Technische Universität Braunschweig

Institut für Geoökologie
Abteilung Umweltchemie

Nutrient cycling in the tropical dry forest: How do different tree species adapt to limited resources and how are water and nutrient uptake strategies connected?

by
Mareike Lacina

Master's thesis
Submitted to the department of Environmental Chemistry,
Institute of Geoecology
Technical University of Braunschweig
In fulfillment of the requirements for a
Master's degree
07. June 2022

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Masterarbeit „Nutrient cycling in the tropical dry forest: How do different tree species adapt to limited resources and how are water and nutrient uptake strategies connected?“ selbstständig verfasst sowie alle benutzten Quellen und Hilfsmittel vollständig angegeben habe und dass die Arbeit nicht bereits als Prüfungsarbeit vorgelegen hat.

Braunschweig, den 06.06.2022

M. Lacine

Technische Universität Braunschweig

Institute for Geoecology

Technische Universität Braunschweig (TUBS)
Institut für Geoökologie | AG Umweltgeochemie
Langer Kamp 19c | 38106 Braunschweig
https://www.tu-braunschweig.de/geooekologie

Dr. Matthias Beyer

Tel. +49 (0) 531 391-5913
Fax +49 (0) 531 391-8130
matthias.beyer@tu-bs.de

Master Thesis for

Mareike Lacina, Matr.-No. 4849889

"Nutrient cycling in the tropical dry forest: How do different tree species adapt to limited resources and how are nutrient and water uptake strategies connected?"

Tropical Dry Forests (TDF) experience one to two dry seasons per year in which hardly any precipitation occurs (D'Odorico & Porporato 2006). Depending on their adaption to drought stress, tree species in the TDF tend to develop different root systems. Deciduous species follow an exploiting strategy and usually have shallow roots, while evergreens tend to behave more conservatively and often develop deep roots in order to maintain a water supply during dry season (Sobrado 1991; Álvarez-Yépiz et al. 2017).
Tree roots not only take up water, but also nutrients. Nutrient cycles are highly dependent on water availability, because many processes such as nutrient uptake, decomposition of litterfall or weathering of bedrock to release nutrients require water (Anaya et al. 2012; Lugo & Murphy 1986; George & Marschner 1996). Hence, variations in the nutrient concentration in different soil layers depending on the rooting depth of the different tree species are expected. Little research has been conducted on how nutrients cycle through TDF's. There are two publications of which the first stresses the differences of nutrient cycling in TDF's to Tropical Rain forests (Raulino et al. 2020) and the second compares macro- and micronutrient contents in leaves of N_2-fixing and non-fixing legumes in TDF in Costa Rica (Alvarado et al. 2018). In both studies, certain tree species of the TDF were "responsible" for the cycling of certain nutrients. Nutrient cycling in TDF's is still not fully understood and even though it is tightly bound to the hydrological cycle, there has been little research conducted which combines water and nutrient uptake in TDF's.

The objectives of the MSc thesis are:

- to characterize nutrient availability and nutrient uptake patterns of four tree species in a Costa Rican TDF with a focus on micronutrients; and
- to investigate how nutrient uptake relates to different water uptake strategies.

The following hypotheses are to be tested:

i. Due to the extreme conditions in dry forest, tree species are strongly adapted to the available resources and different species uses certain elements preferentially.

ii. Deeper rooting dry forest species have access to other nutrients depending on its availability

In order to answer these questions, an extended field campaign at the Estación Experimental Forestal Horizontes in Guanacaste, Costa Rica, was carried out. The goal of this campaign was to collect soil, leave and litterfall samples and analyze macro- and micronutrients in the laboratory. Samples were collected at two specific times: i) at the peak of the dry season and ii) in the beginning of main rainy season. Four species with different characteristics and water uptake strategies were select and their leaves collected. Soil samples were to be collected at three different plots and at different depths (soil surface- 2m). Litterfall was collected once in dry season.

The specific tasks of this MSc thesis are:

1. Literature review and state of the art:
   - Nutrient cycling in tropical dry forests
   - Water vs. nutrient uptake of in tropical dry forest trees
   - Deep roots and their function in regards to nutrient uptake
2. Laboratory analysis:
   - Soil samples:
     - Sample preparation (leaching)
     - Measurement of Macro- (P, K, Ca, S) and Micronutrients (Fe, Cu, Mn, Mo, B, Na, Ni, Zn) in the Leachate
   - Leave samples
     - Sample preparation (washing, freeze-drying, grinding, digestion)
     - Measurement of total nutrient content (Macro- and Micronutrients)
3. Analysis and synthesis of results

The topic will be supervised by Dr. Matthias Beyer and co-supervised by Prof. Harald Biester, both IGÖ. An office workspace will be provided by Dr. Beyer. The completed work should give a well sorted overview over the topic using diagrams and tables. One electronic and three hardcopy versions of the work have to be submitted.

Date of issue: 06.12.2021

Date of start: 06.12.2021

Last date of submission: 07.06.2022

Supervisors: Dr.-Ing. Matthias Beyer (TU Braunschweig)
Prof. Harald Biester (TU Braunschweig)
1. Examiner: Dr.-Ing. Matthias Beyer (TU Braunschweig)
2. Examiner: Prof. Harald Biester (TU Braunschweig)

Acknowledgements

First, I would like to thank Petra Schmidt and Adelina Calean for supervising me in the laboratory and for helping me with the measurements. Thank you for your patience and care!

I would like to thank Marta Pérez-Rodríguez for taking a lot of time and helping me with the statistical analysis and discussing the results.

Special thanks go to the team of the Isodrones Project for helping with the sampling campaign. Alberto Iraheta supported me in the field and Malkin Gerchow provided the drone pictures and helped with controversial conversations. Kathrin Kühnhammer analyzed the sap flow sensor data and I learned a lot from our critical discussions. Thanks for the female empowerment in a male dominated world! I had a great time with you in the field and loved being part of the team!

Of course, I would like to thank Matthias Beyer and Harald Biester for supervising this master thesis. Thanks go especially to Matthias Beyer for corrections, for giving me the opportunity of being part of his team and spending time in the field in Costa Rica.

I. Content

II. List of Figures

III. List of Tables

IV. List of Abbreviations

ACG .... *Área de Conservación Guanacaste*
Al .... *Aluminum*
B .... *Boron*
C .... *Carbon*
Ca .... *Calcium*
Cl .... *Chloride*
Co .... *Cobalt*
Cu .... *Copper*
DBH .... *Diameter of Breast Height*
DOC .... *Dissolved organic carbon*
EEFH .... *Estación Experimental Forestal Horizontes*
Fe .... *Iron*
HL .... *Hydraulic lift*
HR .... *Hydraulic redistribution*
K .... *Potassium*
LOD .... *Limit of Detection*
Mg .... *Magnesium*
Mn .... *Manganese*
Mo .... *Molybdenum*
N .... *Nitrogen*
Na .... *Sodium*
Ni .... *Nickel*
P .... *Phosphorus*
PC .... *Principal Component*
PCA .... *Principal Component Analysis*
S .... *Sulphur*
Se .... *Selenium*
Si .... *Silicon*
SLA .... *Specific Leaf Area*
Zn .... *Zinc*

V. Abstract

This study investigates water and nutrient uptake strategies of deciduous and evergreen tree species in the tropical dry forest (TDF). We hypothesize that (i) tree species in the TDF have to adapt strongly to the limited resources and use some nutrients preferentially and (ii) due to their deep roots, evergreen species have access to deeper water and nutrient pools. To investigate the water and nutrient uptake strategies of tree species in the TDF, two evergreen (*S. capiri* and *H. courbaril*) and two deciduous (*S. macrophylla* and *G. ulmifolia*) species in the TDF in Costa Rica were investigated. Nutrient content in leaves and soil to a depth of 150 cm were measured. Sap flow of the trees and soil moisture was monitored continuously to evaluate water uptake. Results show a higher content of K in *S. macrophylla* for stronger stomata regulation and higher content of Zn in *H. courbaril* for reducing oxidative stress. In *S. capiri* and *G. ulmifolia*, higher B and Ca concentrations could improve cell wall stability under drought conditions. Soil profiles provided strong evidence that bulk fine root density of *S. macrophylla* was at 50 cm soil depth in dry season. *S. capiri* took up water in 200 cm soil depth in dry season, whereas for *H. courbaril* no indicator for rooting activities were found in <200 cm soil depth. Access of deep rooting species on deeper laying nutrient pools could not be evaluated, because soil samples were not taken deep enough. Yet, a decoupling of nutrient and water uptake was observed, which might pose a risk of starvation for the evergreen species in dry season. We conclude that the species-specific nutrient uptake is due to the strong adaption of the tree species to the limited resources for improving drought resistance

1. Introduction

Trees require water, CO_2, energy and mineral nutrients to function. Sunlight is captured and CO_2 is fixed in leaves exposed to the atmosphere in order to do photosynthesis. (Tais and Zeiger, 2003). Tree roots take up water from the soil and transport it in the xylem to the leaves (Tais and Zeiger, 2003). According to the Cohesion-Tension theory, ascent of water in the xylem is driven by negative water pressures which are generated by the loss of water on the leaf surface. The process of water loss on the leaf surface is called transpiration and depends on the differences in water vapor concentration in the leaf and the external air and the diffusional resistance of this pathway (Tais and Zeiger, 2003). This soil-plant-atmosphere continuum is an important factor of the hydrological cycle on Earth. Hence, trees not only influence the Earth's climate by regulating greenhouse gases, but also by being an essential part of the hydrological cycle (Ellison et al., 2017).

Together with water, roots take up nutrients via diffusion. Active nutrient uptake can also occur at specific channels or transporters (Pallardy, 2008). The nutrients are then transported through the xylem to the shoots and leaves (Pallardy, 2008). Tree nutrients are classified as macro- or micronutrients depending on the required amount of the plants. Carbon (C), nitrogen (N), potassium (K), magnesium (Mg), calcium (Ca), sulphur (S) and phosphorus (P) are considered as macronutrients and chloride (Cl), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni), boron (B) and molybdenum (Mo) as micronutrients (White and Brown, 2010). Other elements like cobalt (Co), selenium (Se), sodium (Na), silicon (Si) and aluminum (Al) are considered as beneficial, yet not essential for plant growth (White and Brown, 2010). Information on the function of each nutrient in the plants' metabolism are summarized in Tab. 9 in the appendix.

With their extending root systems, trees can alter the soil properties and are therefore seen as 'ecosystem engineers' (Finzi, Canham, Van Breemen, 1998). Certain tree species affect the biogeochemical cycles of the ecosystems and influence the lithogenic as well as the organic components of the soil (Binkley and Giardina, 1998; Chadwick et al., 2012; Finzi, Van Breemen, Canham, 1998). For example, different organic acids in decomposing litterfall or species dependent uptake of cations can significantly impact the pH of the surrounding soil (Finzi, Canham, Van Breemen, 1998). There are multiple hypotheses why tree species might affect soils in different manners, including species-specific traits to improve the trees fitness, modification of the soil to the disadvantage of other species and indirect effects such as substances in leaves that protect against herbivory which also inhibit the decomposition of the leaves in the soil (Binkley and Giardina, 1998). The "nutrient lift" hypothesis, introduced by

Jobbágy and Jackson (2001), identifies plant cycling as the dominant factor of vertical distribution of nutrients in the soil. Plant cycling increases nutrient concentration in top soil layers due to litterfall and decreases concentrations in deeper soil layers because of root uptake, whereas leaching of nutrients leads to decreased concentration in shallow soil and increased concentrations in deeper soil layers (Jobbágy and Jackson, 2001). Yet, biogeochemical processes such as leaching, decomposition of litter or nutrient uptake depend highly on the water availability in the ecosystem (Da Silva et al., 2011; Hu and Schmidhalter, 2005)

Increasing occurrence of drought events is expected as global climate change proceeds unrestrained, increasing drought induced mortality of trees (IPCC, 2022). Understanding biogeochemical responses as well as adaption of trees to drought stress is crucial to maintain healthy, functioning forests in the near future.

Tropical dry forests (TDF) exhibit one or two pronounced dry seasons per year (Murphy and Lugo, 1986) and are therefore an interesting ecosystem to study plant responses to drought.

Nowadays, TDFs extend to roughly half of the area of humid tropical forests (Murphy and Lugo, 1986; Schröder et al., 2021), can be found in Central and South America, Africa, Asia and Australia and about 25% of the world’s population depends on this ecosystem (Schröder et al., 2021). The TDF biome is the most densely populated forest type and has been exploited for many years (Murphy and Lugo, 1986). TDFs nowadays are threatened and their area is declining worldwide mainly due to wildfires and deforestation (Schröder et al., 2021), converting them from dry forests to grasslands or savannas.

Trees in the TDF need to decide (trade-off principle) between exploiting water efficiently during rainy season and adjusting themselves in order to tolerate droughts during dry season (Pineda-García et al., 2016). Deciduous species in the TDF have a higher water transport capacity, carbon gain and growth rates, but are sensitive to soil desiccation whereas evergreen species are more drought tolerant due to higher resistance against xylem cavitation on the cost of a lower rates of photosynthesis under water sufficient conditions (Pineda-García et al., 2016).

Evergreens therefore generally follow a conservative and deciduous an exploiting water use strategy (Álvarez-Yépiz et al., 2017; Pineda-García et al., 2016; Powers and Tiffin, 2010).

Various adaptions of plants to reduce water stress in drought conditions are known. Leaf traits like a waxy epidermis or microscopic hairs inhibit water loss at the leaf surface (Tais and Zeiger, 2003). Further, use of stored water in stems, roots and leaves or development of deep roots increases drought resistance (Paz et al., 2015).

Evergreen species tend to grow deep roots to assure the water supply during dry season, when upper soil layers are dried out (Hasselquist et al., 2010; Sobrado, 1991). Until today, there is no general agreement on the definition of deep roots because firstly, rooting depth can change considerably depending on topography, soil type, groundwater level and climate (Fan et al., 2017) and secondly, few studies present an entire root profile and therefore neglect the possible existence of deep roots at their study site. Nonetheless, to simplify the rather complicated process of defining deep roots, Pierret et al. (2016) propose to use 1 m depth as threshold for deep roots. The main function of deep roots is water uptake from deeper soil layers, especially in dry and rocky environments (Maeght et al., 2013). Deep roots favor hydraulic lift (HL) or hydraulic redistribution (HR) which is the redistribution of water from moister to drier parts of the soil by roots (Maeght et al., 2013). Like shallow roots, deep roots presumably weather the soil by emitting root exudates and increase the C content in deeper soil layers. Besides a continuous water supply, deep roots might allow access to nutrient pools deeper in the ground. In order to catch scarce nutrients which distribution are usually highest in topsoil, plants either have to construct a dense root system in the top soil, or grow deep roots to access nutrient pools with less competition below the rooting zone of other plants (Jobbágy and Jackson, 2001). Deep roots are therefore a useful strategy of trees to exploit water and nutrient sources, especially if the access to both is limited in the surface soil.

The research on the influence of deep roots on hydrological cycles has increased in recent years, however their effects on biogeochemical cycles is not well understood. Most studies focusing on nutrient use strategies in TDF either did not collect any soil samples (Campo et al., 2000, ; Raulino et al., 2020) or only took samples until 15 cm of soil depth (Lugo and Murphy, 1986; Waring et al., 2019). So, possible effects of deep rooting species on the nutrient supply in the TDF could not be evaluated.

Raulino et al. (2020) compared the nutrient efficiency of tree species in the tropical dry forest to species of the tropical rainforest. In the tropical rainforest, differences of the nutrient concentration of the investigated species were smaller than in the TDF, where the species had specific nutrient efficiencies. Therefore, certain species in the TDF are highly relevant for the cycling of specific nutrients. Tree species in the TDF have to adapt to the limited water supply during dry season. As nutrient uptake is tightly bound to the water availability in the ecosystem (Hu and Schmidhalter, 2005), higher differentiation of water and nutrient uptake strategies are expected in the TDF.

In this thesis we investigate the water and nutrient uptake strategies of two exploiting and two conservative behaving tree species in the TDF in Costa Rica. We hypothesize that (i) due to the extreme conditions in dry forest, the tree species are strongly adapted to the available resources and different species use certain elements preferentially and (ii) that deeper rooting dry forest species have access to other nutrients depending on its availability.

In order to test these hypotheses, leave and soil samples were taken in dry and rainy season of two evergreen (*S. capiri* and *H. courbaril*) and two deciduous (*S. macrophylla* and *G. ulmifolia*) tree species in a TDF in Costa Rica. Total nutrient content in the leaves and leachable nutrient content in the soil was determined to investigate the nutrient uptake of the more exploiting and conservative behaving tree species. Also, sap flow of the trees and soil moisture was monitored during the investigation period to evaluate the water uptake of the trees.

2. Material and Methods

2.1 Field methods

Field site is located in the Estación Experimental Forestal Horizontes (EEFH, 10°42'49.3"N 85°35'44.9"W), in Guanacaste, Costa Rica. Geology of EEFH consists of volcanic rocks and two major formations (Bagaces 8,05 Ma-2,0 Ma. and Liberia 1,59-1,35 Ma) have been identified (Castro et al., 2014). Soil types in the area are Andic and Typic Haplustepts (Alfaro et al., 2001). EEFH is part of the Área de Conservación, Guanacaste (ACG). Before the station became part of the ACG, the area was deforested and used as farmland. Mean temperature is 25°C and mean annual precipitation is 1,800 mm, which mainly occurs from May to October (Waring et al., 2019). Soil texture on the field site is clayey to loamy with a high content of calcium carbonate. A map of the field site is shown in Fig. 1.

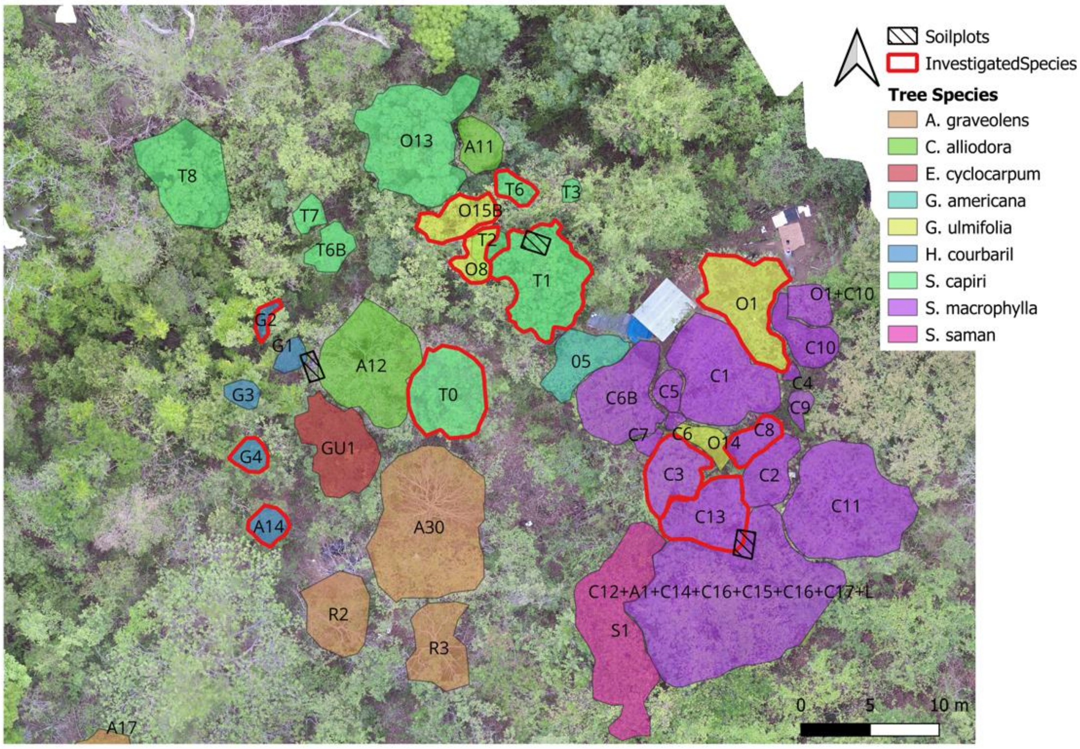

Fig. 1: Drone image by Malkin Gerchow of the field site. Canopy trees are marked by species and investigated tree individuals are highlighted. Location of the soil plots is shown.

2.1.1 Species selection:

Two (semi-)deciduous and two evergreen species were used to in this study. *Guazuma ulmifolia* and *Swietania macrophylla* tend to shed their leaves during dry season and are therefore thought to follow a more exploiting behavior, whereas *Sideroxylon capiri* and *Hymenea courbaril* maintain their leaves all year long, even in dry season which fits to conservative behaving tree species. The investigated trees were planted between 1992-1994. *S. macrophylla*, *S. capiri* and *H. courbaril* were planted in groups (compare Fig. 1), in which mainly these species are growing. *G. ulmifolia* is spread over the research area. Information on the species are summarized in Tab. 1.

Tab. 1. Characteristics of the investigated species.

Species	Family	Ecology	Distribution	Leaves
G. ulmifolia[1]	Sterculiaceae	Common deciduous tree in the secondary forest and on regenerating pasture	-	Simple, alternate, 10-15 cm with serrated edges, hairy
H. coubaril	Fabaceae, non N_2 fixing[2]	Evergreen canopy tree[1], common in dry and wet forests, deciduous or evergreen species[3]	Mexico to South America, Antilles[3]	Bifoliate, alternate, asymmetrical 4-10 cm long and 2-5 cm wide[3], Upper sides of leaflets are glossy and have many translucent points, shedding of leaves briefly and simultaneously in mid dry season[1]
S. capiri[3]	Sapotaceae	Typical of the dry deciduous forest, evergreen, threatened	Mexico and Central America (except Belize), Trinidad; Tobago and Grenada	Simple, alternate, clustered at the end of small branches, coriaceous and glabrous
S. macrophylla (G. King)	Meliaceae	Somewhat deciduous[1], common in dry forests, danger of extinction[3]	Mexico to Brazil and Bolivia[3]	Paripinnate alternate, leaflets 3-6 pairs, 6-18 x 3-5.5 cm, glabrous on both surfaces, shiny on the upper surface[3]

[1] Sullivan and Enquist (2001).
[2] Alvarado et al. (2018).
[3] Jiménes M. et al. (2010).

2.1.2 Weather station

Precipitation, relative humidity, air pressure, temperature, solar radiation and dew point were monitored continuously at a resolution of 1 hour at the field site with a weather station (Hobolink, Onset).

2.1.3 Sap flow measurement

12 sap flow sensors (HPV-06, Implexx) were installed in December 2020 for the majority of investigated individuals. Additional sensors were added in April 2021. Sensors measured the sap flow velocity every 15 minutes a via heat pulse emitted by the three needles probe ("heat ratio method", Marshall (1958)). Data was analyzed by Kathrin Kühnhammer.

2.1.4 Monitoring of soil moisture

Soil pits are located in the middle of the *S. macrophylla*, *S. capiri* and *H. courbaril* groups (compare Fig. 1). They were dug in November 2020 until a depth of 150 (*S. macrophylla*) and 200 cm (*S. capiri*, *H. courbaril*). Soil moisture sensors (SMT100, Truebner for *S. macrophylla* and *H. courbaril* plot, Echo 5TM, Metergroup for *S. capiri* plot) were installed in 5, 15, 30, 50 and 150/200 cm depth. To avoid effects of the opened soil pit, sensors were installed 20-30 cm horizontally into the soil. Pits were then covered to prevent infiltration of rainfall. Special care has been taken to not cover the part, where the soil moisture sensors were installed. Covers were placed with a slope, so that the run off rain water would not influence the soil moisture sensors.

2.1.5 Leaf and soil sampling

Leaves were sampled on 09.04.2021 and 17.06.2021 using a pole pruner. Three individuals of each species were selected and of each individual, three branches were cut. The leaves were separated from the branch by hand (gloves were used) in order to avoid contact to the pole pruner, placed into WhirlPaks and stored in the freezer. Litter of each species was collected from the ground on the 10.04.2021, packed into WhirlPaks and frozen as well. The samples were transported by plane to Germany and analyzed in the laboratory of the Technical University of Braunschweig.

Soil samples were taken on the 09.04.2021 and 17.06.2021 from the soil pits. Samples were taken approximately 30 cm away from the pit walls. A steel bar was used to break down the dry soil. The soil was sieved (Nylon, 2 mm), placed into WhirlPaks and stored in the freezer. The sieve was cleaned with water and dried off with a microfiber towel and a hair blower. The samples were transported by plane to Germany and analyzed in the laboratory of the Technical University of Braunschweig.

Tab. 2 summarizes characteristic information of the investigated tree individuals. Diameter at breast height (DBH) was measured with a tape measure. DBH was measured various times during the investigation period and the mean was calculated. *G. ulmifolia* individuals had either two or three stems, therefore multiple values are given. The development of new leaves was either observed or in case of *H. courbaril* individuals concluded by a rapid drop in the sap flow data. Some sap flow sensors did not function consistently, therefore information of the available data is given.

Tab. 2. Diameter at breast height, sprouting period and information about the installed sap flow sensor of the investigated tree individuals.

Tree ID	Mean DBH in cm	Sprouting	Sap Flow Sensors
S. macrophylla			
C13	26.0	25-30.04.2021	No data available from Jan. to Apr. 2021
C3	20.0	25-30.04.2021	Installed in mid of April 2021
C8	24.1	25-30.04.2021	No data available in Apr. 2021
S. capiri			
T0	25.4	30.04.2021	Functioned consistently
T1	26.1	No information	No data available mid of Jan- April, mid of April and beginning of June 2021
T6	15.9	No information	Installed in April 2021
G. ulmifolia			
O1	18.4/18.3/12.9	20-25.04.2021	No data available after end of April 2021
O8	21.5/28.6	13-20.04.2021	Functioned consistently
O15B	17.3/17.3/10.9	13-20.04.2021	Installed in mid of April 2021
H. courbaril			
A14	13.3	End of February	Functioned consistently
G2	15.8	End of February	No data available after May 2021
G4	11.7	End of February	Functioned consistently

2.2 Laboratory methods

Further analysis of the leaf and soil samples were conducted in the laboratory of the Technical University of Braunschweig.

2.2.1 Digestion of leaf samples

Leaf samples were defrosted, washed with deionized water and freeze dried. They were ground in a ball mill (25 r/s) and digested in bi-distilled nitric acid. Every 8^{th} sample was prepared as a triplicate. Certified references were prepared every 10^{th} sample.

2.2.2 Nutrient leaching from the soil

Soil samples were defrosted and mixed with deionized water in a proportion of 1:10. The mixture was shaken overhead for 24 h (17 r/min). Afterwards, the samples were centrifuged (5000 r/min) and the supernatant was filtered through a 0.45 µm nylon filter. The filtered leachate was stabilized with 4 ml of inverse Aqua Regia (3 ml bi-distilled HNO_3, 1 ml HCl (Roth, Supra-Quality)).

2.2.3 Analysis of Macro- and Micronutrients:

ICP-OES (715-ES, Varian) was used to determine the elements Na, K, Ca, Mg, Al, Fe, Mn, Cu, Zn, Si, S and P and ICP-MS (7700, Agilent-Technologies) to measure B, Cr, Co, and Mo. Detection and quantification limits were calculated by the calibration method according to DIN 32645 (Deutsches Institut für Normung e.V., 2008). Element concentrations below the limit of quantification were set to half of the detection limit.

Element concentrations were expressed in relation to the dry mass of the leaf regarding to equation (1).

$$c_{Leaf} = \frac{c_{solution} * V_{dilution} * V_{digestion}}{m_{dry}} \tag{1}$$

With

c_{Leaf} as concentration of the element in the leaf [mg/kg]

$c_{solution}$ as concentration of the element in the digested sample [mg/L]

$V_{dilution}$ as volume of dilution during the analysis with ICP-OES or ICP-MS [ml]

$V_{digestion}$ as volume of bidistilled HNO_3 during digestion [ml]

m_{dry} as mass of leaf sample [g]

Element concentrations in the soil leachates were related to the soil dry mass by following equation (2)

$$c_{soil} = c_{Leachate} * V_{dilution} * L_{Ratio} \tag{2}$$

With

c_{soil} as leachable concentration of the element from the soil in [mg/kg]

$c_{Leachate}$ as concentration of the element in the leachate [mg/L]

$V_{dilution}$ as volume of dilution during the analysis with ICP-OES or ICP-MS [ml]

L_{Ratio} as the ratio of soil to water for the leaching

L_{ratio} was calculated as the ratio of soil to water for the leaching, corrected by the water content of the soil (equation (3).

$$L_{Ratio} = \frac{V_{Water} + V_{i.A.R.} + (m * \theta_g)}{m - (m * \theta_g)} \tag{3}$$

With

V_{Water} as the volume of water used for the leaching [ml]

$V_{i.A.R.}$ as the volume of inverse Aqua Regia used to stabilize the leachate [ml]

m as mass of soil sample used for the leaching [g]

θ_g as gravimetric water content [%]

Water content of the soil samples was determined for a better comparison of the samples from dry and wet season. The soil was defrosted, weighed and dried at 105°C. The samples were weighed again after 24 and 48 h. The water content θ_g was calculated using equation (4).

$$\theta_g = \frac{m_{wet} - m_{dry}}{m_{wet}} \tag{4}$$

With

m_{wet} as fresh weight of the soil sample [g]

m_{dry} as dried weight of the soil sample [g]

Soil to plant transfer factors (TF) were calculated using(5.

$$TF = \frac{\bar{c}_{leaf}}{\sum c_{soil}} \tag{5}$$

With

$\bar{c}_{leaf}$ as the mean element concentration in the leaves of one tree individual [mg/kg]

c_{soil} as the element concentration in the soil samples [mg/kg]

In order to estimate the uncertainty of the method (heterogeneity of the samples, errors in the digestion or leaching and uncertainty of the measurement with ICP-OES/-MS), coefficient of variation (CV) of the triplicates in percent was calculated with equation (*6*.

$$CV = \frac{\sigma_{triplet}}{\bar{c}_{triplet}} * 100 \qquad (6)$$

With

$\sigma_{triplet}$ as the standard deviation of the triplet

$\bar{c}_{triplet}$ as the mean element concentration of the triplet

2.2.4 Measurement of soil pH

Soil samples were defrosted and shaken with deionized water in a proportion of 1:2 (soil:water) for 2 h. After centrifugation (5000 r/min for 5 min), pH of the supernatant was measured using a pH-Meter (WinLab).

2.2.5 Measurement of dissolved organic carbon in the soil

Soil leachates were diluted 1:10 and stored overnight in the fridge or frozen, if analysis took place more than two days after the leaching occurred. HCl was added to strip inorganic carbon and DOC was measured by (TOC-L, Shimadzu).

2.3 Statistical analysis

Statistical analyses were conducted in RStudio (Version 4.1.2). Principal component analysis (PCA) was carried out with the "psych" package (Revelle, 2022). Graphics were visualized with "ggplot2" (Wickham, 2016).

3. Results

3.1 Results of laboratory analysis

The recovery rate of the certified references (Bushes, twigs and leaves, GBW07603, CNRM and apple leaves, 1515, NIST) of each element was calculated and the means and ranges are shown in Tab. 10 in the appendix. A recovery of >90 % was achieved for Ca, K, Na, Cu, Zn, and B for both references, in Mn and Mg only for the reference of GBW07603. A recovery of 85 % and 78 % of Fe was discovered in both references and of P (88 %) in the GBW07603 reference. For the 1515 reference, no value for P was given. For both references, Al and Si deficiency occurred (36 % and 56 % recovery rate respectively for Al, 5 % recovery rate for Si in the GBW07603). Increased values of >110% of Co, Ni and Mo were detected in both references. Especially in one of the 1515 samples, an exaggerating value for Co, Ni and Mo was detected, in the GBW07603 reference this occurred only for Ni. This outlier has been excluded for the calculation of the mean and the result is given in brackets.

