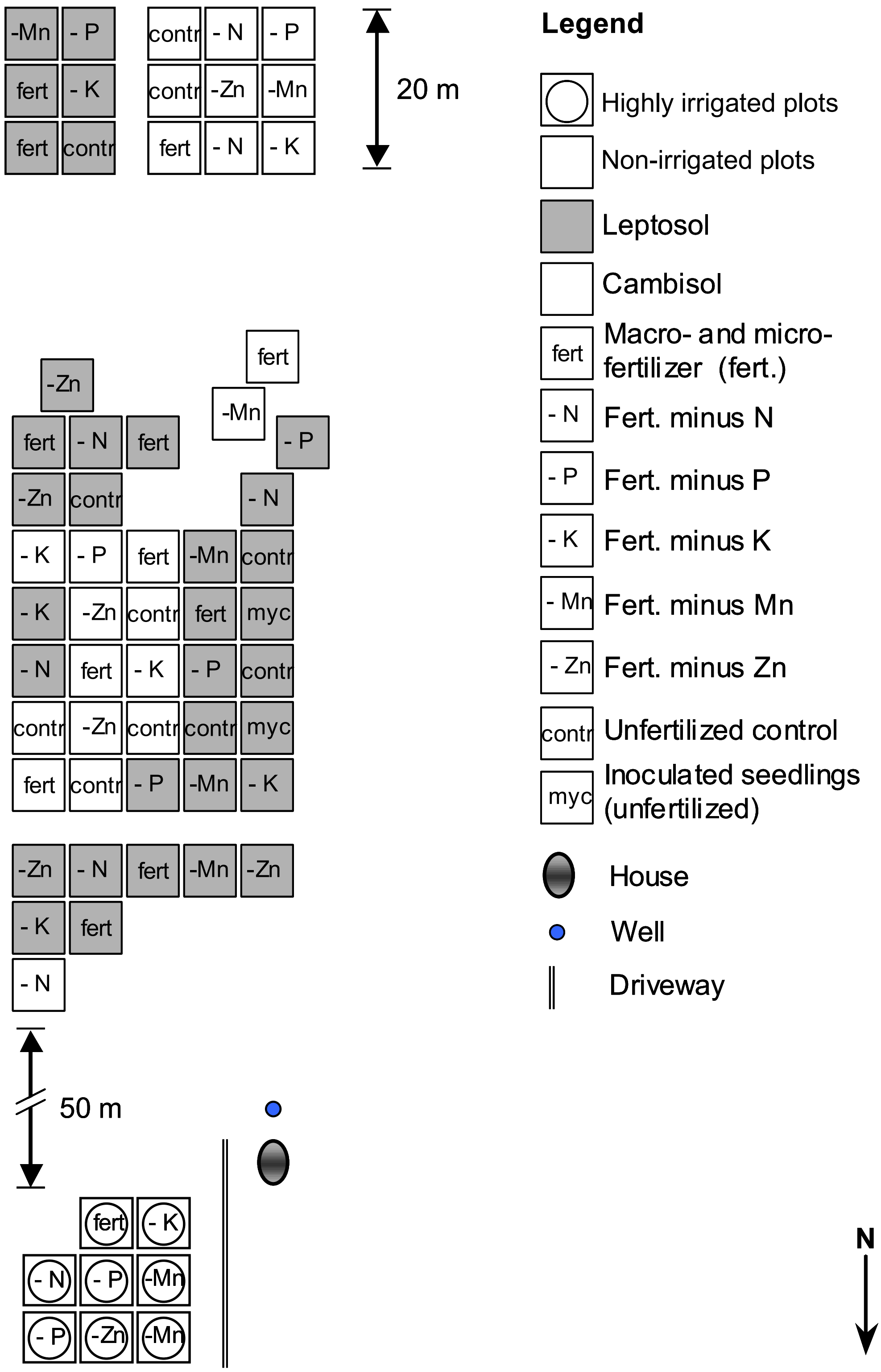

Figure 20: Experimental site 3 at X'matkuil, Mérida, Yucatan, Mexico, owned by J. Castillo, former member of Protrópico (UADY)

type, irrigation level and fertilizer treatment were established, with the exception of site 1, where Leptosol was scarce. Hence, on site 1, eight Leptosol plots were missing (192 plots – 8 Leptosol plots = 184 plots). Hurricane Isidore strongly affected the pumping system on site 3, and the re-established pump was not strong enough to supply the entire experimental area with irrigation water. Therefore, plots on site 3 were not irrigated at all – with the exception of 8 plots located at the entrance of the site, which were irrigated four times a week (highly irrigated) as a result of management decisions of the owner of the site (184 plots – 8 plots = 176 plots). On the remaining sites 1 and 2, the irrigation system was established successfully for regular irrigation of plots. During the dry season, high mortality of seedlings – especially of *B. orellana* – was observed on non-irrigated plots, and therefore we decided to irrigate the plots without regular irrigation on site 1 and 2 during the hottest period of the dry season. As a consequence, there were three irrigation levels instead of two, and the number of plot replications was reduced from six to four. After the dry season, growth results for both species and survival of *B. orellana* were found to be extraordinarily high on sporadically irrigated sub site plots on site 1. The assessment of the micro relief (mostly covered by secondary vegetation) in the surroundings of plots on the entire study area revealed that sub site plots – in contrast to plots on the remaining area - were surrounded on three sides by mounds of heights between 0.75 and 1.5 m. Detailed investigations on the history of the sub site revealed differences in land use history between sub site and the remaining experimental area. Hence, data from sub site plots was analyzed separately (184 plots – 16 sporadically irrigated plots on subsite plots = 160 plots). Due to the resulting reduction of the number of plots, the plot design could no longer be used as the basis for data analysis, and the data analysis was carried out based on the individual seedlings.

3.15 Statistical analysis

Sixteen seedlings per species were planted for each combination of soil type, fertilizer treatment and irrigation level. Seedlings with sporadic and regular irrigation were planted on sites 1 and 2, 8 on each site. Individuals without irrigation were situated on site 3 (located between site 1 and 2). For black soil with sporadic irrigation, 4 individuals (out of 16) were missing due to lack of available area with black soil on experimental site 1. To test for normal distribution, Q-Q-plots and detrended Q-Q-plots, skewness and kurtosis were calculated (SPSS). Data was transformed using log10 (in case of foliar aluminium concentration) to achieve normal distribution. GLM procedure (univariate analysis of variance (ANOVA)) was applied using individuals in a full-factorial model to determine least square means, standard errors (SE) and significance of growth and nutrient data (SAS, SPSS). Subsets for fertilizer treatments – if this factor was identified as significant by ANOVA – were determined using the Duncan test for homogeneous subsets. Significance level was – if not stated otherwise – 0.05. Growth was analyzed as a full factorial treatment, with the main factors irrigation, soil, and fertilizer treatment. The significance of the equality of error variances was assessed by Levene's test. Inoculated seedlings and seedlings on the sub site as well as highly irrigated seedlings on site 3 were not included in the general analysis. For comparison of inoculated and control seedlings, control and inoculated seedlings on sub site were included. Growth results for *B. orellana* were calculated excluding seedlings without irrigation and seedlings on sub site. GLM with repeated measurements was performed to evaluate the influence of the time of measurement on growth. For sporadic and regular irrigation, growth results on Cambisol (red error bars) and Leptosol (black error bars) are displayed separately. Error bars in graphs show means +/- 1.0 SE.

3.16 Discussion of methods

3.16.1 Comparison of digestion procedures for plant and soil samples

The comparison of wet acid digestion methods indicated that the use of nitric acid (HNO3) digestion was suitable for the analysis of leaf samples as well as for possible future analyses of total element content of soils from the project region. The comparison showed that the nitric acid digestion procedure in comparison to digestion with sulfuric acid had very high reproducibility, with little variation between the two repetitions of each sample. The lower amount of Ca detected in leaf samples digested with H_2SO_4 was attributed to the formation of calcium sulfate ($CaSO_4$) during digestion that can occur in tissues rich in Ca. It may lead to the precipitation of other elements (Jones, 2001; Mills and Jones, 1996). At the end of rainy season, mean calcium concentration for Siricote leaves grown on calcareous soils of the Peninsula of Yucatan were 2.5 times higher than the threshold of 10 g/kg that sets the limit for the use of wet sulfuric acid digestion (Mills and Jones, 1996; Jones, 2001).

3.16.2 Use of foliar sprays in semi-arid, stony regions

On the experimental sites, the rocky- and stoniness of the soil made the use of regular soil fertilizer not feasible for the experiment. When applied at each planting site in a circle of 30 cm around the tree, dispersion by wind and the high rock percentage would have made it impossible to guarantee an even distribution of fertilizer in the reach of seedlings root systems. Therefore, nutrients had to be applied as foliar sprays. The use of foliar sprays, especially in high concentrations, may lead to leaf burn. Intense rainfall events shortly after the application may dilute the fertilizer and lead to infiltration of the fertilizer solution into the soil. To avoid these possible negative effects, during the rainy season 2003, the foliar nutrient mix was applied at relatively low concentrations, but several times.

3.16.3 Visual Tree Assessment (VTA) for the tropics

In this study, we concentrated on tree growth as a symptom of nutritional disorders of seedlings, and on the analysis of foliar nutrients. Additionally, nutritional disorders of tropical trees may be assessed by visual assessment of the health status of trees. But so far, detailed descriptions of deficiency symptoms for tropical broadleaved tree species are not available, and no standards for a rapid visual assessment have been developed yet. For further analysis of micronutrient disorders of tropical broad-leaved trees, it would be very useful to develop a universal scheme for the rapid assessment and description of the impact of nutritional disorder on seedlings of tropical broadleaved trees. This would allow the quick and cost-effective monitoring of the individual tree health status on experimental plantations with numerous trees, and comparisons between the nutritional requirements of tree species on different sites would be easier.

4 IMPACT OF WATER, SOIL AND NUTRIENTS ON GROWTH PARAMETERS

4.1 Introduction

Because of the specific hydrological conditions of the Yucatan Peninsula - a groundwater table at 8 m depth, high drainage of the calcareous substrate and underground rivers - so far water has been considered the major growth-limiting factor for plant growth (Jiménez-Osornio, 2002). Few studies have addressed the nutrient requirements of native seedlings on Northern Yucatan soils, and nutrient availability as well as nutrient-water-interactions as an important constraint to seedling growth has not been investigated. The stony, calcareous soils of Northern Yucatan form a small-scale mosaic of the dominant soil classes, black Tsekel on mounds (Leptosol) and red Kankab in plains (Cambisol). Calcareous soils may possess low absolute quantities of macronutrients, especially phosphate, potassium and nitrogen. At pH values above 7.5, the availability of phosphate, manganese, zinc, copper and iron is less than optimum (Jeffrey, 1987). But the analysis of available P and organic matter content of the dominant soil groups of Northern Yucatan did not explain the relative productivity attributed to these soils. However, it indicated that nutrient availability and soil moisture were closely interrelated (Weisbach et al., 2002).

Hypotheses

Under the soil and site conditions in Yucatan, low water availability limits growth of tree seedlings of *C. dodecandra.*

On the calcareous semi-arid soils of Yucatan, low availability of N, P, K, Zn, and Mn, in combination with low water availability limits seedling growth and nutrient uptake of *C. dodecandra.*

4.2 Results and discussion

The first section of this chapter presents our results on the impact of water and the two dominant soil classes of Northern Yucatan, black Tsekel (Leptosol) and red Kankab (Cambisol). The second section provides an overview of our data on foliar nutrient concentrations of unfertilized control seedlings of *C. dodecandra*. They are compared with foliar nutrient concentrations of other tropical broadleaved tree species from the literature, and with our results on foliar nutrient concentrations of mature *C. dodecandra* trees from Mayan homegardens. The third section gives an overview on our results on the impact of the applied subtractive fertilizer treatments on growth of seedlings at three irrigation levels on Leptosol and Cambisol. In the fourth section, our results on foliar nutrient concentrations at sporadic and regular irrigation on the two soils are presented.

4.2.1 Impact of irrigation and soil on growth of *C. dodecandra*

4.2.1.1 Growth response of *C. dodecandra* seedlings

Irrigation was the main influence factor on growth of *C. dodecandra* seedlings (Table 8). With regular irrigation, seedlings obtained the highest total stem length and growth increments (Figures 21a+b). After the first dry season, stems of seedlings without irrigation had reached 63 cm, with sporadic irrigation 85 cm, and with regular irrigation 110 cm ($p_{irr} < 0.0001$) (Figure 21a). At the end of rainy season, non-irrigated seedlings had attained stem lengths of 94 cm, sporadically irrigated 174 cm, and regularly irrigated 206 cm ($p_{irr} < 0.0001$). Stem length increments over the rainy season were significantly different for all three irrigation treatments ($p_{irr} = 0.000$) (Figure 21b). They were comparably high for sporadic irrigation. With regular irrigation, the growth increment was with 96 cm only 0.08 times higher compared to sporadic irrigation with 89 cm. Seedlings without irrigation showed an increment of 32 cm. This meant an increment of stem length from July 2003 to January 2004 in relation to total stem length in July 2003 of 50% for non-irrigated, 106% for regularly irrigated, and 120% for sporadically irrigated seedlings. There was no difference between stem lengths or stem length increments on the two soils.

Table 8: Results of ANOVA of stem length, virtual diameter and crown area of *C. dodecandra* for complete fertilizer and control with three irrigation levels on two soils

Source of variation	**df [1])**	**Stem length of 15-month-old *C. dodecandra*** (n = 183)	**Virtual diameter of 21-month-old *C. dodecandra*** (n = 182)	**Crown area of 21-month-old *C. dodecandra*** (n = 183)
Irrigation (I)	2	***	***	***
Soil type (S)	1	NS	NS	NS
Fertilizer (F)	1	NS	NS	NS
I*S	2	NS	NS	NS
I*F	2	NS	NS	NS
S*F	1	NS	NS	NS
I*S*F	2	*	NS	NS
EEV [2])		***	*	***

*,**,*** Significant at 0.05, 0.01 and 0.001 probability levels, respectively
NS = Non-significant
[1]) df = Degree of freedom
[2]) EEV = Significance of equality of error variances (Levene's Test)

Considering the low irrigation water input during the dry season compared to regular irrigation, growth of sporadically irrigated seedlings was comparably high, especially over the rainy season that followed the dry season during which the irrigation treatments took place. Hence, with sporadic irrigation at the peak of dry season only, seedlings of *C. dodecandra* showed comparably high total stem length at the end of the rainy season, at the age of 21 months. In addition to the main factor irrigation ($p_{irr} = 0.000$), soil by irrigation interactions had a significant impact on virtual diameter growth, with $p_{irr*sol} = 0.009$ for total virtual diameter at the end of rainy season, and $p_{irr*sol} = 0.000$ for virtual diameter increments (Figures 22a+b). After the rainy season, seedlings with sporadic irrigation had higher diameters on red Cambisol (34 mm) than on black Leptosol (31 mm). In contrast to this, regularly irrigated seedlings had higher diameters on Leptosol (42 mm) than on Cambisol (39 mm). Without irrigation, virtual diameters on

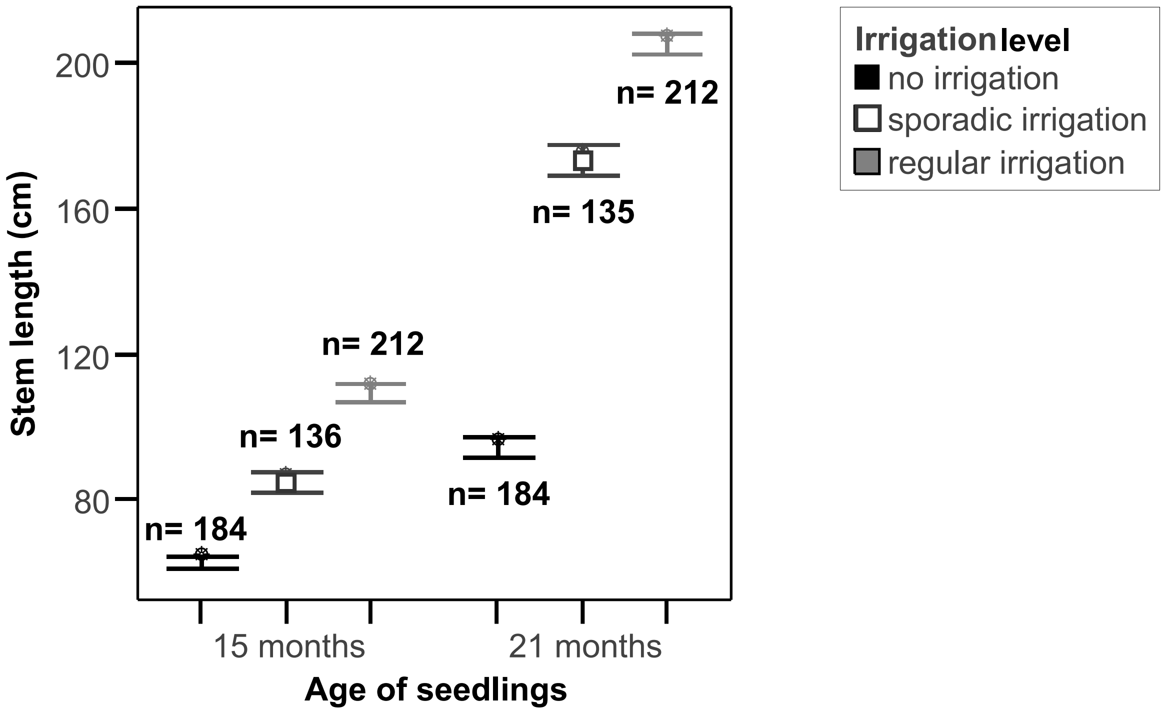

Figure 21a: Stem length of *C. dodecandra* on experimental plots at the age of 15 (mid rainy season) and 21 months (end of rainy season) with three irrigation levels on both Leptosol and Cambisol together (no difference between soils), error bars show mean +/- 1.0 SE

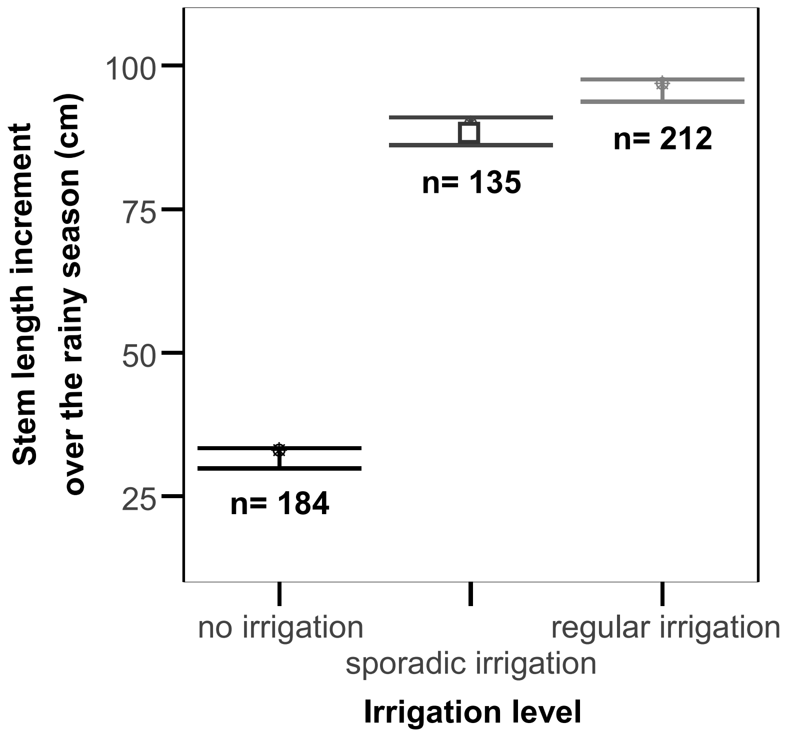

Figure 21b: Stem length increment of *C. dodecandra* seedlings over the rainy season from July 2003 (15 months) to January 2004 (21 months) (expl. see Figure 21a).

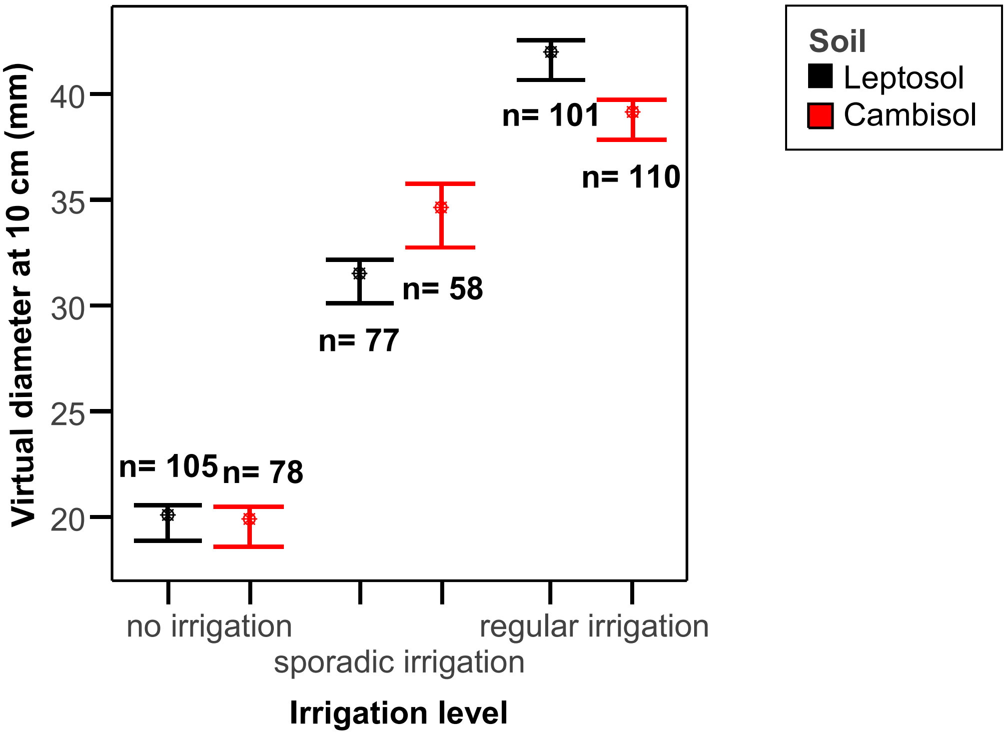

Figure 22a: Virtual diameter (diameter of stem and branches) at 10 cm above ground of 21-month-old *C. dodecandra* seedlings on black Leptosol and red Cambisol at different irrigation levels on experimental plots at the end of rainy season, error bars show mean +/- 1.0 SE

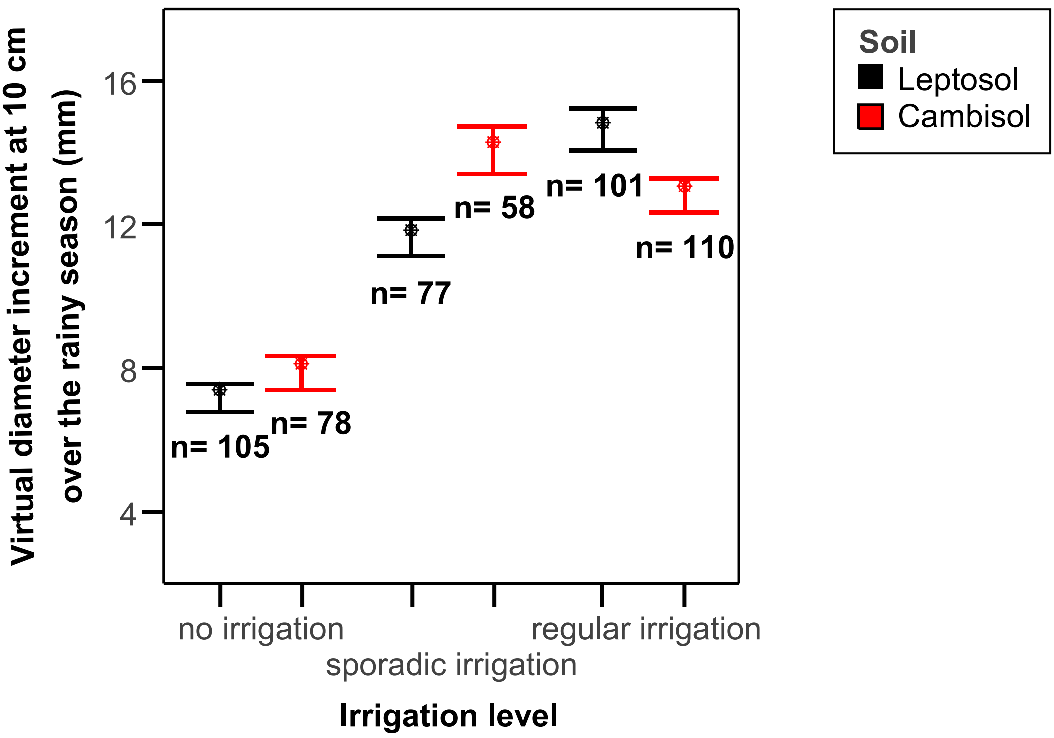

Figure 22b: Virtual diameter increment at 10 cm above ground of *C. dodecandra* from July 2003 (15 months) to January 2004 (21 months) (expl. see Figure 22a)

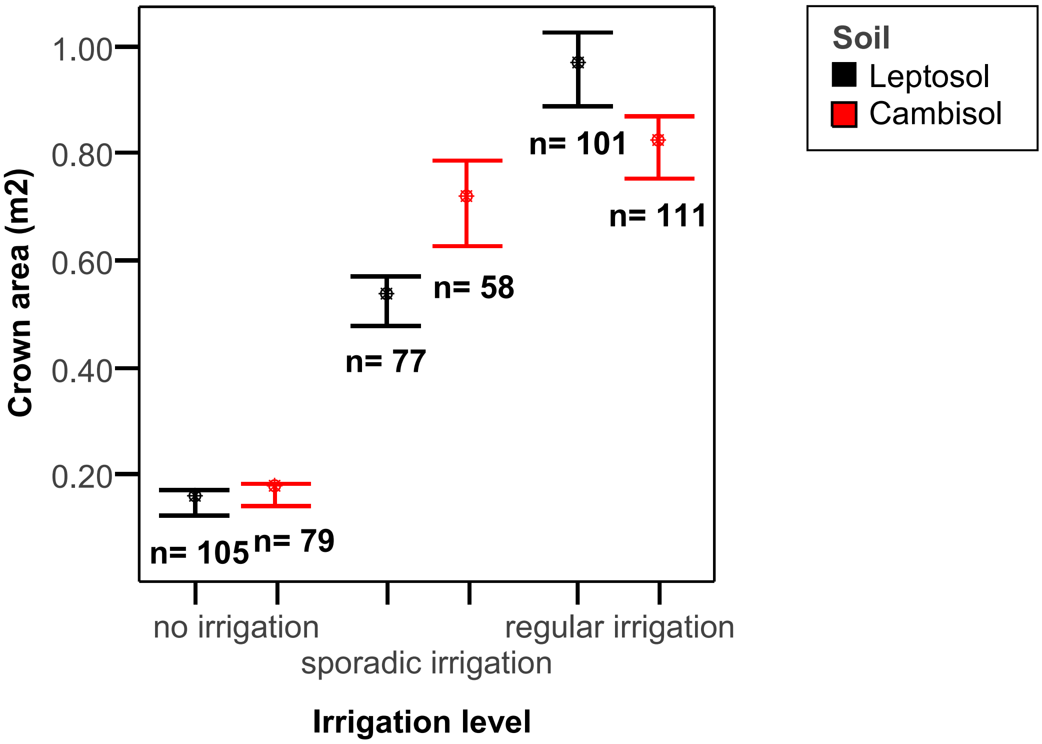

Figure 23: Crown area of 21-month-old *C. dodecandra* on Leptosol and Cambisol at three irrigation levels on experimental plots, error bars show mean +/- 1.0 SE

red and black soil were even (both 19 mm) (Figure 22a). On Leptosol, virtual diameter increments highest with regular irrigation (15 mm compared to 12 mm with sporadic irrigation). On Cambisol, however, virtual diameter increments over the rainy season were not significantly different with sporadic irrigation (14 mm) and with regular irrigation (13 mm) (Figure 22b). In July 2003, at mid rainy season, soil-irrigation interactions did not yet show a significant impact on total virtual diameter of seedlings, irrigation being the main influence factor ($p_{irr} < 0.0001$) (data not shown). At mid rainy season, seedlings with sporadic irrigation had virtual diameters of 20 mm, thereby exceeding virtual diameters of seedlings without irrigation by 8 mm. Regularly irrigated seedlings had virtual diameters of 26 mm.

Growth results for virtual diameter of *C. dodecandra* at different irrigation levels emphasized the comparably high effect of sporadic irrigation on seedling growth. In addition, they revealed the importance of soil-irrigation interactions with increased water additions. On Leptosol, increased irrigation led to higher virtual diameter growth and increment. In contrast, on Cambisol, diameters of stem and branches showed similar growth increments with both sporadic and regular irrigation, even though 9.6 times more water had been added to regularly irrigated seedlings during the dry season.

The crown area of *C. dodecandra* seedlings at the end of rainy season showed a similar picture: regularly irrigated seedlings on black Leptosol obtained most extended crown areas, followed by seedlings on red Cambisol with both sporadic and regular irrigation (Figure 23). The interaction between soil and irrigation had a significant impact on crown area of seedlings ($p_{soil*irr} = 0.033$). Regularly irrigated seedlings had smaller crown areas on Cambisol than on Leptosol. In contrast to this, crown areas of sporadically irrigated seedlings were smaller on black Leptosol than on red Cambisol. At mid rainy season in July 2003, irrigation-soil interactions did not have a significant influence on growth of crown area (data not shown), and irrigation as a main factor explained the variation in crown area (p_{irr} = 0.000).

Highest stem growth on highly irrigated *C. dodecandra* on Cambisol compared to regularly and sporadically irrigated seedlings further supported the result that irrigation was the main influence factor on growth at mid rainy season regarding all evaluated growth parameters (p_{irr} = 0.000) (data not shown). Seedlings with fertilizer minus P additions had highest stem lengths of 164 cm on highly irrigated plots, compared to regularly (109 cm) and sporadically irrigated plots (83 cm) (p = 0.000). Growth parameters of highly irrigated seedlings generally were still higher than (crown area) or similar to (stem length and virtual diameter) regular irrigation after the rainy season. Data for highly irrigated seedlings was not available for unfertilized control seedlings or for black Leptosol (see material and methods).

However, growth increment of stem length on highly irrigated fertilized plots between July 2003 and January 2004 was significantly lower than on fertilized plots with regular and sporadic irrigation (p = 0.000) (data not shown). Highly irrigated seedlings on red Cambisol with complete fertilizer that received 1.3 times more water during dry season than regularly irrigated seedlings, attained only 49% of their stem length increment (49 cm for highly irrigated versus 100 cm for regularly irrigated seedlings). Highly irrigated seedlings with subtractive N applications had stem length increments over the rainy season of 48 cm, similar to seedlings without irrigation, and lower than seedlings with both regular and sporadic irrigation (p = 0.000). Highly irrigated seedlings with subtractive P applications had stem length increments over the rainy season of 47 cm, higher than seedlings without irrigation (26 cm), but lower than seedlings with both regular (83 cm) and sporadic irrigation (91 cm) (p = 0.000). Virtual diameter increments of irrigated seedlings of the respective fertilizer treatments on red Cambisol did not show any significant difference between sporadic, regular and high irrigation (data not shown). At the end of rainy season, crown area on minus N plots on Cambisol was with 1.66 m² still broader than that of seedlings with regular, sporadic or without irrigation (p = 0.003). On Cambisol minus P plots, crown area at mid and end of rainy season did not show any significant difference between sporadically, regularly and highly irrigated seedlings.

The comparison of results on highly irrigated seedlings on site 3 with other irrigation levels confirms the overall importance of water availability for seedling growth on calcareous Cambisol in Yucatan. Even though the effect on non-fertilized plots could not be evaluated, treatment-wise comparisons clearly show the dominant influence of water availability on growth during dry season. Our results indicate that after a certain stage, irrigation during dry season enhances growth until mid rainy season, but ceases to be a trigger for growth during the subsequent rainy season. This points towards the importance of other influence factors on plant growth such as nutrient availability and nutrient-water-interactions.

4.2.1.2 Differences between black Leptosol and red Cambisol

On the experimental sites, the typical colors of black Tsekel (Leptosol) were 10YR3/2 and 10YR2/2. On some sampling sites, black soil showed a darker black color than 10YR2/1, the darkest black found at the Munsell Chart. The average rocky- and stoniness of the selected black Leptosol sites was 70%, varying from 60% to 80%. Thereof, 10% and 50% of surface cover were rocks and rock fragments. The sites with black Leptosol were located on top and on the slope of mounds. The color of red Kankab (Cambisol) was typically 7.5YR4/6. The surface cover of rocks and stones of red Cambisol was around 10%, with less than 10% of rocks and rock fragments. The sites with red Cambisol were situated in the plain. The pH of black Tsekel soil (Leptosol) on research plots was significantly higher than of red Kankab soil (Cambisol) for pH measurements in both water and calcium solution ($p = 0.000$). The pH in $CaCl_2$ of the Cambisol was 7.3; the pH in $CaCl_2$ of the Leptosol was 7.6. The pH in water of the Cambisol on experimental plots was 7.9; the pH in water of the Leptosol was 8.1. Excavations to a depth of 10 to 20 cm on red Kankab soil (Cambisol) on 30 randomly assigned spots at our experimental sites, and the digging of planting holes (up to 40 cm deep) showed the high spatial variability of the rock layer (the so-called laja) that delimited the Cambisol. Its depth varied from 4 cm to over 40 cm, with shallower areas intercalated by deeper areas at short distance on transects. Excavations to 20 to 30 cm on black Tsekel soils (Leptosol) on 30 randomly assigned spots at our experimental sites, as well as the soil profile on a black Leptosol to a depth of about 80 cm, showed that underneath apparently very shallow soil layers delimited by rock and big stones, pockets of black Tsekel soil of several cm diameter were found.

4.2.1.3 Growth differences on black Leptosol and red Cambisol

Better growth of regularly irrigated *C. dodecandra* seedlings on stony Leptosol in comparison to Cambisol on experimental plots may be attributed to the higher amount of available nutrients at adequate soil moisture. Black Leptosol, though shallower and with a higher percentage of stones, has a higher percentage of organic material, and a higher fertility than red Cambisol (Weisbach et al., 2002). When regularly irrigated and hence close to saturation, the high fertility probably enhances faster growth of seedlings.

To explain the high growth response of seedlings to irrigation on stony black Leptosol, the role of the high percentage of stones and rocks as a potential additional water reservoir has to be taken into account. To understand the water regime in calcareous soils, the volume and hydraulic properties of rock fragments should be considered because of their influence on water retention and percolation (Poesen and Lavee, 1994; Cousin et al., 2003). Estrada Medina (2000) found in Northern Yucatan soils a variety of rocks with different ability to retain water. Above-ground biomass production of three indigenous Costa Rican tree species at annual precipitation levels above 2000 mm was best in the upland stony, loamy site compared with more clayey or less well drained non-stony sites in the lowland (Messenger et al., 1997).

In accordance with our result that irrigated seedlings grew better on black Leptosol than on less stony red Cambisol, some farmers in the community Hocabá stated that after heavy rains, black soils on mounds produced higher yields than red soils on flat plains. In contrast to this, other farmers said that both soils produced equally well with abundant rains (Estrada Medina, 2000). This difference in farmers' observation may be attributed to differences in the history of land use of fields such as the age of the fallow vegetation before burning, and to additional soil characteristics such as available soil volume that may have an important impact on plant development.

4.2.1.4 The key role of water for growth

Our results indicate that water availability is the dominant factor influencing growth of *C. dodecandra* seedlings in the former 'Henequén area'. Water availability in the soil is considered as the most critical factor controlling plant productivity and reproduction in semi-arid environments (Noy-Meir, 1973).

In accordance with our results, recent studies on the irrigation of typical fruit trees in Mayan homegardens showed a 4 to 9-fold increase in the photosynthetic rate for *Manilkara zapota*, *Annona squamosa* and *Citrus aurantium* under irrigation (Benjamin et al., 2001). For the establishment of seedlings of the fodder tree species *B. alicastrum,* photosynthetic rates in irrigated plants were three to four times greater than in non-irrigated plants (Gillespie et al., 2004). In contrast to our findings, though, non-irrigated *C. dodecandra* seedlings in homegardens had higher photosynthetic responses than irrigated seedlings (Benjamin et al., 2001). The various additional environmental and anthropogenic influences of homegardens may have resulted in different growth responses than under controlled conditions.

The importance of irrigation on plant growth in arid and semi-arid environments has been acknowledged for a long time (Noy Meir, 1973). Though precipitation in Northern Yucatan with approx. 1000 mm is higher than in regions typically classified as semi-arid, the hydrological and edaphic characteristics of the Peninsula increase the dominant role of water availability on growth. The permeable calcareous rock layers of varying porosity favor the high drainage of the soil, and the slightly undulated micro relief contributes to the minimum overland flow, and hence the absence of aboveground water. The depth of 8 m of the groundwater table enables only deep-rooting species such as trees with a tap root at an adult stage to exploit this water source.

4.2.1.5 Effect of sporadic irrigation at the peak of dry season

Our data suggest that adequate timing of seedling irrigation is important for the efficiency of the irrigation scheme. For *C. dodecandra* seedlings on our experimental area, irrigation at the peak of dry season after several weeks of drought showed relatively more effect on growth than irrigation during the entire period of drought. When assessing the impact of water on plant growth, the timing of rainfall has to be considered (Ogle and Reynolds, 2004). The effect of precipitation pulses on plant growth does not only depend on the amount of annual rainfall, but also on the intensity of pulses and their distribution over time by influencing the amount of infiltration (Schwinning and Sala, 2004) and evaporation (Sala and Lauenroth, 1982). The pronounced drought season in Yucatan from January to May/June with its peak in April/May is a challenge for the development of seedlings in terms of their resistance to drought stress. In our experiment, sporadic irrigation at the peak of dry season just before the beginning of the rainy season shortened the duration of the dry period, and thereby probably mitigated the severity of the drought stress. These two factors determine the physiological status of the seedling at the beginning of rainy season, and hence its ability to resume photosynthetic activity and transpiration (Schwinning et al., 2002; Yan et al., 2000). Sporadic irrigation therefore may alleviate stress of *C. dodecandra* seedlings on the experimental plots, enhance tissue repair and rehydration, and increase the capacity of seedlings to respond to larger events. Occasional pulses during severe drought were found to keep plant activity at an adequate level and reduce stress, even if they do not translate into net carbon gain (Sala and Lauenroth, 1982; Yan et al., 2000). This may give *C. dodecandra* seedlings with sporadic irrigation on our experimental plots a competitive advantage over non-irrigated seedlings. Comparing water input and growth output of sporadically irrigated *C. dodecandra* on our experimental plots with regularly irrigated seedlings, water use was more efficient in sporadically irrigated seedlings. By maintaining an adequate water status and reducing their stress level, sporadic irrigation at the peak of dry season may have enabled *C. dodecandra* to capitalize on the high amounts of soil moisture from the onset of the rainy season on.

4.2.2 Nutrient ranges and ratios of *C. dodecandra*

Table 9a presents the foliar nutrient concentrations and ratios of non-fertilized *C. dodecandra* seedlings at mid rainy season for the comparison of leaf nutrient concentrations with other tropical broadleaved trees. Table 9b gives an overview of leaf nutrient contents of *C. dodecandra* seedlings on control plots at the end of rainy season, with both sporadic and regular irrigation and both red Cambisol and black Leptosol together.

Table 9a: Foliar nutrient content of 15-month-old *C. dodecandra* seedlings (n = 22) from experimental control plots with both sporadic and regular irrigation, on both red Cambisol and black Leptosol, YFML, mid- to upper crown, sampled at mid rainy season, all nutrients except zinc and nitrogen analyzed with ICP-AES, zinc analyzed with AAS, nitrogen analyzed with Elemental Analyzer

Macronutrient	**Min** g / kg	**Max** g / kg	**Mean** g / kg	**SE** g / kg	**Time of sampling**
N	26.7	36.4	30.5	.49	mid rainy season
P	1.4	2.3	1.8	.05	mid rainy season
K	12.8	24.6	19.2	.69	mid rainy season
Ca	23.0	32.0	26.0	.64	mid rainy season
Mg	3.4	6.0	4.5	.16	mid rainy season
S	2.0	2.9	2.5	.05	mid rainy season

Micronutrient	**Min** mg / kg	**Max** mg / kg	**Mean** mg / kg	**SE** mg / kg	**Time of sampling**
Zn	11	20	16	.6	mid rainy season
Mn	9	34	23	1.3	mid rainy season
Fe	30	131	55	4.5	mid rainy season
Al	9	186	14*)		mid rainy season

*) Median instead of mean, not normally distributed

Nutrient ratio	**Min**	**Max**	**Mean**	**SE**	**Time of sampling**
K / sqrt (Ca+Mg)	.72	1.43	1.10	.04	mid rainy season
Ca / Mg	4.3	8.4	6.1	.17	mid rainy season
N / S	10.4	14.3	12.3	.23	mid rainy season
P / Zn	81	151	118	4.1	mid rainy season

Table 9b: Foliar nutrient content of 20-month-old *C. dodecandra* (n = 37) from control plots with both sporadic and regular irrigation, on both soils (explanations see Table 9a)

Macronutrient	Min g / kg	Max g / kg	Mean g / kg	SE g / kg	Time of sampling
N	14.6	27.6	21.5	.47	end of rainy season
P	.7	1.4	1.0	.03	end of rainy season
K	4.1	18.1	9.5	.59	end of rainy season
Ca	24.0	50.2	37.5	1.08	end of rainy season
Mg	2.5	9.1	4.6	.22	end of rainy season
S	2.5	4.9	3.6	.09	end of rainy season

Micronutrient	Min mg / kg	Max mg / kg	Mean mg / kg	SE mg / kg	Time of sampling
Zn	8	26	13	.7	end of rainy season
Mn	10	51	27	1.5	end of rainy season
Fe	40	100	55	2.3	end of rainy season
Al	23	141	41*)		end of rainy season

*) Median instead of mean, not normally distributed

Nutrient ratio	Min	Max	Mean	SE	Time of sampling
K / sqrt (Ca+Mg)	.19	.88	.47	.03	end of rainy season
K / (Ca+Mg)	.08	.45	.23	.02	end of rainy season
K / Mg	.5	7.1	2.4	.24	end of rainy season
Ca / Mg	5.1	15.7	8.6	.39	end of rainy season
N / S	4.3	8.4	6.1	.17	end of rainy season
P / Zn	40	134	81	4.2	end of rainy season

4.2.2.1 Comparison of foliar nutrient contents of *C. dodecandra* and other forest trees

In comparison to other broad-leaved trees growing in Yucatan, mean foliar phosphorus concentration of *C. dodecandra* at mid rainy season with 1.8 g/kg was relatively high (Table 9a). Tissues of temperate forest trees typically contained between 1.5 and 3.0 g/kg of phosphorus (Bergmann, 1993). Foliar P concentrations below 2.0 g/kg have been considered as an indicator for P shortage in plants (Mills and Jones, 1996). In many tropical broad-leaved trees, though, shortage symptoms were only detected at concentrations below 1.0 g/kg, and mean foliar P values of 1.6 g/kg were found in “healthy” seedlings of other species in Yucatan such as *Ceiba pentandra* and *Manilkara zapota*. *Brosimum alicastrum* showed no deficiency symptoms at P concentrations between 0.8 and 1.5 g/kg, while *Gmelina arborea* seedlings had intermediate P contents of 1.4 g/kg in Yucatan (Zech et al., 1991). Low foliar P values in tropical trees on the Yucatan Peninsula without shortage symptoms may be attributed to low P availability combined with an apparent high P use efficiency of the analysed tropical broadleaved species. Considering the literature on foliar P content in relation with health status of trees on the Peninsula, it has to be considered, though, that effects of P shortage on growth of seedlings may become evident only if trees are compared with other individuals of the same species growing under conditions of higher P supply, as it was done in our study.

Nitrogen concentrations of 15-month-old *C. dodecandra* seedlings were with 30.5 g/kg similar or higher than intermediate N concentrations of seedlings of almost all other tropical broad-leaved species from Yucatan. Only *Leucaena lanceolata* N concentrations from Yucatan exceeded N concentrations in *C. dodecandra* by 20 to 30%. Higher N concentrations were found to be characteristic for N-fixing species in comparison with non-fixing broad-leaved tropical trees (Drechsel and Zech, 1991). *Brosimum alicastrum* seedlings in Yucatan had 20 to 30% lower intermediate concentrations (Zech and Drechsel, 1992; Zech et al., 1991). This may be attributed to the low leaf turnover of the evergreen *B. alicastrum*, in contrast to the deciduous *C. dodecandra.* 2-year-old seedlings of *Cedrela odorata* and *Cordia alliodora* planted in Liberia showed equal or slightly higher N concentrations without deficiency symptoms. *C. dodecandra* seedlings were probably far from undergoing N shortage. Seedlings with shortage symptoms of *B. alicastrum*, *C. alliodora* and *C. odorata* had N leaf concentrations half as high as those detected in *C. dodecandra*. Foliar N concentrations of *L. lanceolata* with deficiency symptoms were 20% below the minimum leaf N content measured in *C. dodecandra*. Hence, it may be concluded that in comparison with other tree species from the region (Drechsel and Zech, 1991; Zech et al., 1991), N values of *C. dodecandra* seedlings do not indicate N deficiency, and N seems to be readily available at the site.

Foliar potassium with 19.2 g/kg at mid rainy season was similar or higher than K concentrations of most other tropical broad-leaved trees. Deficiency symptoms in tropical trees were recorded for K concentrations below 6.0 g/kg (Drechsel and Zech, 1991). Different temperate forest tree species contained generally between 10 and 15 g/kg of foliar K (Bergmann, 1993). An inadequate foliar K/Mg ratio may indicate K deficiency. The K/Mg ratio of *C. dodecandra* seedlings was less than half down to a quarter of the ratio considered optimum for crop growth (8/1). This illustrated the extremely low availability of K, combined with the relatively high availability of Mg. At mid rainy season, K/Mg ratios of *C. dodecandra* from this study were close to the critical level detected as a threshold for deficiency symptoms of *G. arborea* in Costa Rica, where very low foliar K/Mg ratios were found to induce K shortage (Stuhrmann et al., 1994). Negative impact on fruit development and quality was reported for grapes on calcareous soils in Austria. Deficiency symptoms occurred under conditions of low K availability, as well as under conditions of low tissue K/Mg ratio (Fardossi, 2001). This is supported by the comparison of base cation concentrations on the sub site, where seedlings grew best, and the remaining experimental area. At the end of rainy season, K/Mg was significantly higher on sub site control plots under sporadic irrigation than on the remaining sporadically irrigated control plots ($p = 0.002$) The same tendency was detected for foliar K/sqrt (Mg+Ca), and for foliar K.

Magnesium was readily available for seedlings on both soils. In Yucatan soils, Mg forms part of composite carbonates such as Ca Mg CO_3 (Duch, 1988). Foliar magnesium concentration with 4.5 g/kg was in the intermediate range of tropical broad-leaved arboreous species. *B. alicastrum*, for instance, had foliar Mg of 3.1 to 4.8 g/kg. Though values between species varied much, low values never exceeded 1.5 g/kg (Zech et al., 1991). Mg forms part of the chlorophyll molecule, and plays an important role as an activator of enzymes e.g. in the light reactions of photosynthesis in the chloroplast (Raven et al., 2000).