The elements Al, Si, Co and Ni have been excluded from further analysis due to the deficient and increased concentrations in the certified references. Mo was kept in the analysis knowing the recovery rate was exceeding, however the values are still close the tolerance given by the certificate. No references for soil leachates were available, so recovery rate for the concentration in the soil leachates could not be determined.
88% of the samples were below the LOQ and 50% below the limit of detection (LOD) of Na in the leaf samples. Concentrations for measuring the references were close to the LOD, yet mean recovery rate for Na was >94 %. Therefore, Na was not excluded from further analysis but it has to be kept in mind that there is a higher uncertainty for the quantification of Na concentrations in the leaf samples. 93% of samples were below the LOQ and 45% below the LOD for Co. Ni was not detected in any leaf sample.
Many samples for the analysis of the soil leachates were below the LOD. Elements with more than 30 % of the samples below the LOD were excluded from further analysis. This included: K, Mg, P, S, Cu, Zn, B, Mo.

Every eighth leaf and soil sample were prepared as a triplet in order to estimate the reproducibility of the procedure. The mean of the coefficient of variation of each element is shown in Tab. 11 in the appendix.
Mean of the coefficient of variation for the leaf samples ranged from 0.9 % for Cu and K to 6.7 % for B. Most elements however had a mean coefficient of variation <2.6 %. The preparation, processing and measurements were consistent and therefore reliable and results

are reproducible. Contrary to this, results for the soil leachates were not as reproducible. Mean coefficient of variation ranged from 30.9 % to 41.3 % for the analyzed metals and 11.3 % and 4.0 % for Ca and Na, respectively. The DOC had a mean coefficient of variation of 14.4 %, whereas the pH-value had one of 0.4 %. The mean coefficient of variation includes the errors made by the preparation, processing and measurement of the samples and should be used as a relative error.

3.2 Results of statistical analysis

3.2.1 Results of the MANOVA

Results of the two-factor MANOVA are shown in Tab. 3. The Shapiro Test showed that the model assumption of normal distribution for Mn in *G. ulmifolia*, Mo and P in *H. courbaril* and B and P in *S. capiri* samples was violated. Also, the boxM test showed that homogeneity of variance was not given for the whole data set. Levene's test revealed that homogeneity of variance was given for Zn, S, Cu and Ca, yet violated for all other elements. Nevertheless, the result of the MANOVA is reasonable because the differences in the element concentrations are visible (Fig. 2-Fig. 8), but it has to be kept in mind that model assumptions were not fulfilled.

*Tab. 3. p-Values and significant codes (0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1) of the two-factor MANOVA*

Element	Species	Season	Species/Season Interaction
Macronutrients			
Ca	2.4^{-09} (***)	0.4	6.4^{-05} (***)
K	1.5^{-13} (***)	0.047 (*)	7.576^{-05} (***)
Mg	8.8^{-14} (***)	0.3	0.00016 (***)
P	0.4	0.009 (**)	0.02 (*)
S	3.5^{-08} (***)	0.04 (*)	0.2
Micronutrients			
Na	3.04^{-11} (***)	0.0003 (**)	0.015 (*)
Fe	1.11^{-08} (***)	1.15^{-06} (***)	9.3^{-12} (***)
Cu	$<2^{-16}$ (***)	0.83	0.101
Mn	1.016^{-09} (***)	0.5	0.6
Zn	$<2.2^{-16}$ (***)	4.97^{-05}(***)	0.0012 (**)
B	5.6^{-05} (***)	0.047 (*)	0.02 (*)
Mo	7.4^{-15} (***)	0.8	0.3

All elements but P showed significant differences in the mean concentrations in the leaves between the species. Significant differences between the concentration in the leaves in dry and rainy season was discovered for Fe, Zn, P, S, Na and B. The interaction between season and species produced differences in mean concentrations for Ca, K, Mg, P, Na, Fe, Zn and B.

3.3 Order of Macro- and Micronutrients

Concentrations of macronutrients in the leaves sampled in rainy season declined in the following order for *G. ulmifolia*, *H. courbaril* and *S. capiri*: Ca>K>Mg>S>P (Tab. 4). In *S. macrophylla* leaves, K concentrations were higher than Ca concentrations (K>Ca>S>Mg>P).

Tab. 4. Mean macronutrient concentrations in % of leaves sampled in rainy season. Standard deviation is given in brackets.

Species	K [%]	Ca [%]	Mg [%]	S [%]	P [%]
G. ulmifolia	1.13 (±0.14)	1.5 (±0.3)	0.32 (±0.04)	0.17 (±0.014)	0.11 (±0.02)
H. courbaril	0.62 (±0.11)	0.74 (±0.16)	0.19 (±0.04)	0.14 (±0.0093)	0.0947 (±0.0102)
S. capiri	1.2 (±0.4)	1.3 (±0.2)	0.29 (±0.04)	0.19 (±0.02)	0.08 (±0.009)
S. macrophylla	1.5 (±0.3)	1.18 (±0.34)	0.16 (±0.02)	0.1616 (±0.0102)	0.09 (±0.02)

Concentrations of micronutrients was more variable than for macronutrients (Tab. 5 Tab. 6) Because too high micronutrient concentrations can lead to toxicity, the optimum range of nutrient concentration for crops (Marschner's, 2012) is given for a better understanding whether the determined concentrations could have caused deficiencies or toxicity. Micronutrient concentrations declined Fe>Mn>B>(Na)>Zn>Cu>Mo in *G. ulmifolia*, Mn>Fe>Zn>B>(Na)>Cu>Mo in *H. courbaril*, (Na)>Fe>B>Mn>Zn>Cu>Mo in *S. capiri* and (Na)>Fe>Mn>B>Zn>Cu>Mo in *S. macrophylla*.

Tab. 5. Mean micronutrient (Fe, Zn, Cu, Mn) concentrations in mg/kg of leaves sampled in rainy season. Standard deviation is given in brackets.

Species	Fe [mg/kg]	Zn [mg/kg]	Cu [mg/kg]	Mn [mg/kg]
G. ulmifolia	51.4 (±10.0)	15.9 (±1.7)	8.8 (±0.7)	44.01 (±6.18)
H. courbaril	42.3 (±9.2)	24.9 (±2.5)	9.5 (±1.6)	332.7 (±96.5)
S. capiri	39.8 (±12.3)	8.05 (±1.44)	3.7 (±0.8)	20.4 (±7.4)
S. macrophylla	32.8 (±2.8)	9.32 (±2.38)	8.8 (±0.9)	18.4 (±4.5)
Optimum range in crops	50-500	15 to 300	1-30	>10*

*toxic Mn concentrations depend highly on the species

Tab. 6. Mean micronutrient (B, Mo, Na) concentrations in mg/kg of leaves sampled in rainy season. Standard deviation is given in brackets.

Species	B [mg/kg]	Mo [mg/kg]	Na [mg/kg]
G. ulmifolia	32.7 (±9.7)	0.5 (±0.2)	18.7 (±6.3)
H. courbaril	17.3 (±4.3)	0.14 (±0.10)	11.2 (±6.3)
S. capiri	35.6 (±17.9)	1.9 (±0.5)	56.2 (±29.9)
S. macrophylla	16.64 (±2.04)	0.59 (±0.12)	68.4 (±18.3)
Optimum range in crops	5-400	0.1-10	-

3.3.1 Absolute nutrient concentrations of the leaves and nutrient uptake rates

The absolute element concentrations and its uptake rates of the elements, which the MANOVA indicated significant differences either by the season or the interaction of species and season, are shown. Uptake rates were calculated differently for the deciduous and evergreen species. For *S. macrophylla* and *G. ulmifolia* (deciduous), the measured concentration of the rainy season sampling was divided by the age of the leaves. For *S. capiri* and *H. courbaril* (evergreen), the element concentration of the rainy season was subtracted from the concentration measured in dry season and this value was divided by the amount of days between the two sampling dates. One *S. capiri* individual (T0) shed its leaves right after taking the samples in dry season. Its uptake rate has been calculated like for the deciduous species. The different ways of calculating the uptake rate should be kept in mind while analyzing the results.

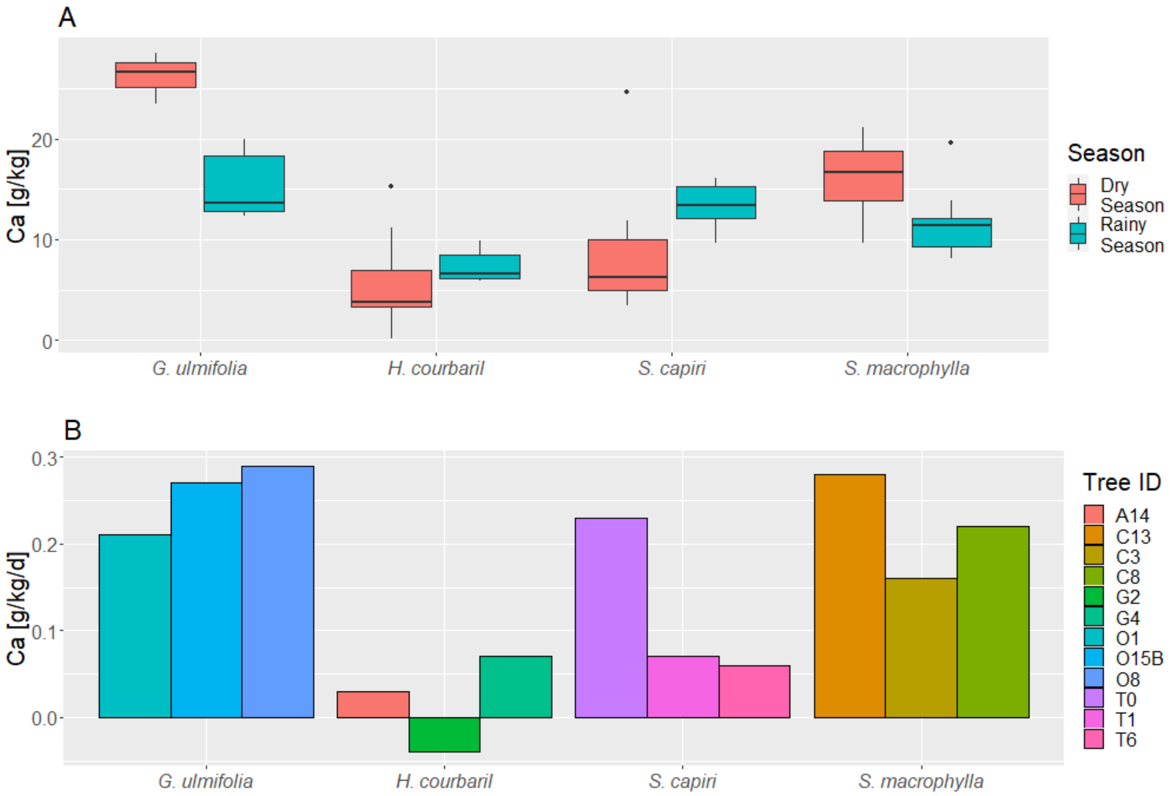

Fig. 2. Absolute Ca concentrations in the leaves in dry and rainy season (A) and Ca uptake rate (B) during the investigation period.

Differences of the Ca concentration in the leaves depending on season and species are visible in Fig. 2. The visible results are consistent with the results by the two-factor MANOVA. *G. ulmifolia* and *S. macrophylla* had higher Ca concentrations in their leaves in dry season than in rainy season. The other way round, Ca concentrations increased in *H. courbaril* and *S. capiri* leaves from dry to rainy season. The concentration differences in the evergreen species can be seen as well in the second plot (B). Individuals A14 and G4 (*H. courbaril*) and T1 and T6 (*S. capiri*) took up between 0.07 and 0.06 g/kg Ca per day. Ca concentrations in G2 decreased about 0.04 g/kg/day. Meanwhile, *S. macrophylla*, *G. ulmifolia* and T0 took up about 0.2-0.3 g/kg Ca per day.

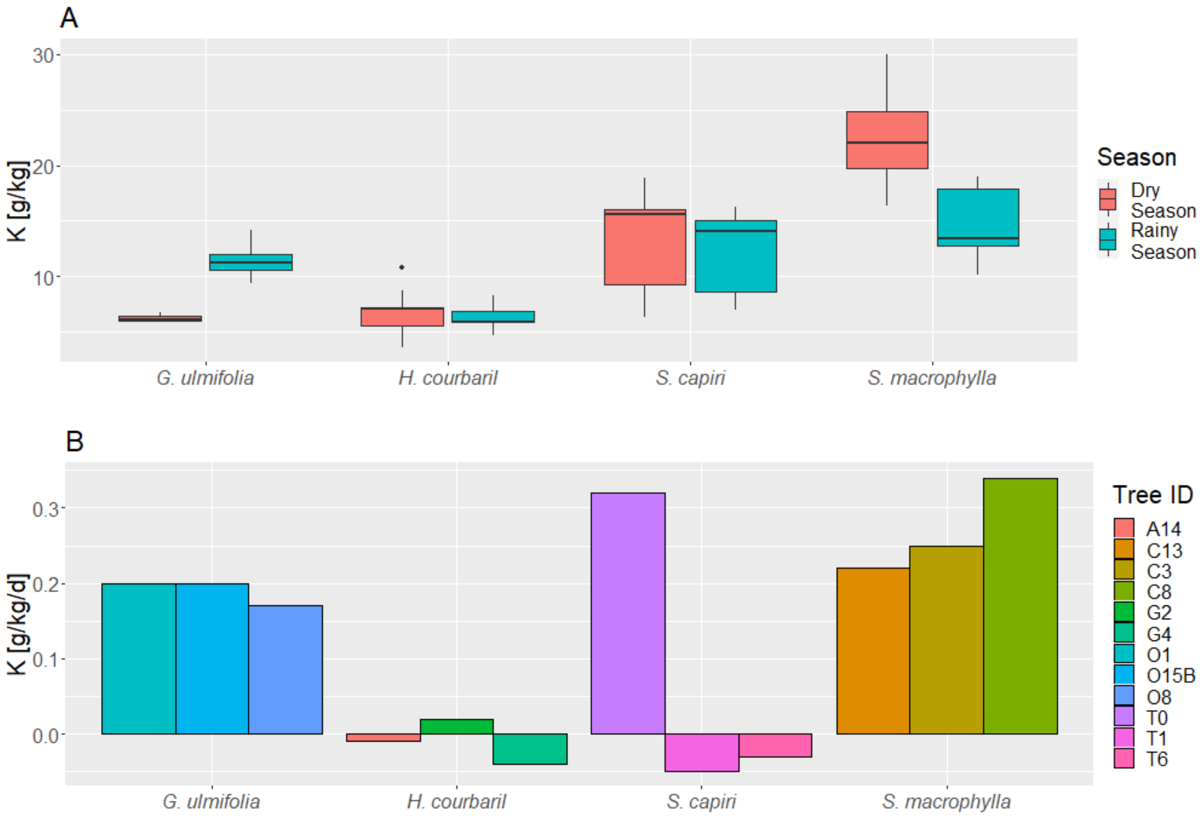

Fig. 3. Absolute K concentrations in the leaves in dry and rainy season (A) and daily K uptake during the investigation period (B).

Absolute K concentrations are shown in Fig. 3. Highest K concentrations were measured in *S. macrophylla* leaves and lowest concentrations in *G. ulmifolia* leaves in dry season. The fresh leaves contained less K for *S. macrophylla* and more K for *G. ulmifolia*. In contrast to the deciduous species, K concentrations in the leaves of *H. courbaril* and *S. capiri* changed little from dry to rainy season. This is also visible in the second plot, where daily uptake rates of K in the leaves of *H. courbaril* and *S. capiri* are close to zero. Uptake rates in fresh leaves of *G. ulmifolia* were lower than for T0 (*S. capiri*) and *S. macrophylla*.

The plot for Na looks similar like Fig. 3 for K. The plot for Na can be found in the appendix (Fig. 28) because Na is not considered and essential nutrient.

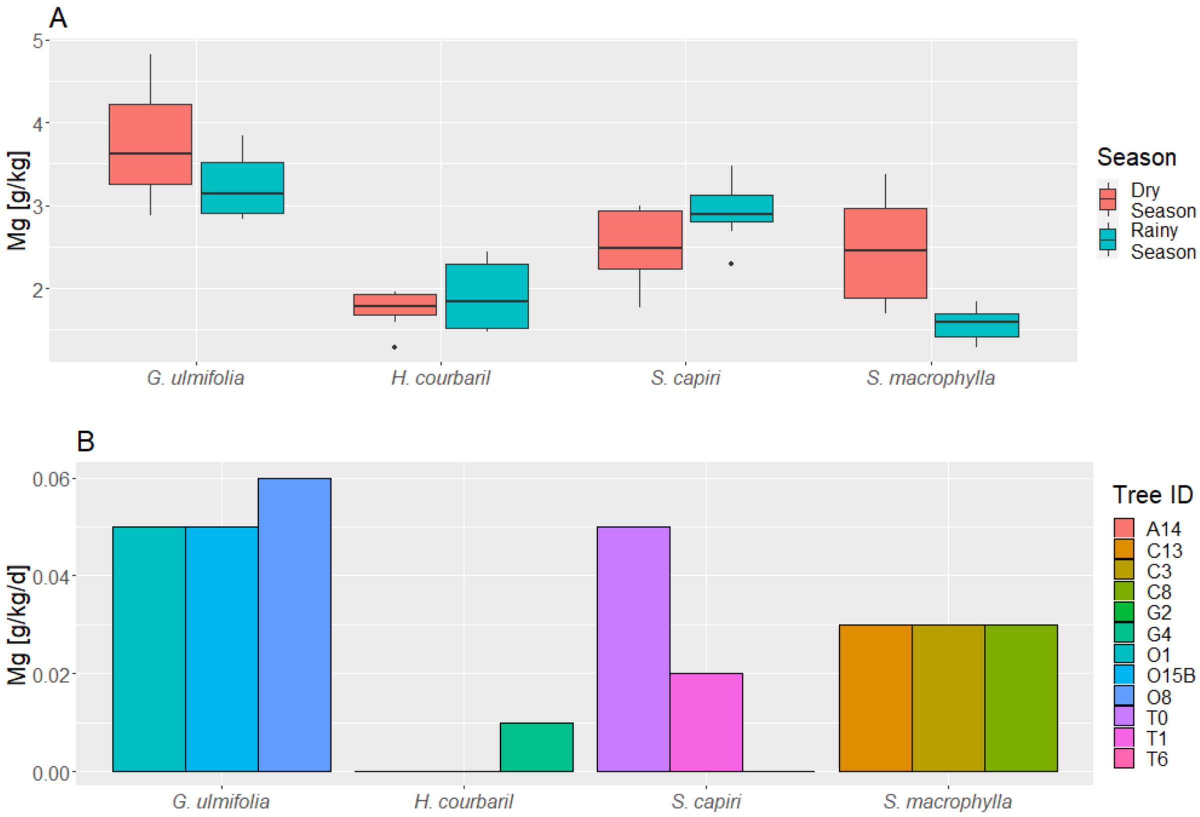

Fig. 4. Absolute Mg concentrations in the leaves in dry and rainy season (A) and Mg uptake rates during the investigation period (B).

G. ulmifolia contained highest Mg concentrations in dry and rainy season (Fig. 4). Mg concentrations were significantly lower in fresh leaves of the rainy season than in old leaves in dry season. Mg concentrations in *S. macrophylla* showed the same pattern with 2.5 g/kg in dry season and 1.7 g/kg in rainy season. Mean concentrations in *H. courbaril* leaves did not change, whereas *S. capiri* leaves contained more Mg in rainy season than in dry season (2.6 and 3 g/kg respectively). This is consistent with plot B where *S. macrophylla* took up less Mg per day than *G. ulmifolia* and T0 (*S. capiri*). No uptake was measured for A14, G2 and T6. An uptake rate of 0.059 g/kg per day and 0.015 g/kg were calculated for G4 and T1, respectively.

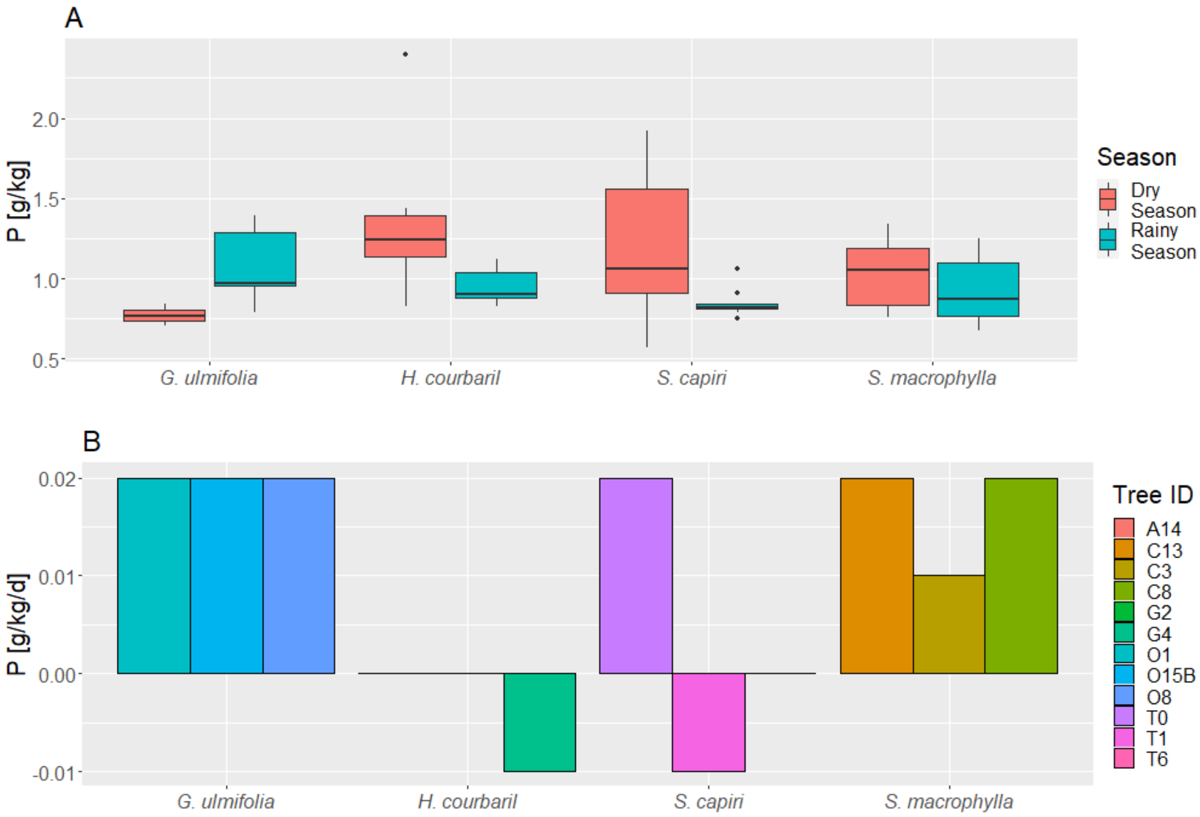

Fig. 5. Absolute P concentrations in leaves in dry and rainy season (A) and daily P uptake into the leaves during the investigation period.

P was the only element with no significant differences in the mean concentration between the species, but between the seasons (Tab. 3). P concentrations ranged between 0.57 g/kg (T0, dry season) and 2.4 g/kg (G4, dry season, Fig. 5). P concentrations were higher in rainy season samples for *G. ulmifolia* leaves, whereas P concentrations decreased for the other species from dry to rainy season. Uptake rates (Plot B) were similar for *G. ulmifolia*, *S. macrophylla* and T0 (*S. capiri*), whereas for A14, G4 (*H. courbaril*) and T1 (*S. capiri*) P concentrations decreased. For G2 and T6, P concentrations stayed the same over the sampling period.

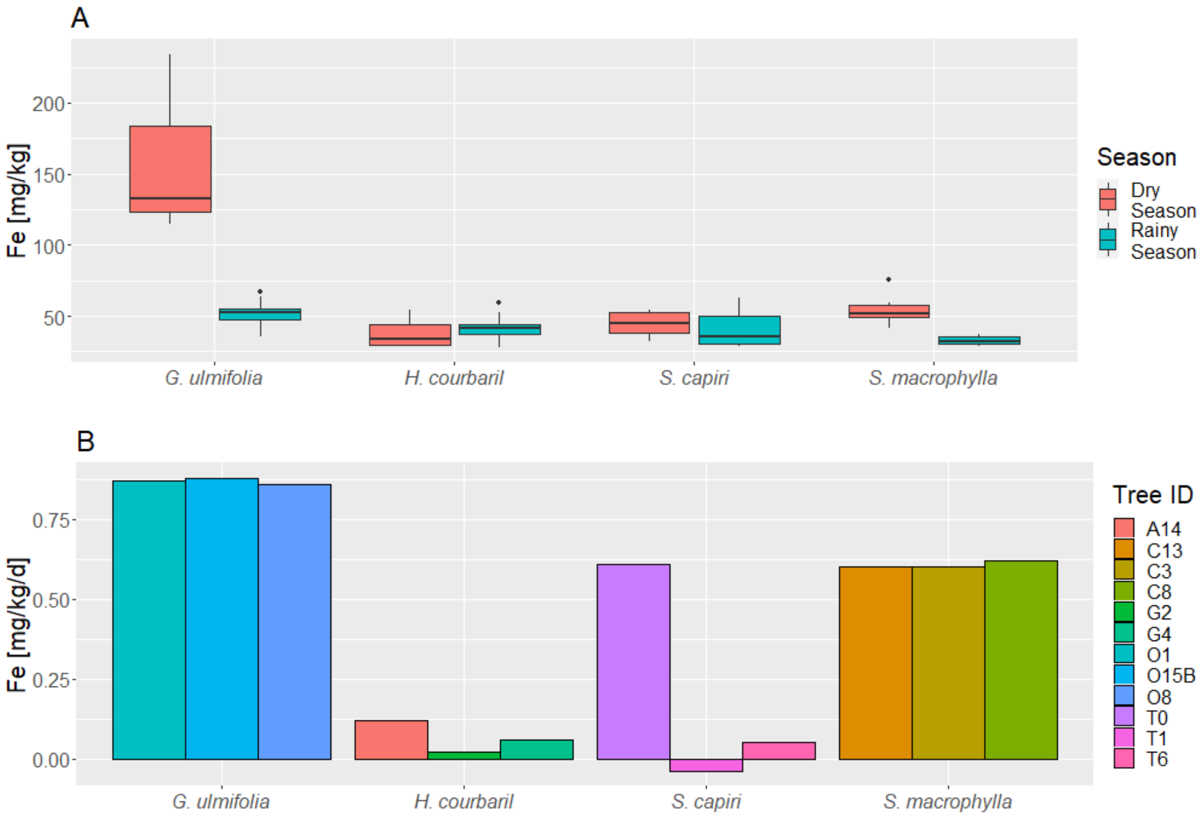

Fig. 6. Absolute Fe concentrations in leaves in dry and rainy season (A) and daily Fe uptake rates into the leaves during the investigation period (B).

Leaves from *G. ulmifolia* sampled in dry season contained significantly higher concentrations of Fe (160 mg/kg) than the other species (Fig. 6). In rainy season, Fe concentration in *G. ulmifolia* leaves (51 mg/kg) were similar to Fe concentrations of the other species (41 mg/kg), regardless the sampling date. Differences in Fe concentration are visible for *S. macrophylla* leaves as well, yet the differences were not as high as for *G. ulmifolia*. Fe concentrations were 55 mg/kg for dry season and 33 mg/kg Fe for rainy season samples. Uptake rate (plot B) was higher for *G. ulmifolia* than for *S. macrophylla* and T0, whereas for *H. courbaril* only A14 showed and increased uptake rate. Uptake rates for G2, G4, T1 and T6 were small, so it is more likely that they occurred due to uncertainties in the measurements of dry and rainy season leaves.

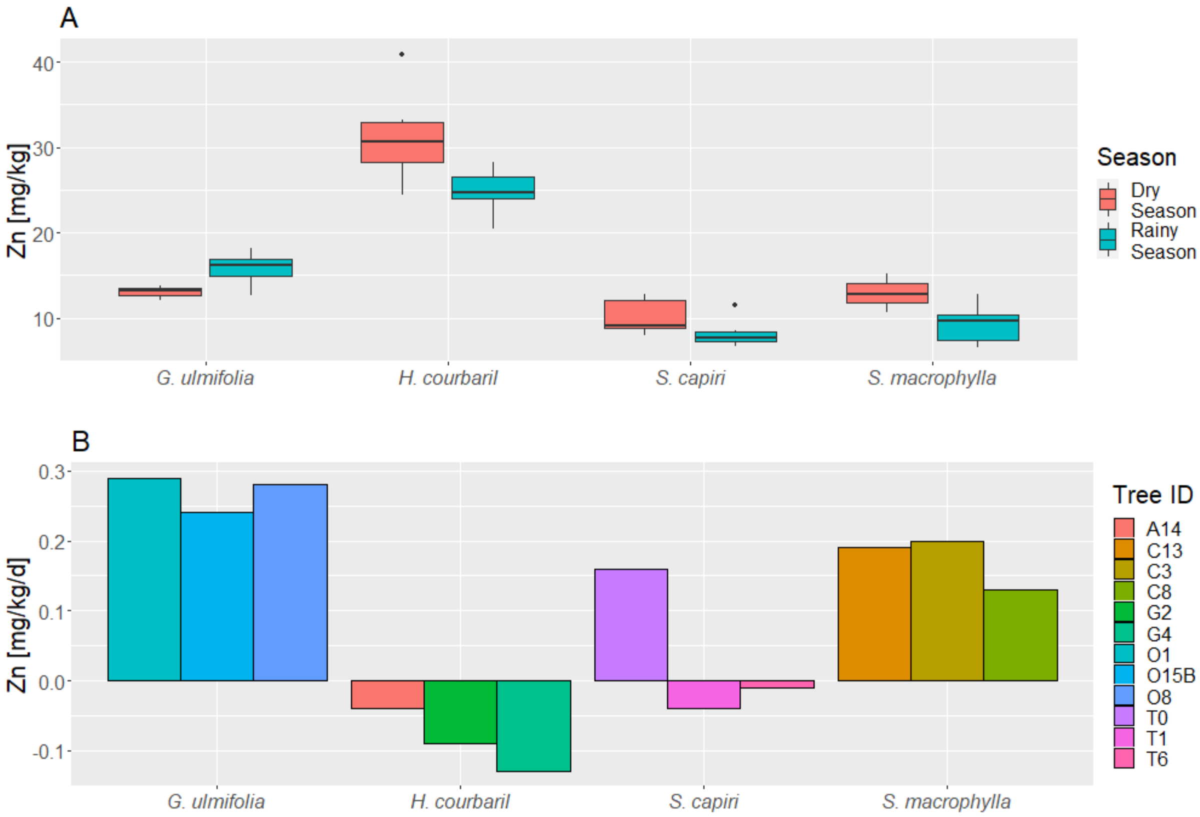

Fig. 7. Absolute Zn concentrations of the leaves in dry and rainy season (A) and Zn uptake rates into the leaves during the investigation period (B).