Calcium to magnesium ratios were up to four times higher than the general optimum for plant growth of 2/1 (Mills and Jones, 1996). The lower Ca/Mg ratio of sporadically irrigated seedlings in comparison to seedlings with regular irrigation (p_{irr} = 0.000) may be partially a result of reduced Ca uptake due to damages on young roots by water stress. Ca^{2+} ions are taken up passively at the tip of young roots with unsuberized endodermis cells. Our results reflect the high availability of Ca^{2+} ions due to the weathering of the calcareous substrate; on the other hand they documented a high calcium tolerance of the species *C. dodecandra*. Leaf calcium concentrations (26.0 g/kg with a range from 23.0 to 32.0) were very high in comparison to other broad-leaved tropical trees. Only very few species, including *B. alicastrum* with 19.3 to 32.0 g/kg and *C. alliodora* with 18.2 to 25.5 g/kg attained similar Ca concentrations. Ca is translocated by transpiration stream, the higher the concentration, the faster the movement. High foliar calcium concentrations did not seem to have a negative impact on *C. dodecandra* growth rates. Hence, *C. dodecandra* may be considered a calcicole species, well adapted to calcareous environments.

Foliar zinc concentrations of *C. dodecandra* seedlings seemed to be at the lower limit, compared to other broadleaved tree species, but without causing deficiency yet. Leaf Zn concentrations with 16 mg/kg (ranging from 11 to 20) at mid rainy season were similar or lower than foliar Zn content reported for other tropical broadleaved tree species. On the Yucatan Peninsula, intermediate Zn concentrations of *B. alicastrum*, *M. zapota*, and *G. arborea* were found to be in the same range. The same was true for *C. odorata* seedlings. Nevertheless, *C. alliodora* in plantations in Liberia had higher Zn concentrations of 28-29 mg/kg. Deficiency symptoms were recorded for tropical seedlings of *G. arborea* and *Ceiba pentandra* with Zn concentrations below 10 mg/kg. Zn concentrations between 10 and 15 mg/kg were generally defined as low (Drechsel and Zech, 1991). The lower limit of leaf Zn contents of temperate forest trees was at 15 mg/kg (Bergmann, 1993).

Compared to foliar Mn concentrations of other tropical trees, it may be concluded that Mn concentrations of *C. dodecandra* seedlings were low, but probably not yet at the deficiency level. Foliar Mn concentrations with 23 mg/kg, and a range from 9 to 34 mg/kg at mid rainy season were at the lower end of Mn concentrations observed in other tropical broad-leaved trees. Generally, foliar Mn concentrations of crops vary between 10 to 200 mg/kg, but sufficiency is attained in the range from 10 to 50 mg/kg (Mills and Jones, 1996). Many tropical tree species in different environments had intermediate Mn concentrations above 35 mg/kg, sometimes up to 300 mg/kg and more. For temperate forest trees, Mn concentrations typically range from 30 to 100 mg/kg (Bergmann, 1993). In Yucatan, Mn contents of *B. alicastrum* varied from 29 to 99 mg/kg, while *C. pentandra* had intermediate concentrations of 75 mg/kg, and low concentrations of 35 mg/kg. Deficiency symptoms were reported for *Swietenia macrophylla* with 13, and for *M. zapota* seedlings with 10 mg/kg. For *C. odorata* in plantations in Liberia, intermediate Mn concentrations of 25 mg/kg had been recorded (Zech and Drechsel, 1992; Drechsel and Zech, 1991).

Leaf iron concentrations with 55 mg/kg in the range of 30 to 131 mg/kg at mid rainy season were at the lower range of Fe contents reported for tropical tree species. For arboreous species on the Peninsula, though, equally low Fe concentrations have been reported (Drechsel and Zech, 1991; Zech et al., 1991). As variations of Fe contents between tree species are high, it is difficult to identify general deficiency levels for this element.

Foliar sulphur content and leaf N/S ratio of *C. dodecandra* at mid rainy season indicated that S status was not limiting growth development of *C. dodecandra* seedlings. At mid rainy season, leaf sulphur concentrations were at 2.5 g/kg. Compared to a range of tropical broad-leaved species, this value was similar or higher than the intermediate levels of S of other arboreous species. Sulphur concentrations of less than 1.2 g/kg were described as low (Drechsel and Zech, 1991). Nevertheless, *C. alliodora* in Costa Rica had mean S concentrations of 2.9 g/kg, and the critical level between healthy and stunted development was set at 2.5 g/kg. *C. alliodora*, though, was found to be highly demanding in macronutrients (Bergmann et al., 1994). Adequate N/S ratio for protein synthesis for most plants is 15 / 1. In the study mentioned above the N/S ratio for "healthy" *C. alliodora* seedlings was 11/1. In our study, *C. dodecandra* seedlings had a N/S ratio of 12.2/1.

According to our results on high growth of *C. dodecandra* on red Cambisol, it was probably not limited by the presence of small amounts of aluminium. The detected low foliar concentrations of aluminium were in accordance with the low expected Al availability at a soil pH of 7 to 8 (Finck, 1991) and in accordance with Al values of other tropical tree species on the Peninsula (Zech et al., 1991). Sensitivity to very low (<5 ppm) concentrations of Al (Jeffrey, 1987) was detected in some species adapted to calcareous environment. Symptoms are similar to phosphate deficiency.

4.2.2.2 Comparison of foliar nutrient contents at mid and end of rainy season

Lower tissue P levels of *C. dodecandra* of 1.0 g/kg at the end of rainy season (Table 9b) compared to mid rainy season (Table 9a) were attributed to the dilution of P in the plant. They may also result from the transport of P to other parts of the seedling before the loss of leaves due to the mobility of P in the plant. Over the rainy season, dilution of available nutrients in plants, especially if they are less mobile in the plant, leads to lower leaf nutrient concentrations of sampled youngest fully matured leaves. At the end of rainy season, leaves export mobile nutrients to stems (Wilson et al., 2000 and 2001). Towards the end of rainy season, N concentrations of YFML dropped by nearly one third. This is attributed to the dilution of N in the plant, and may also be partly explained by the beginning of N translocation to other parts of the seedling. All nitrogen forms are mobile in plants. Increased calcium concentrations of up to 37.5 g/kg at the end of the wet season may be explained by the high accumulation of Ca and its immobility in the plant compared to other nutrients. The increase of S of more than one third over the wet season may be attributed to the low mobility of S in the plant. Younger tissues are provided with S from roots and petioles rather than from older leaves. As other more mobile elements such as N were translocated at the end of rainy season, the percentage of S in dry weight increased. Foliar Zn concentration decreased only slightly towards the end of dry season. As zinc is not very mobile in the phloem, the translocation before leaf loss may have less impact on foliar Zn content. An increased rooting zone may balance the depletion of soil layers from zinc. Over the wet season, Fe concentration remained about constant. This was explained by the low mobility of Fe in the plant that led to an accumulation of Fe in the tissue. As more mobile nutrients started to be transported to other parts of the plant, the relative Fe content of the leaf increased.

4.2.2.3 Foliar nutrient contents of *C. dodecandra* trees in Mayan homegardens

Table 10 shows foliar nutrient ranges and ratios from mature homegarden trees from Northern Yucatan for the comparison of foliar nutrient concentrations of *C. dodecandra* seedlings on the experimental area (Table 9a) with *C. dodecandra* homegarden trees. The selected *C. dodecandra* adult trees had crown diameters from 9 to 13 m² and stem diameters at 1.30 m height (dbh) between 7.2 and 18.5 cm.

Table 10: Foliar nutrient contents of *C. dodecandra* adult trees (n = 5) from homegardens at Hocabá, Northern Yucatan, mid-crown YFML (expl. see Table 9a)

Macronutrient	**Min** g / kg	**Max** g / kg	**Time of sampling**
N	16.8	27.8	mid rainy season
P	.7	1.6	mid rainy season
K	4.7	26.1	mid rainy season
Ca	11.6	56.2	mid rainy season
Mg	4.1	7.8	mid rainy season
S	1.9	3.4	mid rainy season
Micronutrient	**Min** mg / kg	**Max** mg / kg	**Time of sampling**
Zn	8	15	mid rainy season
Mn	7	17	mid rainy season
Fe	32	84	mid rainy season
Al	11	86	mid rainy season
Nutrient ratio	**Min**	**Max**	**Time of sampling**
K / sqrt (Ca+Mg)	.19	2.09	mid rainy season
K / Mg	.61	6.39	mid rainy season
P / Zn	91	112	mid rainy season

While our data show that foliar N concentrations of homegarden trees were probably adequate for fruit production, growth, and tree health status, foliar concentrations of P, Mn and Zn indicated a potential deficiency of these elements (Table 10). In comparison to a range of tropical broad-leaved tree species (Drechsel and Zech, 1991), leaf nitrogen concentrations of homegarden *C. dodecandra* that we assessed may still be considered as low to intermediate, but probably not as limiting seedling development. This may be supported by results of Benjamin et al. (2001) who observed an increase in foliar N content in homegarden trees after N fertilizer additions, though this was not accompanied by an increase in photosynthetic activity. According to our results, foliar P concentrations were low to intermediate, compared to other broad-leaved arboreous species (Drechsel and Zech, 1991). Montañez (2001) observed that the P use efficiency of *C. dodecandra* in Mayan homegardens was similar to that of several other native fruit trees. Foliar Zn contents from homegarden trees that we assessed were located between shortage and low concentrations of Zn of other broad-leaved species. Foliar Mn concentrations in our sampled homegarden trees were clearly on a level where deficiencies have been observed in other tropical species (Drechsel and Zech, 1991). Our results indicate that after the vegetative growth stage, with the onset of flower and fruit production of young trees, low levels of P, Zn and Mn may become limiting for adequate development and further growth. Furthermore, low levels of Zn and Mn may impact fruit set and fruit quality, and hence result in loss of yield and benefit from fruit production. Our data on the cation balance revealed high heterogeneity, reflecting the high variability of nutrient availability of homegarden stands. K, Mg and Ca concentrations of homegarden trees from our investigation reached higher maxima than seedlings of the experimental plots. In accordance with our results, relatively high values of K and Mg in litter of *C. dodecandra* in homegardens were reported from two Mayan communities in Yucatan (Montañez, 2001). In the comparison of nine tree species (mostly native fruit trees) that produced more than half of the litterfall of the homegardens by Montañez (2001), *C. dodecandra* had the lowest K and Mg use efficiency. The adult trees that we evaluated in homegardens at mid rainy season had foliar N, P, Zn and Mn concentrations below the average of *C. dodecandra* seedlings on our experimental area. This may be explained by dilution of the available nutrients. Lower nutrient values in homegardens may be due to competition, especially by neighboring trees with equally deep rooting systems. The possible depletion of nutrients of the rooting zone and the influence of nutrient leaching may be partly balanced by the ability of the tree to forage in deeper soil layers. Additionally, the irrigation of *C. dodecandra* seedlings during dry season on experimental plots possibly increased nutrient availability compared to non-irrigated homegarden trees.

4.2.3 Impact of nutrient–water–interactions on growth of *C. dodecandra*

In this section, the results on the impact of seven fertilizer treatments including the control on growth of *C. dodecandra* seedlings on the experimental area at X'matkuil, Mérida, Yucatan, Mexico, are presented. Figures 24 – 27 show our results from field measurements of stem length and virtual diameter at mid rainy season that reveal the effects of the first fertilizer application on growth.

On both soils, non-irrigated *C. dodecandra* seedlings attained at mid rainy season highest virtual diameters and stem lengths on plots with complete fertilizer minus zinc ($p_{treatment}$ = 0.001 and $p_{treatment}$ = 0.003) (Figures 24 and 25). Virtual diameter (16.0 mm) for the subtractive zinc treatment was higher than for all other treatments (p between 0.000 and 0.012). On both soils, stem length with complete fertilizer minus zinc treatment was significantly higher than other treatments (p between 0.004 and 0.023) including control (p = 0.000), with the exception of subtractive N. Stem length on plots with subtractive N applications was higher than the control (p = 0.004).

On regularly irrigated black Leptosol at mid rainy season, virtual diameter of *C. dodecandra* was higher with subtractive P applications than with complete fertilizer (p = 0.037) (Figure 26). Sporadically irrigated seedlings on Leptosol had higher virtual diameters with subtractive P applications compared to subtractive Mn and subtractive K treatments (p = 0.046 and p = 0.045). On regularly irrigated red Cambisol, seedlings attained higher virtual diameters with complete fertilizer than with complete fertilizer minus K (p = 0.002) and minus Mn (p = 0.048). The difference between complete

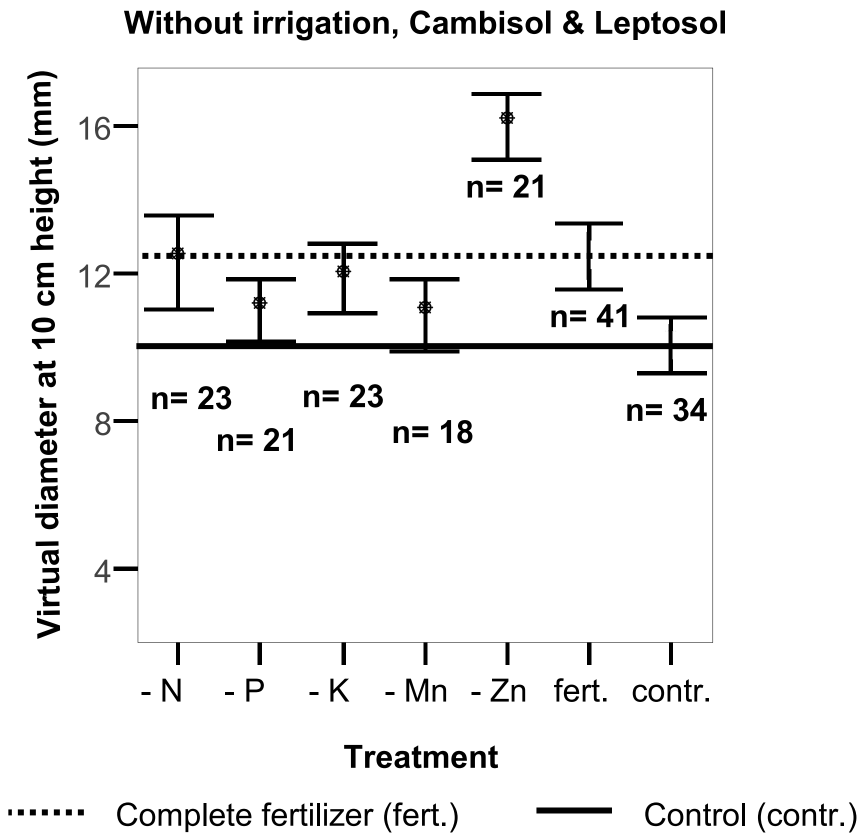

Figure 24: Virtual diameter of 15-month-old *C. dodecandra* on plots without irrigation on both soils (no difference between soils), error bars show mean +/- 1.0 SE

fertilizer and control seedlings on regularly irrigated red Cambisol was close to significant (p = 0.052). There was no growth difference between treatments on sporadically irrigated Cambisol.

At mid rainy season, seedlings on regularly irrigated black Leptosol with complete fertilizer minus P applications were taller compared to seedlings with subtractive Zn applications and complete fertilizer applications (p = 0.014 and p = 0.007) (Figure 27). Sporadically irrigated seedlings on black soil with subtractive N and subtractive P applications had higher stem lengths than control seedlings (p = 044 and p = 0.009). Seedlings on regularly irrigated red Cambisol with complete fertilizer were taller than with subtractive K and Mn applications (p = 0.010 and p = 0.020). On sporadically irrigated Cambisol, no significant growth differences were observed.

4.2.3.1 Availability of phosphorus for seedling growth

Higher growth of seedlings that were provided with complete fertilizer minus zinc (Figures 24 and 25) may indicate a positive impact on growth of the P component of the fertilizer mixture, once the Zn component is omitted. As high plant Zn interferes with normal P metabolism (Mills and Jones, 1996; Bergmann, 1993), and the foliar fertilizer mix contained relatively high Zn amounts, this may have inhibited the positive impact of P applications. Retarded growth is a typical symptom of P deficiency. Hence, low phosphorus availability limited growth of seedlings on experimental plots on Leptosol and Cambisol without irrigation.

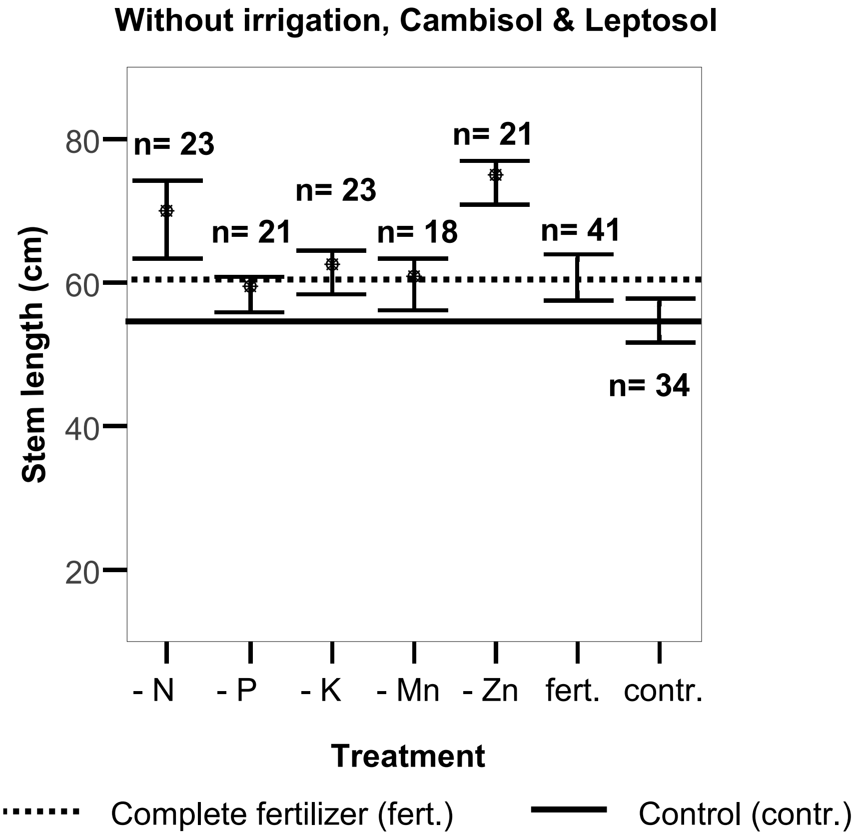

Figure 25: Stem length of 15-month-old *C. dodecandra* on plots without irrigation on both soils (no difference between soils), error bars show mean +/- 1.0 SE

Deficiency in available phosphorus was reported to have a negative impact on growth of seedlings of *C. dodecandra* (Flachsenberg, 2002). Webb et al. (2000) reported for seedlings of *Cedrela odorata* – the native timber species that is best known in Northern Yucatan for its high adaptation to stony, shallow, calcareous soils – a strong growth response to additional P supply on red podzolic soils in north Queensland. Our results show that increased water supply on calcareous substrate reduced the negative impact of Zn additions on P availability for seedlings. When irrigated, growth of seedlings was not higher for the minus zinc treatment compared to other treatments (Figures 26+27). This result indicates that increased water supply mitigates the negative effect of the Zn-P-antagonism for P uptake. The differences in P content of the fertilizer mixtures did not have an evident effect on growth of seedlings, although these differences were reflected in foliar P concentrations at the end of rainy season. Seedlings with complete fertilizer minus zinc additions had significantly higher foliar P contents on black Leptosol with sporadic and regular irrigation (see Figure 28).

Weisbach et al. (2002) found more total P and three times more available P in black Leptosol compared to red Cambisol. These higher amounts of P, nevertheless, seemed not to be available to seedlings on our experimental plots due to reduced water availability in black soils. When plants were irrigated regularly during dry season, growth on black Leptosol was higher than on red Cambisol (see Figures 22a+b and 23), pointing towards higher P availability on black soil under conditions of adequate water supply. Significantly higher growth on irrigated Leptosol without P additions, in contrast to irrigated Cambisol without P additions (Figures 26 and 27)., may be partly explained by higher P availability under conditions of sufficient water availability.

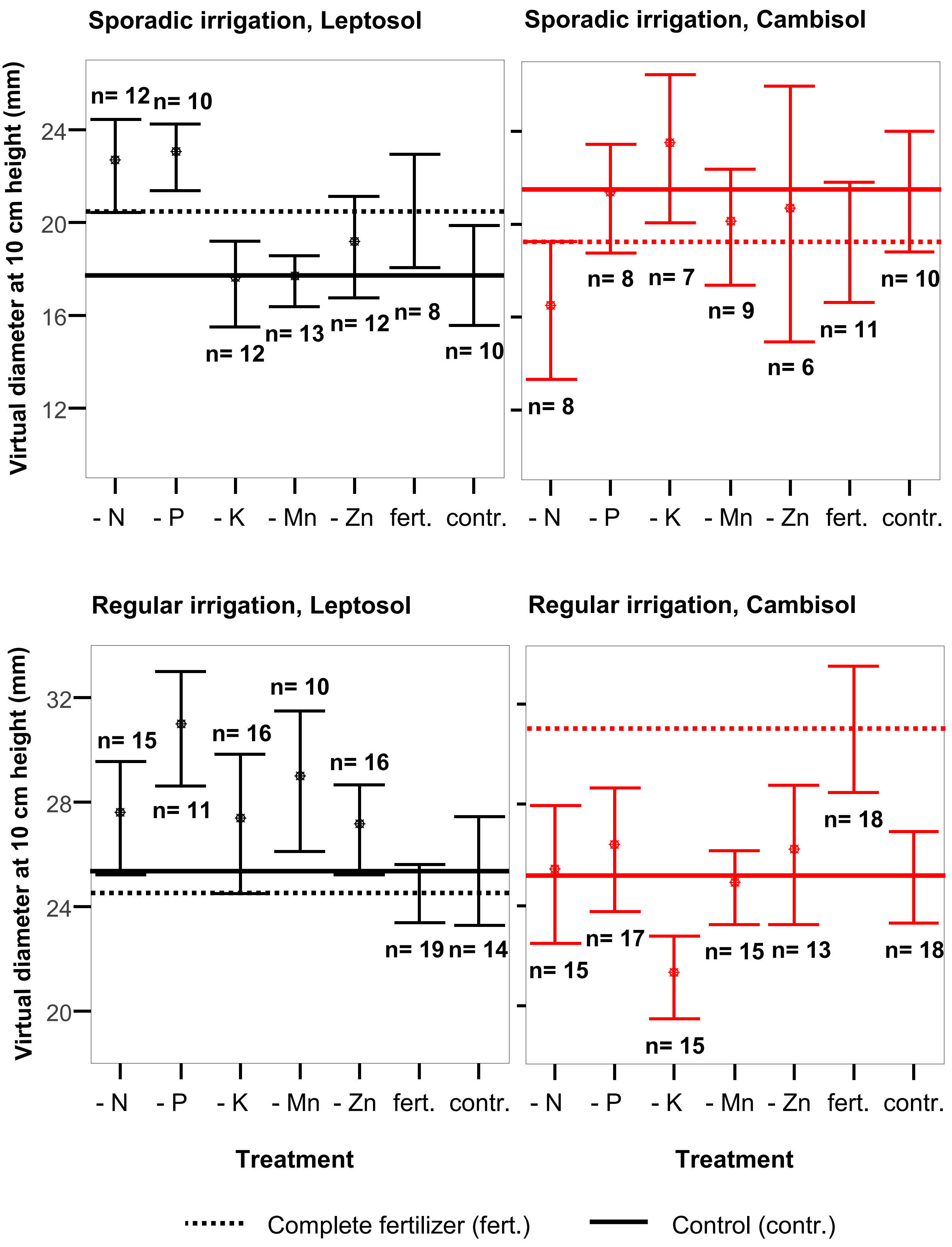

Figure 26: Virtual diameter of 15-month-old *C. dodecandra* at two irrigation levels on two soils with seven fertilizer treatments, error bars show mean +/- 1.0 SE

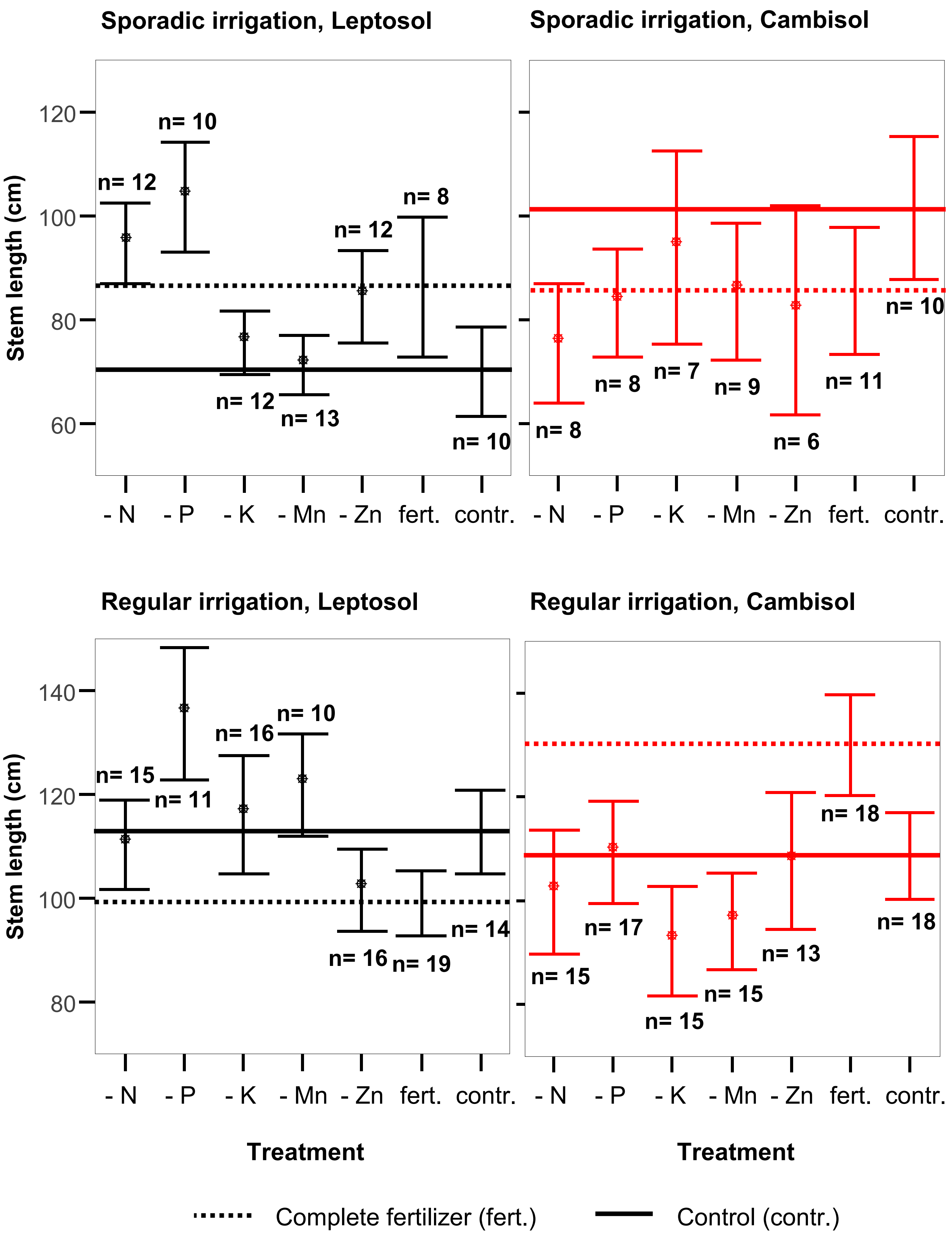

Figure 27: Stem length of 15-month-old *C. dodecandra* seedlings at two irrigation levels on two soils with seven fertilizer treatments, error bars show mean +/- 1.0 SE

Our data show that low P availability impacts plant growth on both soils when seedlings are not irrigated during dry season. When additional water is available to plants, reduced availability of phosphorus seemed to limit growth of seedlings on red Cambisol, but no longer on black Leptosol.