Similar to Fe, results of the MANOVA indicated significant differences between the species and the dry and rainy season samples for Zn (Tab. 3). In contrast to Fe, Zn was accumulated in dry season samples from *H. courbaril* (31 mg/kg, Fig. 7). Zn concentrations dropped from dry season to rainy season from 31 mg/kg, 13 mg/kg and 10 mg/kg to 25 mg/kg, 9 mg/kg and 8 mg/kg for *H. courbaril*, *S. macrophylla* and *S. capiri*, respectively. Zn concentrations in *G. ulmifolia* leaves increased from 13 mg/kg in dry season to 16 mg/kg in rainy season samples. *G. ulmifolia* individuals had higher uptake rates for Zn than *S. macrophylla* individuals and T0. Consistent with the decrease of Zn concentrations from dry to rainy season (Plot A), uptake rates were negative for *H. courbaril* individuals and T1. For T6, the calculated uptake rate is very small and might have been generated for uncertainties in the measurement.

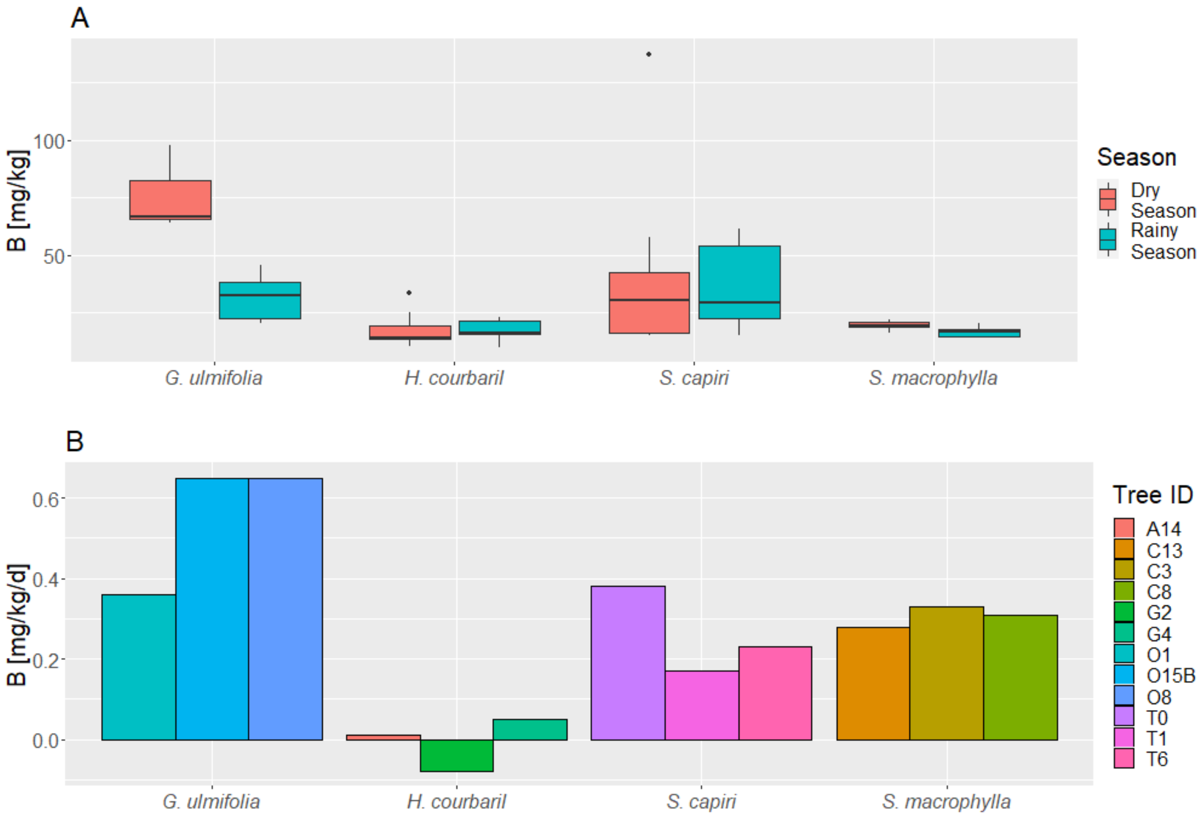

Fig. 8. Absolute B concentration in the leaves in dry and rainy season (A) and daily B uptake rate into the leaves during the investigation period (B).

B concentrations were highest in *G. ulmifolia* samples from dry season (76 mg/kg) and one T0 dry season sample (137 mg/kg, Fig. 8). In rainy season, highest B concentrations were found in *S. capiri* (36 mg/kg) and *G. ulmifolia* individuals (33 mg/kg). B concentrations decreased slightly from dry to rainy season for *H. courbaril* and *S. macrophylla* (18 mg/kg and 17 mg/kg, 20 mg/kg and 17 mg/kg respectively). O15B and O8 had a higher uptake rate for B than O1. For *S. capiri*, individuals with fully grown leaves had half the uptake rate as T0 with new leaves. *H. courbaril* showed little uptake of B, G2 even had less B in rainy season than in dry season.

3.3.2 Results of the Principal Component Analysis (PCA)

The PCA was performed in order to see species or seasonal specific patterns in the element concentrations of the leaves. The PCA explained 88 % of the variance in the data. The elements included in each component as well as the variance explained by this component is given in Tab. 7.

Tab. 7. Percentage of variance explained by and elements included in each principal component.

Principal Component	Elements	Variance (%)
1	Fe, Mg, B, Ca	24
2	K, Mn (-), Zn (-), Na	22
3	Cu (-), Mo, (S)	21
4	P	12
5	S, (Na)	9

S and Na had high loadings in the components 3 (S) and 5 (Na) as well and are therefore included in brackets.

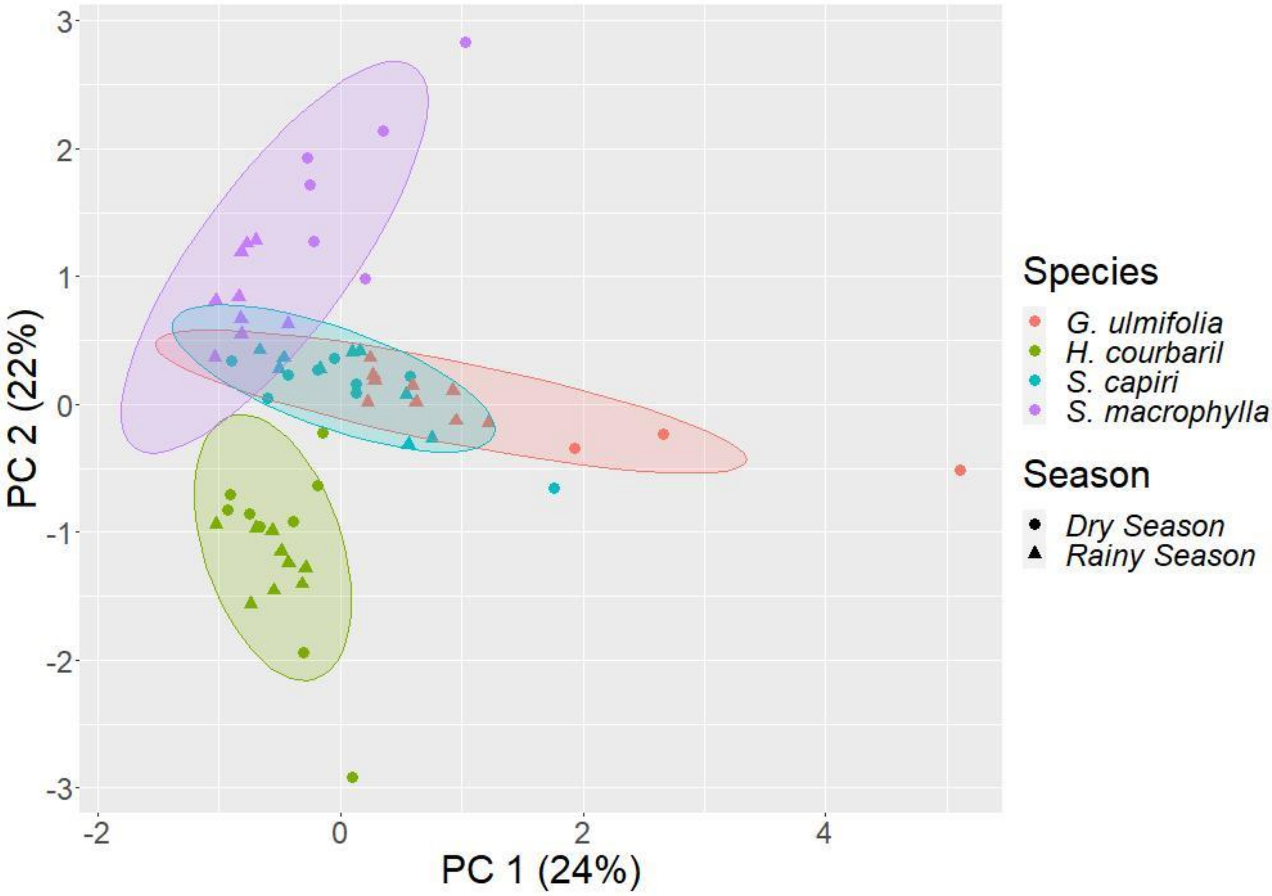

Fig. 9. PC 1 (Fe, Mg, B and Ca) and 2 (K, Na, Mn(-), Zn(-) explain together 46 % of the data's variance.

Principal Components (PC) 1 and 2 separate *S. macrophylla* and *H. courbaril* samples from *S. capiri* and *G. ulmifolia* (Fig. 9). *S. macrophylla* leaves contained more K and Na and less Mn and Zn as the other species. This is even more evident in dry season, where *S. macrophylla* leaves contained the highest K and Na concentrations. Conversely, *H. courbaril* leaves showed lower concentrations of K and N and higher of Mn and Zn in comparison to the other species. *G. ulmifolia* and *S. capiri* samples are separated of PC 1 by season. Dry season samples of *G. ulmifolia* contained more Fe, Ca, B and Mg than samples of the rainy season. For *S. capiri*, individual T6 contained more Fe, Ca, B and Mg in its leaves than individual T0 in rainy season.

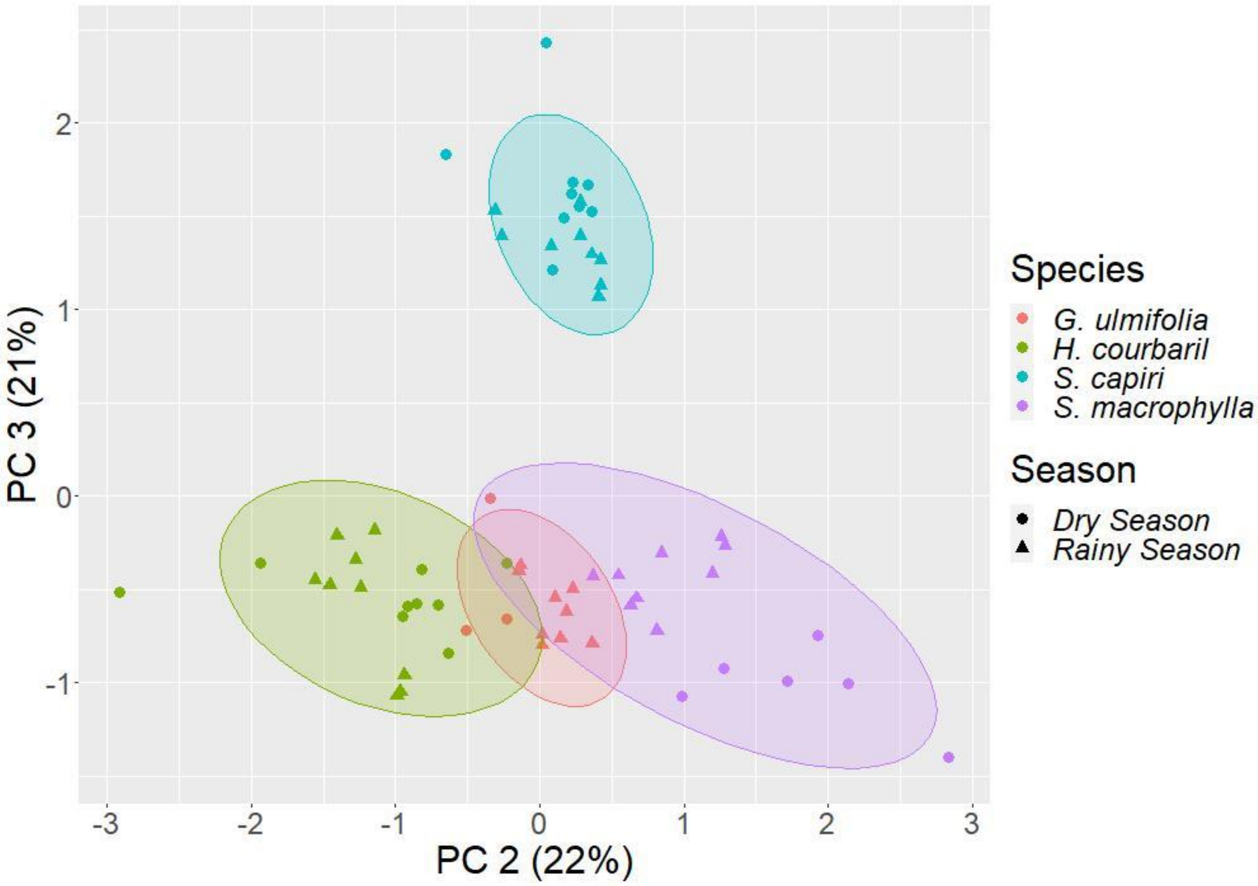

Fig. 10. PC 2 (K, Na, Mn (-), Zn (-)) and PC (Mo, (S), Cu (-)) explain together 43 % of the data's variance.

All Species can be separated by PC 2 and PC 3 (Fig. 10). *S. capiri* had higher loadings in PC 3 which means that this species contained more Mo and S and less Cu compared to the other species. Conversely, *G. ulmifolia*, *H. courbaril* and *S. macrophylla* contained less Mo and S but more Cu than *S. capiri*. Leaf samples from *S. macrophylla* are separated in dry and rainy season samples, with dry season samples containing less Mo and S and more Cu than rainy season samples. *G. ulmifolia*, *H. courbaril* and *S. macrophylla* are mainly separated by PC 2. This means that concentrations of K and Na in the leaves declined in the following order: *S. macrophylla* > *G. ulmifolia* > *H. courbaril*. For Mn and Zn, the order was reversed.

H. courbaril leaves contained the highest concentrations of Zn and Mn, whereas *S. macrophylla* leaves contained lowest concentrations.

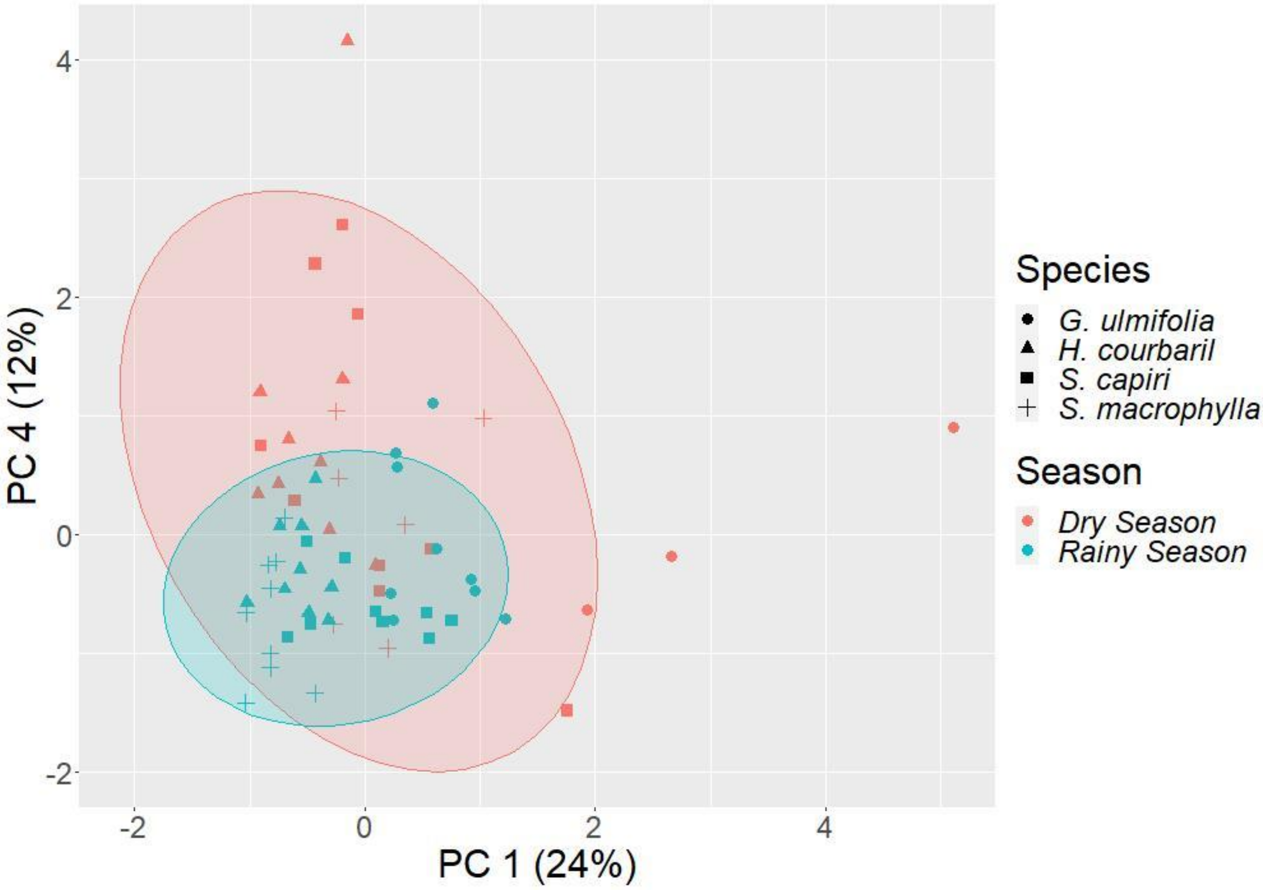

Fig. 11. PC 1 (Fe, Mg, B, Ca) and 2 (P) explain together 36% of the data's variance. Data can be separated by season rather than into the tree species.

In contrast to the elements of PC 1 to 3, P (PC 4) separated the dataset into season, not into species (Fig. 11). This reflects the result of the two-factor MANOVA shown in Tab. 3. For all species, leaves sampled in dry season contained more P than samples taken in rainy season. No information could be concluded by any other combination of the PC. Therefore, these graphics are not presented.

3.4 Continuous monitoring of precipitation, sap flow and soil moisture

Rain events were monitored and are shown in Fig. 12. Little to no rain occurred from January until April. Rain started in mid of April, stopped for a few days and started again in the beginning of May. After the first rains, another month of drought followed. Daily rainfall, characteristic for the beginning of rainy season started in early June 2021.

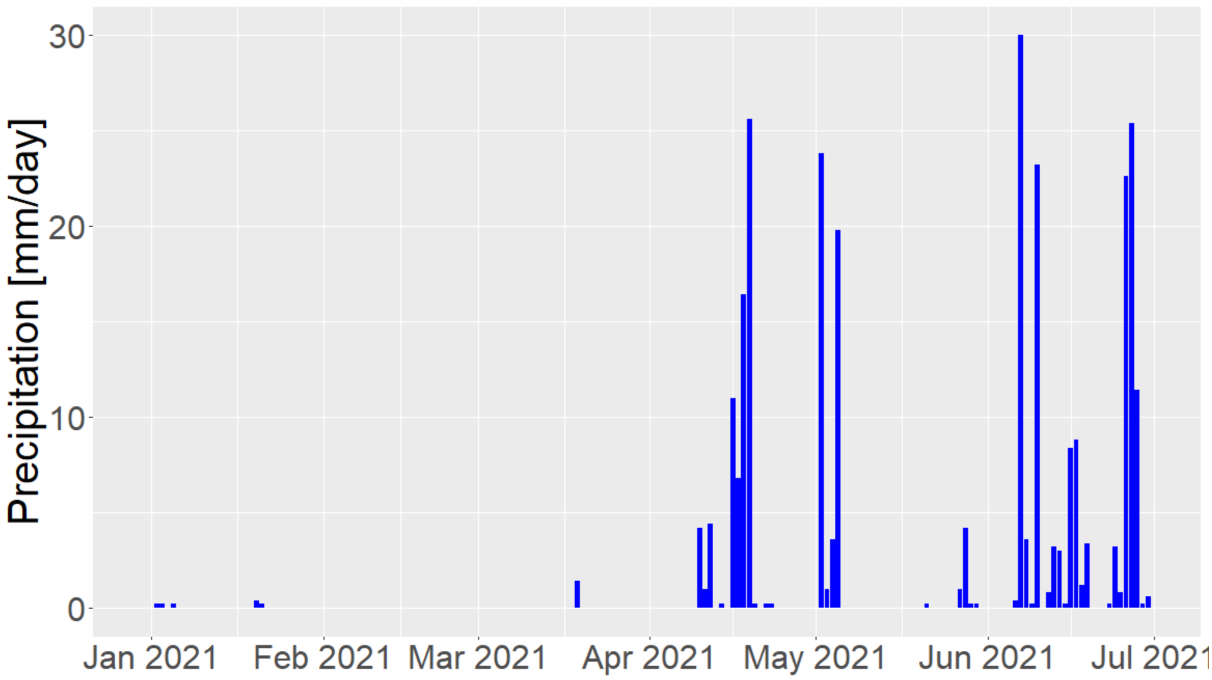

Fig. 12. Precipitation on the field site in the first half of 2021. After some rain events in mid of April and beginning of May, a month of drought followed before rainfall occurred more frequent.

3.4.1 Monitoring of sap flow:

Exemplary, sap flow from the first half of 2021 will be shown for one tree individual of each species. Sap flow plots of the other tree individuals can be found in the appendix (Fig. 30-Fig. 37).

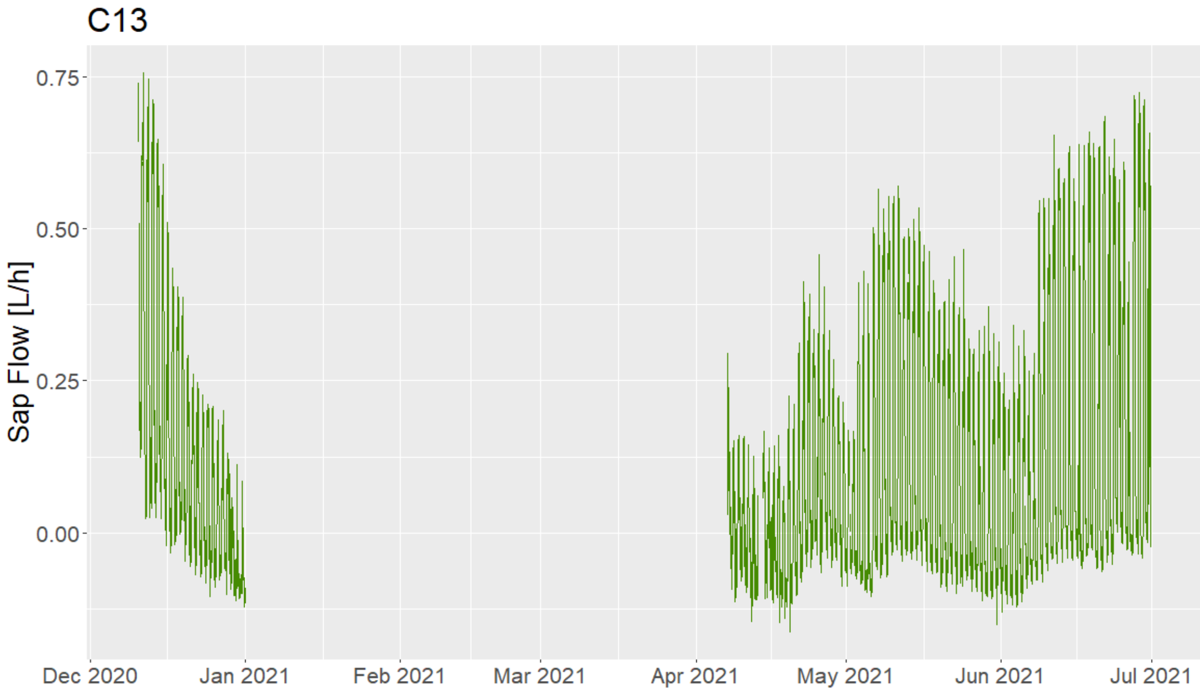

Fig. 13. Sap flow of S. macrophylla individual C13 in the first half of 2021.

Sap flow of C13 (Fig. 13) decreased rapidly as the soil dried out in the beginning of the dry season (Dec 2020 to Jan 2021). The sap flow sensor did not record data between January and April 2021, but somewhen in between C13 must have shed most of its leaves. Sap flow of C13 peaked at the end of April, beginning of May and increased again in mid of June. In between the peaks, sap flow of C13 decreased again. Sap flow plots of C3 and C8 are similar (Fig. 30+Fig. 31), however sensor did not record sap flow as reliable as the sensor of C13.

Sap flow sensors did work constantly in O8 (Fig. 33), however this tree individual different than the other *G. ulmifolia* individuals in the surrounding. It did not shed its leaves until beginning of April, whereas most *G. ulmifolia* individuals shed their leaves in the beginning of dry season like seen in sap flow of O1 (Fig. 32). Sap flow sensor installed in O1 broke after April 2021, so no further data was available. Sensor in O15B did not record data until end of April. In plots of both O8 (Fig. 33) and O15B (Fig. 14), increase of sap flow is visible at the end of April. Similar to the sap flow data of *S. macrophylla*, peaks are visible in the beginning of May and mid of June in the sap flow data of O8.

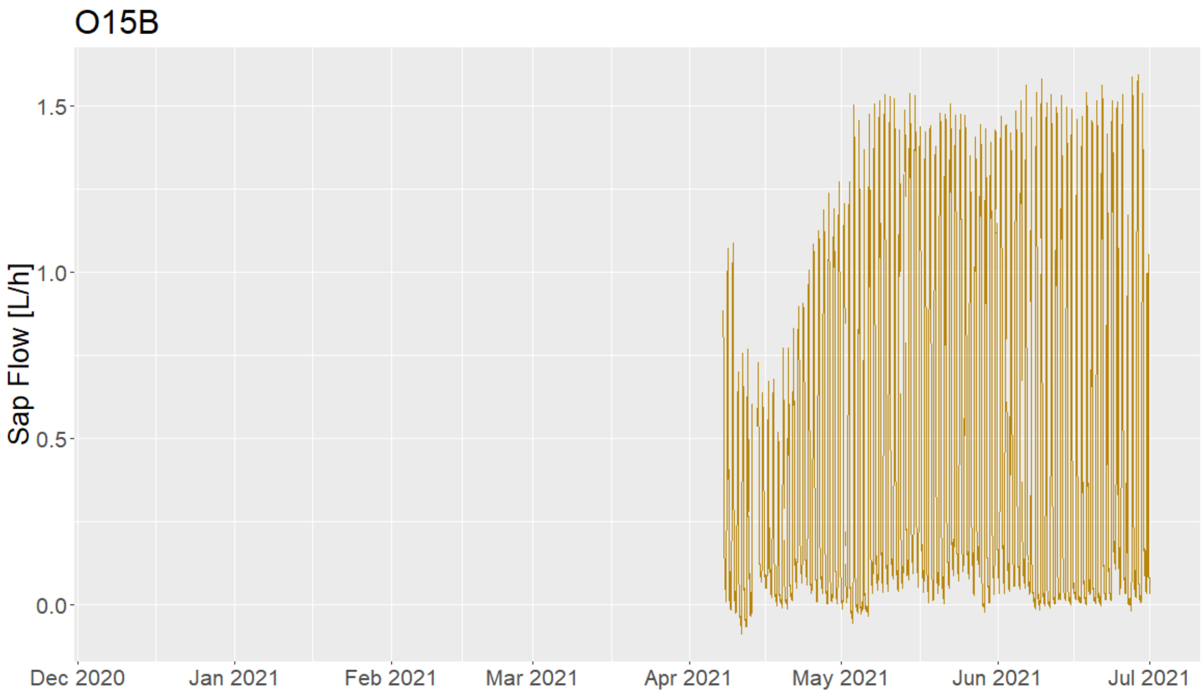

Fig. 14. Sap flow of O15B in the first half of 2021. Sensor started to work in April 2021.

Sap flow of *S. capri* individuals seems more constant than of *G. ulmifolia* and *S. macrophylla*. Sap flow of T0 (Fig. 15) declined steadily over dry season and the lowest point was at the beginning and mid of April, when T0 shed its leaves. After developing fresh leaves, sap flow returned to the same values as observed in dry season from January to March. The sensor installed in T1 did not work consistently (Fig. 34), but the time periods that were monitored show a rather constant sap flow rate. T6 was equipped with a sap flow sensor in early April (Fig. 35), therefore no data about its sap flow in dry season is available. Little fluctuations are visible, yet no such pronounced peaks as in the sap flow data of *S. macrophylla*.

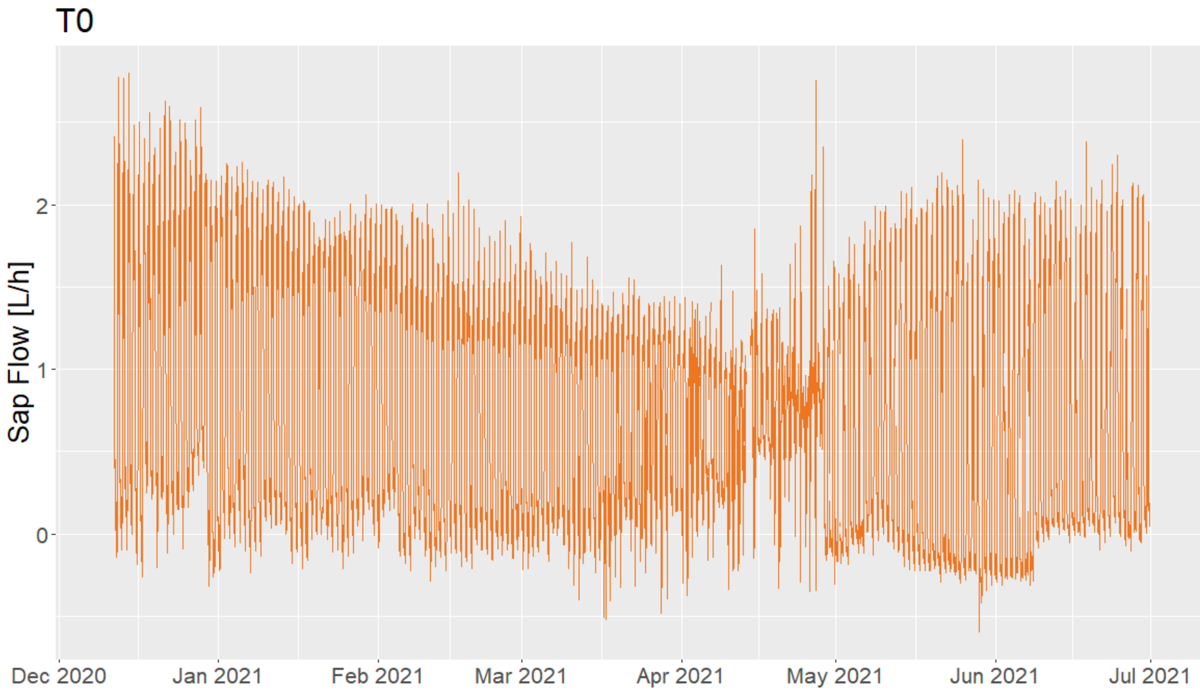

Fig. 15. Sap flow of S. capiri (T0) in the first half of 2021. Leaves were shed in mid of April.

Sap flow of *H. courbaril*, exemplary shown on tree individual G4 (Fig. 16), dropped significantly at the end of February and beginning of March. Except of this sudden decrease of sap flow, which was most likely caused by shedding the leaves simultaneously with the other *H. courbaril* individuals (Fig. 36+Fig. 37), sap flow was constant and showed little fluctuations over the investigation period. Sensor in G2 broke in beginning of May.

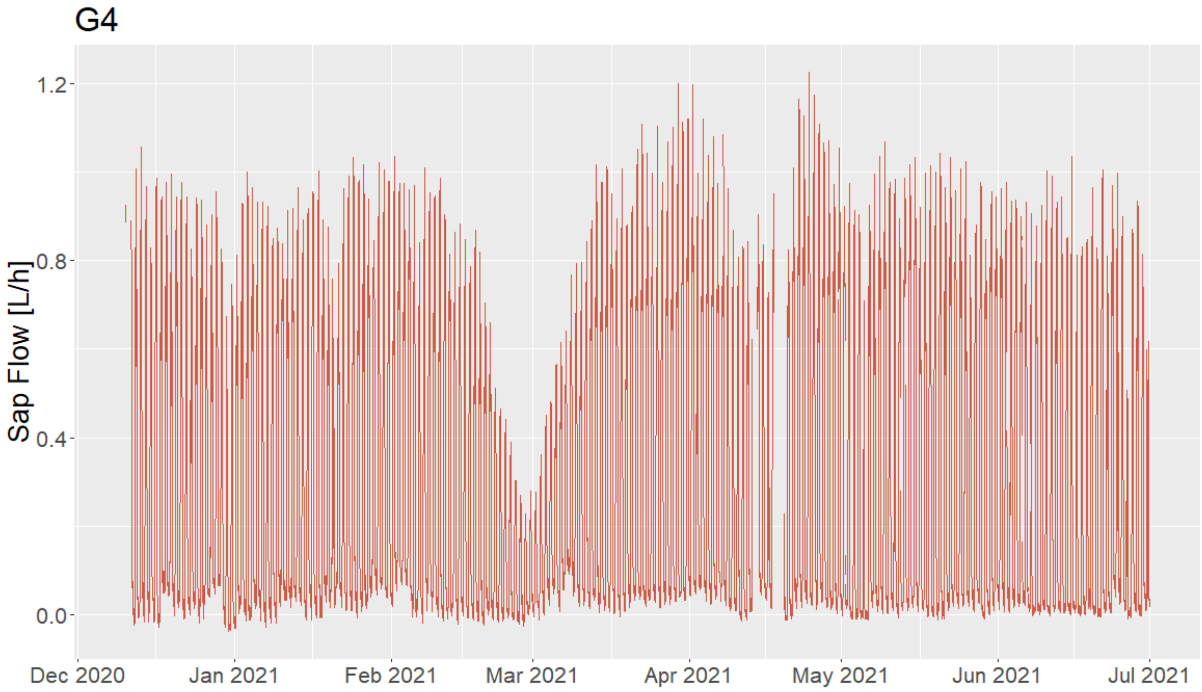

Fig. 16. Sap flow of H. courbaril (Individual G4) in the first half of 2021. Drop of sap flow was most likely caused by shedding old and developing new leaves at the end of February.

Daily mean sap flow was calculated and brought in relation with the daily uptake rate of each measured nutrient over the investigation period. Tree individual O1 was excluded, because the sap flow sensor was broken for the majority of the investigation period. Correlation between nutrient uptake and sap flow for *S. capiri* is distorted, because nutrient uptake rate was calculated differently for T0 than for T1 and T6. A positive correlation between daily nutrient uptake and daily sap flow was found for B in *S. macrophylla*, K in *S. macrophylla* and *G. ulmifolia*, Mg for *H. courbaril* and S for *S. macrophylla* and T1 and T6 of *S. capiri* and Mo in T1 and T6 of *S. capiri* (Fig. 38-Fig. 41;Fig. 46). The remaining nutrients showed either no correlation with sap flow or uptake rate decreased with increasing sap flow (Fig. 42-Fig. 45; Fig. 47-Fig. 49).

3.4.2 Monitoring of soil moisture

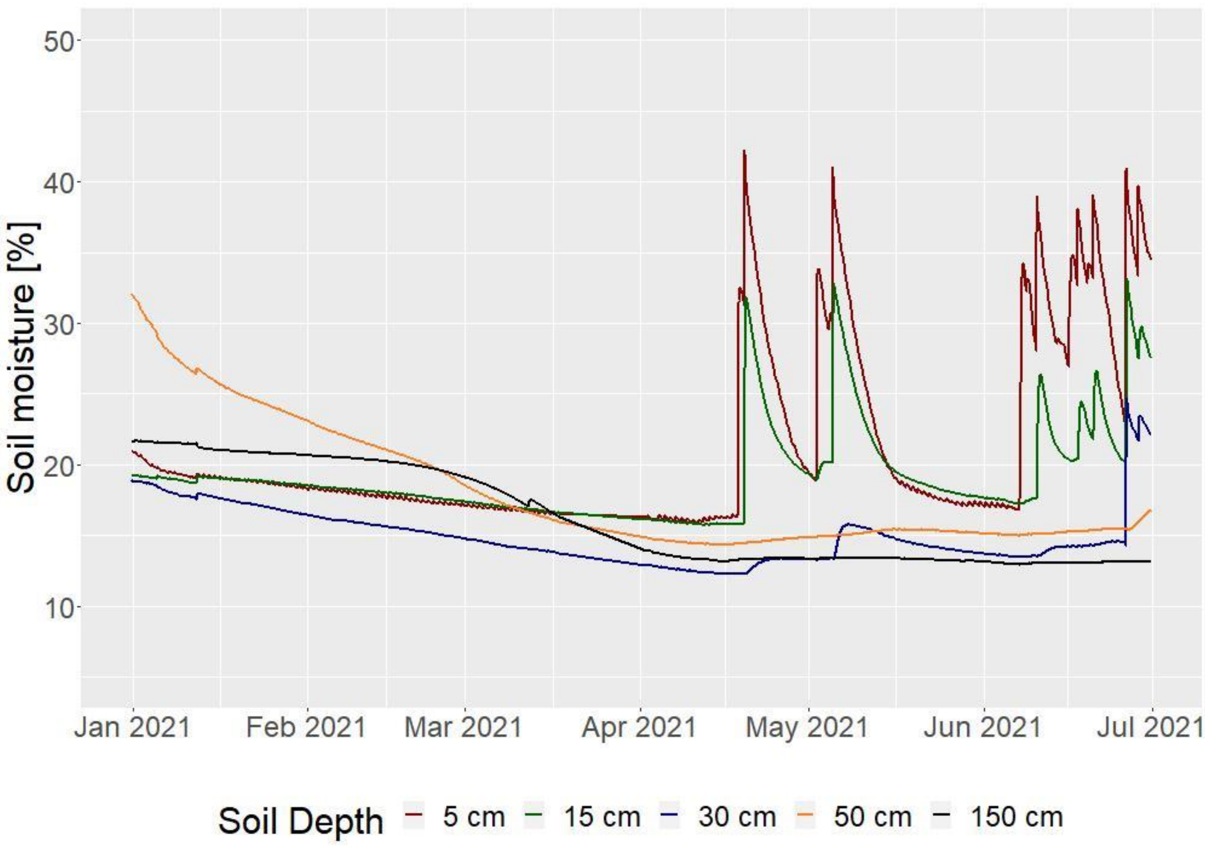

Fig. 17. Monitoring of soil moisture in various depth located in the S. macrophylla group.

Soil moisture in the *S. macrophylla* soil plot decreased during dry season in 30 to 150 cm soil depth (Fig. 17). Steepest decline was monitored in 50 cm depth, in which soil moisture level dropped from 33 % in January to 15 % in April. Rainfall of mid of April infiltrated until 30 cm depth. An increase of 2 % is visible in 50 cm as well, however the increase did not occur with the soil moisture peaks in the top soil layers. As the rainfall stopped again in the beginning of May, soil moisture in the top soil layers decreased again. At the second sampling date on 18. of June, rainfall from the beginning of the month infiltrated until 30 cm depth.

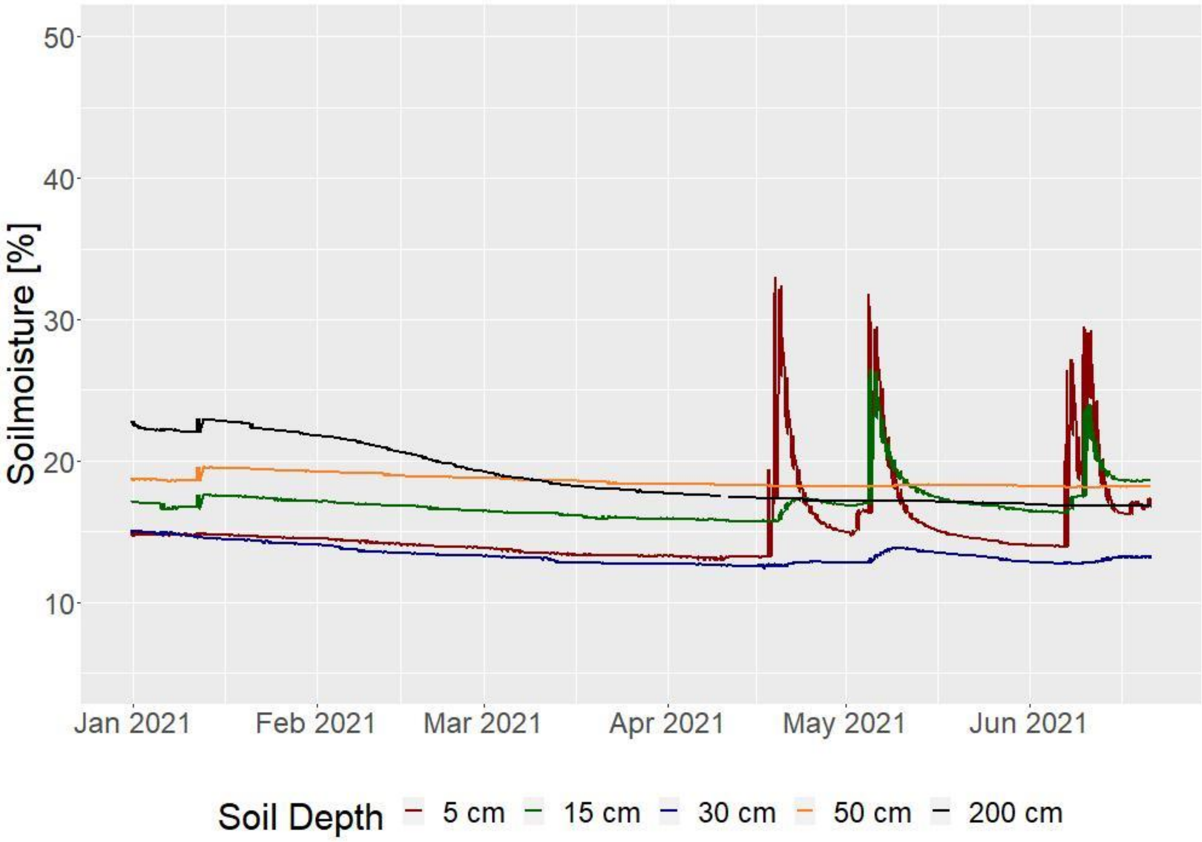

Fig. 18. Soil moisture in various depth in the S. capiri soil pit in the first half of 2021.

Soil moisture in all depth in the *S. capiri* plot declined slightly from January to April 2021 (Fig. 18). Steepest descent was measurable in 200 cm, in which soil moisture decreased from 23 % to 17 %. At the first rain event in mid of April, water infiltrated until 15 cm depth. At the second rain event in beginning of May, water infiltrated until 30 cm. At the second sampling date on 18th of June, water was infiltrated until 30 cm soil depth.

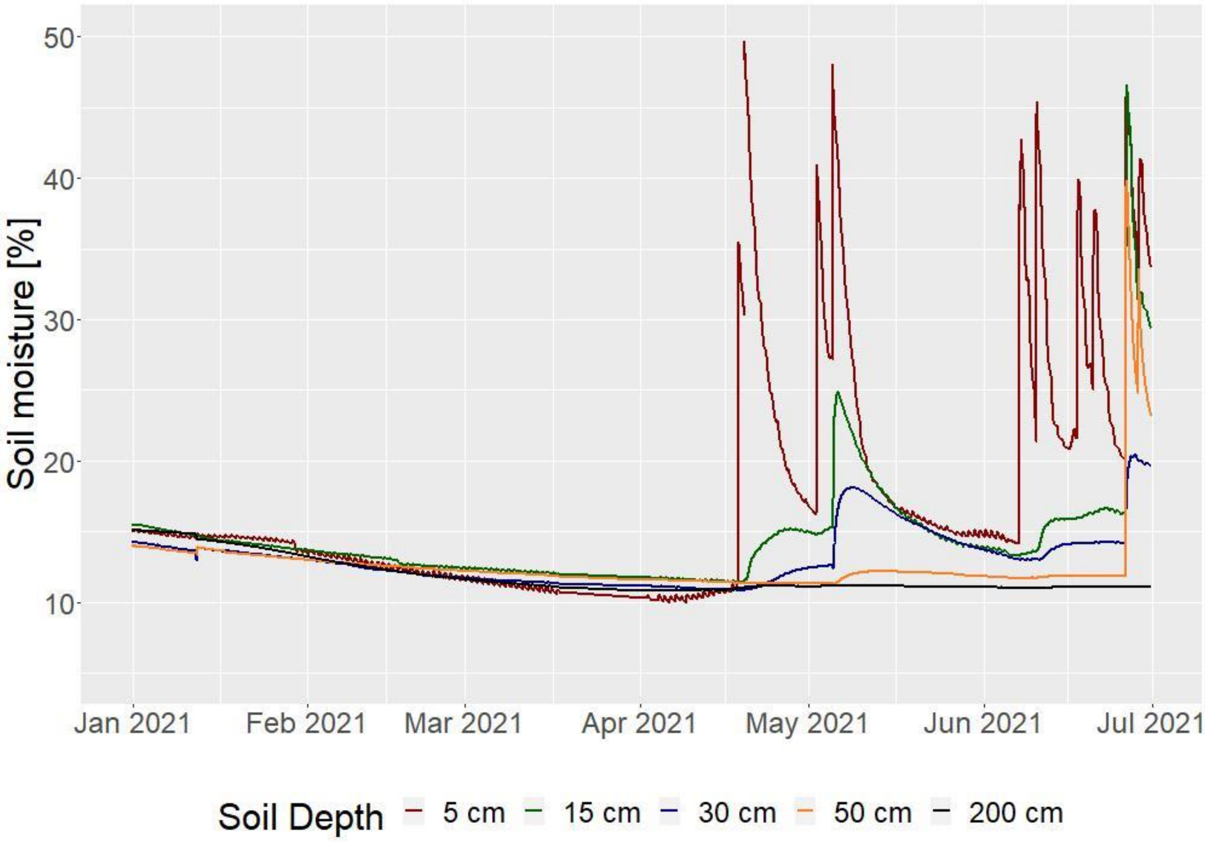

Fig. 19. Continuous monitoring of soil moisture in the first half of 2021 in the H. courbaril plot in various depth.

In comparison to the *S. macrophylla* and *S. capiri* soil plots, soil moisture in all soil depths in the *H. courbaril* plot was lower in January 2021 (Fig. 19). At the end of dry season (April 2021), soil moisture was at 10 to 12 %, with the lowest moisture level in 5 cm depth. When the first rain fell in mid of April, water infiltrated until 50 cm depth. Soil moisture in 5 to 30 cm decreased again in the second dry period in May. At the second sampling date on the 18th of June, water was infiltrated until 30 cm depth.

3.4.3 Leachable Fe and Mn concentrations in the soil profiles

Course of leachable Fe and Mn concentrations were similar in the soil plots and are therefore presented together in Fig. 20 and Fig. 21.

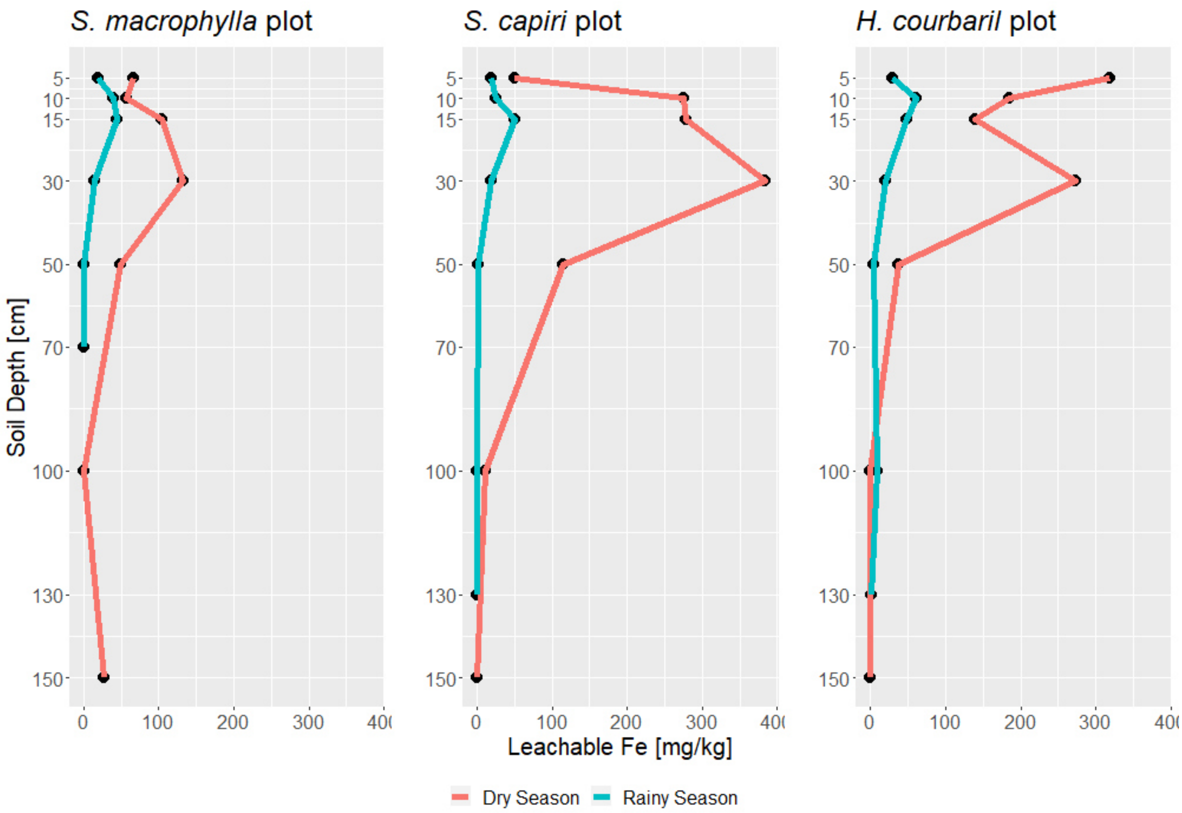

Fig. 20. Course of leachable Fe concentration (± 32.5%) of the three soil plots of dry and rainy season.

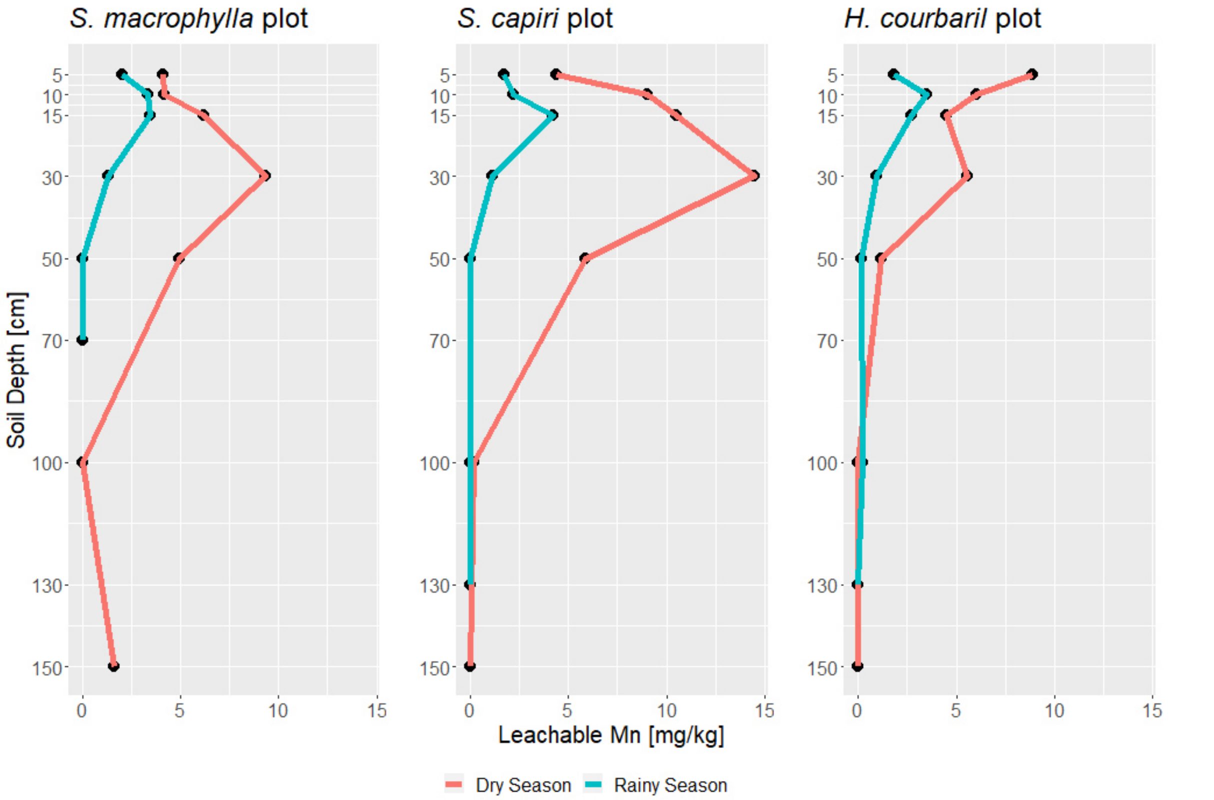

Fig. 21. Course of leachable Mn concentration (± 41.3%) of the three soil plots in dry and rainy season.

Leachable Fe and Mn concentrations were higher in dry season than in rainy season in all soil plots (Fig. 20+Fig. 21). Maximum concentrations (383 mg/kg Fe, 14 mg/kg Mn) were measured in the *S. capiri* plot in 30 cm depth. Leachable Fe and Mn concentration in *S. macrophylla* plot peaked as well in 30 cm depth, however concentrations were not as high as in the *S. capiri* plot. In the *H. courbaril* soil plot, peaks in 5 cm (319 mg/kg Fe, 9 mg/kg Mn) and 30 cm (273 mg/kg, 6 mg/kg Mn) were measured. For samples taken deeper than 50 cm in the *H. courbaril* plot, leachable Fe and Mn concentrations were <LOQ. In *S. capiri* and *S. macrophylla* plots, leachable Fe and Mn concentrations were <LOQ beneath 100 cm soil depth. However, in 150 cm depth leachable Fe and Mn concentrations increased again (26 mg/kg Fe, 1.6 mg/kg Mn) in the *S. macrophylla* soil plot. Mean concentrations of leachable Fe were higher in *S. capiri* (159 mg/kg) and *H. courbaril* (136 mg/kg) than in *S. macrophylla* (62 mg/kg) soil plot in dry season. Mean leachable Mn concentrations were highest in *S. capiri* plot as well (6 mg/kg), but *H. courbaril* had less Mn (3.7 mg/kg) than *S. macrophylla* (4.3 mg/kg). In rainy season, mean concentration declined to 16, 24 and 20 mg/kg of leachable Fe and 1.3, 1.3 and 1.7 mg/kg of leachable Mn for *S. capiri*, *H. courbaril* and *S. macrophylla* plots, respectively. Peak concentrations were measured in 15 cm depth in *S. macrophylla* and *S. capiri* soil and in 10 cm depth in *H. courbaril* soil. However, peaks were not as pronounced as in dry seasons.

Soil profiles of leachable Si and Al can be found in the appendix (Fig. 50+Fig. 51), as both elements showed the same course like Fe and Mn. Though it has to be mentioned that for Al and Si exaggerating values of leachable Si (526 mg/kg) and Al (1254 mg/kg) were measured in the *S. capiri* soil plot.

3.4.4 Soil profiles of dissolved organic carbon and pH

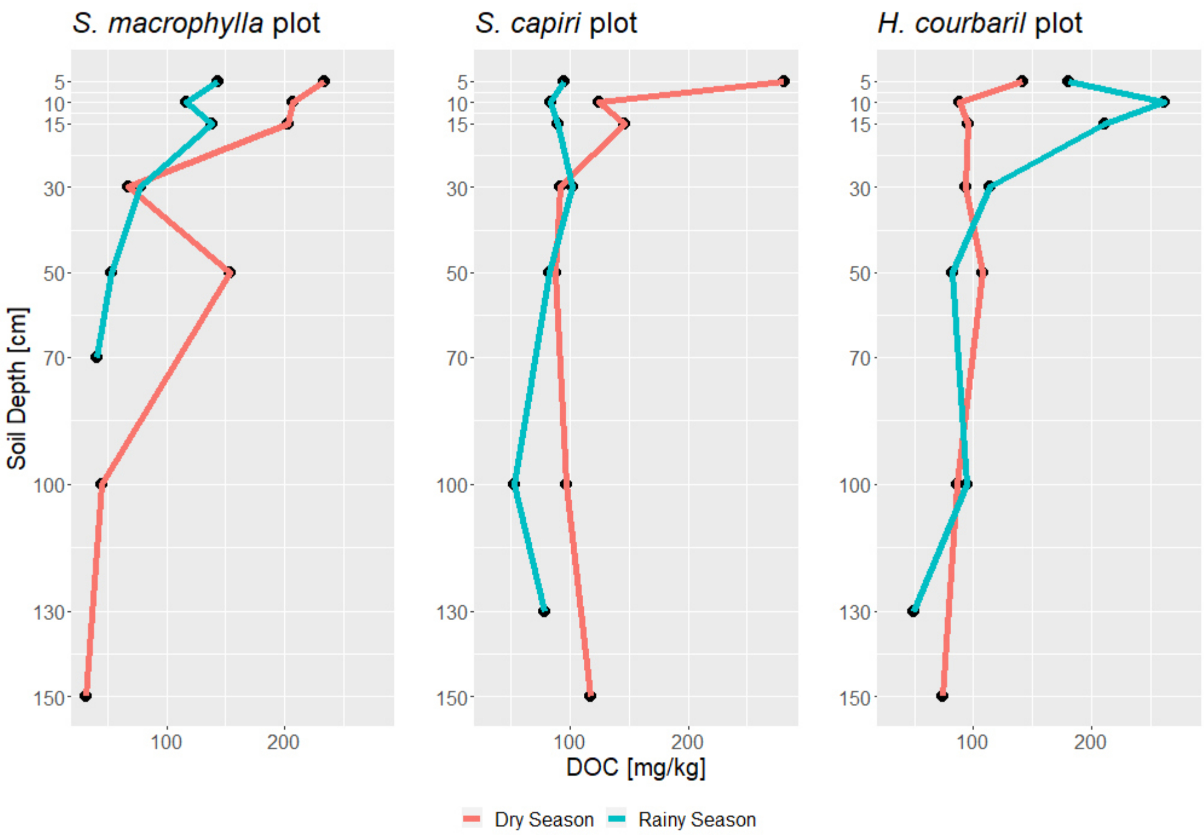

Fig. 22. Course of DOC concentrations (± 14.4%) in the three soil plots in dry and rainy season.

The course of dissolved organic carbon (DOC) was different between dry and rainy season as well as between the tree species (Fig. 22). Highest DOC concentration in *S. macrophylla* were in top soil in 5 to 15 cm (233 to 203 mg/kg). In 30 cm depth, DOC concentrations decreased (68 mg/kg), in 50 cm a peak of 154 mg/kg DOC was measured. In greater depth (100 and 150 cm), DOC concentrations decreased to 32 mg/kg. In rainy season, top soil samples had lower DOC concentrations than in dry season (143, 116 and 137 mg/kg in 5, 10 and 15 cm soil depth, respectively). In 30 cm, DOC concentration in rainy season were similar to samples taken in dry season, yet the peak in 50 cm measured in dry season had disappeared (154 mg/kg to 53 mg/kg).

In *S. capiri* soil, maximum DOC concentration was measured in 5 cm depth in dry season (280 mg/kg). Top soil layers (10 and 15 cm soil depth) had higher DOC concentrations (125 and 146 mg/kg) than deeper soil layers (30 to 100 cm, mean DOC concentration 92 mg/kg). In 150 cm soil depth, DOC concentration increased again (117 mg/kg). In rainy season, DOC concentrations were lower in the whole soil profile (mean DOC rainy season 95 mg/kg, dry season 134 mg/kg), except in 30 and 50 cm depth, where similar DOC concentrations were measured as in dry season. Complementary to dry season samples, DOC concentrations in greater depth (130 cm) increased again (78 mg/kg).
In contrast to the soil profiles of *S. macrophylla* and *S. capiri*, DOC concentration in dry season were lower than in rainy season in the *H. courbaril* plot. Mean concentration was 98 mg/kg in dry and 142 mg/kg in rainy season. Two smaller peaks are visible in 5 and 50 cm soil depth (141 and 108 mg/kg, respectively). In greater depth, DOC concentrations decreased (74 mg/kg in 150 cm depth). In rainy season, maximum concentrations were measured in 10 cm depth (262 mg/kg). In soil samples deeper than 10 cm, DOC concentrations decreased until 50 mg/kg in 130 cm depth. In 100 cm depth, DOC concentrations of dry and rainy season were similar.