Even though the comparison of P values with the literature on foliar nutrients in forest trees indicated that P contents may not be at a deficiency level (see section 4.2.2.1), our results on growth of seedlings clearly suggest that without irrigation, reduced P availability may be limiting growth on both Yucatan soils. Phosphorus shortage in Yucatan may not be evident from field visits and sampling on tree stands alone, if no direct comparison is made with trees of the same species at the same site that dispose of sufficient P supply for adequate growth.

4.2.3.2 Availability of nitrogen for seedling growth

Nitrogen fertilizer application did not have a positive impact on growth. Considering that stunted growth is a major symptom of N deficiency, this indicates that the nitrogen availability in the Yucatan soils is not limiting tree growth. Our results agree with observations in Mayan homegardens by Benjamin et al. (2001), who did not detect any increase in photosynthetic rates of *C. dodecandra* trees as well as of other arboreal homegarden species such as *Manilkara zapota* after N fertilizer application. Though a reduction of N over the cultivation cycle by about 20% was reported from both Yucatan soils (Weisbach et al., 2002), our data show that N is not a limiting factor for growth of seedlings on Yucatan soil. The high organic matter content of Yucatan soils combined with increased water availability due to irrigation seemed to make N readily available. The predominance of Leguminosae species in the natural and fallow vegetation of the Northern Peninsula may contribute to the high availability of N (Flores and Espejel, 1994).

4.2.3.3 Effect of urea-nitrogen applications on growth

High growth rates on non-irrigated plots with subtractive N indicated that nitrogen applications had a negative effect on growth under conditions of water scarcity (Figure 25). This may be explained by urea-N interactions with potassium on N-fertilized plots. The source of N in this study for the complete fertilizer mixture was urea. Shi and Liu (1987) reported that the application of 200 mg/kg N as urea on maize on calcareous soils inhibited the development of fine roots and lateral roots, and led to reduced plant K in roots while K concentration in the soil of the rooting zone increased. This was attributed to the high NH_3 concentration due to urea hydrolysis (Shi and Liu, 1987). Nitrogen loss from urea-N by NH_3 volatilization was found to decrease with increasing precipitation depth, varying from 26% to 11% between topsoil moisture and simulated precipitation treatments in a calcareous clay (Stumpe and Abdel Monem, 1986). Hence, in our study, higher NH_3 concentration on plots without irrigation during dry season may have interfered with root development, reducing K uptake by *C. dodecandra*. On irrigated plots, NH_3 volatilization was probably lower. This may be a reason for the increased growth of seedlings on plots with complete fertilizer minus N compared to other plots with urea-N applications.

4.2.3.4 Availability of potassium and manganese for seedling growth

On black Leptosol with regular irrigation, higher growth results were obtained for subtractive P additions. This may be attributed to higher K content of the fertilizer mixture for the minus P treatment, as the fertilizer mixture for complete fertilizer minus phosphorus plots contained 1.5 times the amount of K compared with all other fertilizer mixtures used for the experiment (see material and methods). Hence, this result indicates that with adequate water supply, K availability is a growth-limiting factor on Leptosol. Seedlings on red Cambisol with regular irrigation attained higher diameters and stem lengths on plots with complete fertilizer than on plots with subtractive K and subtractive Mn treatment. They did not show significantly higher growth rates on subtractive P plots, even though K additions on those plots were 1.5 times higher than on complete fertilizer plots. This indicates that growth on red Cambisol with adequate water supply is limited by a several nutrients: probably by manganese, and primarily – apart from phosphorus - by potassium.

Our results indicate that K supply limited plant growth on both Yucatan soils. Shallow soils with high $CaCO_3$ contents are typically unable to form high amounts of potassium due to leaching (Rowell, 1994). For Northern Yucatan red and black calcareous soil, Weisbach et al. (2002) reported a reduction of resin extractable K due to cultivation, from 8% in red and 11% in black soil of the sum of K, Ca and Mg to 1% in each soil. This equivals a reduction of resin extractable K of 82% and 90%, respectively. Our data confirm the importance of K availability for seedling growth on the two Yucatan soils.

Manganese may be one of the limiting nutrients for growth on red Cambisol with adequate water availability. Complete fertilizer additions on red Cambisol with regular irrigation resulted in higher stem length and diameter of *C. dodecandra* compared to subtractive manganese applications. Application of soluble Mn fertilizer was found to be compulsory to optimize plant growth of soybean on calcareous soils (Gholamalizadeh Ahangar et al., 1995). Nevertheless, our foliar analysis data does not show significantly higher levels of leaf Mn with manganese fertilization. Further investigations are necessary to determine the Mn availability and its effect on plant growth on Yucatan soils.

4.2.4 Impact of nutrient–water–interactions on nutrient uptake of *C. dodecandra*

This section shows our results on foliar nutrient concentrations and nutrient ratios of *C. dodecandra* seedlings from the experimental plots at X'matkuil, Mérida, Yucatan, Mexico (Figures 28-35). The presented results include foliar contents of P, the P/Zn ratio, K, the K/sqrt (Mg+Ca) ratio, N, Zn, and Fe. Data on foliar Mn does not show any clear trends therefore it is not displayed. Data on foliar N only reveals a significant soil by irrigation interaction, but no significances for fertilizer treatments, hence the graph shows this interaction only. For foliar P, an extra graph on the significant soil by irrigation interaction is presented.

4.2.4.1 Foliar phosphorus content

On sporadically irrigated black Leptosol, seedlings reached highest leaf P contents on complete fertilizer minus zinc plots with 1.05 g/kg (Figure 28). Foliar P content on sporadically irrigated minus zinc plots on Leptosol was – at a significance level of 0.15 – higher than on control plots and minus P plots with 0.91 g/kg. On regularly irrigated black Leptosol, foliar P concentration of *C. dodecandra* was higher on complete fertilizer ($p = 0.011$), complete fertilizer minus Mn ($p = 0.003$), and complete fertilizer minus Zn plots ($p = 0.004$) compared with the unfertilized control. This reflects the differences between the applied fertilizer treatments: the subtractive Mn, the subtractive Zn and the complete fertilizer treatment contained 1.5 more P than the subtractive K

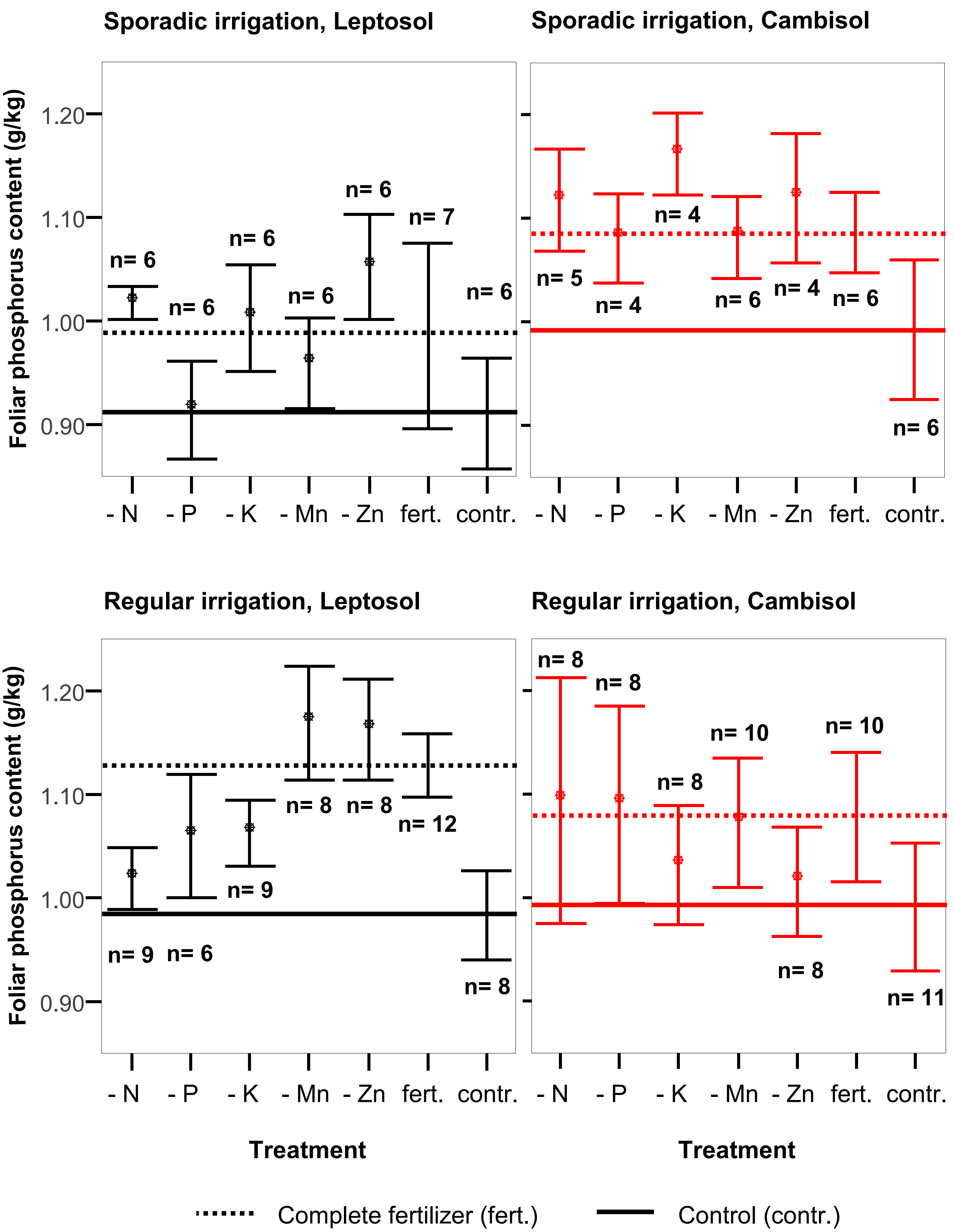

Figure 28: Foliar P concentration of 21-month-old *C. dodecandra* on experimental plots at two irrigation levels on two soils with seven fertilizer treatments; YFML, mid- to upper crown, sampled at the end of rainy season, analyzed using ICP-AES, error bars show mean +/- 1.0 SE

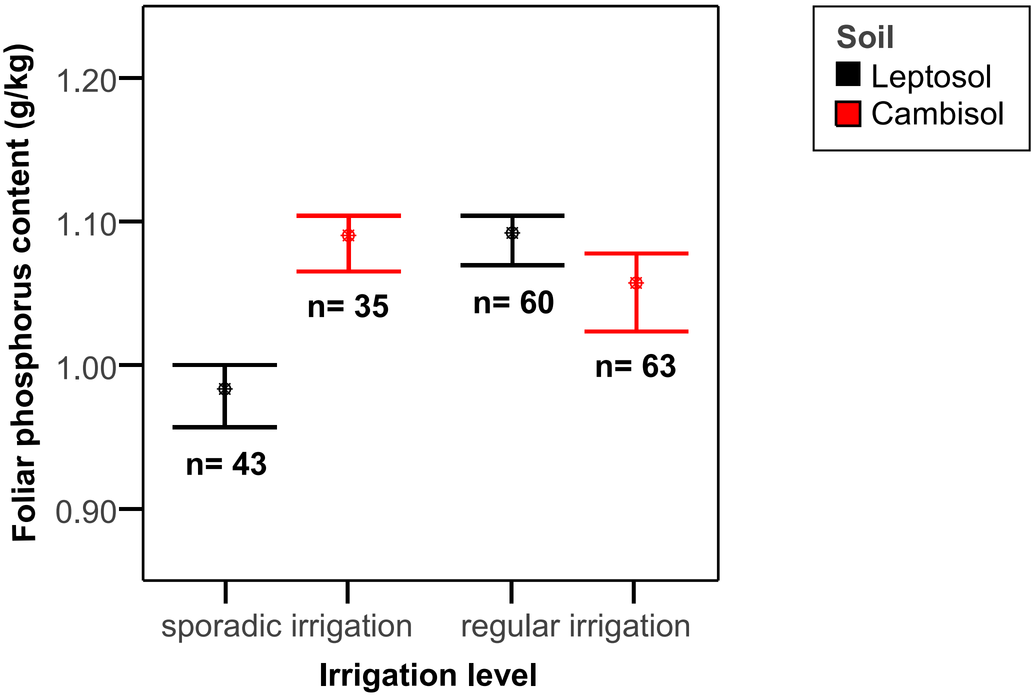

Figure 29: Foliar phosphorus concentration of 21-month-old *C. dodecandra* on plots at two irrigation levels on two soils; error bars show mean +/- 1.0 SE (expl. see Figure 28)

and 3 times more P than the subtractive N treatment. On sporadically irrigated Cambisol, though, only seedlings with complete fertilizer minus K attained foliar P concentrations that were higher than the control ($p = 0.029$).

As shown in Figure 29, the interaction between soil and irrigation had an impact on foliar phosphorus concentration ($p_{soil*irr} = 0.003$). With 0.98 g/kg, phosphorus content in leaves on sporadically irrigated black Leptosol was significantly lower than on regularly irrigated black soil (1.08 g/kg) or on sporadically and regularly irrigated red Cambisol (1.09 g/kg and 1.05 g/kg). For the control treatment, a similar – though not significant – tendency was found: foliar P content was lowest for non-fertilized sporadically irrigated seedlings on Leptosol plots (data not shown). Differences in the underlying rock layers suggest that with similar irrigation, for seedlings on red Kankab (Cambisol) more water is available for growth than on Tsekel (Leptosol) (Estrada Medina, 2005). Hence, reduced availability of water may explain lower foliar P concentrations on sporadically irrigated Leptosol plots.

4.2.4.2 Foliar P/Zn ratio

The foliar P/Zn ratio was explained by the interactions between irrigation and treatment ($p_{irr*treatment} = 0.006$) (Figure 30). On sporadically irrigated Leptosol, leaf P/Zn was with 116 significantly higher with subtractive Zn applications than with any other treatment (all $p = 0.000$), as well as the non-fertilized control ($p = 0.016$). On Leptosol with regular irrigation, the foliar P/Zn ratio was with 91 higher for minus Zn plots than for any other fertilizer treatment and the control (p between 0.000 and 0.019). On sporadically irrigated Cambisol, P/Zn ratio was with 116 significantly higher than minus N, minus P, minus K, and minus Mn treatments (p between 0.001 and 0.027). On regularly irrigated Cambisol, it was with 85 highest for the control, followed with 79 by the subtractive zinc treatment that was significantly higher than the subtractive phosphorus treatment ($p = 0.020$).

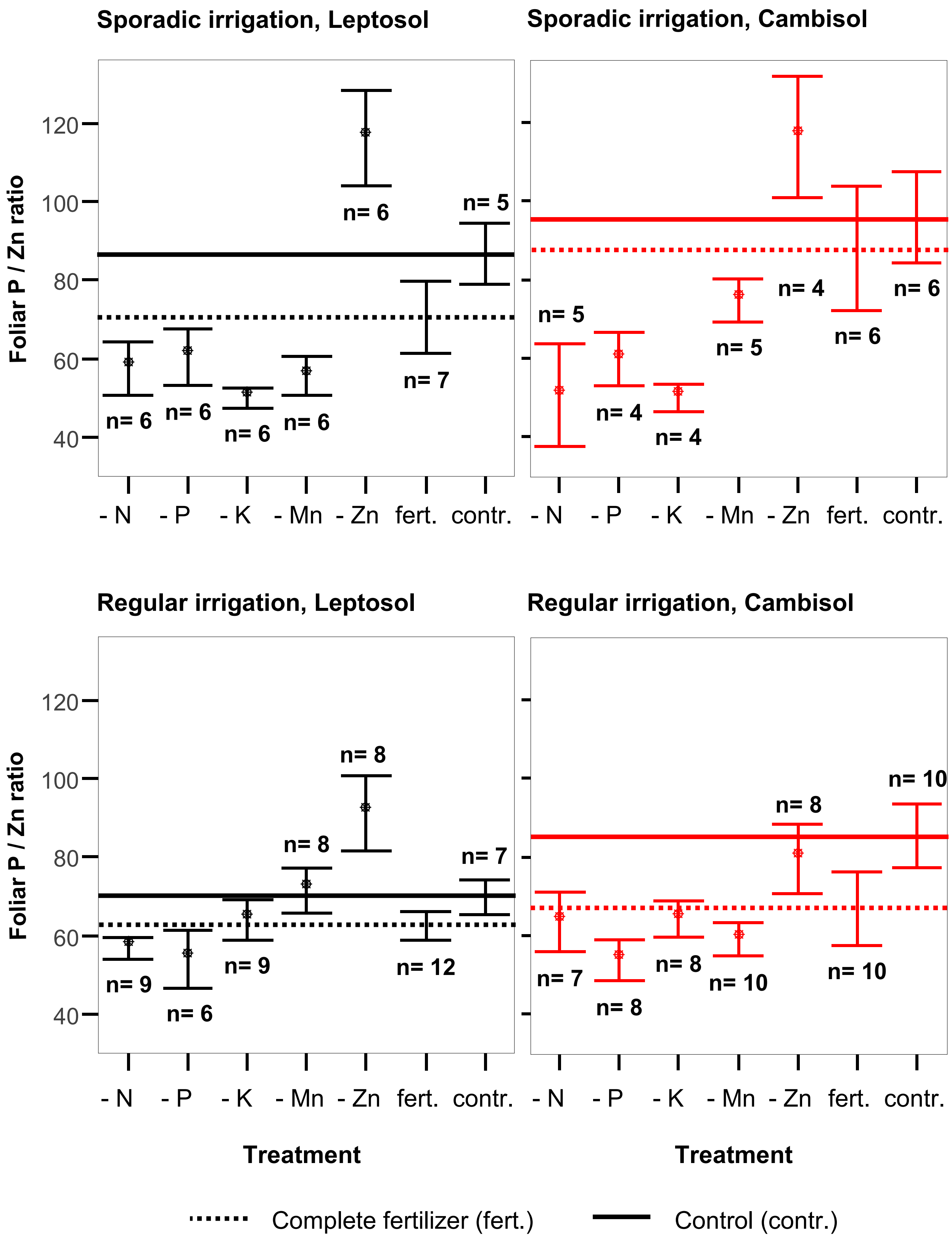

Figure 30: Foliar P/Zn ratio of 21-month-old *C. dodecandra* seedlings at two irrigation levels on two soils with seven fertilizer treatments, error bars show mean +/- 1.0 SE (expl. see Figures 28 and 31)

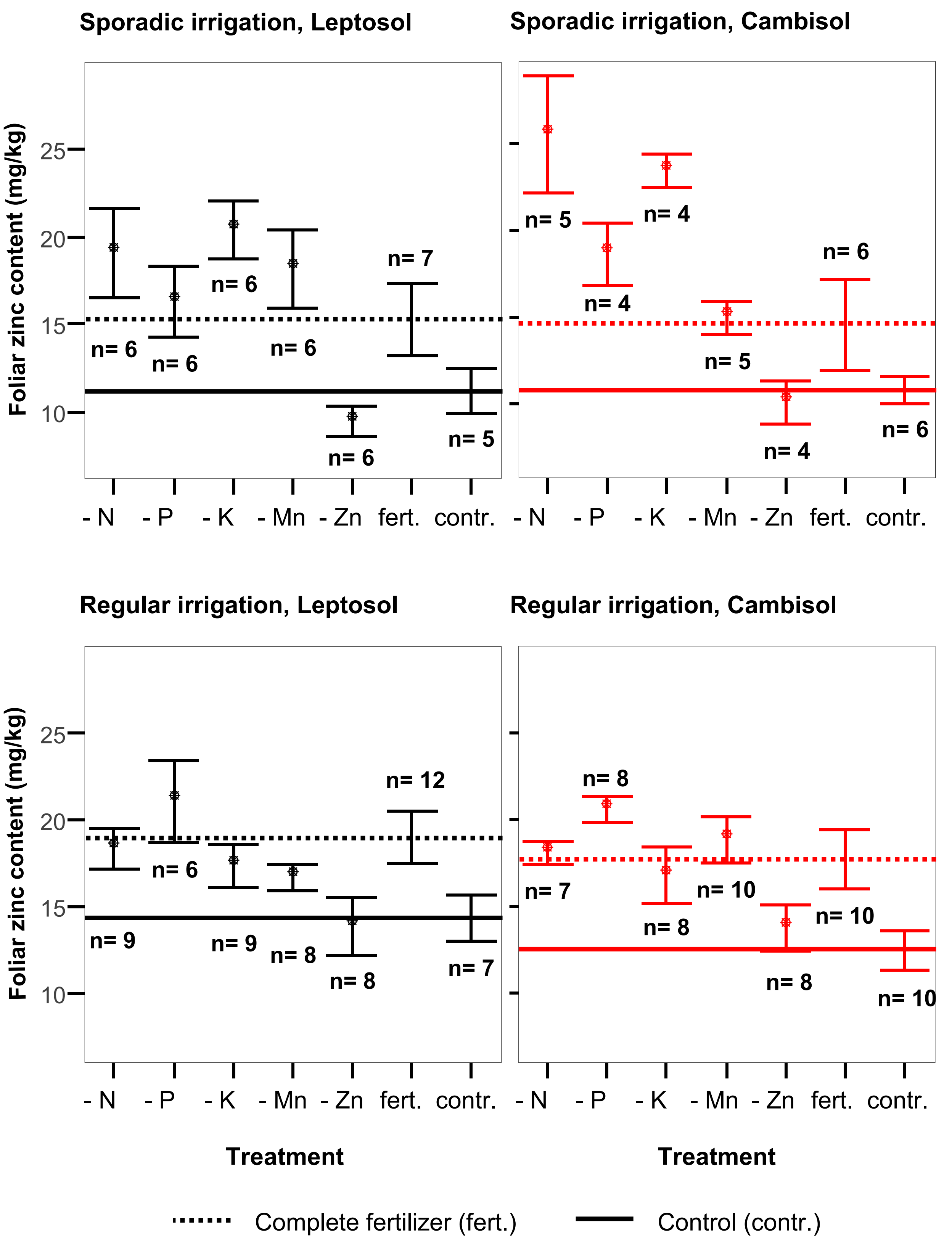

Figure 31: Foliar Zn concentration of 21-month-old *C. dodecandra* seedlings on experimental plots at two irrigation levels on two soils with seven fertilizer treatments, analyzed using AAS, error bars show mean +/- 1.0 SE (expl. see Figure 28)

4.2.4.3 Foliar zinc content

Zinc applications had a strong impact on foliar zinc concentrations ($p_{fertilizer} < 0.0001$). Foliar zinc concentration on control plots and on plots with complete fertilizer minus zinc at the end of rainy season showed the same tendencies for both irrigation levels and on both Leptosol and Cambisol: it was lower, at different levels of significance, than for all other treatment including complete fertilizer. Though GLM did not indicate any significant differences between the two irrigation levels or the two soils, data is displayed here in detail in order to document the influence of the respective foliar zinc values on the P/Zn – ratios shown in Figure 30. With regular irrigation on both Leptosol and Cambisol, foliar zinc concentrations at the end of rainy season were higher for subtractive P plots than for minus zinc plots ($p = 0.001$ for Cambisol and $p = 0.003$ for Leptosol) and control plots ($p = 0.000$ for Cambisol and 0.006 for Leptosol) (Figure 31).