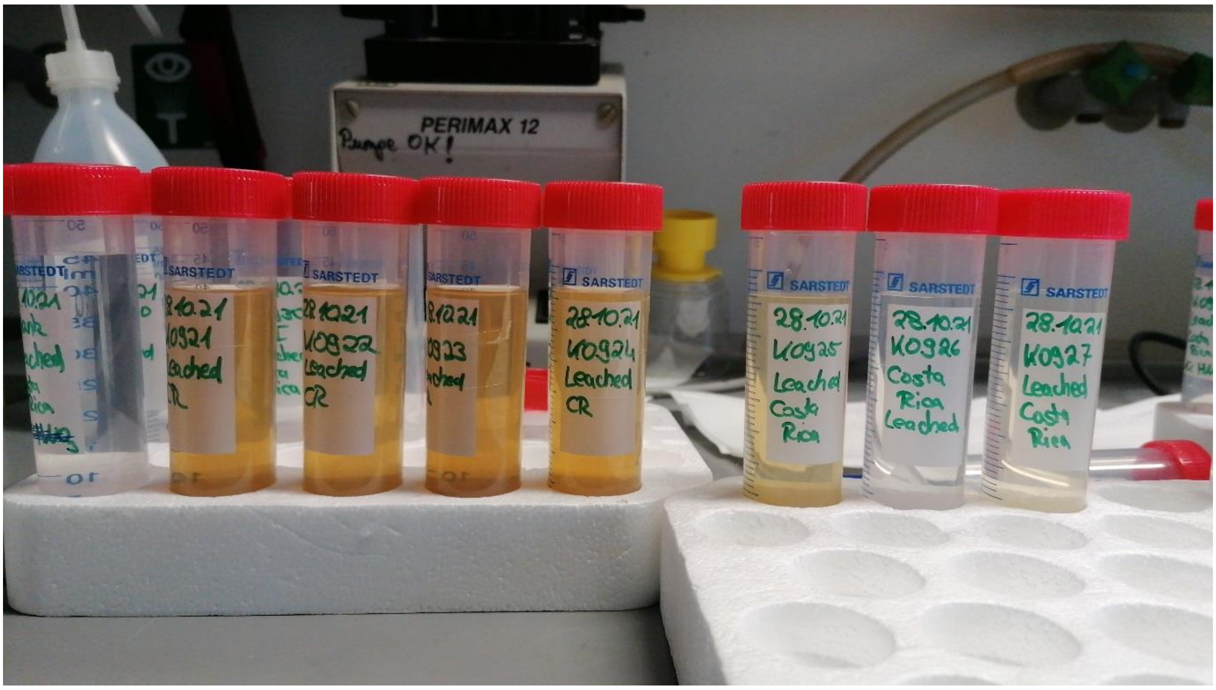

Fig. 23. Image of the leachates of the S. macrophylla soil profile. Samples are: Blank, 5, 10, 15, 30, 50, 100, 150 cm soil depth.

Color of the soil leachates (Fig. 23) changed from top soil (brown) to deep soil (no color). Also, coloring was not consistent in one of the triplicates (Fig. 24).

Fig. 24. Colors of the leachates of one triplet.

Tab. 8. Element and DOC concentrations of one triplet, which color differed significantly within the triplet.

Replicate	Al [mg/kg]	Fe [mg/kg]	Mn [mg/kg]	Si [mg/kg]	Ca [mg/kg]	Na [mg/kg]	DOC [mg/kg]
1	47.3	20.5	0.7	90.14	7.6	4.5	113.4
2	196.4	70.8	1.9	237.9	11.9	4.8	144.07
3	68.6	31.16	0.97	112.8	8.8	4.5	65.17

Similar to the color, DOC concentrations as well as the metal concentrations varied immensely in the triplicates (compare Tab. 8). Base cations such as Ca or Na were not affected.

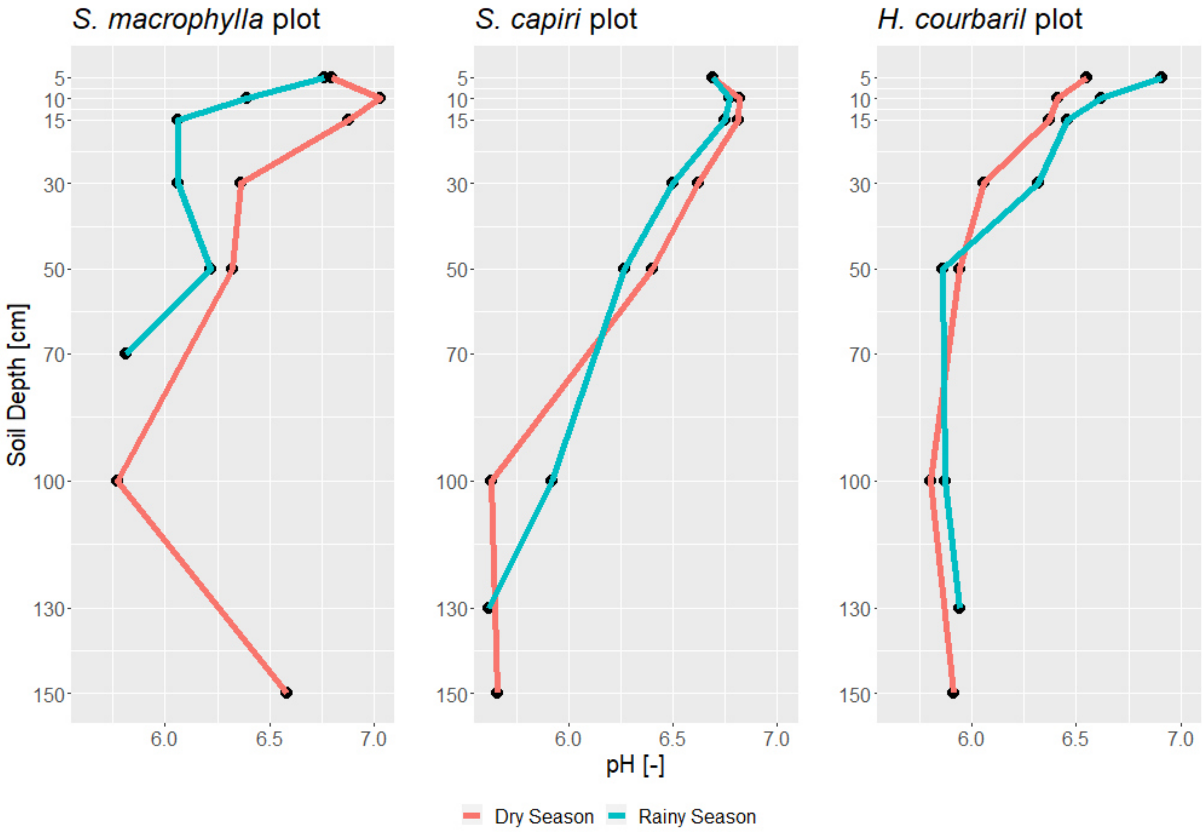

Fig. 25. Course of pH in the three soil plots in dry and rainy season.

pH of the soil ranged between 5.6 and 7.0 (Fig. 25). In the *S. capiri* and *H. courbaril* plot, pH decreased from top to bottom (6.8 to 5.6 in dry and rainy season in *S. capiri*; 6.6 and 6.9 to 5.9 in dry and rainy season in *H. courbaril*). In rainy season, pH was higher in top soil samples in *H. courbaril* plot. In contrast to the *S. capiri* and *H. courbaril* soil plots, the course of pH in the *S. macrophylla* plot showed opposing values in dry and rainy season until 50 cm depth. In 5 cm depth, pH measured in dry and rainy season was the same (6.8). In 10 to 30 cm depth, pH decreased to 6.0 in rainy season, whereas in dry season maximum pH value was measured in 10 cm depth (7.0). In 100 cm in dry season, and 70 cm in rainy season, pH decreased to 5.8. In contrast to the *S. capiri* and *H. courbaril* plots, pH increased (6.6) again in 150 cm depth in the *S. macrophylla* plot.

3.4.5 Leachable Ca and Na concentrations in the soil profiles

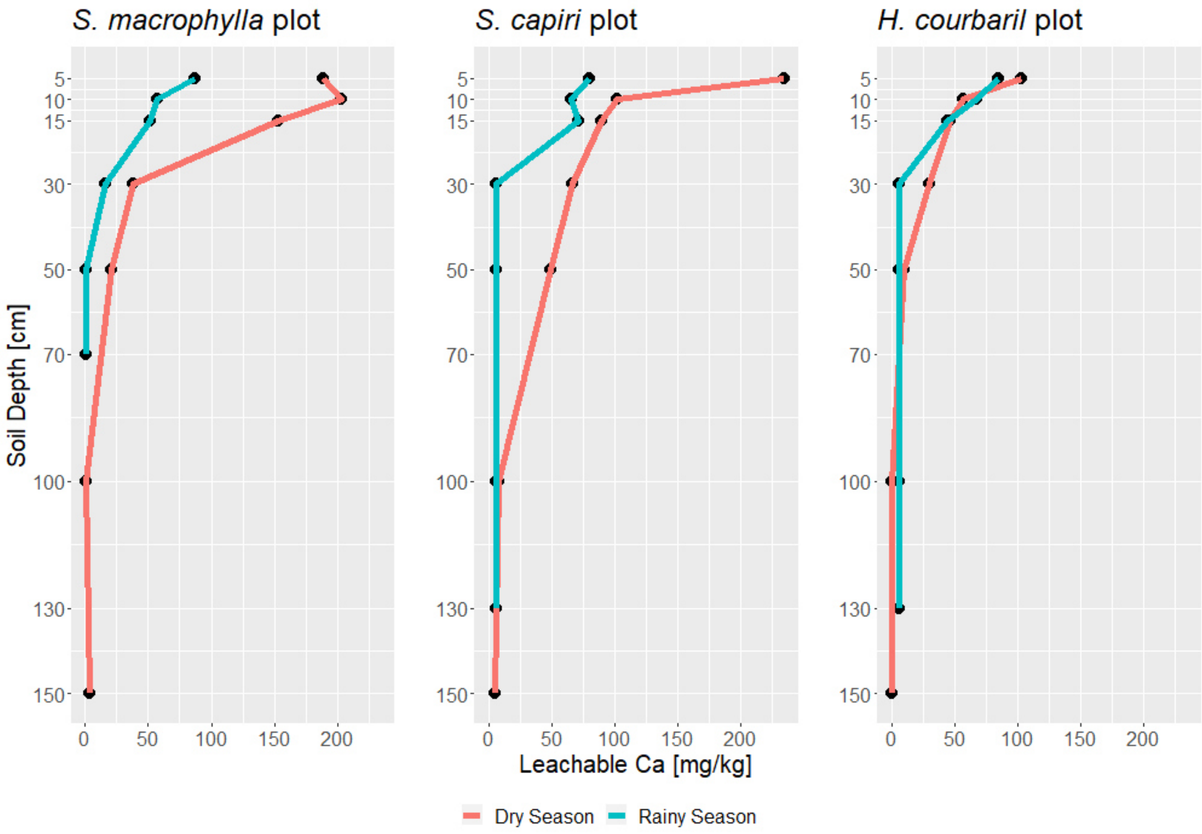

Fig. 26. Course of leachable Ca concentrations (± 11.3 %) in the three soil plots in dry and rainy season.

Leachable Ca concentrations were highest in the top soil and decreased in deeper soil layers in all plots (Fig. 26). Ca concentrations were higher in *S. macrophylla* and *S. capiri* soil in dry season (121 mg/kg, 109 mg/kg) than in rainy season (43 mg/kg, 46 mg/kg) until 50 cm depth. In dry season, leachable Ca concentration in 100 cm in *S. macrophylla* soil was <LOQ but increased slightly in 150 cm again (4 mg/kg), whereas in rainy season Ca concentrations were <LOQ in 50 and 70 cm depth. In *S. capiri* plot, leachable Ca concentrations in samples deeper than 30 cm were <LOQ in rainy season. In the *H. courbaril* plot, no difference in the leachable Ca concentration between dry and rainy season is visible. Mean concentrations were 35 mg/kg in dry and 31 mg/kg rainy season for the whole soil profile. In dry season, Ca concentration in 100 and 150 cm depths were <LOQ.

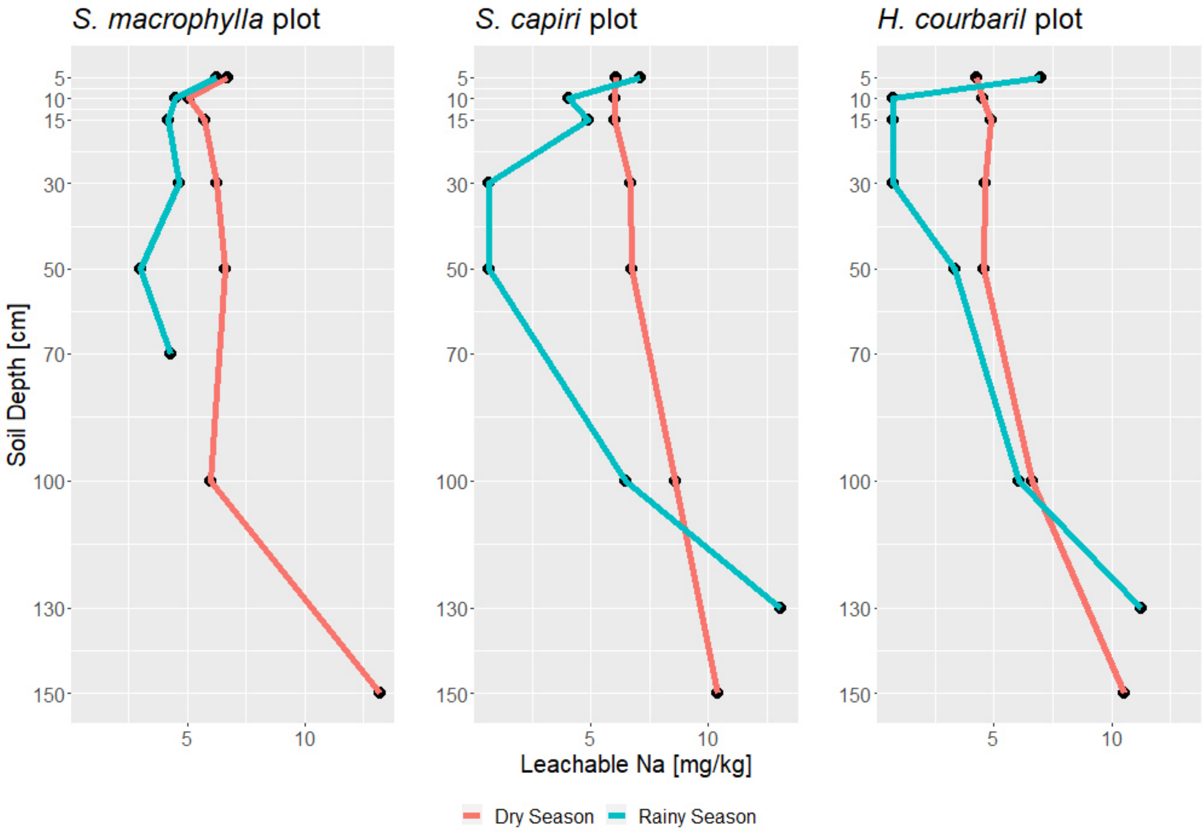

Fig. 27. Leachable Na concentration (± 4%) in the soil plots of S. macrophylla, S. capiri and H. courbaril in dry and rainy season.

Leachable Na concentrations, shown in Fig. 27, are in a contrasting course to the leachable Ca concentrations (Fig. 26). Leachable Na concentrations in dry season ranged from 5.1 to 6.7 mg/kg in *S. macrophylla* until 100 cm, 6.0 to 6.7 mg/kg in *S. capiri* until 50 cm and 4.3 to 4.8 mg/kg in *H. courbaril* until 50 cm. Leachable Na concentrations increased in 150 cm (13.2 mg/kg) in *S. macrophylla*, 100 and 150 cm (8.6 and 10.4 mg/kg) in *S. capiri* and 100 and 150 cm (6.6 and 10.5 mg/kg), in *H. courbaril* soil plot. In rainy season, leachable Na concentrations declined to 4.3 mg/kg from 10 to 30 cm and to 3 mg/kg in 50 cm in *S. macrophylla* soil. Leachable Na concentration increased in 70 cm depth again (4.3 mg/kg). In the *S. capiri* soil plot, leachable Na concentrations decreased from 7 mg/kg in the top soil to <LOQ in 30 and 50 cm depth. Leachable Na concentrations increased in 100 and 150 cm (6.5 and 13.1 mg/kg) again. Similar, leachable Na concentrations in *H. courbaril* plot decreased from 7 mg/kg in 5 cm depth to < LOQ in 10 to 30 cm and increased again in 50 to 130 cm (3.3 and 11.2 mg/kg).

3.5 Soil to plant transfer factors

Transfer factors shown in Fig. 52-Fig. 55 reflect the decrease in leachable nutrient concentrations from dry to rainy season in the soil plots (Fig. 20+Fig. 21; Fig. 26+Fig. 27). As the concentration in the soil leachates decreased, transfer factors in rainy season increased. This is obvious for Ca, Fe, and Mn. For Na, transfer factors in dry and rainy season stayed the same, because the sum of Na in the soil plots did not significantly change from dry to rainy season. The transfer factors are shown in the appendix because they do not provide any new information, but merely reflect the change of leachable nutrient concentrations from dry to rainy season.

4. Discussion

4.1 Preferential uptake of specific nutrients by the tree species

When the nutrient concentration of living biomass is studied over a period of time, it is advisable to keep track of biomass growth to avoid dilution effects of the nutrients due to increase of living matter. Unfortunately, leaf dry matter was not measured to determine the growth rate of the trees. In case of linear uptake of nutrients with the growth rate, nutrient concentrations should stay the same if divided by the leaf age from samples taken at the two sampling dates. Leaf age for both, dry season and rainy season samples is only known for *H. courbaril* because of the decrease of sap flow when the trees shed their leaves (Tab. 2). Linear nutrient uptake was not the case for all nutrients except for Mn, however *H. courbaril* seemed to accumulate Mn in high levels (section 4.1.7). Also, specific leaf area (SLA) measured from 23. May 2021 until 11. June 2021 did not show an increase over the investigation period for all tree species (data not shown). Waring et al. (2019) also state, that biomass growth is lower in dry season. It can be concluded that differences in the nutrient concentrations determined in dry and rainy season are most certainly not caused by dilution effects, as leaf growth was inhibited during the investigation period.

Experimental design was constructed for taking samples at the end of dry season (beginning of April) and, as rainy season usually starts in beginning of May, after roughly six weeks of rain (mid of June). High differences in nutrient concentrations in soil and leaves were predicted and information on water and nutrient concentrations as well as information on rooting depth were expected. However, rainy season was delayed. After little rainfall at the end of April and beginning of May, another month of drought followed (Fig. 12). Samples which were taken in mid of June and were thought of representing biogeochemical processes of rainy season, represent now transition processes of dry to rainy season. In order to keep it simple, samples taken in beginning of rainy season are still referred to as rainy season samples.

4.1.1 Macro and Micronutrient concentrations in the tree species

Results by the two-factor MANOVA indicated species specific requirements of each element but P (Tab. 3). The absolute concentrations show, which species was in especially high need of some elements (Fig. 2-Fig. 8; Fig. 28).
Samples taken in rainy season were used to compare nutrient contents of the different tree species, because leave age was rather similar than in samples from dry season. Yet it has to be kept in mind that *S. macrophylla* leaves were approximately 54 days, *G. ulmifolia* 59 and *H. courbaril* 107 days old (compare Tab. 2). The leaf age of *S. capiri* was known for T0 (44 day), leaf age of the other individuals could not be determined.
Macronutrient concentrations in the leaves of the investigated tree species declined in the following order Ca>K>Mg>S>P for *G. ulmifolia*, *S capiri* and *H. courbaril* (Tab. 4). Alvarado et al. (2018) measured the same order in 33 *H. courbaril* individuals in Costa Rica, whereas Hunter and Stewart (1993) found the order K>Ca>P>Mg>B in one year old *H. courbaril* seedlings in a field experiment in Honduras. Grown in nutrient solution, 240 days old *H. courbaril* seedlings showed the same order as in the field experiment in Honduras (Bessa et al., 2022). In *G. ulmifolia* seedlings, the same order was detected as in fully grown individuals in this study (Hunter and Stewart, 1993). *S. macrophylla* individuals investigated in this study contained more K than Ca and more S than Mg in their leaves (Tab. 4). Macronutrient concentrations declined in a different order than for the other species: K>Ca>S>Mg>P. Gonçalves et al. (2005) found the following order of macronutrients in three year old *S. macrophylla* individuals grown in the shadow and sun exposed: N>Ca>K>P>Mg. However, individuals grown in the sun had higher N, K, Fe and Mn concentrations than those grown in shade (Gonçalves et al., 2005). No information on the nutrient content of *S. capiri* leaves was found in publications.

G. ulmifolia, *S. macrophylla* and *S. capiri* contained more Fe than Mn, whereas *H. courbaril* had higher Mn than Fe concentration (Tab. 5). *S. macrophylla* and *S. capiri* contained higher Na than Fe concentrations. There were higher concentrations of Zn than Cu and Mo in all species but *H. courbaril* which had higher Zn than B concentrations (Tab. 5+Tab. 6). *S. capiri* contained more B than Mn, which is in contrast to the other species. The findings of micronutrients in *S. macrophylla* are consistent with the results of Gonçalves et al. (2005). Grown in a nutrient solution, 180 days old *H. courbaril* seedlings contained more Mn than Fe which is consistent with this study, however Cu concentrations were higher than B and Zn concentrations (Bessa et al., 2022).

Results by the MANOVA already indicated species specific nutrient requirement (Tab. 3). Yet, some elements were especially important for the prevailing species.

H. courbaril seems to have a higher need of Zn and Mn, *S. macrophylla* of K and Na and *S. capiri* and *G. ulmifolia* of B and Ca. These results support the first hypothesis that species in the tropical dry forest use certain elements preferentially. The question now is, if these differences in the nutrient concentrations are due to species´ specific traits, the adaption to endure dry season or if these species have access to other nutrient pools, for example by developing deep roots.

4.1.2 Nutrient Uptake Rates

Nutrient uptake rates for each element are shown underneath the absolute concentrations measured in dry and rainy season (Fig. 2B-Fig. 8B). Nutrient uptake rates were calculated differently for *S. macrophylla* and *G. ulmifolia* and one *S. capiri* individual (T0) than for *H. courbaril* and the remaining *S. capiri*, because *S. macrophylla*, *G. ulmifolia* and T0 developed new leaves during the investigation period. Consequently, the uptake rates of *S. macrophylla*, *G. ulmifolia* and T0 cannot be compared to *H. courbaril* and T1 and T6 of *S. capiri*. Trees store mineral nutrients in the leaves, stems (especially in the bark) and roots (Pallardy, 2008). Especially when new leaves developed in *S. macrophylla*, *G ulmifolia* and T0, usage of stored nutrients of the shoots was likely because the trees had little to no sap flow to transport the nutrients from either the soil or from storage tissue in the roots or bark to the shoots and new leaves. For none of the species, nutrient uptake rates were correlated positively with the sap flow of the trees (Fig. 38-Fig. 49). Exception was the positive correlation of B, K and S uptake rates in *S. macrophylla* (Fig. 38, Fig. 39, Fig. 41), K in *G. ulmifolia* (Fig. 39), Mg in *H. courbaril* (Fig. 40) and S and Mo in *S. capiri* (T1 and T6) trees (Fig. 41+Fig. 46). It is possible that the trees took up nutrients with rainwater from April and May, which infiltrated in the topsoil, however transport was too slow to reach the leaves before the second sampling campaign in mid of June. Consequently, nutrient uptake would not have been detected. However, sap flux velocities of *S. macrophylla* were between 350 and 460 cm/day, *G. ulmifolia* 70 to 600 cm/day, *S. capiri* 120 to 270 cm/day and *H. courbaril* 320 to 710 cm/day. Water was therefore transported fast enough, to notice a correlation between mobile elements like K and water uptake. K and Mg are both mobile in the tree (Farhat et al., 2016; Wilkinson, 2000), and usually abundant in the soil. Soil profiles could not be established for both elements, because many samples were <LOQ. However, in topsoil samples, both elements were determined, suggesting a similar distribution to Ca (Fig. 26). Because of the mobility of K and Mg and their abundance in the topsoil, the positive correlation between K and Mg uptake and the sap flow of *S. macrophylla* and *G. ulmifolia* (K) and *H. courbaril* (Mg) could truly be based on uptake from the rewetted, shallow soil to the leaves. Mo is mobile in trees (Tais and Zeiger, 2003), however due to the Mo concentrations <LOQ in the soil samples, uptake of Mo from the soil

into *S. capiri* individuals cannot be clarified. Another option is that the trees used internal nutrient storage, so that the uptake rates calculated in Fig. 2B- Fig. 8B were no uptake rates from the soil to the plant, but merely translocation or use of storage. S is relatively immobile (Wilkinson, 2000), and Boron mobility depends on the species (Pallardy, 2008). Due to the immobility of these elements, it is more likely that other effects influenced the calculated nutrient uptake than uptake of these elements from the soil to the leaves. For the remaining elements, no correlation or even negative relations to the sap flow were discovered (Fig. 42-Fig. 45; Fig. 47-Fig. 49). This suggests limited access, either by restricted uptake, transport or availability, to nutrients during the investigation period. Yet *H. courbaril* and *S. capiri* maintained a moderate sap flow (compare to Fig. 15+Fig. 16) which indicates a decoupling of water and nutrient uptake in these species. The data does not resolve the various influences, namely storage, translocation or uptake from the soil, well enough to truly speak of nutrient uptake from the soil to the leaves. Subsequently, nutrient uptake will be used in quotation marks, because use of stored nutrients or translocation cannot be excluded.

4.1.3 Potassium and Sodium in *S. macrophylla* leaves

K is required in large amounts by plants and is, among other functions, a major part of stomatal opening and closure and osmoregulation (Pallardy, 2008). It is thought that stomata pores can be opened or closed by regulating turgor in the guard cells which is controlled by the K^+ concentration (Pallardy, 2008). Effects of K on stomatal closure are not fully understood, however a study by Benlloch-González et al. (2008) on stomatal conductance of olive trees suggests that low K supply inhibits the plants possibility to close its stomata. Vice versa, water use efficiency was improved in *Hibiscus rosa-sinensis* under drought stress with higher K supply (Egilla et al., 2005).

S. macrophylla contained higher K and Na concentrations in dry season than in rainy season (Fig. 9). According to Hu and Schmidhalter (2005) K and Na uptake occurs simultaneously because of antagonism of Na und K at uptake sites in the roots. This could explain, why in addition to K, Na concentrations were elevated in *S. macrophylla* leaves as well (Fig. 28), even though Na is not considered as an essential nutrient.

Gonçalves et al. (2005) state that higher K concentrations in sun exposed *S. macrophylla* might have been used for stomata regulation to control water loss. Subsequently, increased K concentrations in *S. macrophylla* leaves in dry season was required for higher stomatal regulation because the trees were exposed to the sun due to the missing cover of the canopy of surrounding trees (compare Fig. 56+Fig. 57). Younger *S. macrophylla* leaves sampled in rainy season contained less K, yet concentrations were higher than for the other species (Fig.

9). Combined with the fact that *S. macrophylla* leaves have a higher stomata density (data not shown) and no physical protection against transpiration like a waxy epidermis or hair on the leaf surface, it is possible that *S. macrophylla* has to regulate its stomata stronger than the other species in order to reduce water loss in dry season.

In rainy season, the elevated stomatal density might allow *S. macrophylla* an increased water and therefore nutrient uptake compared with the other species. Sap flow of the monitored *S. macrophylla* individuals increased rapidly after the first rainfalls at the end of April and decreased again in the second dry period until June (Fig. 13). The rapid reaction to the increased soil moisture in the top soil suggests a high density of fine roots in 5 to 30 cm in which the water infiltrated. With the water, nutrients could have been taken up provided that they were plant available. This seems to be the case for K (Fig. 39), which “nutrient uptake” rate was positively correlated with the sap flow of *S. macrophylla* trees. *S. macrophylla* seems to follow an exploiting water use strategy with rapid water uptake when water is available. The higher stomata density suggests a higher transpiration rate but leads also to the urgency to regulate water loss in dry season, either by closing stomata or shedding its leaves in threatening drought conditions.

4.1.4 Boron, Calcium and Magnesium in *G. ulmifolia* and *S. capiri* leaves

Dry season samples of *G. ulmifolia* showed especially high concentrations of Fe, B, Mg and Ca which were similar to concentrations of litter samples. Most likely, dry season samples of *G. ulmifolia* were senescenced leaves. Nevertheless, fresh leaves of *G. ulmifolia* and *S. capiri* leaves had higher Fe, Mg, B and Ca concentrations than *H. courbaril* and *S. macrophylla* (Fig. 9). Of these four elements, B is an important micronutrient regulating the plant water status. In *G. ulmifolia* and *S. capiri* leaves, B was the third most common micronutrient whereas in *H. courbaril* and *S. macrophylla* B was less abundant (Tab. 6). B is essential for plants as it is necessary for stabilizing the cell wall pectic network and regulating cell wall pore size (Pallardy, 2008). B dependent processes in plants which are connected to plant water status include root and shoot growth, vessel formation, barrier function of leaf surfaces and photosynthesis (Wimmer and Eichert, 2013). B deficiency can cause lower rates of water absorption and transpiration, as well as poor stem form and leaf malformation (Pallardy, 2008). In B sufficient conditions, B is taken up passively by diffusion, whereas in B deficient situations, B can be taken up actively via an efflux B transporter (BOR1) or channels (NIP5) (Wimmer and Eichert, 2013). However, little information of B and its effect on trees under drought stress are available. B seems to affect drought resistance of trees directly through membrane integrity, which might be affecting stomatal function (Lehto et al., 2010). Indirectly, B can affect hydraulic conductivity and root growth (Lehto et al., 2010). In a study by Möttönen et al. (2001), increased B concentrations elevated water uptake in Norway spruce seedlings by increasing the amount of root tips and mycorrhizas. Secondary effects of the higher amount of root tips were faster soil water depletion as well as faster stomatal closure and a decrease in net photosynthetic rate compared to seedlings with lower B concentrations (Möttönen et al., 2001). Mobility of B in the tree depends on the species and its available concentration. Excessive B which has not been used as a constituent of the cell walls is potentially mobile (Lehto et al., 2010). High concentrations of B in litter samples of *G. ulmifolia* and *S. capiri* indicates that B in these tree individuals was immobilized by being used to stabilize their cell walls. Higher B concentrations in *G. ulmifolia* and *S. capiri* could therefore increase their drought resistance by stabilizing their cell walls and improving stomatal function.

In analogy to B, Ca functions among others, on membrane structure, stomatal function and cell-wall synthesis, as well as in plants defense and repair of damage from biotic and abiotic stress (Hu and Schmidhalter, 2005). Contradicting results have been found on whether Ca concentrations in plants increase or decrease under drought conditions. Ca concentrations increased in some drought experiments, suggesting that Ca could improve drought resistance. In other publications Ca concentrations decreased in plants under drought stress, mainly due to the reduction of transpiration (Da Silva et al., 2011). In this study, Ca concentrations increased in *H. courbaril* and *S. capiri* leaves during the investigation period (Fig. 2). Yet, the Ca supply rate of *S. capiri* was higher than for *H. courbaril*. *G. ulmifolia* contained highest absolute Ca concentration of all species in rainy season, whereas *S. macrophylla* preferred K over Ca (Tab. 4). The high affinity of *G. ulmifolia* and *S. capiri* of Ca supports the hypothesis that both species increase their drought resistance by stabilizing their cell walls. However, as Ca plays a major role in many other physiological processes like cell division or respiratory metabolism (Hu and Schmidhalter, 2005), the increase of Ca in *H. courbaril* and *S. capiri* and the high concentrations in *G. ulmifolia* cannot sorely be attributed to the trees adaption on drought conditions.

In contrast to Ca, little information is available on how Mg affects the plant water status (Hu and Schmidhalter, 2005). Vice versa, few research has been conducted on how water stress affects Mg concentration in plants (Da Silva et al., 2011). Mg is an important macronutrient for development and growth and is especially associated with photosynthesis, as up to 35 % of total Mg content of the plant is located in chloroplasts (Farhat et al., 2016). In this study, Mg was taken up similar to Ca. *G. ulmifolia* contained highest concentration in rainy season and *S. capiri* had higher “uptake rates” than *H. courbaril* (Fig. 4). Lower Mg concentrations in *S. macrophylla* in rainy season might have been caused by its elevated need of K. Competition between Ca, Mg and K may occur as they behave antagonistic (Farhat et al., 2016). As no further information of Mg and its role in plant water status is available, no conclusion on the water and nutrient use strategies can be drawn based on Mg concentrations.

Elevated B and Ca concentration in *G. ulmifolia* and *S. capiri* suggest increased cell wall stability (Pallardy, 2008) and membrane integrity, which affects stomatal function (Lehto et al., 2010). Data does not explain, whether those two species are more efficient in taking up B and Ca or if they have access to other nutrient pools. Also, *G. ulmifolia* and *S. capiri* seem to have different water use strategies, as *G. ulmifolia* is a deciduous species with higher sap flow in rainy season (Fig. 14), when water is readily available than *S. capiri* which has a consistent sap flow during the whole year (Fig. 15). Therefore, the higher B and Ca concentrations found in a more exploiting and conservative behaving tree species indicate, that both elements influence the water status of the trees, however they might not be the driving factor for surviving dry season.

4.1.5 Zinc concentrations in *H. courbaril* leaves

Plants take up Zn either passively with water molecules or actively by pumping H^+ ions into the rhizosphere which decreases soil pH and therefore increases the uptake rate of Zn^{2+} (Umair Hassan et al., 2020).

Zn concentrations decreased in the leaves of *H. courbaril* and *S. courbaril* from dry to rainy season (Fig. 7). This suggests that the Zn supply was interrupted. Zn is relatively immobile in trees (Wilkinson, 2000), so a translocation of the element into other tissue can be neglected. Sap flow did not decrease between the two sampling dates in beginning of April and mid of June, therefore it is unlikely that *H. courbaril* and *S. capiri* were under much greater water stress in June than in April. The negative correlation between Zn supply and sap flow indicates the decoupling of water and nutrient supply in the evergreen species in dry season (Fig. 49). Zn must have either been plant unavailable or absent in the water source of *H. courbaril* and *S. capiri*.

In contrast to the other species, *G. ulmifolia* contained less Zn in dry season than in rainy season samples (Fig. 7). *G. ulmifolia* leaves sampled in dry season contained the same Zn concentrations as litter samples collected from the ground, which stresses that Zn is rather immobile in *G. ulmifolia* and that dry season samples of *G. ulmifolia* were senescenced leaves. Zn in *S. macrophylla* samples taken in dry season were higher than litter samples collected from the ground. Therefore, leaves were not senescenced as in the case of *G. ulmifolia*. Fresh *S. macrophylla* leaves had lower Zn concentrations than older leaves (Fig. 7). Either

S. macrophylla accumulates Zn with increasing leaf age due to its immobility or *S. macrophylla* individuals were suffering from Zn deficiency due to the prolonged dry season and the resulting insufficient water and nutrient supply.
Zn concentrations were two to three times higher in *H. courbaril* than in the other species in rainy season (Tab. 5). It cannot be explained why *H. courbaril* contained more Zn than the other species, because soil profiles could not be provided to fill the missing link of more efficient Zn uptake or higher availability of Zn in the soil. High Zn concentrations in its leaves might be an adaption strategy of *H. courbaril* to endure dry season. Zn is known to enhance drought resistance of plants in multiples ways. Zn fertilization has shown to improve membrane stability, hormone synthesis, photosynthesis and the scavenging of reactive oxygen species in various crops under drought stress (Umair Hassan et al., 2020). In an experiment with cotton seedlings, Wu et al. (2015) stated that Zn treated plants performed better in drought conditions. Shoot dry matter, net photosynthesis, chlorophyll a and chlorophyll b concentrations as well as the buildup of antioxidative defenses was enhanced in Zn treated plants (Wu et al.; Wu et al., 2015). In experiments with chickpea, Zn treated plants developed water stress more rapidly, however the authors noted that they had a higher biomass production than Zn deficient plants which resulted in higher water stress (Khan et al., 2004). Nevertheless, Zn sufficient plants showed a higher water use efficiency (Khan et al., 2004). No information was found on the effect of Zn on trees under drought conditions. However, it is possible that *H. courbaril* had a higher demand of Zn in order to endure drought season by reducing oxidative stress and improving membrane stability. Enduring drought stress rather than avoiding it fits the idea of a more conservatively behaving evergreen species. To test this hypothesis, controlled experiments with *H. courbaril* individuals treated with varying Zn concentrations under drought conditions are necessary.
Decreasing Zn concentrations from dry to rainy season suggest an interruption of the Zn supply of *S. macrophylla*, *S. capiri* and *H. courbaril*. For latter, the deficiency might have caused further stress, because *H. courbaril* seems to endure drought stress by Zn induced reduction of oxidative stress and improvement of membrane stability.

4.1.6 Phosphorus concentrations in the leaves

According to Hu and Schmidhalter (2005), P deficiency could be an early symptom of drought stress. P uptake is inhibited by low soil moisture, as its uptake occurs mainly by diffusion (Da Silva et al., 2011). In this study, P concentrations decreased from samples taken in dry season to samples taken at the beginning of rainy season (Tab. 3; Fig. 11). This was obvious in all tree species, suggesting that independently of their survival strategy, trees were under nutrient stress during this time period.

In a three years fertilization experiment with P and N by Waring et al. (2019), conducted as well in EEFH, a strong response of below ground biomass was observed. The additional nutrient capital was used for root growth to promote water and nutrient uptake (Waring et al., 2019). Trees treated with P had higher nodulation of arbuscular mycorrhizae which can enhance the plant water status (Waring et al., 2019). The authors concluded that trees invested the additional available nutrients into their fungal symbionts to increase water uptake (Waring et al., 2019). Even though P plays no direct role in the plant water status, it might influence it indirectly via fungal symbionts in the tropical dry forest in EEFH. It is possible that due to the P deficiency in the trees caused by the drought stress in the extended dry season, water uptake was reduced further due to disturbed symbioses to the arbuscular mycorrhizae. Further information on which tree species prefers symbiosis with soil microorganism might be helpful to understand the nutrient and water uptake of the species.

The fact that P concentrations declined regardless the water uptake strategy (evergreens- continuous water supply, deciduous- reduced water supply) stresses the decoupling of water and nutrient uptake of the evergreen species (*H. courbaril* and *S. capiri*) during dry season as mentioned in section 4.1.5.

4.1.7 Sulphur, Iron, Manganese, Copper and Molybdenum in the leaves

The supply of the nutrients S, Fe, Mn, Cu and Mo are essential in proteins, amino acids, for photosynthesis or the metabolism (Da Silva et al., 2011). However, none of these elements are associated directly with the water status of the plants. Therefore, the role and uptake of these elements in the investigated tree species will not be discussed in detail. Differences in the concentrations of each element between samples taken in dry and in rainy season might be because nutrient uptake was inhibited due to low soil moisture (Hu and Schmidhalter, 2005). *S. capiri* samples had higher scores on PC 1 (which included Fe) and PC 3 (more Mo as well as S (lower loading), less Cu) than the other species (Fig. 9+Fig. 10). Fe and Mo are constituents of the Fe protein and MoFe protein which are required to reduce nitrogen (Tais and Zeiger, 2003). The MoFe protein has four subunits, in which two Mo-Fe-S clusters are located (Tais and Zeiger, 2003). Increased concentrations of Fe, Mo and S indicate that *S. capiri* might be superior in reducing N. It could also be possible that *S. capiri* had a different access to Fe, Mo and S. However, Mo and S concentrations were <LOQ in the soil samples. Therefore, this possibility cannot be clarified. It is also possible that *S. capiri* was more efficient in taking up Mo and S than the other species. Fe uptake is discussed in section 4.2.4.

H. courbaril accumulated Mn in its leaves (333 mg/kg compared to <44 mg/kg in the other species, Tab. 5). Even though critical Mn concentrations highly depend on the species (Marschner's, 2012), these elevated Mn concentrations might lead to toxicity symptoms. According to Marschner's (2012), symptoms of Mn toxicity are brown spots on mature leaves, which have been observed on *H. courbaril* leaves on the field site (Fig. 58). It might be possible that on top of experiencing drought and nutrient stress, *H courbaril* accumulated Mn in toxic levels.

Results by the MANOVA show species specific requirements of nutrients (Tab. 3), yet some elements were identified which are useful to improve adaption to drought conditions.
S. macrophylla seems to have a high affinity to K which is necessary for stomata regulation and helps maintain plant water status under drought conditions. In combination with the fact, that *S. macrophylla* has a higher stomata density and increases its sap flow under sufficient water supply, it can be concluded that *S. macrophylla* pursues an exploiting strategy, at least in regard to its water uptake. This allows the species to react fast to available water. *S. capiri* and *G. ulmifolia* contained more B and Ca than the other species. Both elements are important for stabilizing cell walls and in the case of B, for root growth, vessel formation and functioning of the stomata. Both species could use these elements preferentially to improve the water supply by increased root growth and higher stability of the cell walls. *H. courbaril* contained higher Zn concentrations than the other species. Its strategy to endure dry season seems to be reducing stress by antioxidating regulation.
Even though *H. courbaril* and *S. capiri* maintained a continuous water supply in dry season, decreased of Zn and P concentrations was observed. The decoupling of water and nutrient supply could lower the plants performance and could imply serious risks for the tree`s survival.

4.2 Indicators of rooting depth within the soil profiles

Leachable macro- and micronutrient concentrations in the soil profiles were <LOQ for many elements. One reason was that measurement of the elements in the soil leachates was difficult because of the high amount of dissolved organic carbon (DOC) in the samples. When the leachates samples were stabilized with 1 % HNO_3, precipitation of most likely DOC occurred. Inverse aqua regia had to be added to avoid co- precipitations of metals on the DOC, but the chloric acid must have disturbed the measurement which resulted in high LOQs. Nevertheless, it was possible to establish soil profiles for Al, Si, Fe and Mn, Ca and Na, as well as for DOC and pH.

The dominant factor of vertical nutrient distribution is plant cycling (Jobbágy and Jackson, 2001). Therefore, nutrient uptake and consequently rooting depth should be visible in a decline of nutrient concentration and increase of elements, which are of no use for the plants.
Advective transport of substances occurs with the movement of soil water (Amelung et al., 2018). Also, uptake of substances, especially nutrients occurs with sufficient soil moisture (Hu and Schmidhalter, 2005). When soil moisture was reduced to 10-15 % in dry season (Fig. 17-Fig. 19), both processes were inhibited. Soil profiles taken at the end of dry season can therefore be interpreted as “artefacts” from when soil dried out in the beginning of dry season and the plants took up the remaining water. Soil profiles from the beginning of rainy season can be seen as rainy season samples only in 5 to 30/50 cm depth, because rainwater did infiltrate only that far.

4.2.1 Soil profiles of leachable Calcium and Sodium concentrations

Leachable Ca concentrations in the soil plots (Fig. 26) show the typical profile of strongly cycled elements, as suggested in the hypothesis of “nutrient uplift” by Jobbágy and Jackson (2001). Base cations, which are required by plants in large amounts (K, Ca and Mg) are depleted in the subsoil by the plants and return to the top soil through litterfall (Jobbágy and Jackson, 2001). In all soil plot, leachable Ca concentrations were highest in the first 5-10 cm soil depth. When soil was rewetted by the first rains (Fig. 12; Fig. 17-Fig. 19, infiltration until 30 to 50 cm), leachable Ca concentrations declined drastically in the *S. macrophylla* and *S. capiri* plot until 50 cm. No increase of leachable Ca concentrations was observed below 50 cm in the *S. macrophylla* or in the *S. capiri* plot so that transport of Ca into deeper soil layer does not explain the decrease of leachable Ca concentrations in rainy season. It might be possible that Ca was removed from the top soil by surface run off, yet in the TDF in Chamela, Mexico only 10 % of Ca was lost in surface runoff, which means that the macronutrient was held tightly in the ecosystem (Campo et al., 2000). However, results of Campo et al. (2000) cannot be transferred directly to the field site in EEFH because of natural differences and heterogeneity of the both field sites. As Ca concentrations declined as deep as to 30 and 50 cm, surface runoff cannot be the main reason for the decrease of leachable Ca concentration in *S. capiri* and *S. macrophylla* plot. Leachable Ca concentrations in the *H. courbaril* plot were generally lower in dry season than in the other plots, which could be explained by lower Ca concentrations in litter of *H. courbaril* than in litter of the other species (1.1 % in *H. courbaril*, 2.9, 2.4 and 2.8 % Ca in *G. ulmifolia*, *S. capiri* and *S. macrophylla* litter). Campo et al. (2000) reported that 99 % of Ca was returned to the soil in the TDF in Mexico. Consistently, as *H. courbaril* litter contained less Ca, less of the cation was returned to the soil in comparison to the other tree species. In contrast to the *S. macrophylla* and *S. capiri* plots, leachable Ca concentrations in the *H. courbaril* plot did not decline when the top soil layers were rewetted. Only uptake could explain the disappearance of leachable Ca in the *S. macrophylla* and *S. capiri* plot. "Uptake" of Ca was measurable in *S. capiri* individuals (Fig. 2), yet the correlation of the uptake rate and the sap flow failed (Fig. 42). Controversially, "uptake" of Ca was measured in two *H. courbaril* individuals (Fig. 2), yet no decline of the leachable Ca concentration in the soil of either dry or rainy season was measured. Therefore, it cannot be proved that the investigated tree species took up the missing Ca in the *S. capiri* and *S. macrophylla* plots. It could be possible that fungi, microorganisms or other plants took up the Ca as soon as the soil rewetted in the top layers.

Focusing on deeper soil layer, were rain water has not been infiltrated until the second sampling date, leachable Ca concentration did not change over the investigation period. In the *S. capiri* and *H. courbaril* plot, leachable Ca concentrations <50 cm soil depth were below the detection limit, whereas in the *S. macrophylla* plot leachable Ca concentration increased slightly again in 150 cm depth in samples taken in dry season. The increase of the leachable Ca concentration in 150 cm depth in the *S. macrophylla* plot could mean that in this plot, Ca depletion stopped below 100 cm depth. Consequently, plant available Ca was still being depleted in 150 cm soil depth in the *H. courbaril* and *S. capri* plot. This alone is no proof for the different rooting depths of the species, however leachable Na concentrations in the soil profiles (Fig. 27) support this idea: in soil samples taken at the end of dry season, leachable Na concentrations below 100 cm soil depth in the *S. macrophylla* plot doubled in comparison to soil samples taken in shallower soil. Increased Na concentrations in greater soil depth can be considered as an indicator of the end of rooting zone (Joggáby and Jackson, 2004). Roots take up the infiltrated water, yet tend to exclude substances which are of no use for the plants, which results in higher contents in greater depth according to the profiles of leached substances (Joggáby and Jackson, 2004). Based on the increase of leachable Na concentrations below 100 cm soil depth it can be concluded that *S. macrophylla* roots did not reach much further than 100 to 150 cm. This conclusion is supported by the steep descent of soil moisture in 50 cm, but a softer decrease in 150 cm soil depth in the *S. macrophylla* soil plot (Fig. 17). Therefore, bulk fine root density must have been highest in approximately 50 cm soil depth. Information of the soil moisture in 100 cm depth would have been helpful to support this statement. The increase of leachable Ca concentration in 150 cm fits perfectly and supports the hypothesis that water uptake and nutrient depletion mainly occurred above 150 cm soil depth in the *S. macrophylla* soil plot.

In contrast, leachable Na concentrations in soil samples from dry season did not increase in greater depth in the *S. capiri* and only slightly in the *H. courbaril* plot. Soil moisture in the *S. capiri* plot decreased only in 200 cm soil depth in dry season (Fig. 18). In shallower soil depth, no change of soil moisture was monitored during this time period. As mentioned earlier, Ca depletion in the *S. capiri* plot occurred until at least 150 cm soil depth. Adding up the information given by the decrease of soil moisture in 200 cm, the depletion of Ca in minimum 150 cm and the missing increase of Na concentration at the end of the rooting zone implies that water and nutrient uptake occurred deeper than 150 cm depth in dry season in the *S. capiri* plot.

In the *H. courbaril* plot, soil moisture in all depth decreased consistently, yet in 5, 30 and 200 cm soil moisture was lower than in 15 and 50 cm (Fig. 19). These differences might occur due to small changes in soil texture which have a great influence on the retention capacity of the soil (Amelung et al., 2018). Leachable Na concentrations increased in 150 cm depth which implies end of the rooting zone, yet the increase was not as strong as in the *S. macrophylla* plot. Leachable Ca concentrations did not increase in greater depth. Because of the contradicting indicators in the *H. courbaril* plot, no conclusion can be drawn of in which soil depth *H. courbaril* took up its water and nutrients when soil dried out in dry season.

Leachable Na concentrations in rainy season samples decreased drastically in 10 to 50 cm in the *H. courbaril* and 10 to 100 cm in the *S. capiri* plot. Similar to the Ca profiles, leachable Na concentration did not increase below the infiltration depth of the rainwater, therefore leaching into deeper soil layers can be excluded. Also, surface runoff can be excluded because leachable Na concentration declined in soil depths up to 30 and 50 cm. Again, the decrease of leachable Na concentration cannot be explained other than by uptake, even though Na is not considered as an essential nutrient. This fact weakens the argumentation made above, that Na is an indicator for rooting depth because it cannot be excluded that Na depletion might occur due to uptake by plants or microorganisms. In the case of *S. macrophylla* plot, the decrease of Na concentration in rainy season was not as severe as in the *H. courbaril* and *S. capiri* plot.

Leachable Ca and Na concentrations as well as the soil moisture monitoring suggest bulk fine root density in 50 cm for *S. macrophylla* and water uptake of *S. capiri* in 200 cm in dry seasons. Bio-available Ca must have been taken up when the top soil layer rewetted, yet it could not be clarified if these trees, other plants or microorganisms took up the Ca. For *H. courbaril* neither indicators for rooting depth nor Ca uptake were visible in the soil plot.

4.2.2 pH in the soil profiles

Plants can influence soil pH by emitting CO_2 and organic acids in the rhizosphere (Kelly et al., 1998). Therefore, pH in the rhizosphere can vary significantly from the bulk soil (Kelly et al., 1998). The availability of nutrients depends highly on soil pH: availability of micronutrients which are present as cations (such as Mn, Fe or Zn) increases with lower pH and the availability anionic nutrients like $B(OH_2)$ or MoO_4^{2-}) increases with higher pH (Rengel, 2015). Subsequently, soil pH increases or decreases in the rhizosphere depending on whether H^+ or HCO_3^- are emitted by the roots, this however depends on either the plants higher need of cations (release of H^+) or anions (release HCO_3^-) (Rengel, 2015).

pH of all soil plots was slightly acidy (pH 5.5-6.5) for most of the soil samples (Fig. 25). pH of the *H. courbaril* and *S. capiri* plots decreased with soil depth for both sampling dates. In rainy season, pH of *H. courbaril* top soil slightly increased (neutral). During dry season, pH tends to decrease because salts accumulate in the top soil layers. Due to the increased salt concentrations, exchangeable H^+ ions are forced into the soil solution (Rengel, 2015). Vice versa, when salts are been washed out by rainfall, pH increases again (Rengel, 2015). Therefore, increased pH in the top soil of the *H. courbaril* plot could have been either due to washing out of salts, which increases pH or due to the release of HCO_3^- by roots to promote uptake of anionic nutrients. Soil salinity was not measured, however leachable Na concentration (Fig. 27) could be an indicator of salinity as Na is the cation of NaCl. Leachable Na concentrations were elevated in the top soil of the *H. courbaril* plot, but decreased significantly in 10-30 cm. Therefore, pH could have been increased on rainy season samples due to the decreased leachable Na concentrations and consequently decreased salinity. Below 50 cm, pH as well as leachable Na concentrations of dry season and rainy season samples were similar. In the *S. capiri* plot, no major differences between the pH of dry and rainy season samples were discovered. In dry season samples, pH was lowest in 100 cm depth and reached pH 5.5 which is exactly the threshold, of which cationic metals like Mn, Zn or Fe start to become more soluble (Wilkinson, 2000). Concurrently, leachable metal concentrations in the soil profiles were <LOQ in the deeper soil layers the *S. capiri* plot (Fig. 20+Fig. 21; Fig. 50+Fig. 51).

In the *S. macrophylla* plot, dry season and rainy season samples showed opposite courses. The decrease of pH in the topsoil in rainy season could have been caused by increased root activity as organic acids were emitted to increase cationic uptake. However, leachable metal concentration did not decrease significantly more than in the other soil plots, which would have been expected if root exudates would have lowered pH to promote plant availability of the metals in the *S. macrophylla* but not in the other soil plots. Therefore, decrease of pH due to root exudates seems not to be logical.

Joggáby and Jackson (2004) state that the uplift of Ca from subsoil to topsoil layer might explain soil acidification in deeper soil layers. Similarities can be detected when comparing the pH and leachable Ca concentrations of the soil plots. As the Ca concentration in the soil layers decreased when leachable Ca was removed by probably uptake by either plants or microorganisms in the *S. macrophylla* plot (Fig. 26), pH (Fig. 25) decreased as well. Ca concentrations did not decline in the top soil layers of the *H. courbaril* plot and pH in this plot even increased, but more likely due to the wash out of accumulated salts. Contradicting, Ca concentrations decreased in the *S. capiri* plot in the top soil, yet pH did not decrease as significantly as in the *S. macrophylla* plot. Conversely to the decreased Na concentrations in the top soil of the *H. courbaril* plot, increased leachable Na (and therefore salinity) in 150 cm soil depth (Fig. 27) could have been the reason for increased pH in 150 cm depth in the *S. macrophylla* plot.

It can be concluded that soil pH was rather indirectly influenced by root activity in the *S. macrophylla* and *H. courbaril* plot. pH varied in the soil profile depending on the depletion of Ca. As Ca was removed from the soil, pH increased, as suggested by Joggáby and Jackson (2004). Additionally, salinity might have affected pH of the soil as well. pH decreased in the *S. macrophylla* plot when Na concentration peaked and conversely pH increased in the *H. courbaril* plot when Na concentrations decreased. This is only an assumption, because electrical conductivity of the soil solution as indicator of salinity was not measured. In the *S. capiri* plot, pH variations could not be explained by fluctuation of Ca or Na concentrations. Therefore, decrease of pH caused by root activity in the top soil cannot be excluded.

4.2.3 Dissolved organic carbon concentrations in the soil profiles

Dissolved organic carbon (DOC) consists of low molecular organic compounds which either emerge by the degradation of solid organic material or by the emission of organic molecules by roots (Amelung et al., 2018). Roots exudates released to the soil contain carbohydrates, organic acids and enzymes (Pallardy, 2008). These biological weathering agents are usually found in the O and in the A horizon as well as in the rhizosphere (Kelly et al., 1998). Yuan et al. (2020) showed that the increased DOC in the rhizosphere was higher for trees than for herbs and shrubs (Yuan et al., 2020). Therefore, an increase of the DOC content in the soil profiles close to the rooting zone of the trees is expected.

Higher DOC concentrations were found in the *S. macrophylla* and *S. capiri* plot in the top soil layers in dry season than in rainy season (Fig. 22). In 50 cm, DOC concentrations in the *S. macrophylla* plot increased significantly, which could have been caused by root exudates.

However, pH did not decrease in this soil depth in the *S. macrophylla* plot (Fig. 25) which is the logical consequence of the elevated presence of organic acids. Therefore, it is more likely that DOC concentrations increased in 50 cm soil depth due to the degradation of biomass, like fine roots. This supports the hypothesis that bulk root density of *S. macrophylla* individuals during the drying of soil was located in 50 cm depth (section 4.2.1). In contrast, no peak of DOC concentrations was visible in the *S. capiri* plot in dry season samples. In rainy season, DOC concentration declined in both soil plots which might have been caused by C mineralization by microorganism, attachment to the soil matrix or leaching (Amelung et al., 2018). No increased DOC concentrations were detected below 30 to 50 cm, the depth until which the rain water infiltrated at the sampling date in rainy season. Therefore, leaching is rather unlikely, and the decreased DOC concentrations from dry to rainy season are probably caused by mineralization or fixation to the soil matrix.
DOC concentrations in the *H. courbaril* plot showed an opposing course. DOC concentrations were relatively constant in all depth but 5 cm in dry season. Increased DOC concentrations in the top soil are most likely caused by the organic layer on the soil surface. In rainy season, DOC concentrations increased until 30 cm soil depth. Similar to the DOC peak of the *S. macrophylla* plot in 50 cm, the peak in 10 cm in the *H. courbaril* plot cannot be related to decreasing pH value due to the emission of organic acids by the roots. DOC concentration might have increased in the top soil due to the breakdown of organic matter by microorganisms like litter or dead fine roots, which have been accumulated during dry season. The discrepancy of DOC mineralization or fixation between the top soil of *S. macrophylla* and *S. capiri* plots and the construction of DOC in the topsoil of the *H. courbaril* plot might have been caused by the different chemical composition of the litter fall. *H. courbaril* has waxy leaves, which are usually harder to break down (Amelung et al., 2018). Therefore, the decomposition of the litter and the resulting formation of DOC and later mineralization or fixation of the DOC might have been delayed in the top soil of the *H. courbaril* plot in comparison to the *S. macrophylla* and *S. capiri* plots.

The DOC concentrations in the soil profiles provides more evidence that bulk rooting depth of *S. macrophylla* must have been around 50 cm when soil dried out. In contrast, no such pronounced peaks like in the *S. macrophylla* plot were discovered in the *S. capiri* and *H. courbaril* plot in dry season samples, which suggests again that rooting depth was deeper than 150 cm. In rainy season, a great proportion of the DOC in the *S. macrophylla* and *S. capiri* top soil might have been already mineralized or fixed to the soil matrix, whereas in the *H. courbaril* plot, DOC concentrations might have increased by breaking down of organic matter.

4.2.4 Leachable metal (Fe, Mn and Al) and metalloid (Si) concentrations in the soil profiles

Considering the soil properties, which include clayey to loamy soil, with a high content of Ca and pH higher than 5.5, rather immobile metal species are expected. Also, O_2 concentrations are higher in soil under drought conditions which leads to an increase of the oxidized form of Fe (Fe^{3+}) which is not bioavailable and less mobile in the soil (Sardans et al., 2008). Similar, Mn deficiency may even occur in soils with neutral or alkaline pH because Mn gets oxidized and is not further plant available as Mn^{2+} (Rengel, 2015). Surprisingly, high concentrations of leachable and therefore plant available Fe, Mn, Al and Si concentrations were detected, especially in dry season (Fig. 20+Fig. 21; Fig. 50+Fig. 51).

Joggáby and Jackson (2004) state that micronutrients can be cycled according to their “nutrient lift hypothesis” as well. For example, Mn concentrations in the soil of an eucalyptus stand (which accumulates Mn) were depleted in 5-50 cm, but highly increased in organic horizon and in the top mineral soil layer (Joggáby and Jackson, 2004). The soil profiles of the metals (Fe, Mn and Al) and metalloid (Si) (Fig. 20+Fig. 21; Fig. 50+Fig. 51) look differently than for example the profile of Ca (Fig. 26) which was mainly shaped by plant cycling (section 4.2.1). Slight increase of metal and Si concentrations was found in *S. macrophylla* plot in 150 cm in dry season. However, depletion of the metals did not occur on shallower soil layers. Hence, it is difficult to relate the increasing metal and Si concentrations to the end of rooting zone. Therefore, plant cycling might not be the driving factor for the vertical distribution of these elements in the soil.

Rengel (2015) states that in the case of Mn, the supply from the soil does not only depend on plant responses but also on soil chemistry and the activity of microorganisms. Mn as well as Fe are both mobile along the redox gradient of the soil: in reducing conditions, Fe^{2+} and Mn^{2+} are mobile and bioavailable and in aerobic conditions, the metals are oxidized and therefore immobilized and are not bioavailable for plants (Amelung et al., 2018). Redox conditions could change in this soil because anaerobic conditions can arise in clayey soils in rainy season (Amelung et al., 2018), which could influence the distribution of Fe and Mn in the soil profile. However, Al and Si profiles were similar to those of Mn and Fe, and these elements are not redox sensitive. Ergo, peak concentrations of the metals and Si cannot be explained by changing redox conditions.

In all soil profiles, leachable Fe, Mn, Al and Si concentrations accumulated until 50 to 100 cm soil depth with pronounced peaks in 30 cm soil depth. Mn^{2+} or Fe^{3+} and Al^{3+} are known for building stabile complexes with organic compounds (Amelung et al., 2018), and are therefore often associated with the DOC content. Also, one reason for high coefficient of variance of the metal and Si concentrations might have been the DOC content in the leachate (compare Tab.

8). However, metal peaks in 30 cm soil depth in dry season cannot be explained by the DOC dynamic, because no DOC peaks occurred in the *S. capiri* and *H. courbaril* plot. In the *S. macrophylla* plot, DOC concentrations even decreased in 30 cm, so the peak in the metal concentrations could be explained by a dilution effect in this case. As DOC concentrations decreased in the soil samples, metal concentration automatically increased. This provides only a weak explanation, as this effect is not visible in the *S. capiri* and *H. courbaril* plot.
Consisting with the results of this study, drought treatment increased Fe solubility by 65% in an experiment on a Mediterranean field site in Spain (Sardans et al., 2008). Just as in this study, the increased Fe solubility in soils under drought conditions did not fit to the hypothesis that Fe becomes oxidized and therefore insoluble in dry soil in the experiment in Spain (Sardans et al., 2008). The authors explained the elevated Fe solubility in dry soil by the high mortality of microorganism, which releases nutrients into the soil, yet the soluble Fe is not plant available because of the low soil moisture (Sardans et al., 2008), and therefore accumulates in the soil. A high mortality of soil organisms and the accumulation of the released nutrients could explain the increased leachable Al, Fe, Mn and Si concentrations in 30 cm depth. One could argue that the lyse of microorganisms would have resulted in higher DOC concentration in the same depth, yet if there are no decomposers left it would have not been possible to degrade the organic matter of the deceased organisms. I admit that this is highly speculative. However, little research has been done on soil metal concentrations under drought conditions and the study by Sardans et al. (2008) was the only one found which described these circumstances. Also, the possibility that these elements were just more abundant in 30 cm soil depth cannot be excluded because total element concentrations were not measured. More research should be conducted in order to understand the complex interactions of plants, microbes and soil chemistry under drought conditions.
In rainy season, leachable metal concentrations declined drastically and no pronounced peaks are visible. As in the case with the other indicators (Ca, Na and DOC), leaching did not occur because metal concentrations did not increase in deeper soil layers, and surface runoff is also unlikely because metal concentration declined until 50 cm depth. In contrast to Ca, Fe, Mn, Al and Si could not only been taken up by microorganism or plants, but also immobilized for example at clay minerals as so called coatings (Amelung et al., 2018). Considering the possible effect of the microorganisms on the metal concentrations in dry season, it is more likely that uptake decreased the metal concentrations.