As seedlings of this study were in their vegetative stage, the question remains whether the relatively low zinc concentration of the seedling will have a negative effect on *C. dodecandra* fruit set and quality. Hence, if *C. dodecandra* trees are intended for fruit production, it will be important to monitor bud development and fruit production, and eventually investigate the impact of foliar zinc applications. Zinc deficiency was found to have a negative impact on the number of buds, fruit growth and quality. Poor fruit set and small fruit were among the first symptoms of Zn shortage observed in apples (Swietlik, 2002; Swietlik and Faust, 1984).

4.2.4.4 Phosphorus – zinc interactions

Our results show that uptake of additional P was reduced by simultaneous zinc supply, and that zinc-phosphorus interactions limited P uptake and thereby growth at low water availability (Figures 24 and 25). High foliar P/Zn ratios on subtractive zinc plots with both regular and sporadic irrigation, though, point towards an interference of additional Zn with P uptake (Figure 30). High foliar Zn concentrations on minus P plots of both soils with regular irrigation demonstrate that the P-Zn-antagonism also led to the inhibition of Zn uptake by additional P from fertilizer applications. With adequate water supply, plant zinc uptake from fertilizer seemed to be reduced by P applications. Similarly, eight barley cultivars showed reduced Zn uptake and foliar zinc contents with increased P availability (Zhu et al., 2002). Two wheat cultivars had significantly increased foliar zinc concentrations with higher P supply (Zhu et al., 2001). Hence, P applications may have interfered in zinc uptake of *C. dodecandra*. Our data did not indicate a positive impact of zinc applications on growth. On the contrary, seedlings without complete fertilizer minus zinc grew significantly better than non-fertilized seedlings or seedlings of fertilizer mixtures including zinc. This may be explained by the interference of the P and Zn antagonism regarding uptake, translocation and metabolism.

Our results for the P/Zn ratio reflect the significant Zn uptake after fertilizer applications, and show that P uptake after fertilizer applications was significant when Zn was absent in the fertilizer mixture, and that Zn uptake on regularly irrigated plots increased in the absence of additional P (Figures 28, 30, and 31). On highly calcareous soil from a semi-arid region in Australia, zinc applications in combination with low P additions resulted in slight reductions in biomass of barley cultivars. In contrast to this, P applications alone increased shoot biomass and foliar P concentrations (Li et al., 2003). Hence, phosphorus-zinc interactions probably led to reduced growth under conditions of low water availability, when zinc and phosphorus were supplied simultaneously.

4.2.4.5 Foliar nitrogen content

Considering foliar nitrogen contents of *C. dodecandra* seedlings on experimental plots, only the soil by irrigation interaction had a significant impact on N concentrations ($p_{soil*irr}$ = 0.0001) (Figure 32). Highest foliar nitrogen content was found on sporadically irrigated Cambisol, with N concentrations of 23.16 g/kg at the end of rainy season. This was significantly more than on regularly irrigated Cambisol (21.02 g/kg) or on black Leptosol (20.97 g/kg on sporadically, 21.73 g/kg on regularly irrigated plots). Seedlings on sporadically irrigated Cambisol grew significantly faster than on sporadically irrigated Leptosol – and had at the same time higher foliar N concentrations. Considering dilution, this indicated a higher availability of N under conditions of higher water availability.

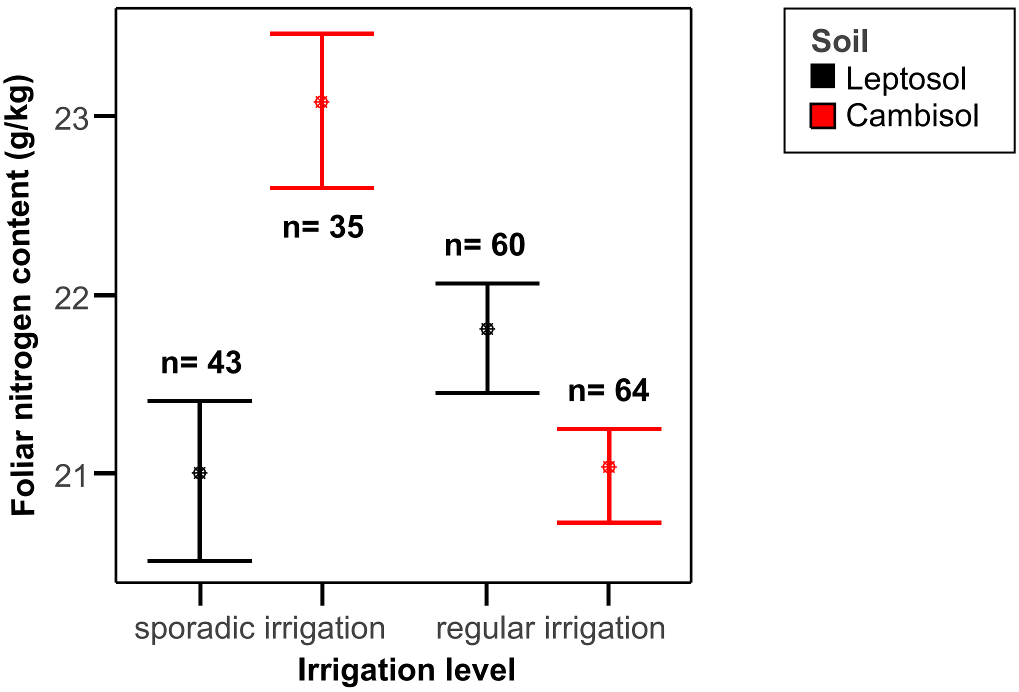

Figure 32: Foliar N concentration of 21-month-old *C. dodecandra* at two irrigation levels on two soils, analyzed with Elemental Analyzer, error bars show mean +/- 1.0 SE (expl. see Figure 28)

4.2.4.6 Foliar potassium content

Potassium concentrations in leaves varied according to soil and irrigation (p_{soil} = 0.011, p_{irr} = 0.022). When regularly irrigated, foliar potassium was as high as 10.24 g/kg, when sporadically irrigated, it decreased to 9.20 g/kg. A higher content of potassium in leaves was found on black Leptosol (10.29 g/kg) in comparison to red Cambisol (9.14 g/kg). This was emphasized by similar results at mid rainy season (p_{soil} = 0.0100) (data not shown).

With complete fertilizer minus P additions on sporadically irrigated Leptosol, foliar K concentrations were higher than with subtractive zinc or complete fertilizer additions (p = 0.035 and p = 0.005), and close to significantly higher than with subtractive K additions and on control plots ($p = 0.059$ and $p = 0.057$) (Figure 33). Foliar K concentration on regularly irrigated Cambisol at the end of rainy season was higher for seedlings with subtractive P applications than for other treatments (p between 0.004 and 0.021) with the exception of complete fertilizer applications and subtractive N applications. Differences were most pronounced for minus P with 12.21 g/kg compared to the control (8.63 g/kg) and to minus K plots with 8.01 g/kg ($p = 0.008$ and $p = 0.004$).

On sporadically irrigated black Leptosol, seedlings with complete fertilizer minus N additions had higher foliar K concentrations than seedlings with complete fertilizer additions ($p = 0.036$) (Figure 33). Higher rates of N were reported to lead to reduced foliar K content in *Ilex opaca* leaves (Mills and Jones, 1996). In a study on nutrient requirements of Eureka lemon seedlings on calcareous soil, N applications were found to increase foliar N, Ca and Mg content, while at the same time decreasing foliar K content (Khalidy and Nayyal, 1974). Considering our results on high growth rates on non-irrigated plots with complete fertilizer minus N additions shown in Figure 25, N fertilizer additions may have reduced K uptake and foliar K concentration under conditions of reduced water supply, with subsequent negative effects on seedling growth. Significantly higher foliar potassium contents for complete fertilizer minus phosphorus may be explained by the 1.5 times higher potassium content of this fertilizer compared to all other fertilizer mixtures (see material and methods).

4.2.4.7 Foliar basic cation ratios

Foliar K/sqrt (Mg+Ca) ratio was higher in leaves of seedlings on black Leptosol than on red Cambisol ($p_{soil} = 0.017$). Treatment by soil interactions were significant at $p_{fertilizer*soil} = 0.042$. On black Leptosol at the end of rainy season, foliar K/sqrt (Mg+Ca) reached a peak on subtractive P plots with both sporadic and regular irrigation, where it was significantly higher than on control plots (Figure 34). On sporadically irrigated red Cambisol, foliar K/sqrt (Mg+Ca) peaked on complete fertilizer plots. The difference between the two soils was at the significance level of $p_{soil} = 0.017$.

At mid rainy season, on plots with regular irrigation during dry season, comparing only complete fertilizer with control plots, the difference between control and complete fertilizer was significant for red Cambisol ($p_{treatment} = 0.039$). Foliar K/sqrt (Mg+Ca) ratios on red soil were higher on complete fertilizer (1.20) than on control plots (1.03). On black Leptosol, complete fertilizer and control plots were not significantly different. Foliar K/sqrt (Mg+Ca) on black soil was 1.18 at mid rainy season (data not shown).

The foliar K/Mg ratio was significantly different among the treatments, irrigation levels and soils ($p = 0.014$), with highest values for complete fertilizer minus P, and lowest values for the control treatment. Leaf K/Mg ratios of *C. dodecandra* on sporadically irrigated Cambisol plots were significantly lower than for regularly irrigated Cambisol or Leptosol with both irrigation levels (data not shown).

The Ca/Mg ratio was significantly lower for sporadically irrigated seedlings (6.9) than for seedlings with regular irrigation (8.2) ($p_{irr} = 0.000$). It was significantly lower for inoculated seedlings (6.2) than for seedlings of control and fertilizer treatments (between 7.2 and 8.3) ($p_{treatment} = 0.049$) (data not shown).

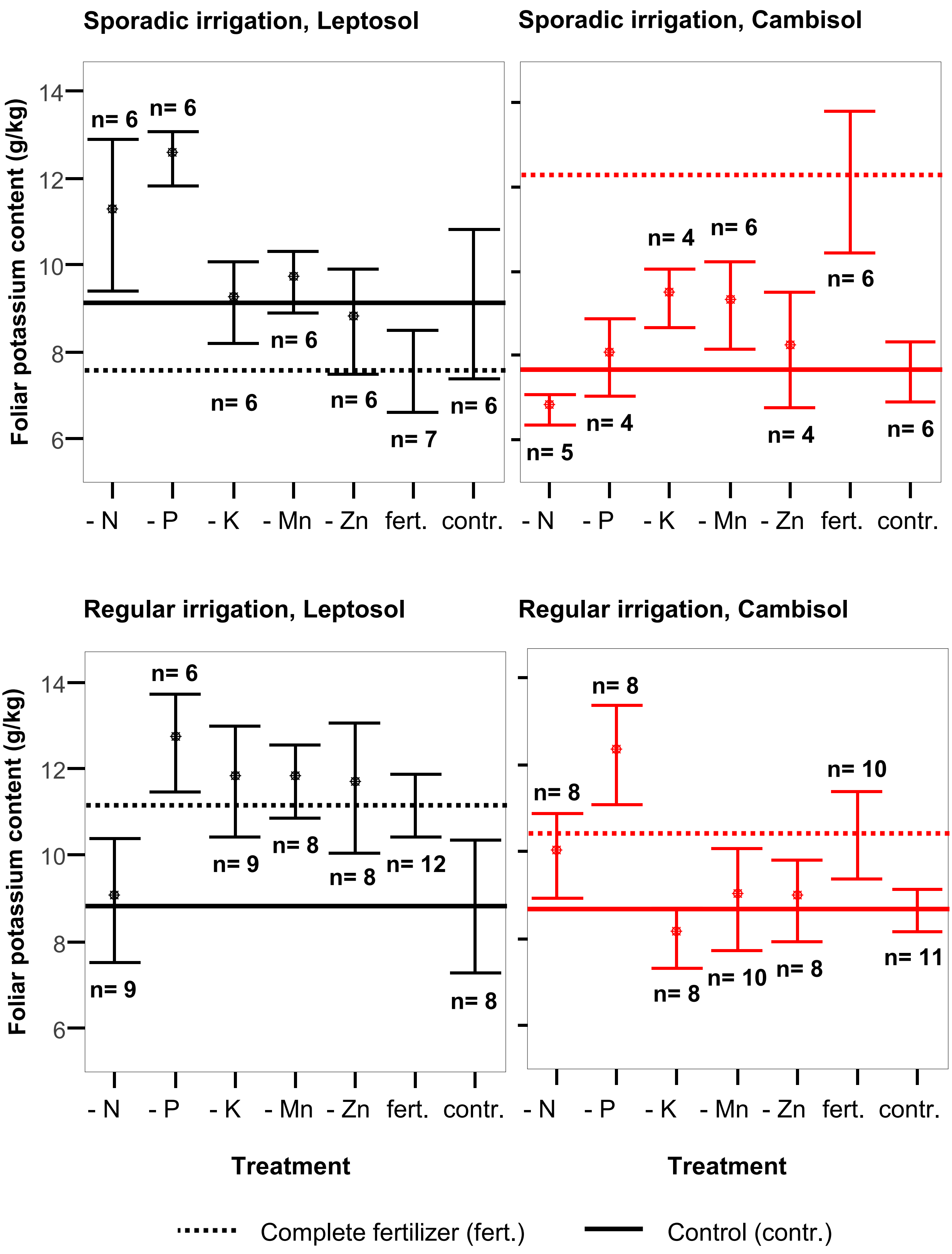

Figure 33: Foliar potassium concentration of 21-month-old *C. dodecandra* at two irrigation levels on two soils with seven fertilizer treatments, error bars show mean +/- 1.0 SE (expl. see Figure 28)

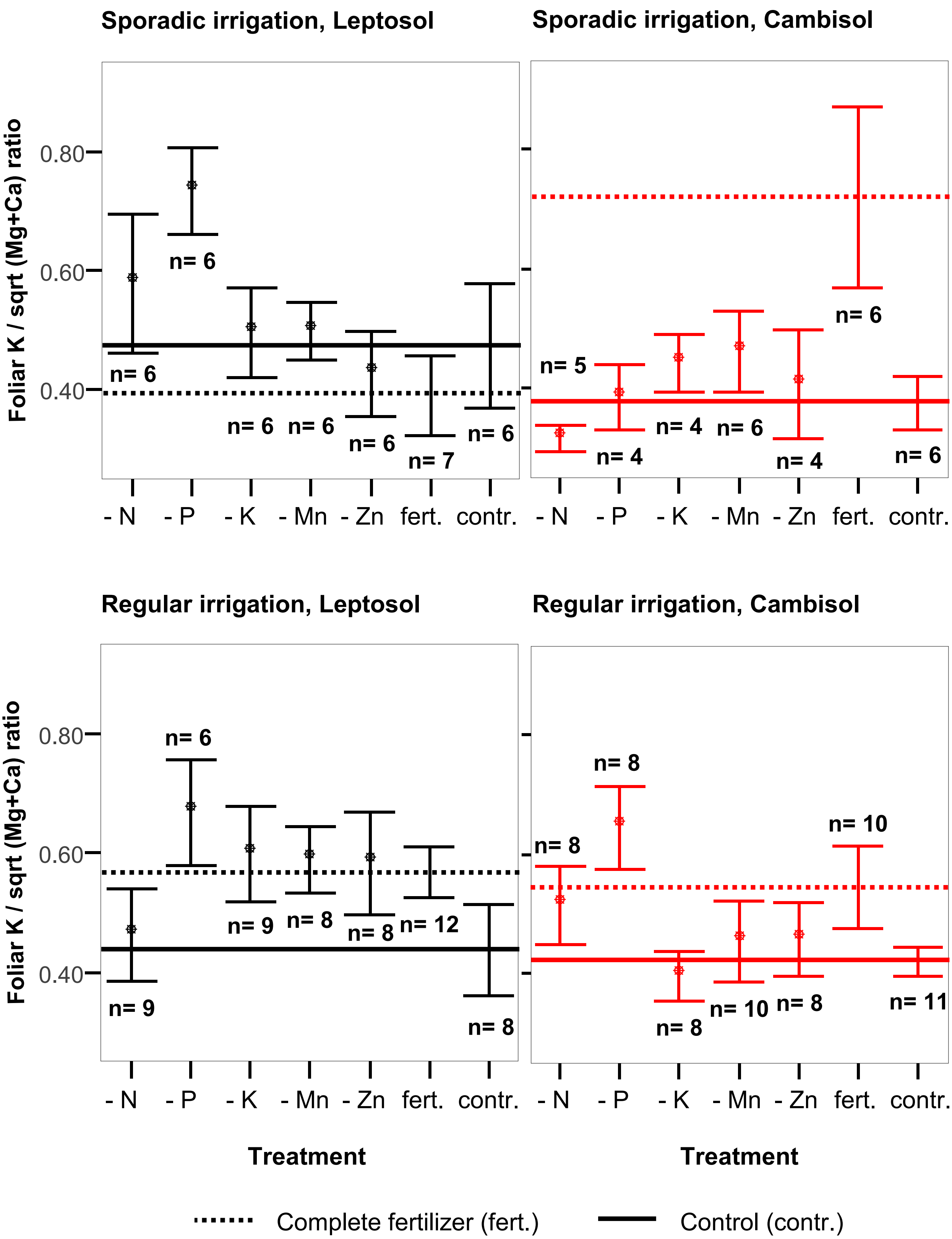

Figure 34: Foliar K to square root of (Mg plus Ca) ratio of 21-month-old *C. dodecandra* at two irrigation levels on two soils with seven fertilizer treatments, error bars show mean +/- 1.0 SE (expl. see Figure 28)

4.2.4.8 Foliar magnesium content

Foliar magnesium also responded to differences in soil type and irrigation level. On sporadically irrigated plots magnesium concentration in leaves reached 5.23 g/kg, while on regularly irrigated ones it was only 4.42 g/kg. It was higher on red soil (5.05 g/kg) than on black soil (4.60 g/kg). Considering the interactions between soil type and irrigation level, a significant difference between soils could only be found on sporadically irrigated plots ($p_{soil*irr}$ = 0.0046), where magnesium concentration was 5.62 g/kg on red soil and 4.85 g/kg on black soil. There was no difference in magnesium concentration on the two soils for regularly irrigated plots, therefore the interaction failed to be significant ($p_{soil*irr}$ = 0.0602) (data not shown).

4.2.4.9 Availability of basic cations

Potassium availability for plants in combination with water availability may be limiting plant growth on Yucatan soils. Variations in foliar K concentrations and foliar K/sqrt (Ca+Mg) ratios corresponded with significant variations in growth of seedlings on both soils at different levels of water availability, even though *C. dodecandra* seedlings had relatively high foliar K concentrations compared to other tropical broadleaved trees (see Table 9a+b). In *C. dodecandra* leaves on our experimental plots, the K/sqrt (Mg+Ca) ratio was very low for control plots on both soils. On sporadically irrigated red Cambisol, it was highest for complete fertilizer plots, and showed the same tendency on regularly irrigated plots (Figure 34). High K concentrations on minus P plots are explained by the 1.5 higher amount of K in the fertilizer mixture for this treatment (see material and methods). On black Leptosol, the K/sqrt (Mg+Ca) ratio was highest for complete fertilizer minus P plots, due to the relatively higher amounts of K in the fertilizer mix. Leptosol probably provided more readily available K for plant uptake than Cambisol. Comparing the two soils, foliar K/sqrt (Mg+Ca) was significantly higher in leaves of seedlings on black Leptosol than on red Cambisol. Together with the adequate growth of seedlings on subtractive K plots versus control plots on Leptosol, this pointed towards higher amount of K readily available for plant uptake on black Leptosol compared to red Cambisol.

Variations in foliar magnesium concentrations of seedlings were attributed to soil differences in exchangeable Mg, to higher availability of Mg with increased soil moisture, and to K–Mg–uptake interactions. Our results showed higher foliar Mg concentrations on red soil. 32% higher exchangeable Mg was reported for red Yucatan soil compared to black soil (Weisbach et al., 2002). Mg is taken up passively by mass flow. Hence the concentration in tissue is closely related to the available soil moisture. There is a competition on uptake with other cations, especially with K. Therefore, higher foliar Mg values on irrigated plots were probably influenced by reduced competition due to a decreased availability of potassium, and by the positive impact of soil moisture on Mg availability.

Our results documented the high tolerance of *C. dodecandra* for calcareous environments. Available Ca^{2+} is always high in calcium carbonate containing soils. Ca^{2+} and Mg^{2+} together may be nearly 100% of the CEC in alkaline soils. The distribution of *C. dodecandra* all over the Yucatan Peninsula with its calcareous soils documented a high tolerance of the species to these specific soil conditions. In the tissue of species adapted to calcareous environment, high Ca^{2+} concentrations have been found (Jeffrey, 1987). High calcium content of leaves may be favourable for resistance of *C. dodecandra* against reduced water availability. Calcium ions participate in the regulation of plant responses to drought stress (Gong et al., 1996). The Ca/Mg ratio of *C. dodecandra* on experimental sites was three to four times as high as the ratio (2/1) considered generally adequate for best growth of plants. Whether this indicates "luxury absorption" and a high tolerance of the species to Ca^{2+} or whether the species has a high Ca demand remains to be investigated.

4.2.4.10 Foliar manganese content

Foliar manganese of *C. dodecandra* varied with soil type and with irrigation level (p_{soil} < 0.0001, p_{irr} < 0.0001). It was as high as 31.9 mg/kg on red Cambisol, and only 24.1 mg/kg on black soil. Sporadically irrigated seedlings showed higher concentrations of manganese (30.2 mg/kg) than regularly irrigated ones (25.8 mg/kg) (data not shown).