Another interesting aspect of the metal and Si soil profiles are the increased leachable concentration in top soil of the *H. courbaril* plot. As mentioned in section 4.2.3, increased DOC concentrations in the topsoil indicate the slower decomposition of the waxy leaves of this species. In the *S. capiri* and *S. macrophylla* plots, tops soil concentrations are low because degradation of the litter and recycling of the nutrients might have occurred already. Further, the *H. courbaril* soil plot is special in regard to the Mn cycling. This species accumulated Mn, as discussed earlier (section 4.1.7), most likely even to toxic levels. Yet, the Mn soil profile of *H. courbaril* does not differ significantly from the soil plots of *S. macrophylla* and *S. capiri*, which did not accumulate Mn in such high concentrations. Also, no strong increase or decrease of leachable Mn was visible but the peak in 30 cm in dry season, but this might have been caused by microorganisms as discussed earlier. It can be concluded that *H. courbaril* must have taken up the Mn in depths greater than 150 cm. This is supported by the fact that soil moisture in the *H. courbaril* plot did not decline (Fig. 19) like in the *S. macrophylla* in 50 cm (Fig. 17) or in *S. capri* plot in 200 cm depth (Fig. 18). *H. courbaril* must have had access to a water and at least Mn source which was located deeper than 200 cm. Bedrock was found below 200 cm, so the possibility of *H. courbaril* rooting in the bedrock requires further scientific attention.

Similar, *S. capiri* contained more Fe in its´ leaves than the other species (Fig. 9), yet soil profile of leachable Fe concentrations did not differ significantly from the other two plots. As in the case for Mn uptake in *H. courbaril*, a soil plot of 150 cm depth might not have been deep enough to determine Fe uptake of the *S. capiri* individuals. This is supported by the decline of soil moisture in 200 cm depth in the *S. capiri* plot, which indicates water and possibly nutrient uptake deeper than 150 cm.

In summary, Fe, Mn, Al and Si concentrations in dry and rainy season might have been strongly influenced by microbiological activities. Peaks in dry season samples could have been caused by the death of microorganism as the soil dried out. Contrary, the decrease of metal and Si concentrations in the beginning of rainy season might have been occurred due to strong microbiological activity. The missing link between the Mn concentration in the soil profile of *H. courbaril* and its possibly toxic concentrations of Mn in its leaves suggests that *H. courbaril* takes up Mn which lays deeper than 150 and water which is deeper than 200 cm. Similar, *S. capiri* contained more Fe in its leaves than the other species, yet Fe concentrations in the soil were not significantly different from the other soil plots. This indicates that *S. capiri* took up water and possibly Fe deeper than 150 cm.

Considering the decline of soil moisture in dry season, leachable Ca, Na, and DOC concentrations as indicators for rooting depth, strong evidence is provided that *S. macrophylla* contained its bulk rooting density until 50 cm in dry season. *S. capiri* most likely contained roots to a minimum of 200 cm due to the decline of soil moisture in this soil depth during dry seasons and missing indication of the end of rooting zone above 150 cm. In the *H. courbaril* plot, no indicators for the end of the rooting zone were visible. The increased Mn concentrations indicate access to a Mn and most likely water pool deeper than 200 cm, maybe even located in the bedrock.

4.3 Soil to plant transfer

Soil to plant transfer factors are usually calculated for the uptake of rare earth elements or radionuclides into crops (f.e. Alharbi and El-Taher, 2013; Mesa-Pérez et al., 2018; Uchida et al., 2007). In this study, transfer factors indicate higher transfer from soil to the plant in rainy season (Fig. 52-Fig. 55), even though concentrations in the leaves stayed the same (Fe (Fig. 6), Mn in S. capiri (Fig. 29)) or decreased (Na (Fig. 28)). No positive correlation of nutrient supply and sap flow was visible but for K, B and S in *S. macrophylla*, K in *G. ulmifolia*, Mg in *H. courbaril* and Mo and S in *S. capiri* (Fig. 38- Fig. 49). However, these elements were below the LOQ in the soil leachates, so transfer factors for these elements could not be calculated. Ca concentrations in the leaves of *S. capiri* and *H. courbaril* increased (Fig. 2), yet correlation of Ca uptake and sap flow failed (Fig. 42). The transfer factors calculated in this study neglect the availability of trees to translocate nutrients in the trees because the element concentration of the soil is merely put in relation to the element concentration in the tree leaf. As in the example of the metals, leachable metal concentrations might have declined by building coatings on the soil matrix or by being taken up by microorganisms (section 4.2.4). Transfer factors in this study are no adequate indicator for the complex interaction between plants, soil and microorganisms because too many influences are completely neglected when the complex system in broken down to one ratio.

5. Conclusion

Water and nutrient uptake strategies of two evergreen and two deciduous TDF tree species were investigated. Nutrient concentration in the leaves and leachable nutrient concentration of the soil were measured to evaluate nutrient uptake. Sap flow of the trees and soil moisture were monitored to investigate the water use of the trees.

The first hypothesis that the investigated trees contain different nutrient concentrations due to their adaption to the limited resources was approved. *S. macrophylla* contained more K for stronger stomatal regulation, *G. ulmifolia* and *S. capiri* more B and Ca for higher cell wall stability and improved stomatal function and *H. courbaril* endures drought stress by Zn induced reduction of oxidative stress and improved membrane integrity. Second hypothesis that the trees obtain these elements because of their rooting depth could not be clarified. Bulk root density of *S. macrophylla* was most likely in 50 cm depth, as indicated by soil moisture, Ca, Na and DOC concentrations. Therefore, water supply of *S. macrophylla* individuals was drastically reduced in dry season, when soil moisture declined until a depth of 150 cm. In order to avoid water stress, *S. macrophylla* requires large amounts of K to regulate its stomata. The exploiting strategy seems like a disadvantage in comparison to the evergreen species, because water and nutrient supply gets interrupted annually. Yet, the higher stomata density and rapid reaction to soil moisture in the beginning of rainy season might allow *S. macrophylla* to scavenge nutrients and water of the top soil, like in this case K, before the more conservative behaving species are able to react.

G. ulmifolia which is also thought to behave rather exploiting must have found other adaption strategies. Developing hairy leaves is one strategy to reduce transpiration and therefore water stress. The increased B and Ca concentrations could have also improved drought resistance by stabilizing cell walls and improving stomata functioning. No information of how *G. ulmifolia* roots influence the soil properties were available, because *G. ulmifolia* grows distributed on the field site and no specific soil plot for *G. ulmifolia* could be established.

H. courbaril reduces loss of water with waxy leaves and seems to have access to a water supply deep into the ground. No indicator of the end of rooting zone was found in the *H. courbaril* plot until 150 cm depth. Development of physical defense of drought stress and deep roots allows the tree to steadily transpire water during dry season. In order to endure oxidative stress in drought conditions, *H. courbaril* requires more Zn than the other species. This endurance of drought stress rather than avoiding it fits to a conservative behaving species. Similar to *G. ulmifolia*, *S. capiri* contained more B and Ca in its leaves. Higher concentrations of these elements could improve cell wall stability and stomatal function. Indicators for the end of rooting zone were absent in the soil profile of *S. capiri*. Soil moisture declined in 200 cm during dry season, indicating a rooting depth of *S. capiri* of at least 200 cm. Increased Fe, Mo and S concentrations were discovered in *S. capiri* which might be connected to the N metabolism. It was not possible to evaluate, if *S. capiri* was superior in taking up these elements or had access to deeper laying nutrient pools.

Therefore, the second hypothesis that deeper rooting species had access to other nutrient pools could not be clarified. Due to the high LOQ for the elements in the soil leachates, many soil profiles had to be dismissed from further analysis. However, data indicates rooting depths of 200 cm for *S. capiri* and even greater for *H. courbaril*. So, it is doubtful, if the required information on nutrient uptake (like Zn for *H. courbaril* or Mo and S for *S. capiri*) would have been found in soil samples <150 cm soil depth. This is already obvious for *S. capiri* which contained more Fe than *S. macrophylla* or *H. courbaril*, yet no significant difference was discovered between the soil profile of *S. capiri* in comparison to the soil profiles of the other species.

Further, a decoupling of water and nutrient uptake in dry season was observed in the evergreen species *H. courbaril* and *S. capiri*. Zn, Fe, Cu, Na and P concentration declined during the investigation period although water supply was maintained. This disconnection of water and nutrient supply could seriously threaten the tree's survival and evergreen, drought resistant species might face a higher threat of starvation than of desiccation.

This study neglects the influence of soil microorganism on nutrient as well as water uptake. Investigating symbiosis partners of the species could be helpful to better understand the plant-microorganism-soil interactions. Also, fine root densities were not analyzed which could help to understand the root morphology of the investigated tree species.

Nevertheless, this study indicates a strong adaption of the tree species on the climatic conditions and major differences in the nutrient and water uptake of evergreen and deciduous species in the tropical dry forest. Leachable element concentrations, pH and DOC of the soil profiles revealed a strong interaction of plant, microbes, and soil properties but also of the climatic conditions. Little information is known on how biogeochemical cycles are influenced by drought. Considering the fact, that drought events will increase with proceeding climate change, the influence of droughts on biogeochemical cycles requires further scientific attention.

6. References

Alfaro, A, E., Alvarado, Alfredo, Chaverri and Adelaida (2001) ‘Cambios edáficos asociados a tres etapas sucesionales tropical seco en Guanacaste, Costa Rica’, *Agronomía Costarricense*, no. 25, pp. 7–20.

Alharbi, A. and El-Taher, A. (2013) ‘A Study on Transfer Factors of Radionuclides from Soil to plant’, *Life Science Journal*, no. 2, pp. 532–539.

Alvarado, A., Mora, A., Chacón, E., Villalobos, J. and Sandí, C. (2018) ‘Concentración foliar de macro- y micro-nutrimentos en cuatro leguminosas maderables del trópico estacionalmente seco de Costa Rica’, *Revista de Biología Tropical*, vol. 66, no. 3, p. 969.

Álvarez-Yépiz, J. C., Búrquez, A., Martínez-Yrízar, A., Teece, M., Yépez, E. A. and Dovciak, M. (2017) ‘Resource partitioning by evergreen and deciduous species in a tropical dry forest’, *Oecologia*, vol. 183, no. 2, pp. 607–618.

Amelung, W., Blume, H.-P., Fleige, H., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K. and Wilke, B.-M. (2018) *Scheffer/Schachtschabel Lehrbuch der Bodenkunde*, Berlin, Heidelberg, Springer Berlin Heidelberg.

Benlloch-González, M., Arquero, O., Fournier, J. M., Barranco, D. and Benlloch, M. (2008) ‘K(+) starvation inhibits water-stress-induced stomatal closure’, *Journal of plant physiology*, vol. 165, no. 6, pp. 623–630.

Bessa, L. A., Oliveira Reis, M. N., Vitorino, L. C. and Silva, F. G. (2022) ‘Evaluation of Requirements and Efficiency Parameters in the Use, Absorption, and Translocation of Nutrients in the Production of Hymenaea courbaril L. Seedlings, a Fruit Tree of Neotropical Importance’, *Journal of Agricultural Studies*, vol. 9, no. 2, p. 1.

Binkley, D. and Giardina, C. (1998) ‘Why do tree species affect soils? The Warp and Woof of tree-soil interactions’, in Van Breemen, N. (ed) *Plant-induced soil changes: Processes and feedbacks,* Dordrecht, Springer Netherlands, pp. 89–106.

Campo, J., Maass, J. M., Jaramillo, V. J. and Martinez Yrizar, A. (2000) ‘Calcium, potassium, and magnesium cycling in a Mexican tropical dry forest ecosystem’, *Biogeochemistry*, no. 49, pp. 21–36.

Castro, J., Chamarro, C., Fallas, M., Miller, R. and Villalobos, G. (2014) *Aspectos geológicos de la Estación Experimental Forestal Horizontes Guanacaste, Costa Rica: Geological mapping of the horizontes experimental forest station, Guanacaste*.

Chadwick, O. A., Chorover, J., Eissenstat, D. M., Hobbie, S. E., Jagodzinski, A. M., Mueller, K. E., Oleksyn, J. and Reich, P. B. (2012) ‘Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment', *Biogeochemistry*, vol. 111, 1-3, pp. 601–614.

Da Silva, E. C., Custódio Nogueira, R. J. M., Da Silva, M. A. and De Albuquerque, M. B. (2011) 'Drought Stress and Plant Nutrition', *Plant Stress*, no. 5, pp. 32–41.

Deutsches Institut für Normung e.V. (2008) *32645: Chemische Analytik- Nachweis-, Erfassungs- und Bestimmungsgrenze unter Wiederholbedingungen- Begriffe, Verfahren, Auswertung*.

Egilla, J. N., Davies, F. T. and Boutton, T. W. (2005) 'Drought stress influences leaf water content, photosynthesis, and water-use efficiency of Hibiscus rosa-sinensis at three potassium concentrations', *Photosynthetica*, vol. 43, no. 1, pp. 135–140.

Ellison, D., Morris, C. E., Locatelli, B., Sheil, D., Cohen, J. and et al. (2017) 'Trees, forests and water: Cool insights for a hot world', *Global Environmental Change*, vol. 43, pp. 51–61.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B. and Otero-Casal, C. (2017) 'Hydrologic regulation of plant rooting depth', *Proceedings of the National Academy of Sciences of the United States of America*, vol. 114, no. 40, pp. 10572–10577.

Farhat, N., Elkhouni, A., Zorrig, W., Smaoui, A., Abdelly, C. and Rabhi, M. (2016) 'Effects of magnesium deficiency on photosynthesis and carbohydrate partitioning', *Acta Physiologiae Plantarum*, vol. 38, no. 6.

Finzi, A. C., Canham, C. D. and Van Breemen, N. (1998) 'Canopy tree-soil interactions within temperate forests: species effects on pH and cations', *Ecological Applications*, no. 8, pp. 447–454.

Finzi, A. C., Van Breemen, N. and Canham, C. D. (1998) 'Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen', *Ecological Applications*, vol. 8, no. 2, pp. 440–446.

Gonçalves, J. F. d. C., Vieira, G., Marenco, R. A., Ferraz, J. B. S., Santos Junior, U. M. d. and Barros, F. C. F. (2005) 'Nutritional status and specific leaf area of mahogany and tonka bean under two light environments', *Acta Amazonica*, vol. 35, no. 1, pp. 23–27.

Hasselquist, N. J., Allen, M. F. and Santiago, L. S. (2010) 'Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence', *Oecologia*, vol. 164, no. 4, pp. 881–890.

Hu, Y. and Schmidhalter, U. (2005) 'Drought and salinity: A comparison of their effects on mineral nutrition of plants', *Journal of Plant Nutrition and Soil Science*, vol. 168, no. 4, pp. 541–549.

Hunter, I. R. and Stewart, J. L. (1993) ‘Foliar nutrient and nutritive content of Central American multipurpose tree species growing at Comayagua, Honduras’, *Commonwealth Forestry Review*, no. 72, pp. 193–197.

IPCC (2022) *Climate Change 2022 - Impacts, Adaptions and Vulnerability*.

Jiménes M., Q., Rojas R., F., Rojas Ch., V. and Rodríguez S., L. (2010) *Timber trees of Costa Rica. Ecology and silviculture*, Instituto Nacional de Biodiversidad.

Jobbágy, E. G. and Jackson, R. B. (2001) ‘The distribution of soil nutrients with depth: Global patterns and the imprint of plants’, *Biogeochemistry*, no. 53, pp. 51–77.

Joggáby, E. G. and Jackson, R. B. (2004) ‘The uplift of soil nutrients by plants: biogeochemical consequences across scales’, *Ecology*, no. 85, pp. 2380–2389.

Kelly, E. F., Chadwick, O. A. and Hilinski, T. E. (1998) ‘The effect of plants on mineral weathering’, *Biogeochemistry*, no. 42, pp. 21–53.

Khan, H. R., McDonald, G. K. and Rengel, Z. (2004) ‘Zinc fertilization and water stress affects plant water relations, stomatal conductance and osmotic adjustment in chickpea (Cicer arientinum L.)’, *Plant and Soil*, vol. 267, 1-2, pp. 271–284.

Lehto, T., Ruuhola, T. and Dell, B. (2010) ‘Boron in forest trees and forest ecosystems’, *Forest Ecology and Management*, vol. 260, no. 12, pp. 2053–2069.

Lugo, A. E. and Murphy, P. G. (1986) ‘Nutrient dynamics of a Puerto Rican subtropical dry forest’, *Journal of Tropical Ecology*, no. 2, pp. 55–72.

Maeght, J.-L., Rewald, B. and Pierret, A. (2013) ‘How to study deep roots-and why it matters’, *Frontiers in plant science*, vol. 4, p. 299.

Marschner's (ed) (2012) *Mineral Nutrition of Higher Plants*, 3rd edn, Elsevier.

Marshall, D. C. (1958) ‘Measurement of Sap Flow in Conifers by Heat Transport’, *Plant Physiology*, no. 33, pp. 386–396.

Mesa-Pérez, M. A., Díaz-Rizo, O., Tavella, M. J., Bagúe, D. and Sánchez-Pérez, J. M. (2018) ‘Soil-to-Plant Transfer Factors of Rare Earth Elements in Rice (Oryza sativa L.)’, *Revista Ciencias Técnicas Agropecuarias*, no. 27, pp. 1–8.

Möttönen, M., Aphalo, P. J. and Lehto, T. (2001) ‘Role of boron in drought resistance in Norway spruce (Picea abies) seedlings’, *Tree physiology*, vol. 21, no. 10, pp. 673–681.

Murphy, P. G. and Lugo, A. E. (1986) ‘Ecology of tropical dry forest’, *Annual Review of Ecology, Evolution, and Systematics*, no. 17, pp. 67–88.

Pallardy, S. G. (2008) *Physiology of woody plants*, 3rd edn, Elsevier.

Paz, H., Pineda-García, F. and Pinzón-Pérez, L. F. (2015) ‘Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest’, *Oecologia*, vol. 179, no. 2, pp. 551–561.

Pierret, A., Maeght, J.-L., Clément, C., Montoroi, J.-P., Hartmann, C. and Gonkhamdee, S. (2016) 'Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research', *Annals of Botany*, vol. 118, no. 4, pp. 621–635.

Pineda-García, F., Paz, H., Meinzer, F. C. and Angeles, G. (2016) 'Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest', *Tree physiology*, vol. 36, no. 2, pp. 208–217.

Powers, J. S. and Tiffin, P. (2010) 'Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches', *Functional Ecology*, no. 24, pp. 927–936.

Raulino, W. N. C., Freire, F. J., Assunção, E. A. d. A., Ataide, K. M. P., Da Silva, H. V. and Da Silva, A. C. F. (2020) 'Nutrition of tree species in tropical dry forest and rainforest environments', *Rev. Ceres*, vol. 67, no. 1, pp. 70–80.

Rengel, Z. (2015) 'Availability of Mn, Zn and Fe in the rhizosphere', *Journal of soil science and plant nutrition*, no. 15, pp. 397–409.

Revelle, W. (2022) *psych: Procedures for Psychological, Psychometric, and Personality Research* [Online].

Sardans, J., Peñuelas, J., Prieto, P. and Estiarte, M. (2008) 'Changes in Ca, Fe, Mg, Mo, Na, and S content in a Mediterranean shrubland under warming and drought', *Journal of Geophysical Research*, vol. 113, G3.

Schröder, J. M., Ávila Rodríguez, L. P. and Günter, S. (2021) 'Research trends: Tropical dry forests: The neglected research agenda?', *Forest Policy and Economics*, no. 122, pp. 1–5.

Sobrado, M. A. (1991) 'Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species', *Functional Ecology*, no. 5, pp. 608–616.

Sullivan, J. and Enquist, B. J. (2001) *Vegetative key and descriptions of tree species of the tropical dry forests of upland Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica* [Online].

Tais, L. and Zeiger, E. (2003) *Plant Physiology*, 3rd edn, Sinauer Associates.

Uchida, S., Tagami, K. and Hirai, I. (2007) 'Soil-to-Plant Transfer Factors of Stable Elements and Naturally Occurring Radionuclides (1) Upland Field Crops Collected in Japan', *Journal of Nuclear Science and Technology*, vol. 44, no. 4, pp. 628–640.

Umair Hassan, M., Aamer, M., Umer Chattha, M., Haiying, T., Shahzad, B., Barbanti, L., Nawaz, M., Rasheed, A., Afzal, A., Liu, Y. and Guoqin, H. (2020) 'The Critical Role of Zinc in Plants Facing the Drought Stress', *Agriculture*, vol. 10, no. 9, p. 396.

Waring, B. G., Pérez-Aviles, D., Murray, J. G. and Powers, J. S. (2019) ‘Plant community responses to stand-level nutrient fertilization in a secondary tropical dry forest’, *Ecology*, vol. 100, no. 6, e02691.

White, P. J. and Brown, P. H. (2010) ‘Plant nutrition for sustainable development and global health’, *Annals of Botany*, vol. 105, no. 7, pp. 1073–1080.

Wickham, H. (2016) *Ggplot2: Elegant Graphics for Data Analysis* [Online], 2nd edn, Cham, Springer international publishing; Imprint; Springer. Available at https://ebookcentral.proquest.com/lib/kxp/detail.action?docID=4546676.

Wilkinson, R. E. (ed) (2000) *Plant-environment interactions*, 2nd edn, New York, Marcel Dekker.

Wimmer, M. A. and Eichert, T. (2013) ‘Review: mechanisms for boron deficiency-mediated changes in plant water relations’, *Plant science : an international journal of experimental plant biology*, 203-204, pp. 25–32.

Wu, S., Hu, C., Tan, Q., Li, L., Shi, K., Zheng, Y. and Sun, X. (2015) ‘Drought stress tolerance mediated by zinc-induced antioxidative defense and osmotic adjustment in cotton (Gossypium Hirsutum)’, *Acta Physiologiae Plantarum*, vol. 37, no. 8.

Yuan, Y., Dai, X., Fu, X., Kou, L., Luo, Y., Jiang, L. and Wang, H. (2020) ‘Differences in the rhizosphere effects among trees, shrubs and herbs in three subtropical plantations and their seasonal variations’, *European Journal of Soil Biology*, vol. 100, p. 103218.

VI. Appendix

Tab. 9. Function and mobility of each measured element in plants, according to Wilkinson (2000), Pallardy (2008) and Tais and Zeiger (2003).

Element	Function	Mobility
P	Energy transport, part of nucleoproteins and phospholipids	Mobile
K	Enzyme activation, protein synthesis, osmoregulation, stomatal opening and closing, photosynthesis and cell expansion	Highly mobile
S	Constituent of amino acids (cysteine, methionine, coenzymes, ferredoxin, biotin, thiamine) and sulfolipids	Relatively immobile
Ca	Cell wall elasticity, involved in N metabolism, activator/regulator of enzymes (f.e. amylase)	Relatively immobile
Mg	Constituent of chlorophyll end several enzyme systems, ribosomes	Gets translocated easily
Fe	in chloroplasts, synthesis of chloroplast proteins. As well in respiratory enzymes (peroxidases, catalase, ferredoxin, cytochrome oxidase)	Relatively immobile
Mn	Chlorophyll synthesis, O2 evolution step in photosynthesis	Somewhat mobile
Zn	Part of enzymes and enzyme cofactor, protein synthesis (cofactor of RNA polymerase)	Relatively immobile
Cu	Part of enzymes (f.e. ascorbic acid oxidase and tyrosinase)	Relatively immobile
B	Complexes with sugars, stabilizing cell wall pectic network and regulating cell wall pore size	Depending on the species
Mo	Nitrate- reducing enzyme system	Mobile

Tab. 10. Mean and range of reproduction rate (RR) of the certified references, measured for quality control.

Element	RR in % GBW07603		RR in % 1515	
	Mean	Range	Mean	Range
Al	36	30-46	56	40-75
Ca	102	96-112	94	91-101
Fe	85	74-96	78	72-84
K	95	91-103	92	87-110
Mn	100	93-106	88	86-90
Na	100	96-103	94	88-102
Mg	93	82-103	89	85-98
P	88	81-92	-	
S	95	83-105	-	
Cu	97	83-106	97	89-112
Si	5	5-6	-	
Zn	99	93-104	95	85-107
B	100	93-104	102	94-125
Co	135	124-161	1750 (124)	100-9878 (133)
Ni	180 (117)	106-498 (129)	4981 (142)	129-29175 (159)
Mo	142	129-154	5418 (313)	106-30947 (457)

Tab. 11. Mean of the coefficient of variation of each element in %, calculated by the standard deviation and mean concentrations of the analyzed triplicates.

Element	Mean coefficient of variance in %	
	Leaves	Soil leachate
Al	-	30.9
Ca	1.10	11.3
Fe	1.4	32.5
K	0.9	-
Mn	1.13	41.3
Na	2.2	4.0
Mg	1.4	-
Zn	1.08	-
P	0.99	-
S	2.6	-
Cu	0.9	-
Si	-	18.0
B	6.7	-
Mo	2.3	-
pH	-	0.4
DOC	-	14.4

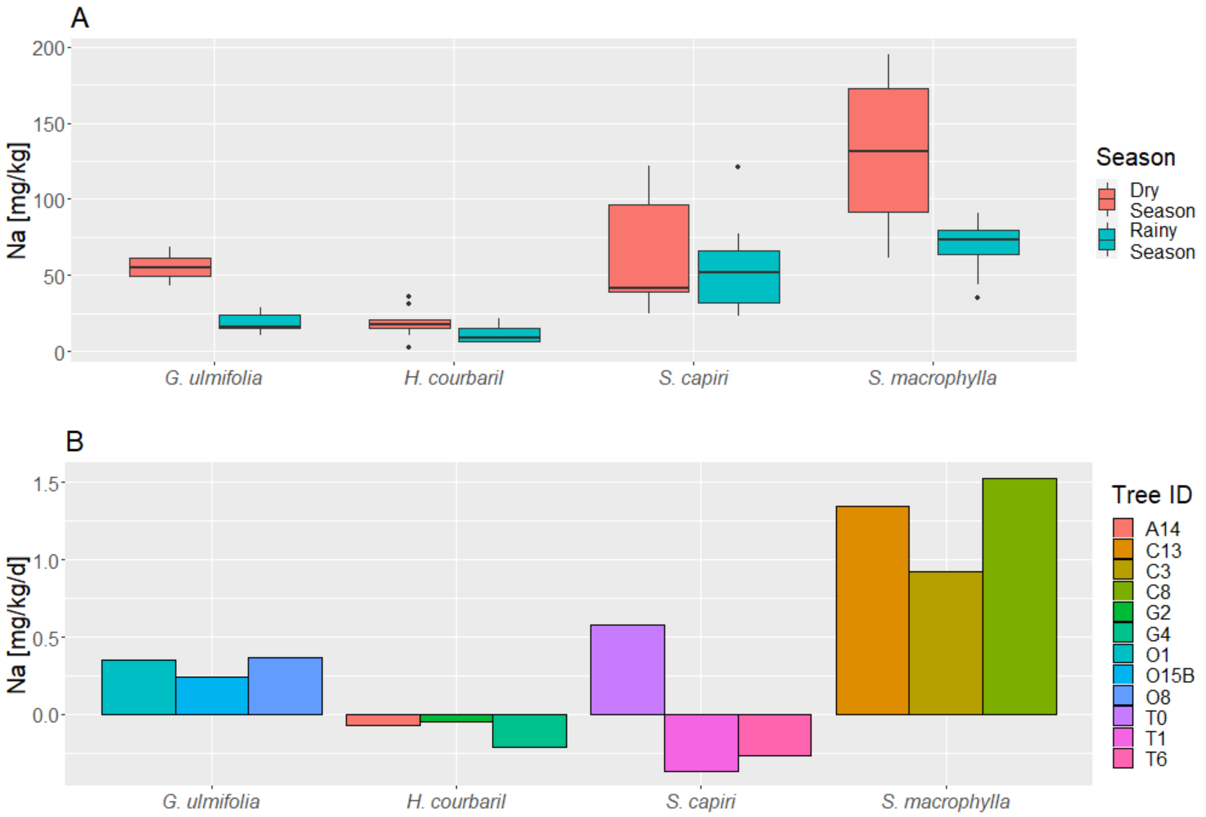

Fig. 28. Absolute Na concentrations in the laves of dry and rainy season (A) and Na uptake rates into the leaves during the investigation period.

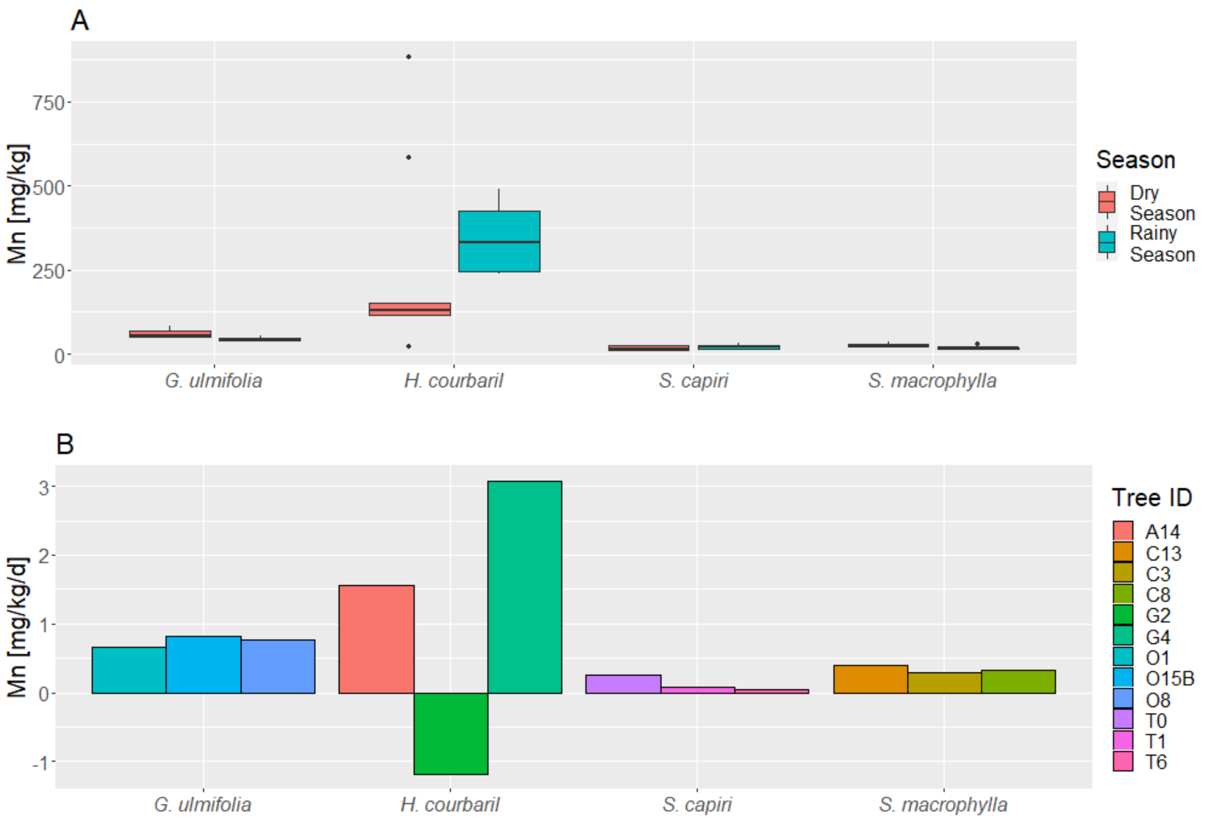

Fig. 29. Absolute Mn concentrations (A) and daily Mn uptake rates (B) into the tree species.