Higher manganese content in tissue of regularly irrigated seedlings may be attributed to the higher availability of manganese from the organic matter content of both soils with increased water supply. Mn is a cofactor for various enzymes. It contributes to the stability of the chloroplast membrane, and it participates in oxido-reduction processes (Raven et al., 2000). Availability of Mn increases with organic matter content. In contrast to this, besides calcium carbonate, organic matter was detected to be a major site of retention of Mn in calcareous soils (Karimian and Gholamalizadeh Ahangar, 1998). This may partly explain lower concentrations of manganese in black Leptosol with its higher organic matter content. More detailed studies are needed to fully understand availability of manganese for plant growth on Yucatan soils.

4.2.4.11 Foliar iron content

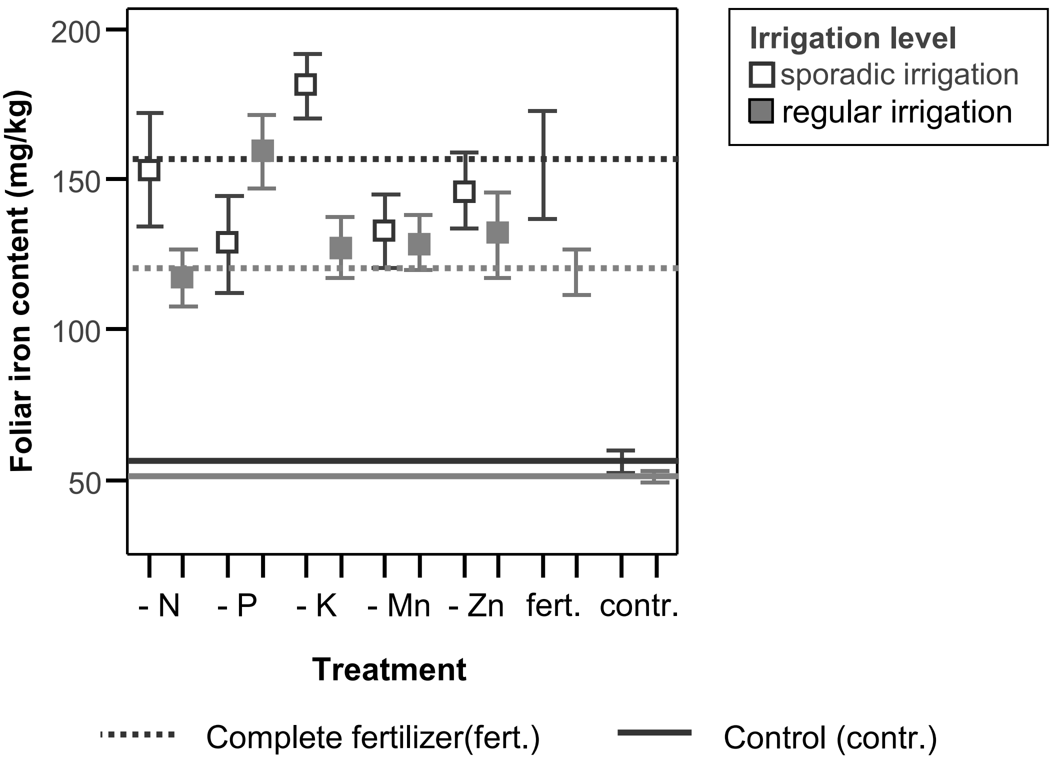

Figure 35: Foliar iron concentration of 21-month-old *C. dodecandra* seedlings at two irrigation levels with seven fertilizer treatments, error bars show mean +/- 1.0 SE (expl. see Figure 28)

Fertilizer application by irrigation had a significant impact on iron concentration in leaves ($p_{fertilizer*irr}$ = 0.0112). Iron content of leaves on control plots was 50.7 mg/kg with regular, and 56.1 mg/kg with sporadic irrigation, while fertilized leaves had an iron content between 118.1 and 181.9 mg/kg (Figure 35). On sporadically irrigated plots, iron content was either similar or higher than on regularly irrigated plots. It was significantly higher for complete fertilizer minus nitrogen, minus potassium as well as for complete fertilizer.

Similar or higher concentrations of iron in sporadically irrigated seedlings may be attributed to the dilution effect. The same amount of Fe was applied to the seedlings of both irrigation levels, and seedlings on regularly irrigated plots grew significantly more, so the final concentration of Fe was lower. *C. dodecandra* seedlings on our experimental plots, as well as mature trees in homegardens, did not show symptoms of iron-induced chlorosis. The plant genotype as well as the availability of iron in the soil determine Fe uptake rates. *C. dodecandra* may be described as an iron efficient species. Tree species that are able to take up iron in adequate amounts under conditions of low Fe availability are considered to be “iron-efficient”. Calcicoles are reported to possess a high iron-efficiency (Rowell, 1994).

4.2.4.12 Foliar sulphur content

C. dodecandra leaves contained less sulphur when trees had been regularly irrigated than when they were irrigated at the peak of dry season only (p_{irr} = 0.007). This was shown for the end of rainy season (3.33 g/kg with regular vs. 3.56 g/kg with sporadic irrigation) (p_{irr} = 0.007) as well as for mid rainy season (p_{irr} = 0.005) (data not shown). The comparably lower leaf S content on plots with regular irrigation may be attributed to dilution of foliar S in faster growing seedlings. As 90% of available S is found in association with organic matter, it may be assumed that the high organic matter content of the soils in Yucatan accounted for adequate amounts of available S. The absorption of S is not influenced by soil pH. It is mainly taken up by mass flow, and the uptake depends on available water (Mills and Jones, 1996).

4.2.4.13 Foliar aluminium content

Aluminium content of leaves on red Cambisol was higher (51.8 mg/kg) than on black Leptosol (36.6 mg/kg) (p_{soil} = 0.002). Data for foliar aluminium was not normally distributed, though. By transforming the data using log10, normal distribution of the data set was achieved. The transformed data confirmed our observation that leaves on red soil had higher aluminium content than on black soil (p_{soil} = 0.000). Additionally, these data indicated that foliar aluminium was higher on sporadically irrigated than on regularly irrigated plots (p_{irr} = 0.012) (data not shown). Higher soil moisture and slightly lower pH of Cambisol may have lead to an increased amount of available Al ions on this soil compared to Leptosol.

4.3 Summary

Irrigation was the main influence factor on growth of *C. dodecandra*. Sporadic irrigation during the peak of dry season led to comparably high growth increments over the subsequent rainy season. Sporadically irrigated 21-month-old *C. dodecandra* had higher virtual diameters and broader crowns on red Cambisol. In contrast to this, regularly irrigated 21-month-old *C. dodecandra* attained higher virtual diameters and broader crowns on black Leptosol.

Reduced P availability limited growth of non-irrigated *C. dodecandra* seedlings on experimental plots on Leptosol and Cambisol. On irrigated experimental plots, reduced P availability limited growth of seedlings on red Cambisol. Our data show that with adequate water supply, K availability was a growth-limiting factor on Leptosol. Seedling growth on red Cambisol with adequate water supply was limited by low availability of phosphorus, potassium, and manganese. Nitrogen availability was no limiting factor for growth of seedlings on Yucatan soils. Urea-N applications had a negative effect on growth of non-irrigated seedlings. Though there was no effect of zinc applications on growth, foliar zinc concentrations showed a significant response to zinc fertilizer applications. Phosphorus applications interfered with Zn uptake of regularly irrigated *C. dodecandra*. Zinc applications interfered with P uptake, resulting in reduced growth of non-irrigated *C. dodecandra* on both Leptosol and Cambisol.

5 CONDITIONS AND IMPACTS ON SEEDLING SURVIVAL OF *C. DODECANDRA*

5.1 Introduction

The semi-arid climate with its pronounced dry period and the karstic Yucatan plains with subterranean rivers and groundwater at 8 m depth present a challenge for the establishment of agroforestry plantations. The two dominant soil classes of the region are the shallow black Tsekel soil (Leptosol) with a high percentage of rock fragments and stones, and the less stony red Kankab soil (Cambisol). Due to high drainage of the calcareous substrate, water availability for plant growth, especially during dry season, is crucial. Veenendaal et al. (1995) and Turner (1990) have related decreased survival of tropical plants to drought. This was the first time that survival of *C. dodecandra* seedlings on the dominant soils of Northern Yuactan was investigated.

Hypothesis

Under the soil and site conditions in *Yucatan*, low water availability limits survival of tree seedlings of *C. dodecandra.*

5.2 Results and discussion

5.2.1 Survival of *C. dodecandra*

On our experimental plots, drought did not have an effect on survival of *C. dodecandra* over the first dry season after transplanting. Using the number of *C. dodecandra* seedlings at the beginning of dry season as the baseline, survival rate of seedlings after the first dry season was 93% for seedlings with regular irrigation during dry season. Compared to this, survival rates were higher for sporadically irrigated and non-irrigated seedlings (both 96%). Survival of *C. dodecandra* was not affected by soil type, neither was it affected by fertilizer additions. From the total number of 56 planted seedlings (equal to the number of planting holes) on control Leptosol plots, 84% survived until July 2003, from 60 originally planted seedlings on non-fertilized Cambisol plots, 83% survived until the following rainy season. No relationship was detected between soil depth in planting holes and mortality of seedlings. The root system of 20-month-old seedlings had developed in between stones, with medium size and fine roots on the surface of rock fragments. The strong taproot, sometimes developing strong side branches, had grown around rock fragments.

In contrast to our hypothesis, low water availability did not limit survival of tree seedlings of *C. dodecandra* under the soil and site conditions in Yucatan. *C. dodecandra* was able to establish and survive under the harsh environmental conditions. Seedlings were highly adapted to pronounced drought, low groundwater table, stony soils, and hurricane incidents. High adaptability to periods of drought is in accordance with the high number of drought-resistant arboreous species reported from a study in the tropical forest of Panama where survival of seedlings of 43% of the investigated 28 native tree species did not decline during a period of severe drought (Engelbrecht and Kursar, 2003). Our results showed that survival of *C. dodecandra* seedlings even without irrigation was unexpectedly high on both soils. On our experimental plots, survival on sporadically and regularly irrigated plots was with 93 to 96% similar to survival without irrigation (96%). *Cordia alliodora* seedlings in Costa Rica had with 88% equally high survival rates (Wightman et al., 2001). Our results did not show any effect of soil type, though, while Somarriba et al. (2001) reported that *C. alliodora* had lower survival rates on soils with high clay content. High survival on both Leptosol and Cambisol in our study may be attributed to the ability of *C. dodecandra* to adapt easily to different sites. In Tabasco, Southern Mexico, high survival of seedlings was reported for native species that adapt to a wide range of environments and a variety of environmental factors such as *Ceiba pentandra* and *Tabebuia species* (Martínez Bravo, 2001). In Yucatan, *C. dodecandra* trees were found on different soils, in closed and open environments, and along the precipitation gradient of the Peninsula (Flachsenberg, 2002). This may indicate that the low water table and high drainage of calcareous Yucatan soils are favorable for survival of *C. dodecandra*. Our finding confirmed farmers experiences from homegardens in Northern Yucatan, where natural regeneration of *C. dodecandra* survived well without irrigation. In Southern Yucatan, seedlings of *C. dodecandra* in regeneration plantings in the forest or in alleys on agroforestry plots survived and grew well without additional irrigation; still it has to be taken into account that precipitation is with 1200 mm about 20% higher and the period of drought is not as pronounced in the Southern Peninsula as in the Henequén area. Survival of *C. dodecandra* seedlings on our experimental plots was not affected by fertilizer applications. In accordance with our results, Vincent and Davies (2003) did not report any effect of nutrient applications on survival of tropical seedlings. In contrast to this, survival of seedlings of several native species in Tabasco decreased with increased fertilizer applications, because applied fertilizer mixtures probably had damaged the roots and contributed to the drought stress (Martínez Bravo, 2001).

5.2.2 Survival of *C. papaya* seedlings

Two months after the transplanting of seedlings, the survival of *C. papaya* seedlings (56%) was low in comparison to *C. dodecandra* seedlings. Survival of *C. papaya* seedlings was with 43% lower on one site with less regular initial water supply than on the other sites (58% resp. 68%).

Lower survival of *C. papaya* shortly after transplanting was primarily attributed to drought stress. Inadequate water status of the seedlings led to weakness of the plant. Weakness of stems led to bending, followed by disruption of the transpiration flow that resulted in plant death. In contrast to the literature (CONABIO, 2005) that mentioned the susceptibility of *C. papaya* to diseases and pests, seedlings were not found to die from virus or insect attack. Another factor for lower survival of *C. papaya* was the consumption by herbivores on a limited number of plots, due to the higher palatability of its leaves. The high mortality even during rainy season indicated that *C. papaya* was more sensitive to low soil moisture than *C. dodecandra*. This was supported by the observation that on one of the sites, where irrigation on dry days of the rainy season was less consistent due to failure of the water pump, survival of *C. papaya* seedlings was 15 to 25% lower than on the other sites. *C. dodecandra* survival, on the contrary, did not vary much between sites.

5.2.3 Impact of hurricane Isidore on survival

In September 2002, two months after transplanting, survival of *C. dodecandra* seedlings was 73%. Of these seedlings, an estimated 95% survived hurricane Isidore in

September 2002. Only about 5% of *C. papaya* seedlings survived hurricane Isidore in September 2002.

Higher survival of *C. dodecandra* seedlings in comparison to *C. papaya* during hurricane Isidore with wind velocities of 220 km/h was primarily explained by two factors. On the one hand, rooting patterns of *C. dodecandra* and *C. papaya* differ considerably. While *C. papaya* roots grew close to the surface, forming a shallow root circle around the seedling, *C. dodecandra* developed a deeper rooting system. The taproot of *C. dodecandra* prevented the seedlings from uprooting by winds. *C. papaya* seedlings, in contrast, were found to be entirely uprooted by the hurricane. Winds of 64 km/h are able to uproot *C. papaya* trees (Nakasone, 1998). On the other hand, stems of *C. papaya* seedlings were less flexible than stems of *C. dodecandra* , and could not withstand the strong winds. *C. papaya* seedlings, even if most of them were bent and had to be fixed to sticks to resume regular growth, were not killed by the hurricane. High survival of *C. dodecandra* of the strong precipitation events that accompanied hurricane Isidore may be attributed to the strong adaptation capacity of the species, to the age of seedlings and the resulting flexibility of their stems, and to the high drainage capacity of the calcareous soils.

5.3 Summary

In contrast to our hypothesis, over the first dry season after transplanting water availability did not limit seedling survival of *C. dodecandra*. During this dry season, *C. dodecandra* seedlings had survival rates between 93 and 96% regardless of irrigation.

6 SURVIVAL AND GROWTH OF *B. ORELLANA*

6.1 Introduction

The semi-arid climate with its pronounced dry period and the karstic Yucatan plains with subterranean rivers and groundwater at 8 m depth present a challenge for the establishment of agroforestry plantations. The two dominant soil classes of the region are the shallow black Tsekel soil (Leptosol) with a high percentage of rock fragments and stones, and the less stony red Kankab soil (Cambisol). Mean annual precipitation in Mérida, close to the experimental site, was 984.4 mm (Duch, 1988). Due to high drainage of the calcareous substrate, water availability for plant growth, especially during dry season, is crucial. According to Geilfus (1994), the traditional agroforestry species *Bixa orellana* L. (with the common name Achiote) requires a minimum annual precipitation of 1000 mm. Still, *B. orellana* is one of the structural species of Mayan homegardens, and there is an established local and export market for its seeds (Godoy Hernandez, 2002). The species prefers well-drained, slightly alkaline soils (ICRAF, 2005). We wanted to study the importance of water availability for growth and survival of *B. orellana* on the two dominant Yucatan soils, Leptosol and Cambisol.

Hypothesis

Under the soil and site conditions in *Yucatan*, low water availability limits growth and survival of tree seedlings of *B. orellana.*

6.2 Results and discussion

6.2.1 Influence of soil and irrigation on survival

Highest survival of *B. orellana* seedlings after the first rainy season was found on red Cambisol plots with regular irrigation (99%), followed by black Leptosol with regular irrigation (78%). On sporadically irrigated plots, survival was low: 34% on Cambisol, and only 11% on Leptosol. Regular irrigation during first dry season had a major impact on survival. 92% of *B. orellana* seedlings survived under regular, 41% under sporadic irrigation. Survival of *B. orellana* seedlings was lower on unfertilized control plots than on plots with complete fertilizer application, for sporadic irrigated seedlings (28% vs. 38%) as well as for regularly irrigated seedlings (83% vs. 93%) (data not shown). Without irrigation, survival was too low (2% on Leptosol, and 5% on Cambisol) to include the irrigation level in growth analysis. This was mainly due to technical reasons (planting just before the peak of dry season, in March 2003, without subsequent irrigation, see material and methods).

Water availability seemed to be the major influence on *B. orellana* survival during the first dry season. Regular water supply during the first dry season seemed to have more importance for the survival of *B. orellana* than for *C. dodecandra. B. orellana* seedlings were probably more susceptible to drought stress than *C. dodecandra. B. orellana* leaves were – in contrast to *C. dodecandra* leaves – thin and smooth. The shoots were less robust than *C. dodecandra* shoots. The shallower root system of *B. orellana* probably relied more on the increase in soil moisture in the upper soil layer. Regarding low survival of *B. orellana* with sporadic water additions, the late planting date of

B. orellana seedlings during the last months of the rainy season due to the incidence of hurricane Isidore (see material and methods). The pronounced higher survival of *B. orellana* seedlings on sub site on both soils, and especially on black Leptosol, may be attributed to higher availability of soil moisture on the sub site. This indicated again that survival was primarily related to water availability. It corresponded with results from a tropical dry forest in Jamaica, where water availability was the key factor for tree seedling survival (McLaren and McDonald, 2003).

6.2.2 Influence of irrigation on growth

Biomass of *B. orellana* evaluated as crown area was significantly affected by irrigation combined with the time of measurement ($p_{irr*time}$ = 0.015) and the main factor irrigation (p_{irr} = 0.003). With sporadic irrigation, crown area was 0.07 m² at mid rainy season and with 0.06 m² about similar at the end of rainy season. With regular irrigation, *B. orellana* crowns reached mean areas of 0.16 m² after the first dry season that increased up to mean areas of 0.27 m² six months later. Standard variations were high compared to *C. dodecandra*.

Virtual diameter of *B. orellana* was explained by irrigation-time-interactions ($p_{irr*time}$ = 0.001), and by the main factors irrigation (p_{irr} = 0.001) and time of measurement (p_{time} = 0.000). At mid rainy season, mean diameter of stem and branches together was 7.1 mm with sporadic, and 10.0 mm with regular irrigation. Six months later, seedlings with less irrigation had virtual diameters of 12.2 mm, and with regular water additions 19.6 mm.

The height of *B. orellana* seedlings, though, was explained by the interaction between time and irrigation ($p_{irr*time}$ = 0.000) and the main factor time only (p_{time} = 0.003). At mid rainy season, seedlings of both irrigation levels were of about the same height: 65 cm with sporadic, and 60 cm with regular water additions. At the end of rainy season regularly irrigated seedlings had grown in height (77 cm), while the mean height of sporadically irrigated stagnated (59 cm).

Our results showed that water availability was the dominant influence factor not only for growth of *C. dodecandra*, but also for growth of the intercalated *B. orellana*. The major impact of irrigation during the dry season on growth development over the subsequent rainy season was demonstrated by the results for diameter, height and crown area, reflecting the impact of water availability on biomass production.

6.2.3 Influence of soil and fertilizer on growth

The influence of irrigation by soil by time interactions on virtual diameter was with $p_{soil*irr*time}$ = 0.052 very close to significant. *B. orellana* seedlings on both soils with regular irrigation grew equally well over the rainy season. Virtual diameter growth of seedlings on sporadically irrigated red Cambisol plots was higher (from 7.3 mm to 13.0 mm) than that of seedlings on black Leptosol (from 6.7 mm to 10.2 mm) (data not shown). This result for sporadic irrigation coincides with growth results from *C. dodecandra* that showed higher virtual diameter on sporadically irrigated Cambisol compared to Leptosol (Figures 22a+b).

Our data show no influence of fertilizer treatments on growth of *B. orellana*. On our experimental plots, the growth response of seedlings of *B. orellana* to nutrient applications did not follow any clear pattern. As fertilizer treatments did not indicate any obvious effect on growth of *B. orellana*, it might be argued that even on regularly irrigated plots, water availability was still limiting seedling development to a point where nutrient deficiencies did not yet become obvious. This assumption is supported by the high mortality of *B. orellana* on our less irrigated plots. It has to be considered that seedlings on the experimental plots were planted very late in the rainy season, so that water requirements during the first dry season after transplanting were probably even higher as if they had been planted at the beginning of rainy season, as it is usually recommended. The optimum annual precipitation for *B. orellana* is reported as 2000 mm, with preferably continuous rainfall throughout the year (Geilfus, 1994). *B. orellana* has a preference for neutral to slightly alkaline soils, and a high adaptability to different soil conditions; it prefers fertile, deep soils with good drainage (ICRAF, 2005). The higher virtual diameter increment on red Cambisol in comparison to seedlings on black Leptosol with sporadic irrigation may suggest better drainage of Leptosol due to differences in underlying rock layers. This assumption will have to be investigated in further studies, though.

Standard variations for growth variables were much higher for *B. orellana* seedlings than for *C. dodecandra*. This may be related to high genetic variability of *B. orellana* seeds in Yucatan, or to the higher sensitivity of *B. orellana* seedlings to environmental micro-site influences during the establishment phase. Due to their less robust physical constitution in comparison to *C. dodecandra*, considering leaves, stem, and root system, *B. orellana* seedlings may be more prone to react on different shade percentage and other environmental factors. Regular irrigation of *B. orellana* seemed to act as a trigger to virtual diameter increment and crown diameter growth during the subsequent rainy season.

Regular irrigation during first dry season probably provided the plants with the basis for even stronger diameter growth during rainy season. The importance of irrigation for survival during the first dry season was on the one hand due to the late planting date; on the other hand the climatic environment was with 1000 mm at the lower limit of the mean annual precipitation range for *B. orellana* (Geilfus, 1994). Soil conditions, nevertheless, were very favorable for *B. orellana*, with slightly alkaline soils and good drainage, and high organic matter content (ICRAF, 2005). The shallowness of the soils and the high percentage of rock fragments may have represented an obstacle to *B. orellana* development, as *B. orellana* tends to develop an extensive layer of roots (Voß et al., 1998).

6.3 Summary

Water availability seemed to be the major influence on *B. orellana* survival and growth performance during the first dry season. Highest survival of *B. orellana* seedlings after the first rainy season was found on red Cambisol plots with regular irrigation (99%), followed by black Leptosol with regular irrigation (78%). On sporadically irrigated plots, survival was comparably low: 34% on Cambisol, and only 11% on Leptosol. Fertilizer applications had no significant impact on growth of *B. orellana*. This may be partly attributed to the late planting date of *B. orellana* seedlings.

7 EFFECTS OF EXOTIC VA MYCORRHIZAE ON SURVIVAL AND GROWTH

7.1 Introduction

While tropical mycorrhizae have been studied in tropical rainforests, the relevance of mycorrhizae for water and nutrient dynamics under conditions of seasonal water scarcity in the tropics remains poorly investigated (Huante et al., 1993). Hyphae of VA mycorrhiza may extend the zone for nutrient uptake by several centimeters. They have the capacity to deliver a high proportion of the plants demand of P, as well as Zn and Cu (Marschner, 1992). As VA mycorrhizal dependency was documented for *Cordia alliodora* (Huante et al., 1993), *Cordia* was classified as a VAM genus, and the inoculation of *C. dodecandra* seedlings with exotic VA mycorrhizae was assumed to have positive effects on growth and survival.

Hypothesis

The inoculation with exotic strains of Vascular Arbuscular Mycorrhiza (VAM) enhances survival and growth of *C. dodecandra* on calcareous semi-arid Yucatan soils.

7.2 Results and discussion

7.2.1 Survival of inoculated seedlings

Survival in the field during the first rainy season was slightly lower for inoculated seedlings than for non-inoculated seedlings on control plots. In December 2002, one month after replacing lost seedlings in November, survival rate on control plots was 87%, compared to 79% on plots with seedlings that had been inoculated in the nursery (data not shown).

Four weeks after inoculation with the mycorrhizal mixture, *C. dodecandra* seedlings transplanted into plastic bags with sterilized red Yucatan soil in the nursery had a survival rate of about 97%. High survival of seedlings on sterilized red Kankab soil in the nursery showed that high soil pH did probably not have a negative impact on the establishment of inoculated seedlings. While *C. dodecandra* seedlings developed well after inoculation in the nursery, about 40% of the inoculated *C. papaya* died directly after the inoculation, even before transplanting.

In the field, after the first dry season, survival of inoculated seedlings on Leptosol was with 60% higher than survival of seedlings on Cambisol (37.5%). On both soils, considering the irrigation level, survival was more than 20% higher when seedlings were irrigated only at the peak of dry season compared to seedlings that were irrigated regularly during dry season (Table 11).

Table 11: Survival of inoculated *C. dodecandra* compared to the non-inoculated control on two soils with different irrigation levels after the first dry season

Soil, Irrigation level	**No. of seedlings at mid rainy season**	**No. of originally planted seedlings**	**Survival of inoculated seedlings (%)**	**Survival of non-inoculated seedl. on control plots, based on the no. of originally planted seedlings (%)**
Leptosol (total)	12	20	60	84
Cambisol (total)	9	24	37.5	83
Leptosol, without irrigation	6	8	75	80
Leptosol, sporadic irrigation	4	4	100	85
Leptosol, regular irrigation	2	8	25	87.5
Cambisol, without irrigation	0	0	no data	75
Cambisol, sporadic irrigation	6	12	50	87.5
Cambisol, regular irrigation	3	12	25	90

7.2.2 Growth of inoculated and control seedlings

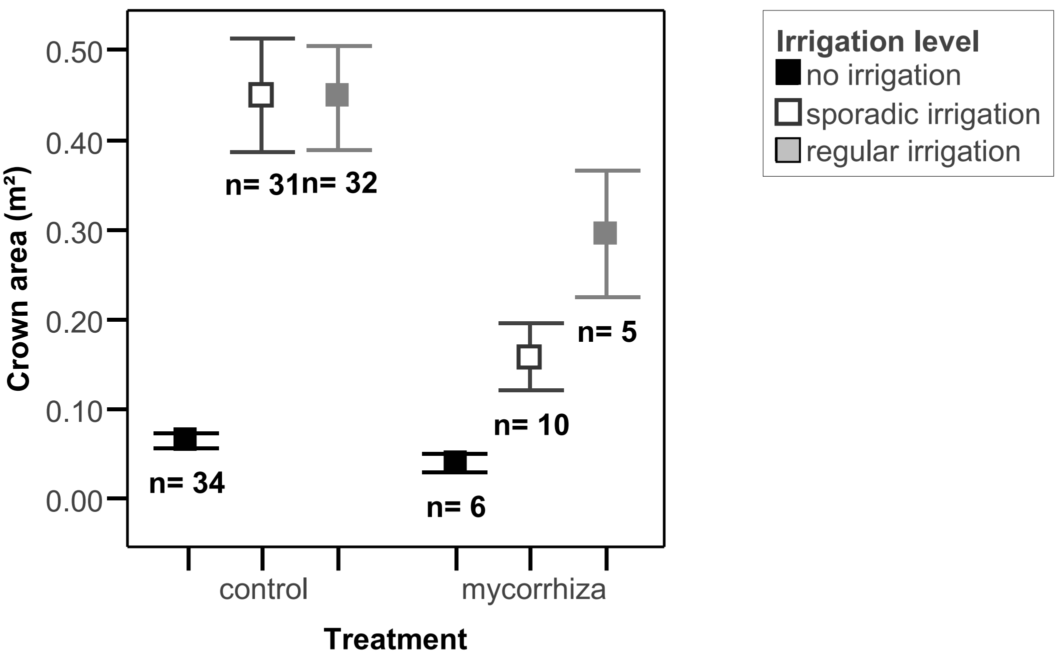

Figure 36: Crown area of inoculated vs. non-inoculated 15-month-old *C. dodecandra* at three irrigation levels on both soils (no difference between soils), error bars show mean +/- 1.0 SE

Comparing non-inoculated control and inoculated seedlings, growth of crown area was explained by the main factors irrigation and treatment (p_{irr} = 0.000; p_{tre} = 0.004). Crown area of *C. dodecandra* at mid rainy season on sporadically and regularly irrigated control plots was 0.44 m² and 0.45 m², respectively (Figure 36). Inoculated seedlings had crown areas of 0.15 m² with sporadic, and 0.31 m² with regular irrigation. Without irrigation, control seedlings had crown areas of 0.06 m², in comparison to 0.04 m² of inoculated seedlings. Crown area on irrigated plots was higher than on non-irrigated plots.

Virtual diameter increment from July 2003 to January 2004 was significantly influenced by the main factors treatment (p_{tre} = 0.006) and irrigation (p_{irr} = 0.000), and to a lesser extent by soil (p_{soil} = 0.049). Seedlings without inoculation had higher stem and branch diameters at 10 cm above ground (12.9 mm) than seedlings with mycorrhizal treatment (10.0 mm). For inoculated as well as for control seedlings, growth of stem and branch diameter on non-irrigated plots was significantly lower than on irrigated plots. On black Leptosol the difference between virtual diameter growth of inoculated and control seedlings was more pronounced than on red Cambisol (data not shown).

The stem length of *C. dodecandra* after the first dry season was explained by interactions between treatment and irrigation ($p_{tre*irr}$ = 0.035), and by the main factors treatment and irrigation (p_{tre} = 0.001; p_{irr} = 0.000). Control seedlings were always taller than inoculated seedlings, and stem length increased significantly with each irrigation level. The most notable difference in stem length was recorded on sporadically irrigated plots, where control seedlings were 91 cm tall, compared to a mean stem length of 42 cm of seedlings with mycorrhiza treatment (data not shown).

Our results on the influence of irrigation and soil on growth of control seedlings in this section vary from our overall results presented in chapter 4 on the influence of Leptsol and Cambisol on growth of seedlings. The reason for this is that due to the reduced number of surviving inoculated seedlings, inoculated as well as control seedlings from sub site were included into the analysis.

The remarkable growth difference of control seedlings and seedlings with mycorrhizal inoculation on sporadically irrigated plots emphasized the lack of benefit for seedlings of an inoculation with exotic VAM. For the evaluation of the differences between control and inoculated seedlings, sporadic irrigation included “sub site” plots from the experimental site owned by the Faculty, where probably higher amounts of soil moisture and nutrients were available for inoculated and control seedlings. While control seedlings translated this supply into growth, inoculated seedlings did not respond to it. This indicated that the mycorrhizal treatment rather inhibited nutrient uptake of *C. dodecandra*.

7.2.3 Impact of mycorrhizal inoculation on foliar nutrient concentrations

Phosphorus tissue contents of inoculated plants were not significantly different from control treatments. The P/Zn ratio was significantly lower for inoculated seedlings compared to control seedlings. No difference in foliar K concentrations between inoculated seedlings and control seedlings was found. Ca/Mg ratio was significantly lower for inoculated seedlings (6.2) than for seedlings of control and fertilizer treatments (between 7.2 and 8.3) ($p_{treatment}$ = 0.049).

The lack of increase in leaf P concentration after mycorrhizal inoculation in comparison with control treatments was surprising. Generally, an increase in P availability due to a larger volume of explored soil is a typical benefit related to inoculation. The significantly lower P/Zn ratio for leaves of inoculated seedlings in comparison to leaves of control plots may indicate that inoculated seedlings absorb less P than seedlings without additional VAmycorrhiza. There was no indication that mycorrhizal infection improved nutrient uptake. On the contrary, the more fertile the soil, the larger the difference between virtual diameter growth of inoculated and control seedlings.

A reduction of capacity for uptake of K as a result of exotic VAM inoculation may have decreased survival and growth of seedlings. Considering the significantly lower growth of inoculated seedlings compared to control seedlings and the high mobility of K in the plant, the lack of a significant difference in foliar K concentration between the two treatments implied a higher K uptake by control seedlings. In the semi-arid environment of Northern Yucatan, especially adequate K seemed to play a vital role for the ability of *C. dodecandra* seedlings to grow well. Inoculation may impede uptake and delivery of K due to decreased root surface area and less root exsudation after VAmycorrhizal infection. It may also reduce uptake and delivery of Mn and Ca (Sieverding, 1991).

7.2.4 Mycorrhizal trial in the nursery

Survival of transplanted seedlings from the mycorrhizal trial in the Protropico nursery after 14 weeks was 100% on Cambisol and 80% on black soil. Survival by treatment was 100% for seedlings inoculated with *G. mosseae*, 90% for seedlings inoculated with *G. manihot* and the mycorrhizal mixture, and 80% for non-inoculated control seedlings.

Height growth of seedlings was explained by the interaction between mycorrhizal treatment and time of measurement ($p_{time*myc}$ = 0.035). Seedlings without inoculation and seedlings inoculated with mycorrhizal mixture increased significantly in height between the 8th and the 14th week after transplanting, from 19 cm to 20 cm, and from 20 cm to 21 cm, respectively. In contrast, *C. dodecandra* inoculated with *G. manihot* and *G. mosseae* did not show any height growth. No difference in growth between seedlings on red and black soil was found.

The high survival of seedlings with inoculation in the nursery during our nursery trial 2003 to 2004 may be attributed to less physical stress by drought and heat in comparison to field conditions. This coincided with high survival after inoculation in the nursery in 2002. Higher mortality of control seedlings and similar growth improvement in the nursery compared to seedlings inoculated with the mycorrhizal mixture during the second trial after 14 weeks indicate that the granular mycorrhiza was not contaminated.

7.2.5 Impact of exotic VA mycorrhizae on growth and survival

The - beneficial or parasitic - effect of vesicular arbuscular mycorrhizal fungi (VAMF) may be determined by a variety of factors, including environmental conditions, soil quality, and the VAMF strain and ecotype (Vlek et al., 1996). The use of *Glomus species* from different latitudes and climatic conditions may have had a negative effect on growth and survival. Allen et al. (2001) found a positive impact of inoculation with inoculum from Yucatan soils on growth of native tree seedlings in Yucatan. Their result compared with our data points towards a better adaptation of local mycorrhiza to local climatic and site conditions than imported mycorrhizae. The mycorrhizal inoculum from Göttingen University used for our nursery trial originated from Columbia and Zaire (Schultz, 2002), while the mycorrhizal mixture originated from tropical regions in Africa (see material and methods). More detailed information on the climatic conditions of the site of origin of mycorrhizal mixtures are necessary to evaluate the impact of site characteristics on potential benefits for growth of plants on other sites. Introduced vesicular arbuscular mycorrhizal fungus species and/or populations from other latitudes and climates may result in differences of physiological response of the host plant. Plant growth responses were found to vary with mycorrhizal fungi from different latitudinal sites (Allen et al., 1992; Allen et al., 1995). Physiological responses of *Agropyron smithii* to different populations of VAMF showed that fungal populations from soil of drier regions improved the water status of the host plants (Stahl and Christensen, 1991; Stahl and Smith, 1984).

Our data from the nursery trial show significantly lower growth after inoculation with *G. mosseae* and *G. manihot* in non-sterilized Yucatan field soil. They indicate that exotic mycorrhizal treatments have a negative effect on plant growth. Allen et al. (2001) reported that inoculation with native mycorrhizae leads to higher growth of ten tree species of the tropical deciduous forest of Southern Mexico: in their study, soil from early and late successional forests was used for inoculation, and best growth results were recorded for inoculum collected from 2-3 years old burnt sites, and inoculated plants showed higher growth even four years after transplanting to the field. It may be deduced that the imported mixture that was applied in our study colonized the roots of seedlings, thereby impeding beneficial interactions between roots and the native soil microorganisms. The lack of mutual acceptance and/or positive interactions between introduced VA mycorrhizae from other sites and autochthonous mycorrhizae may determine future plant growth more than initial plant response under nursery conditions.

Our results indicate that exotic VAMF used for inoculation of *C. dodecandra* did survive and colonize the roots under field conditions, limiting the opportunity of native mycorrhizae to generate a benefit for the seedling by the symbiosis. Berta et al. (1995) reported that time course and level of mycorrhizal infection of roots of *Prunus cerasifera* varied between different *Glomus species*: it was faster for *G. mosseae*, but finally higher for *Glomus intraradices*. Hence, high colonization by *Glomus intraradices* may reduce the possible colonization with native mycorrhizae that are more adapted to the soil and climate conditions. Introduced mycorrhizal species may play a dominant role regarding time and intensity of mycorrhizal colonization compared to native mycorrhizal species. Results of a study by Ortas et al. (2002) emphasized the importance of the colonization by indigenous VAMF for adequate nutrient uptake. They found that the removal of native mycorrhizal spores by soil sterilization completely stopped positive response of sour orange (*Citrus aurantium* L.) to additional P and Zn supply on high pH soil. Voß et al. (1998) suggested that colonization by exogenous VA mycorrhizae was suppressed in the field by competing colonization with autochthonous mycorrhizae. In our field experiment, the inverse may have happened: preceding colonization of exogenous VA mycorrhizae may have blocked potentially beneficial colonization by autochthonous mycorrhizae.

By illustrating the decrease in survival and growth of inoculated *C. dodecandra*, our results controvert the positive impact of VAmycorrhizal infection documented for many tree and crop species in nurseries of temperate and tropical regions (González Chávez and Ferrera Cerrato, 1997). Seedling growth in the nursery of various tree species including *Cordia ovalis* and fruit crops such as *C. papaya* was improved by VAMF inoculation in semi-arid regions of Kenya (Ishii, 2000). Schultz (2002) reported higher survival and shoot dry weight for VAM inoculated vs. non-inoculated oil palm (*Elaeis guineensis* Jacq.) plantlets. Both inoculations with *G. mosseae* and *Glomus intraradices* led to higher survival and growth of *Prunus cerasifera* L. (Berta et al., 1995).

Nevertheless, in accordance with our results, other authors showed that inoculation with mycorrhiza did not always produce higher growth rates of seedlings: one of four inoculated tree species from the Mexican tropical deciduous forest, *Ipomoea wolcottiana* Rose (Convolvulaceae), did not respond by an increase in relative growth rate, biomass production, and leaf area (Huante et al., 1993). After inoculation with

Glomus etunicatum and *G. mosseae*, *Citrus aurantifolia* Swingle (one of three investigated Citrus species) did not show any increase in height or biomass (Athipunyakom, 1988). In accordance with our results, no beneficial effect of inoculation with *G. deserticola* was found for growth of *Leucaena leucocephala* (Lam.) de Wit. in simulated eroded soils (Fagbola et al., 2001). Macêdo et al. (1998) studied the response of a variety of tropical fruit and timber trees and crop species on VAMF inoculation in polyculture systems in the Western Amazon. Inoculated plants showed higher growth responses in the nursery and higher survival rates after transplanting, but for most species the apparent competitive advantage regarding growth of inoculated seedlings was no longer detected in the field.

7.3 Summary

Inoculation of *C. dodecandra* with a mixture of *G. mosseae*, *G. intraradices* and *G. deserticola* reduced both survival as well as growth of *C. dodecandra*. Reduced growth of *C. dodecandra* seedlings may be explained by the use of *Glomus species* and strains from different latitudes and climatic conditions. Mycorrhizal infection did not lead to an increase in foliar P concentration of seedlings compared to the non-inoculated control. Our results indicate that exotic VAMF used for inoculation of *C. dodecandra* did survive and colonize the roots under field conditions, thereby possibly limiting the opportunity of native mycorrhizae to generate a benefit for the seedling by the symbiosis.

8 INSECTS ASSOCIATED WITH *C. DODECANDRA*

8.1 Introduction

So far, with few notable exceptions, the entomofauna of agroforestry species has not been part of the investigations on the respective agroforestry schemes (Rao et al., 2000; Schroth et al., 2000). On the Yucatan Peninsula, *Hypsipyla grandella* and *Chrysobothris yucatanensis* caused major damages on plantations of *C. odorata* and *S. macrophylla* (Diaz Maldonado, 2002). Hence, the risk of the incidence of damaging insects on plantations of multi-purpose trees such as *C. dodecandra* has to be assessed before recommending them as useful species to farmers.

8.2 Results and discussion

8.2.1 Insect populations associated with *C. dodecandra*

In June 2003, at the end of the first dry season, no major insect damage or insect populations were observed on the experimental plots. In August and September 2003, an increased population of Coleoptera, of the family Chrysomelidae, subfamily Cassidinae was observed on the experimental area, manifested by accumulations of larvae on *C. dodecandra* leaves and the green-golden beetles. At the peak of the incidence, an estimated 60 to 70% of seedlings on the experimental area were subject to damages by Chrysomelidae, subfamily Cassidinae, but the percentage of leaf damage per tree was generally low and did not impact growth variables such as crown diameter. Shoots were not affected. By November, the population had decreased considerably. In January 2004 during leaf sampling, seedlings were occasionally found to host insects of this subfamily.

In Southern Yucatan, on a private *C. dodecandra* plantation for fruit production, there was a strong incidence of Coleoptera (probably Chrysomelidae, subfamily Cassidinae) observed in November 2003. About 90% of the trees were attacked; some of them hosted large populations of phytophagous insects and larvae. The high percentage of leaf damage per tree was severely reducing leaf area. On *C. dodecandra* regeneration plantings in forests in Southern Yucatan, and on farmers' land, where *C. dodecandra* was planted in lines (aisles) in between fallow vegetation, no comparable presence or damage by *Chrysomelidae* was observed.

On our experimental plots, occasional incidence of stem-, petiole- and leaf-sucking insects was observed on *C. dodecandra* seedlings. The insects were of the order Homoptera. During rainy as well as dry season, ants (order Hymenoptera, family Formicidae) were observed on *C. dodecandra* seedlings all over the experimental area. Mining insects were observed mainly in July and August 2003, at mid rainy season. Highest incidence was found on *C. dodecandra* seedlings in an area of site three that had been irrigated during dry season three times a week. Very few damage by mining occurred on seedlings in the area without irrigation on the same experimental site.

Our observations on insects associated with *C. dodecandra* corresponded with results of an assessment of the phytosanitary conditions of forest and fruit tree plantations on the Yucatan Peninsula. In the evaluation of plantations of valuable timber species including *C. dodecandra*, leaf mining insects, ants, and larvae of the family Chrysomelidae were detected (Diaz Maldonado, 2002). Phytophagous insects of the order Coleoptera, of the family Chrysomelidae, subfamily Cassidinae, were observed mainly causing leaf damage on *C. dodecandra* on experimental plots at mid rainy season. Riley (2005) and Windsor et al. (1992) reported the association of insects of this subfamily with plant species of the genus *Cordia*. For Panama, highest populations of adults and larvae were reported for the beginning of rainy season (Riley, 2005). In accordance with this, Cassidinae were found on the experimental plots mainly at mid rainy season. The slight shift of the period of occurrence may be attributed to high rainfall intensity during the first weeks of rainy season in Northern Yucatan. Some insect species of the order Hymenoptera, family Formicidae, may cause leaf damage to seedlings. On the other hand, as species that are specialized on killing larvae of other phytophagous insects, their presence may have a beneficial effect. The presence of *Azteca longiceps* on *Cordia alliodora* trees was found to be beneficial for the tree species, as it protected trees from damages by larvae and adults of *Psalidonota leprosa* (order Coleoptera, family Chrysomelidae, subfamily Cassidinae) (Quiroz Robledo and Valenzuela González, 1998).

8.2.2 Impact of insect incidence on growth of *C. dodecandra*

Insect incidence did not interfere with seedling growth on the experimental area throughout the experiment. Field observations showed that shoot tips were not subject to insect attack, and insect damage occurring on leaves was not leading to any substantial reduction of biomass of seedlings. Observed leaf damages were mainly attributed to insects of the order Coleoptera, of the family Chrysomelidae, subfamily Cassidinae. Leaf damages were also associated with populations of the order Hymenoptera, family Formicidae. Limited damages on stems, petioles and leaves were caused by the order Homoptera. Damages by leaf-sucking insects increased towards the dry season.

Insect populations associated with *C. dodecandra* do not seem to impact seedling growth in small scale agroforestry systems as the one designed for this study. Though some insect damage was observed on *C. dodecandra* on the experimental agroforestry plots, no severe or growth-limiting insect incidence was recorded. In accordance with this, at present, there are no reports of severe insect attacks on *C. dodecandra* seedlings (CONAFOR, 2004b; Tamayo Rivera, 2004). Nevertheless, considering the observed high insect damage on a predominantly monoculture plantation of *C. dodecandra* in Southern Yucatan, the possibility of potential severe insect damages may not be disregarded.

8.2.3 Comparing insect incidence in Mayan homegardens and on study sites

The fluctuations in insect populations on the experimental plots seemed to be similar to those in Mayan communities. In homegardens, low insect incidence was found in July, and a high insect population was recorded for January (Tamayo Rivera, 2004). This coincided with high incidence of insect damage on experimental plots in January 2004, and the lack of insect damage on seedlings in July 2003. Apart from precipitation (Tamayo Rivera, 2004), temperature probably played a major role in fluctuations of insect populations related to *C. dodecandra*. The observed lack of insect incidence on the experimental plots at the end of dry season may indicate that at the peak of dry season, temperatures in Northern Yucatan have a lethal effect on insects. The development of insects is strongly affected by temperature, and the lethal temperature limit is generally about 40° C (Apablaza, 1995). Temperatures during May in Mérida may reach 40° C (Duch, 1988), causing the death of both phytophagous insects as well as their natural enemies.

Comparing the extent of insect populations of Cassidinae and the related damage on *C. dodecandra* in homegardens with field observations on insect incidence on our experimental plots, a higher variety of species in the neighborhood of seedlings seemed to reduce insect incidence and the related damage in homegardens. In the complex multi-strata homegardens of Mayan farmers, with up to more than 350 plant species including *C. dodecandra* as a pillar species (Ruenes Morales et al., 1999), low incidence of Cassidinae was recorded. Though there were numerous other phytophagous insects sampled in the homegardens with *C. dodecandra* trees, the equally high number of natural enemies seemed to maintain the system in balance (Tamayo Rivera, 2004). On our experimental plots that were rather scattered and mostly surrounded or bordered by secondary vegetation, the insect populations of Cassidinae during mid rainy season were comparably higher than in homegardens including *C. dodecandra* trees. Rao et al. (2000) recommended small fields and scattered distribution of fields within the agroforestry system as management components favoring low pest incidence. Our results indicate that the same holds true for the design of agroforestry plots within secondary vegetation in Yucatan. Severe damage and high populations of the same insect were observed in the *C. dodecandra* plantation on a meadow in Southern Yucatan in November 2003. At the same time, regeneration plantings in the forests and *C. dodecandra* line plantings in aisles between fallow vegetation in the southern peninsula did not show any severe insect incidence. This may indicate that the species-richness of the surrounding vegetation plays a role in assuring lower populations of pests on seedlings. Plant species diversity by itself, though, is not a guarantee against low pest incidence in agroforestry systems (Rao et al., 2000). While shade trees, for example, may have the beneficial effect of harboring natural enemies of crop pests, they may on the other hand provide physical protection to crop pests, diseases and their vectors (Schroth et al., 2000).

When selecting crop and other perennial species in order to combine them with *C. dodecandra*, their susceptibility to pests that occur in association with *C. dodecandra* should be taken into account. In simultaneous systems, high diversity with widely differing species, high number of species, close spatial arrangement and high density of trees help maintaining insect damage at a low level (Rao et al., 2000). If one plant species attracts the pests of other species, it may be used as a “trap crop”, such as *Cordia verbenacea*. This tree species was employed successfully in Citrus orchards in Bahia, Brazil, in order to “trap” the Citrus pest *Cratosomus flavofasciatus* (Nascimento et al., 1986). It would be very useful to identify plants that may act as trap crops for phytophagous insects associated with *C. dodecandra*, or plant species that harbor predators or parasites of these damaging insects.

More research and technical assessment in the field of biological control of insects and infections of native trees will be substantial for successful sustainable management of agroforestry systems. For the efficient control of insect pests and diseases in Yucatan, more technical assistance is required (Diaz Maldonado, 2002). An evaluation of management practices for fruit trees and fruit crops in Chiapas, Southern Mexico, showed that costs and potential health hazards make the use of chemical insecticides disadvantageous for the farmer (Pohlan et al., 1997). On-going and future studies on the ecology of insects associated with *C. dodecandra* shall be a potential measure to protect agroforestry systems with *C. dodecandra* from future damage.

8.3 Summary

Phytophagous insects of the order Coleoptera, of the family Chrysomelidae, subfamily Cassidinae, were observed mainly causing leaf damage on *C. dodecandra* on experimental plots at mid rainy season. Occasional incidence of stem-, petiole- and leaf-sucking insects was observed on *C. dodecandra* seedlings. The insects were of the order Homoptera. During rainy as well as dry season, ants (order Hymenoptera, family Formicidae) were observed on *C. dodecandra* seedlings all over the experimental area. Mining insects were observed mainly in July and August 2003, at mid rainy season. On our experimental plots, the insect populations of Cassidinae during mid rainy season were comparably higher than in homegardens including *C. dodecandra* trees. Insect incidence did not interfere with seedling growth on the experimental area throughout the experiment.

9 ADDITIONAL INFLUENCES ON GROWTH OF SEEDLINGS

9.1 Introduction

The sub site differed from the remaining experimental area in the history of site as well as in surrounding micro relief (Figure 18). The secondary vegetation on sub site had been slashed and burnt in 2001, 2-3 years later than the remaining area. In contrast to the other experimental plots, sub site plots were surrounded on three sides by mounds that were covered with secondary vegetation.

9.2 Results and discussion

This chapter presents the differences in growth and foliar nutrient concentrations of *C. dodecandra* and in survival and growth of *B. orellana* on sub site compared to the remaining experimental area, and reports the impact of additional factors on growth of seedlings such as bordering mounds, surrounding secondary vegetation, climbing vines, light availability, preceding land use, and small ruminants.

9.2.1 Growth of *C. dodecandra* on sub site plots

Considering our entire experimental area, highest growth of *C. dodecandra* seedlings after 15 and after 21 months was observed on the sporadically irrigated Cambisol sub site, especially on plots with complete fertilizer minus P. Control plots with sporadic irrigation on black Leptosol on sub site vs. the remaining experimental area showed significantly higher growth of seedlings at mid and end of rainy season of crown area, virtual diameter (both $p = 0.006$ mid rainy season, and 0.003 end of rainy season), and growth increment of virtual diameter and stem length from July 2003 to January 2004 ($p = 0.017$ and $p = 0.028$). Stem length was higher at the end of rainy season ($p = 0.014$). On sporadically irrigated red Cambisol with complete fertilizer additions, seedlings on sub site versus non-sub site seedlings showed significant differences in growth of crown area ($p = 0.019$ in July 2003, 0.012 in January 2004), stem length and virtual diameter in January 2004 ($p = 0.005$ and $p = 0.038$), and growth increment of stem length and virtual diameter over the rainy season ($p = 0.000$ and $p = 0.022$).

There were significant differences between crown areas at mid rainy season of seedlings on plots with complete fertilizer minus manganese on sub site (0.75 m²) versus seedlings on remaining plots (0.35 m²) ($p_{\text{sub site}} = 0.015$). Though control plots on sporadically irrigated red Cambisol showed no difference in growth between sub site and non-sub site plots, seedlings with complete fertilizer additions minus zinc ($p_{\text{stem length increment (sti)}} = 0.000$ and $p_{\text{virtual diameter increment (vdi)}} = 0.007$), minus nitrogen ($p_{sti} = 0.000$ and $p_{vdi} = 0.003$) and minus phosphorus ($p_{sti} = 0.000$ and $p_{vdi} = 0.006$) all had significantly higher growth increment of stem length and virtual diameter over the rainy season.

The growth difference between sub site and non-sub site plots was especially strong for plots on red Cambisol with subtractive phosphorus. On sporadically irrigated plots, significance for differences in crown area at the end of rainy season was $p = 0.001$, for virtual diameter $p = 0.001$, and for stem length $p = 0.000$ for minus P. With complete fertilizer minus phosphorus additions, 21-month-old *C. dodecandra* seedlings attained heights of 311 cm on sub site with sporadic irrigation, compared to 174 cm with sporadic and 192 cm with regular irrigation on the remaining area.

The comparison of fresh weight biomass of two 19-months-old *C. dodecandra* seedlings showed that total biomass of the seedling on sub site was with 4.95 kg 3.3 times higher than total biomass of the seedling outside the area (1.51 kg). Both seedlings were located on red Cambisol with sporadic irrigation, the one on sub site with complete fertilizer, the other one with complete fertilizer minus manganese. Biomass of roots was 2.4 times higher for the seedling on sub site (0.84 kg vs. 0.35 kg), stem biomass was 1.9 times higher (0.54 kg vs. 1.01 kg), and total aboveground biomass was 3.6 times higher on sub site versus the remaining area (1.15 kg vs. 4.12 kg). The ratio of root biomass to stem biomass was 0.83 for the seedling on sub site, versus 0.65 on the plot outside the “sub site” area.

The difference in belowground growth between the two excavated seedlings confirmed the observation that provision with nutrients and water for growth was better on sub site than on the remaining area. While the seedling on sub site received complete fertilizer treatment, and the other one complete fertilizer minus manganese, the missing element may have had a negative influence on biomass increment. Nevertheless, there were significant differences between crown areas at mid rainy season of seedlings on plots with complete fertilizer minus manganese on sub site versus seedlings on remaining plots. Also, seedlings of complete fertilizer treatment differed significantly in aboveground biomass according to whether located on sub site or not. Hence, it is suggested that the missing manganese was not the main reason for difference in biomass growth, and that growth differences reflected better resource availability on sub site.

9.2.2 Impact of K availability on growth of *C. dodecandra*

The comparison of foliar nutrient concentrations of *C. dodecandra* on control plots under sporadic irrigation on the sub site and the rest of the research area showed that at the end of rainy season, K/Mg was significantly higher on sub site (4.4) than on the remaining area (1.8) ($p = 0.002$). The same tendency held true for foliar K/sqrt (Mg+Ca), and for foliar K. No difference was detected for foliar P and N concentrations. Highest growth of *C. dodecandra* on substractive P plots confirmed the extraordinarily high importance of adequate K supply and water for seedling growth. Higher K additions from the fertilizer mixture on substractive P plots may explain highest growth on these plots. On the remaining area, growth of *C. dodecandra* seedlings on red Cambisol indicated a reduced availability of P on red Cambisol compared to black Leptosol. On sub site plots, additional factors such as higher soil moisture leading to increased nutrient availability, nutrient supply from litter of the surrounding vegetation, more recent burning with subsequent planting of cover crops and the precending longer fallow period may have relieved this constraint to growth.

9.2.3 Survival and growth of *B. orellana* on sub site plots

Survival of *B. orellana* seedlings was much higher on sporadically irrigated plots on the sub site than on plots with similar irrigation level on the remaining area. On Leptosol control plots, survival on the sub site was 87.5%, compared to 0% on the rest of the experimental area. On Cambisol control plots – only one of them located on the sub site – two *B. orellana* out of four survived on sub site, while only one out of twelve (8.3%) survived on the remaining area. On Cambisol plots with fertilizer minus N treatment and sporadic irrigation, 100% (eight out of eight) survival was recorded on sub site, compared to 12.5% survival on other plots with the same treatment.

For treatments with an adequate number of surviving individuals on sporadically irrigated plots outside the sub site area, growth rates outside and on sub site were compared. On the sub site, significantly higher growth rates were found for *B. orellana* seedlings with subtractive manganese additions for virtual diameter at mid and end of rainy season ($p = 0.003$ and $p = 0.001$), for virtual diameter increment over the rainy season ($p = 0.000$), for crown diameter at mid and end of rainy season ($p = 0.004$ and $p = 0.011$), and for the height of *B. orellana* bushes in January 2004 ($p = 0.012$). *B. orellana* seedlings on minus P sub site plots had higher crown diameters and virtual diameters (both $p = 0.008$) in July 2003 in comparison to other minus P plots with sporadic irrigation. Over the rainy season, they attained heights of 123 cm compared to 62 cm on the remaining area ($p = 0.019$), and virtual diameters of 39.8 mm compared to 9.0 mm ($p = 0.010$).

High growth of *C. dodecandra* and *B.orellana seedlings* on the sub site was attributed to higher availability of water due to surrounding vegetation and microrelief, combined with higher availability of nutrients caused by the recent slashing and burning of older fallow vegetation, and preceding cultivation of cover crops.

9.2.4 Impact of mounds bordering the sub site on growth

A delimited area on experimental site of the Faculty for Veterinary Science - the so-called sub site - was surrounded on three sides by mounds of 0.75 to 1.5 m height (see map of the experimental site), with summit levels at a distance of 8 to 16 m from research plots. On the remaining experimental area of all three sites, mounds of 0.75 to 1 m height were recorded along the experimental plots, too, but never bordering the plot area on more than one side.

The remarkably high height and diameter growth response to only sporadic irrigation on Cambisol plots on site 1 might be explained by differences in the micro relief surrounding some of the scattered research plot areas. The chain of mounds with heights between 0.75 and 1.5 m covered by secondary vegetation that surrounded the sub site on three sides at distances between 8 and 16 m may have contributed to higher available soil moisture for seedlings. In a study on Miocene calcareous sandy marls, the vigour of olive trees (*Olea europaea* L.) on slopes increased significantly with distance from summit of terrain elevations (Gálvez et al., 2004).

9.2.5 Impact of climbing cover plants on growth

Mucuna plants in neighbourhood of *C. dodecandra* seedlings had a negative impact on seedling growth. *Mucuna* tended to bend the seedlings and to compete with them for light and space availability. Hence, all plots had to be weeded every 6 weeks especially to hinder climbing vines to interfere with growth of straight stems and adequate crown development.

The regular removal of climbers was found to be essential for straight stem growth and adequate crown development of seedlings. Due to their tendency to invade tree crowns and bend branches and stems, they represent competition for light, and may considerably affect development of seedlings in the open. Horvitz and Koop (2001) stated that in a tropical hardwood forest, the removal of vines might improve recruitment of seedlings and saplings of native trees. This may as well hold true for tree seedling planting schemes on areas cleared from secondary vegetation. For the ecologically sound cultivation of the tropical fruit tree guanábana (*Annona muricata* L.), an important measure is to prevent species such as *Ipomoea spp.*, *Momordica spp.*, and *Pueraria spp.* from climbing the stem (Pohlan et al., 2001).

During the first year of establishment, competition between seedlings and grasses may have a relevant influence on the establishment of woody species in temperate savanna ecotones (Weltzin and McPhearson, 2000). In Costa Rica, *Cordia alliodora* seedlings responded positively in leaf habitus to competition control during the first weeks after transplanting. This was attributed to higher nutrient availability (Wightman et al., 2001). Gehring et al. (1999) attributed the missing initial effect of fertilization treatments on woody biomass accumulation of secondary vegetation in Eastern Amazonia to competition by grasses. Removal of all non-tree vegetation during early secondary forest succession in Uganda did have a positive impact on growth of trees for the first two years (Duncan and Chapman, 2003). Belowground competition had a strong impact on seedling growth on a degraded hillside in Hong Kong (Hau and Corlett, 2003). Nevertheless, a comparison of ten native multi-purpose tree species from Southern Mexico on plots with different types of plant cover showed no significant impact of ground vegetation on aboveground seedling growth (Martínez Bravo, 2001). Competing vegetation may have a stronger negative impact on survival than on growth. Densely resprouting secondary vegetation was reported to cause high seedling mortality in restoration trials at the El Eden Ecological Reserve in Quintana Roo, Southern Mexico (Allen at al., 2001). Due to its deep tap roots, *C. dodecandra* probably gains relatively fast access to soil moisture and nutrients from deeper soil layers, and hence competition with grasses for water and nutrients will probably not have a significant impact on seedling growth beyond the first two rainy seasons (including the one when seedlings are planted). In this study, grass competition was reduced by manual weeding, removing the graminoid roots in a circle around the individuals.

9.2.6 Impact of surrounding woody vegetation on growth

On the experimental site 2 towards the end of rainy season 2003, *C. dodecandra* seedlings of about six interconnected research plots (an area of 14 m by 21 m) lost most of their leaves, several weeks earlier than all other seedlings on the same site, about 10 days after the bordering secondary vegetation had been felled.

Surrounding secondary vegetation including woody perennials may increase water availability and hence growth of seedlings. Greater infiltration and increased soil moisture was found beneath plant canopies in the Chihuahuan desert (Bhark and Small, 2003). Secondary vegetation with tree species that surrounded the sub site on three sides was older than secondary vegetation bordering research plots on the remaining area. Natural vegetation by low deciduous and medium subdeciduous forests increased soil organic matter content and soil moisture of Yucatan soils (Duch, 1995). Other benefits of neighboring tree crowns on sub site plots of our experimental area were probably lower temperatures, and the related reduction of soil evaporation. *C. dodecandra* in homegardens was found to have highest photosynthetic activity in the early morning, and hence to respond positively to low temperatures, in combination with high humidity and CO_2 concentrations and light availability (Benjamin et al., 2001). Soil temperatures beneath trees in semiarid piñon-juniper woodland may be reduced by up to 10° C in comparison with intercanopy patches (Breshears et al., 1998).

Removal of secondary vegetation may reduce available soil moisture for *C. dodecandra* seedlings, leading to premature loss of leaves. The earlier shedding of leaves by seedlings at the end of rainy season 2003 occurred one to two weeks following the removal of the secondary vegetation bordering the respective plots. The fallow vegetation had been covering a terrain elevation bordering the experimental plots. Probably the secondary vegetation protected *C. dodecandra* seedlings from drought stress, increasing available soil moisture, and providing shelter against high temperature and winds.

For successful establishment of seedlings in existing woody vegetation, thinning of planting areas combined with continuous removal of regrowth during the first two rainy seasons may increase growth of seedlings. Prior clearing of stripes of 2 to 3 m width and removing regrowth of competing vegetation during the establishment phase seemed to have a beneficial impact on seedling establishment and growth on agroforestry plots in Quintana Roo. On those plots, seedlings of *C. dodecandra* showed fast growth during the early establishment phase (Wightman, 2002).

9.2.7 Impact of light on growth of *C. dodecandra*

Light as a major influence factor has been largely discussed regarding growth of tropical forest species, especially considering tree fall gaps (e.g. Barker et al., 1997; Allen and Pearcy, 2000). The ability of tropical forest seedlings to adapt to situations of open areas, with light levels considerably higher than in intact forest, though, remains largely unknown. Shrubs in early-successional fields in Costa Rica did apparently not improve growth of 1.5-year-old tree seedlings of four tropical forest species (Loik and Holl, 2001). High light tolerance of *C. dodecandra* was documented by fast growth on our experimental sites, and by observations in *C. dodecandra* regeneration plantings in Southern Yucatan.

The tropical forest species *C. dodecandra* seemed to adapt well to high light level environments, and growth did not seem to be limited by high light intensities. On the one hand, field observations did not indicate better seedling development on plots adjacent to secondary vegetation compared to other plots. On the other hand, growth of seedlings on black Leptosol plots was high, even though these plots were typically located on the top of terrain elevations, and therefore most exposed to direct sunlight. Hence, it is not probable that light was a growth-limiting factor. At high light levels, *C. dodecandra* trees had maximum net photosynthetic rates of around 50 µmol m^{-2} s^{-1} in Mayan homegardens (Benjamin et al., 2001). One of the typical forest species for forest regeneration plantings in Yucatan, *Cedrela odorata*, showed best growth performance under maximum openness (Ricker et al., 2000). At high light conditions, both *Cedrela odorata* and *Cordia alliodora* had higher maximal rates of photosynthesis than two other tree species from the Yucatan Peninsula (Ramos and Grace, 1990).

As *C. dodecandra* developed well in partly shaded forest regeneration plantings, too (field observations 2003, Quintana Roo, Southern Peninsula), it seemed to adapt well to different light environments. This concurred with the results of an assessment of shade tolerance and potential growth of 73 canopy tree species in Panama. Most species were found to be neither extremely shade tolerant nor extremely light demanding at the seedling stage, but to have intermediate light requirements (Wright et al., 2003). Shading might have an additional positive influence on seedling survival and growth (McLaren and McDonald, 2002). Facilitation of tree seedling establishment by taller vegetation is a recommended management strategy for the restoration of forests on degraded tropical lands (Duncan and Chapman, 2003). This is supported by observations on a limited area of experimental plots where seedlings lost their leaves after the removal of adjacent secondary vegetation. This effect might be a consequence of subsequent changes in wind and light intensity, or of a change in the amount of available water due to vegetation removal. Shade of higher bordering vegetation may also have led to a reduction in soil temperature, resulting in higher soil moisture that may have been beneficial to seedling development.

9.2.8 Impact of preceding land use on growth

According to the history of the three different experimental sites, the record of the sub site was exceptional in terms of the potential nutrient availability for plant growth. The fallow vegetation on this sub site was with an age of 50 years 10 years older than fallow vegetation on the remaining area on the site of the Veterinary Faculty, and about 40 years older than the fallow on the other two sites. The length of the fallow period has a relevant impact on the amount of available nutrients after burning (Weissbach et al., 2002). As the amount of available nutrients declines with time and cultivation, it has to be taken into account that the sub site was cleared by slash-and-burn practices only in 2001, one year before starting this experiment. Most of remaining area of the site was burnt and cultivated from 1999 on. The shorter period of time between the burning event may have contributed to a higher potential availability of mobile nutrients, combined with less nutrient export by harvest of cultivated crops. In addition, the sub site was planted with different varieties of *Mucuna* during the year before starting the experiment. This led to a potentially higher amount of available soil nitrogen for seedlings in comparison to the remaining experimental area.

9.2.9 Impact of small ruminants on growth of *C. dodecandra*

When animals entered 16 plots of our planting site in August 2002, recently planted *C. dodecandra* seedlings were not consumed by goats or local deer. In contrast, leaves of planted *C. papaya* on our experimental plots were completely consumed. The protection of *C. dodecandra* seedlings from consumption by small ruminants such as goats is attributed to the roughness of its leaves, and makes it a suitable species for agroforestry systems in Northern Yucatan. As many farmers in Northern Yucatan keep goats, *C. dodecandra* would be a potential species for agrosilvopastoral systems including small ruminants. Furthermore, without being harmed by animals, seedlings could develop rapidly extensive tree crowns in order to provide shade to livestock of farmers for most of the year (Vlek et al., 2004).

9.3 Summary

Considering our entire experimental area, highest growth of *C. dodecandra* and *B. orellana* seedlings was observed on sporadically irrigated plots located on the so-called “sub site” on experimental site 1. High growth seedlings on the sub site may possibly be attributed to higher availability of water due to surrounding vegetation and micro relief, higher availability of nutrients caused by the recent slashing and burning of older fallow vegetation, and preceding cultivation of cover crops. Climbing vines had a negative impact on seedling growth. The protection of *C. dodecandra* seedlings from consumption by small ruminants such as goats is attributed to the roughness of its leaves, and makes it a suitable species for agroforestry systems in Northern Yucatan.

10 CONCLUSIONS

Nutrient-water-interactions and nutrient availability on Yucatan soils

The effect of nutrient-water-interactions on plant growth and nutrient uptake on Yucatan soils deserves much more attention than previously thought. This study shows that nutrient availability and nutrient-water-interactions have a significant impact on growth and foliar nutrient levels of *C. dodecandra* seedlings on Yucatan soils. On the experimental area, growth of *C. dodecandra* on red Cambisol with adequate water supply was limited by low availability of P, K, and Mn. With adequate water supply, K availability was a growth-limiting factor on Leptosol. When water was scarce, low phosphorus availability had a significant impact on growth on both soils. Zinc-phosphorus interactions limited P uptake and growth at low water availability. With adequate water supply, plant zinc uptake from fertilizer was reduced by P applications. Further studies should be carried out to reveal the importance of the detected low nutrient availability and nutrient-water-interactions for growth of other economically important crops and multi-purpose tree species.

The impact of low availability of P, K (considering basic cation uptake ratios), Mn and Zn on plant growth and yields on Yucatan soils should be investigated further. Our results show the importance of P and K availability for seedling growth on both soils, and of Mn availability for growth on Cambisol. Variations in foliar K levels and foliar K/sqrt (Ca+Mg) ratios corresponded with significant variations in growth of irrigated seedlings on both soils. Foliar nutrient concentrations from adult trees of *C. dodecandra* in homegardens indicated a deficiency of P, Mn, and Zn. Although no impact of zinc on growth of seedlings was detected, foliar zinc as well as manganese concentrations of *C. dodecandra* on both soils were at the lower limit for adequate growth compared to other tropical broadleaved tree species on the Peninsula.

In addition, the development of sustainable and cost effective measures for the mitigation of nutrient deficiencies of multi-purpose tree seedlings and crops should be a research priority. Our results indicate that irrigation is an option to increase P availability on black Leptosol. The application of P fertilizer is recommended in order to improve plant growth on Cambisol. The high cost of P fertilizer for farmers may be covered for instance by micro credit programs in cooperation with regional institutions. The application of K is recommended on both soils in order to improve growth of seedlings. Compost may be used as a source of K. In the long run, the enrichment of fallows with native tree species with economic potential such as *C. dodecandra* may create incentives for longer fallow periods, in order to mitigate soil nutrient constraints in a sustainable way. As the seedlings of this study were in their vegetative stage, the question remains whether low Zn, Mn and K availability will have a negative effect on *C. dodecandra* fruit set and quality. Hence, if *C. dodecandra* trees are intended for fruit production, it will be important to monitor nutrient status of trees when fruit production starts.

Our results indicate that nitrogen is not a limiting nutrient for growth of *C. dodecandra* seedlings on Yucatan soils. The application of urea-N fertilizer seems to interfere with growth, and is therefore not recommended during seedling establishment. Further studies will have to show whether nitrogen availability on Yucatan soils is adequate for other species.

This study demonstrates that native tree species with economic potential may be successfully used as indicator species for the assessment of nutrient-water-interactions in field trials, especially under harsh environmental conditions. Their advantage is that they are highly adapted to climatic and soil conditions of the region. An additional benefit is the generation of information on adequate management of native species with economic potential for farmers.

Recommendations for the establishment of agroforestry systems

The Mayan homegarden species *C. dodecandra* is a promising multi-purpose tree for agroforestry systems in Northern Yucatán. The species is recommended as the tree component in agrosilvopastoral schemes for the recultivation of abandoned sisal plantation areas.

Apart from its economic potential for providing short-term income by fruit production and long-term income by its valuable timber, *C. dodecandra* possesses a number of characteristics beneficial to small-scale farmers.

- For the establishment of *C. dodecandra* as a tree component, management requirements in terms of labor input are very low. With only sporadic irrigation at the peak of the dry season, high growth of *C. dodecandra* during the subsequent rainy season was achieved compared to the non-irrigated control. Concentrating the application of a limited amount of water to the hottest period of the drought season should be verified as a management option for other economically interesting Mayan tree species in further studies.
- *C. dodecandra* shows high growth response on different soils. It established and grew well on the two dominant soils of the area, on stony black Leptosol as well as on red Cambisol. To assess the role of rock fragments for tree seedling growth in the calcareous soils of the peninsula, more research will be necessary.
- The risk of loss due to seedling mortality when planting *C. dodecandra* in agrosilvopastoral schemes is low. Survival of seedlings was high whether irrigated or not during the first dry season after planting, although growth suffered.

The planting of *B. orellana* in Northern Yucatan is recommended only if irrigation during the first dry season is feasible. *B. orellana* requires irrigation during this season in order to ensure high survival and adequate growth.

The use of exotic VA mycorrhizae for seedling inoculation on Yucatan soils is not recommended unless further research shows benefits of exotic VAMF for semi-arid Yucatan soils. As knowledge is scarce on the suitability of exotic VA mycorrhizae application for the establishment of native tree species in semi-arid environments, the impact of drought stress on the effectiveness of the symbiosis should be verified in nursery trials.

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