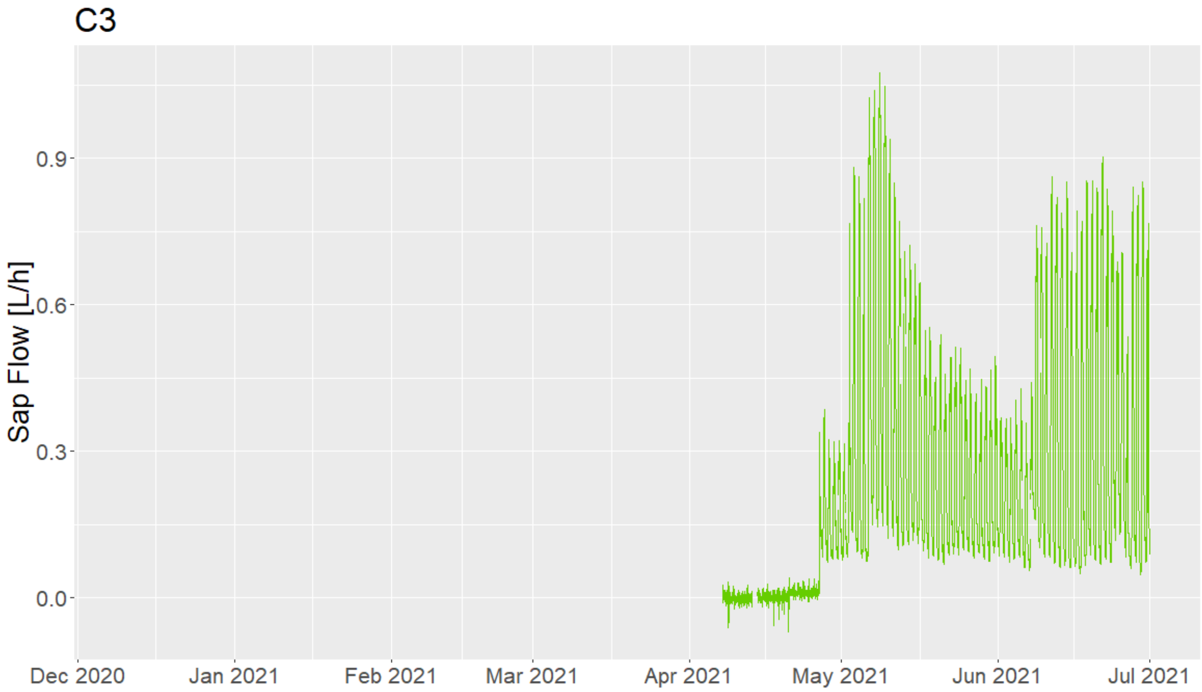

Fig. 30. Sap flow of S. macrophylla (individual C3) in the first half of 2021.

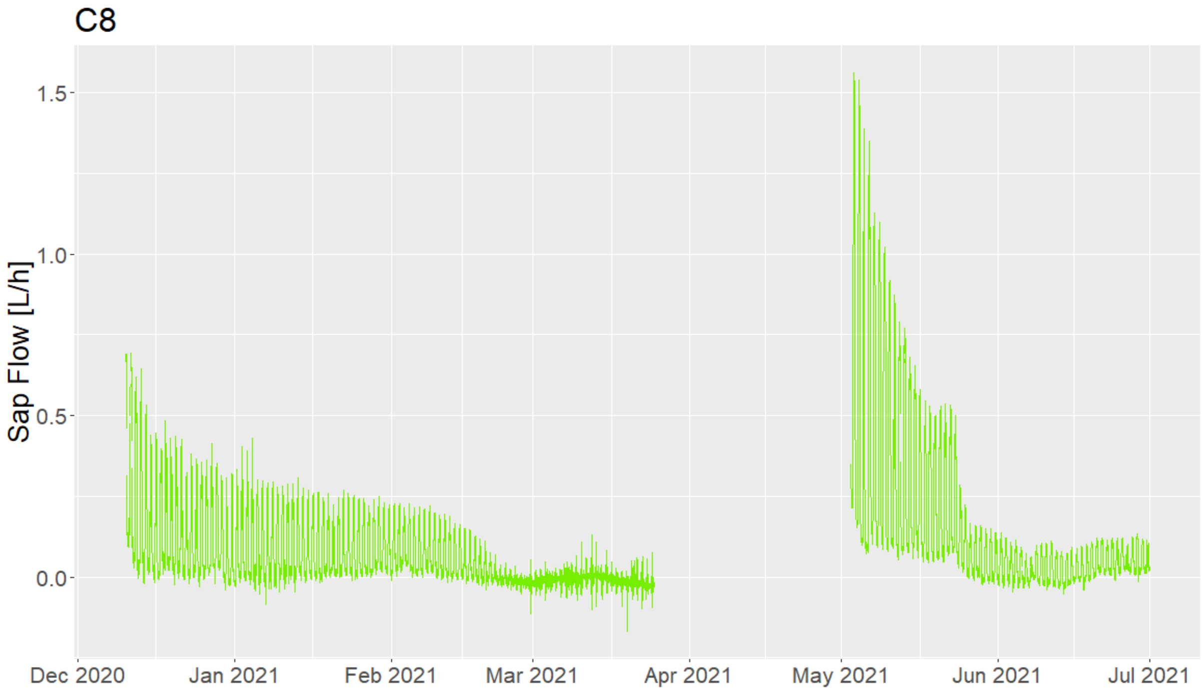

Fig. 31. Sap flow of S. macrophylla (individual C8) in the first half of 2021. Sensor was not functioning in April.

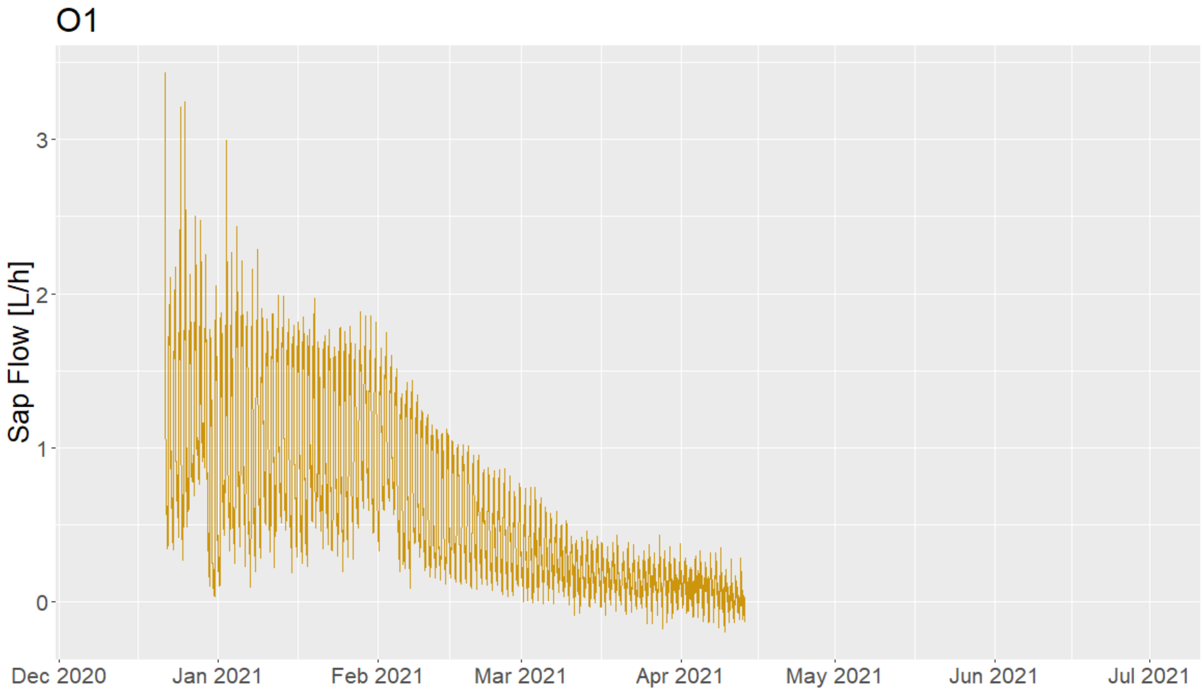

Fig. 32. Sap flow of G. ulmifolia (individual O1) in the first half of 2021. Sap flow sensor broke after mid of April.

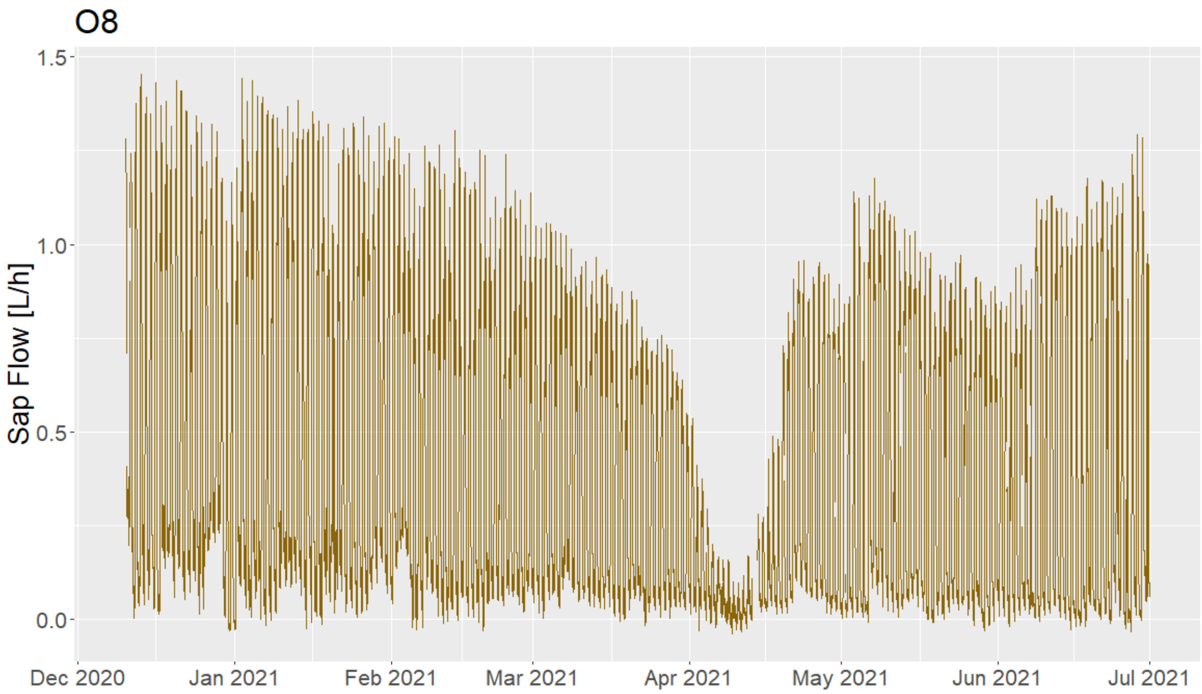

Fig. 33. Sap flow of G. ulmifolia (individual O8) in the first half of 2021. Sap flow decreased in the beginning of April when the tree shed its' leaves.

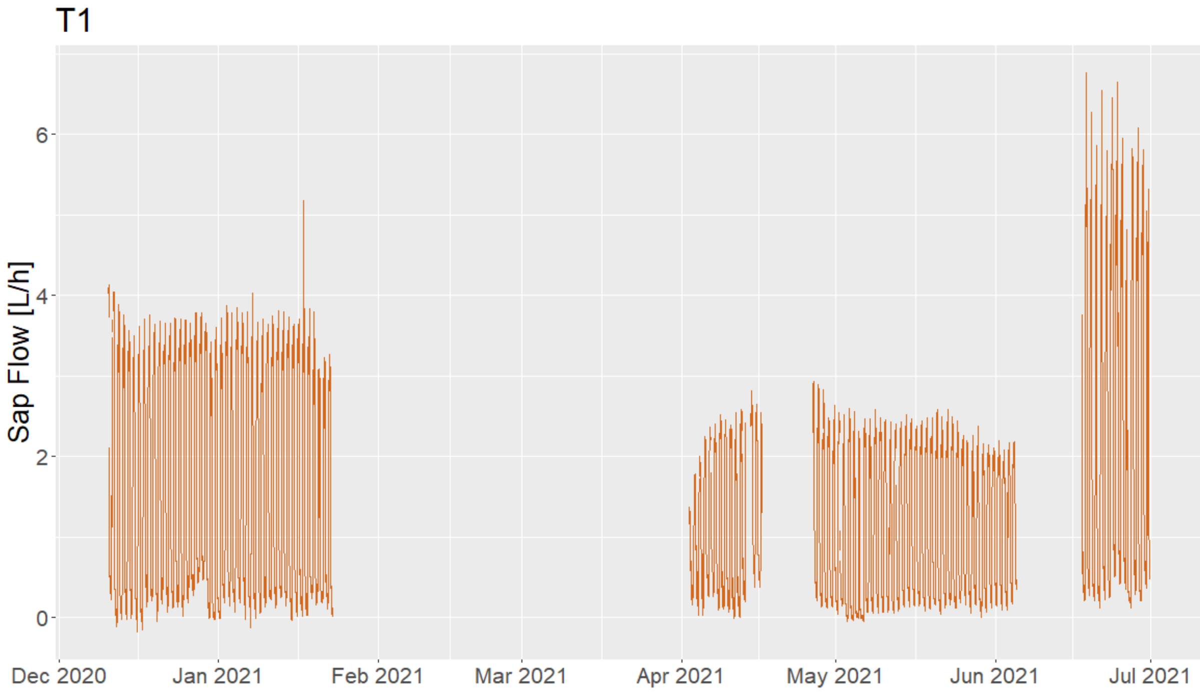

Fig. 34. Sap flow of S. capiri (individual T1). Sensor did not record data from February until April, beginning of May and mid of June.

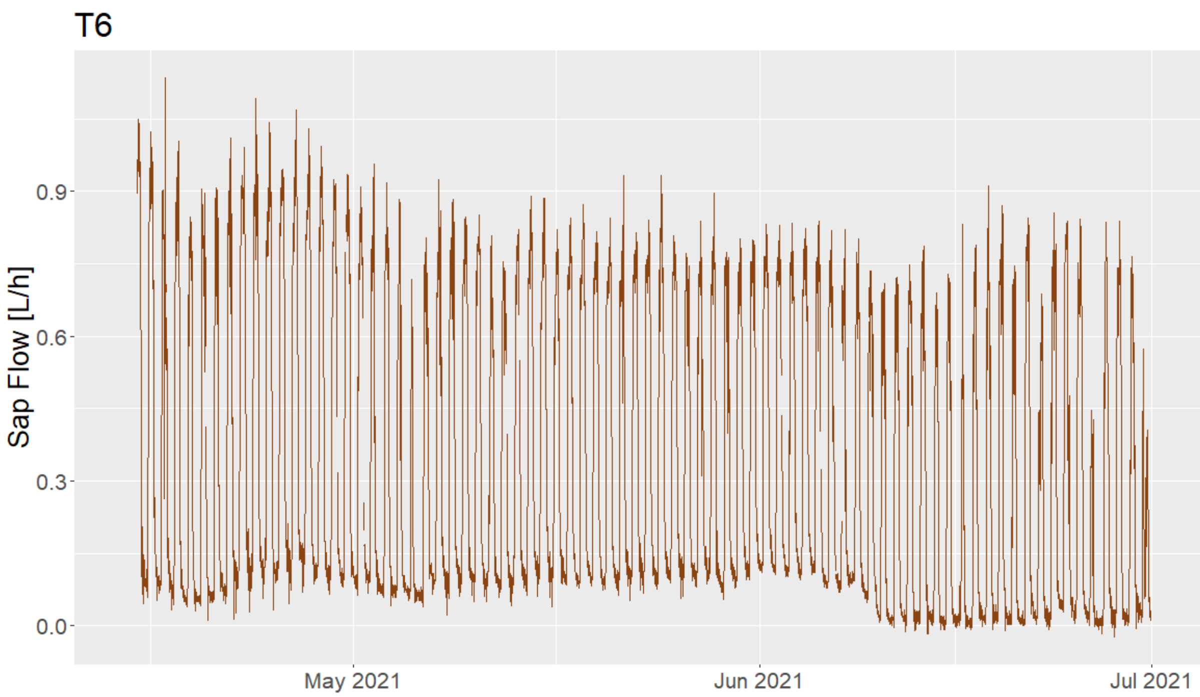

Fig. 35. Sap flow of S. capiri (individual T6). Sap flow sensor was installed in April 2021.

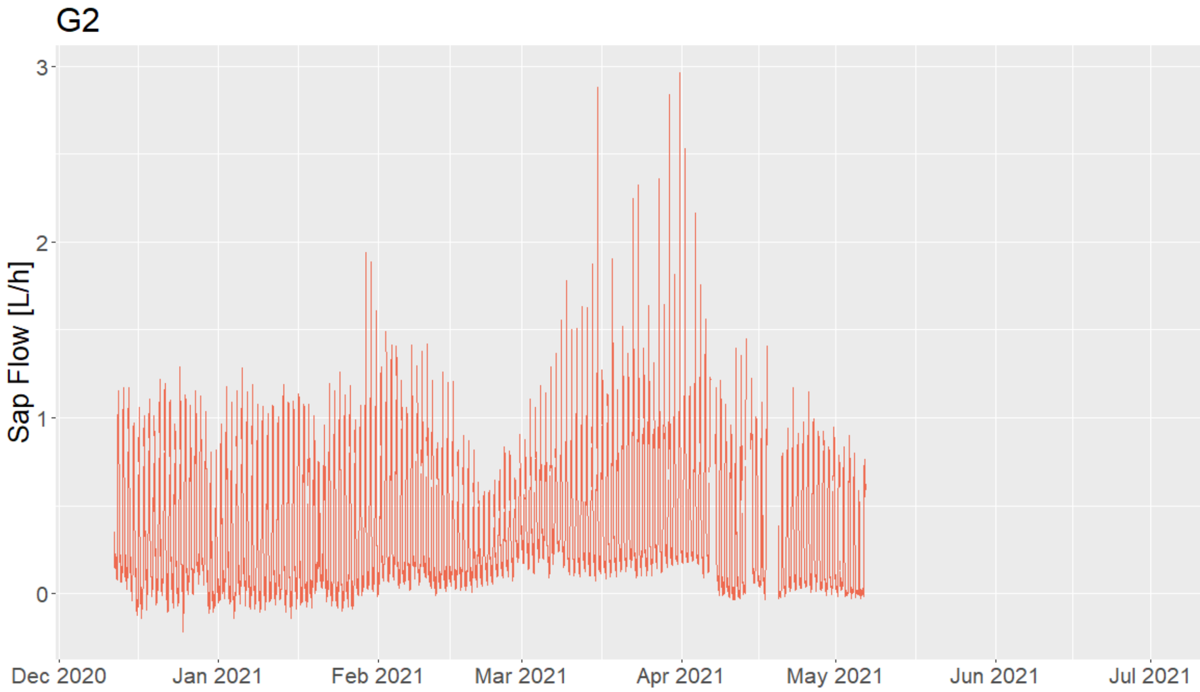

Fig. 36. Sap flow of H. courbaril (individual G2) in the first half of 2021. Drop of sap flow was most likely caused by shedding old and developing new leaves at the end of February.Sap flow sensor broke after May.

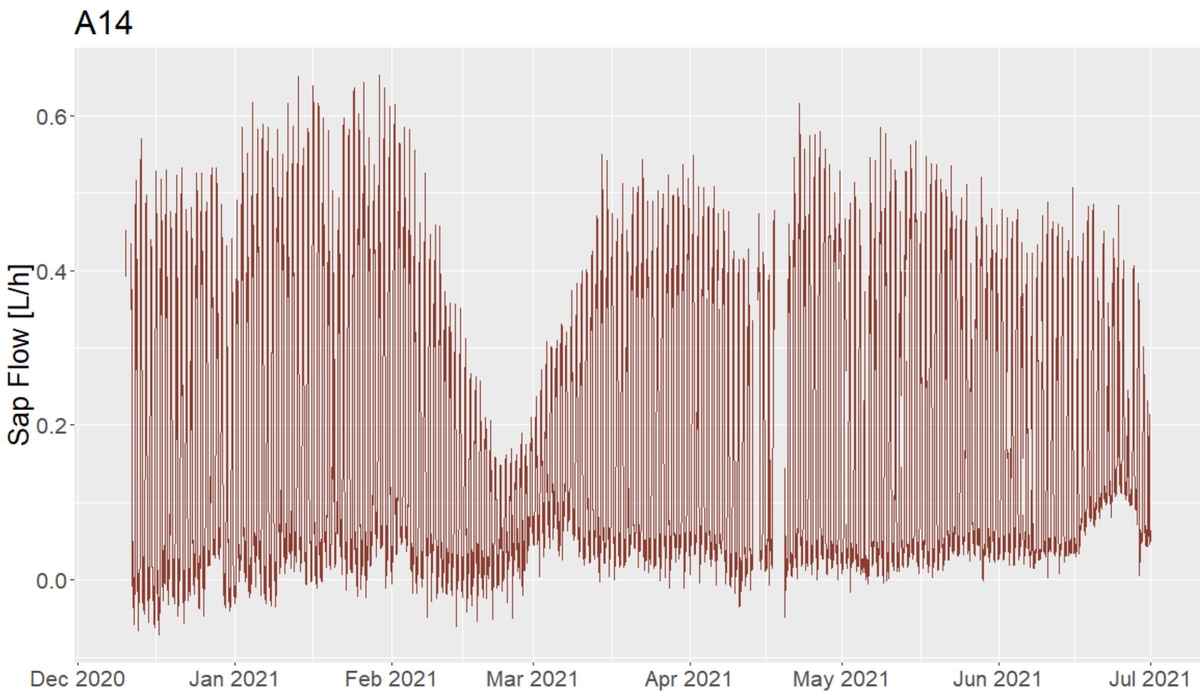

Fig. 37. Sap flow of H. courbaril (individual A14) in the first half of 2021. Drop of sap flow was most likely caused by shedding old and developing new leaves at the end of February.

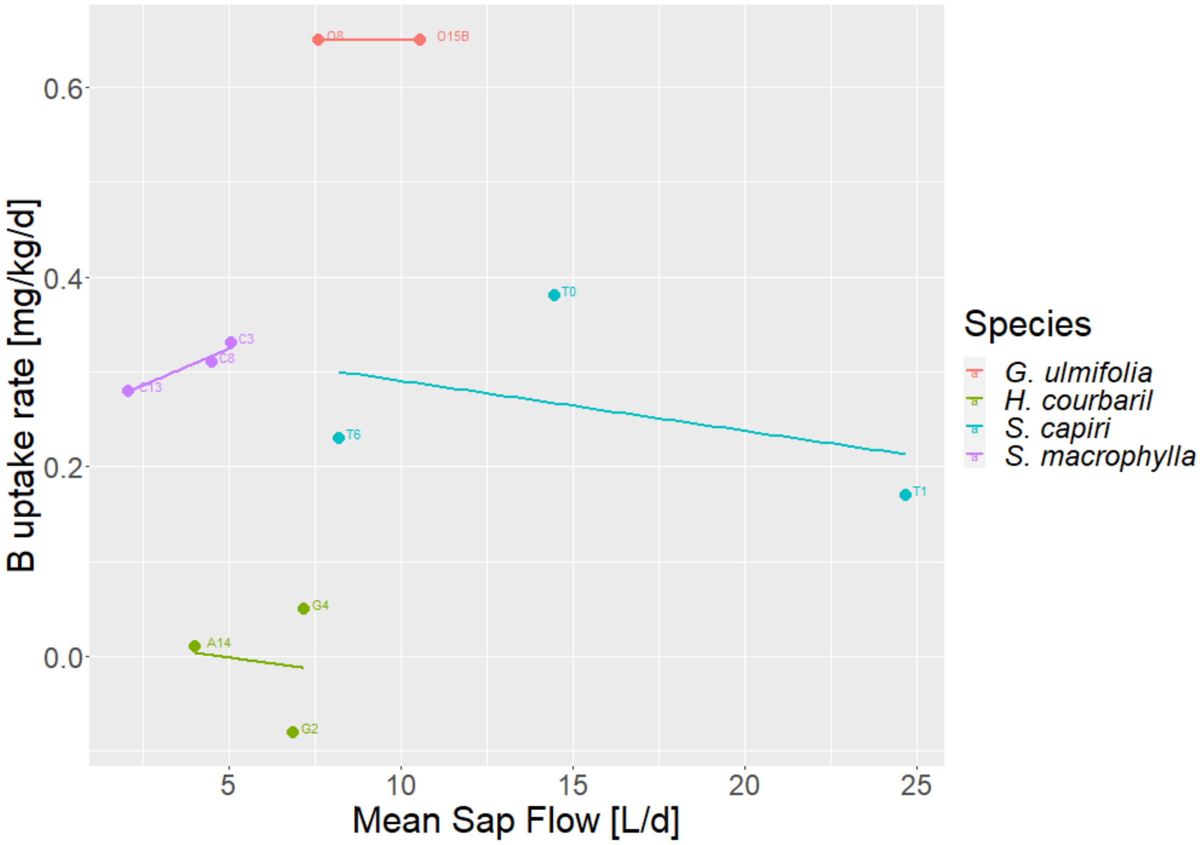

Fig. 38. Scatterplot of daily B uptake in mg/kg/day and daily mean sap flow in L/d.

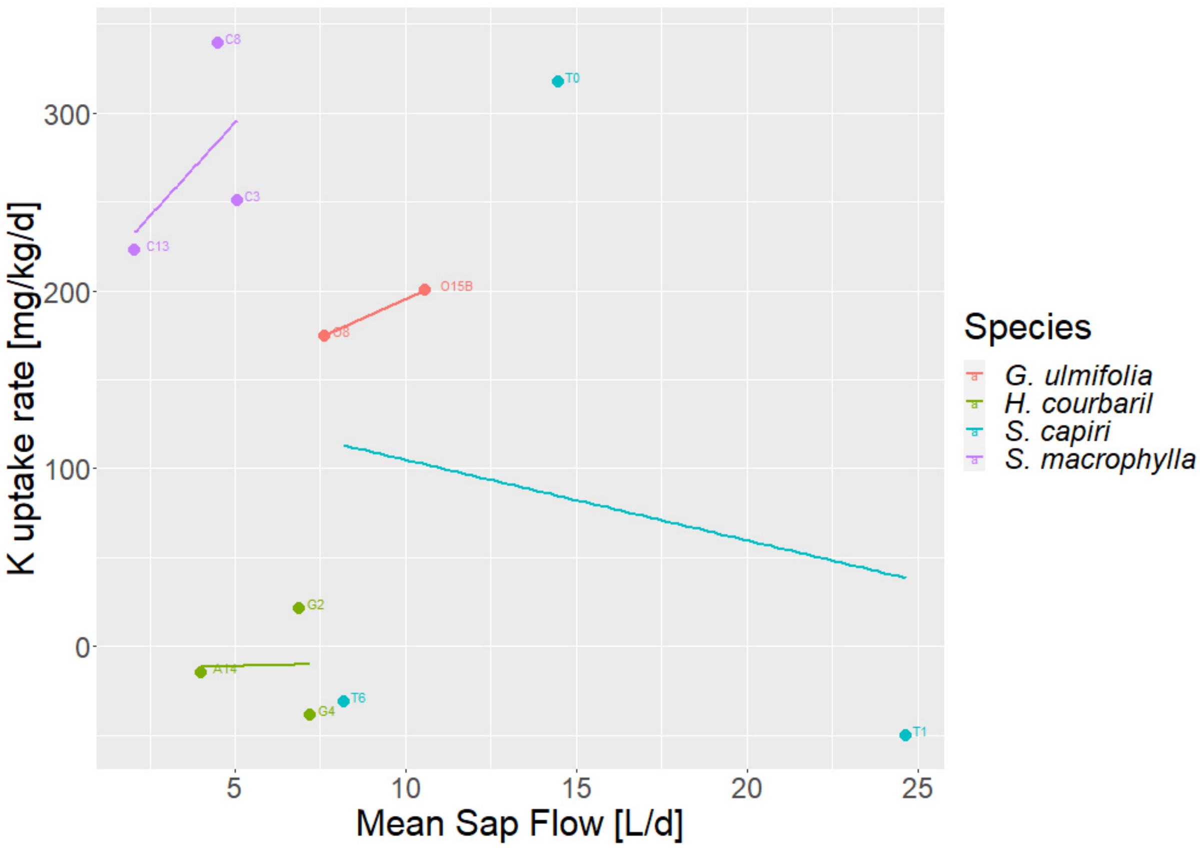

Fig. 39. Scatterplot of daily K uptake in mg/kg/day and mean daily sap flow in L/d.

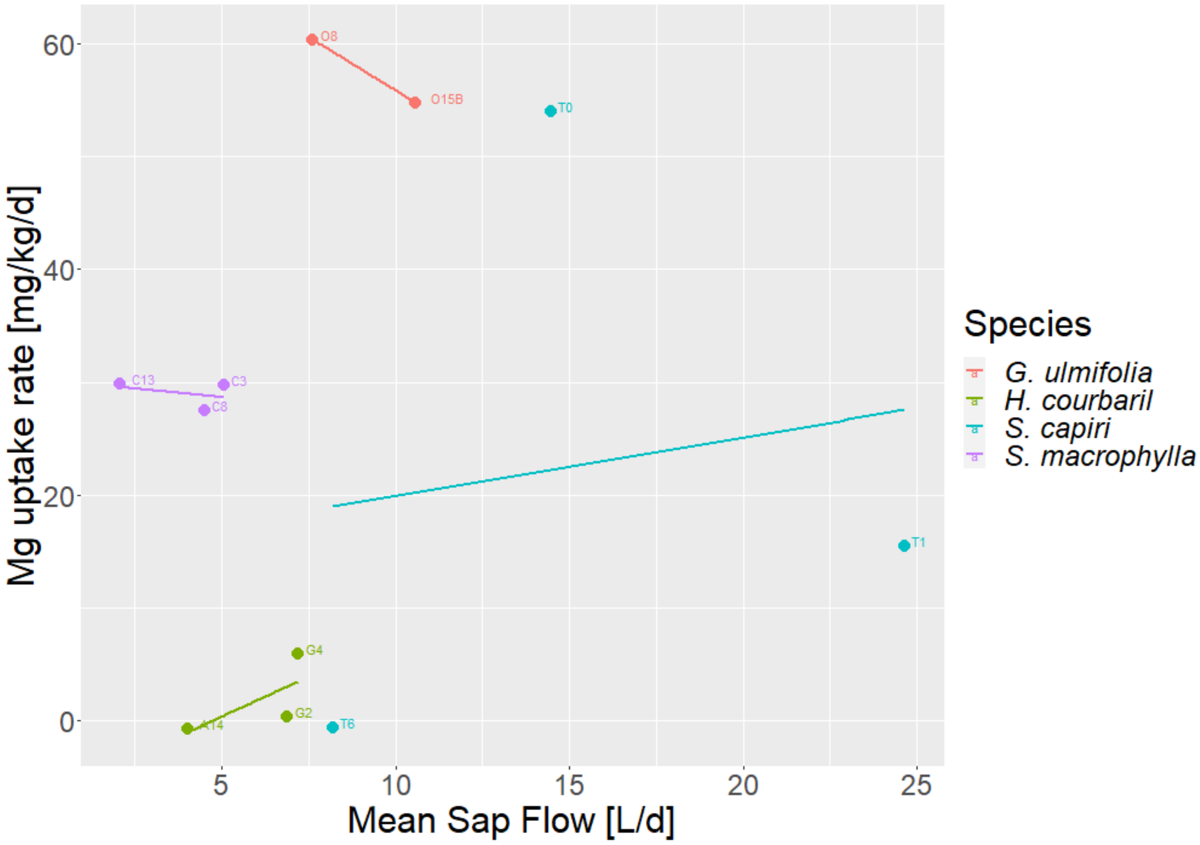

Fig. 40. Scatterplot of daily Mg uptake in mg/kg/d and mean daily sap flow in L/d.

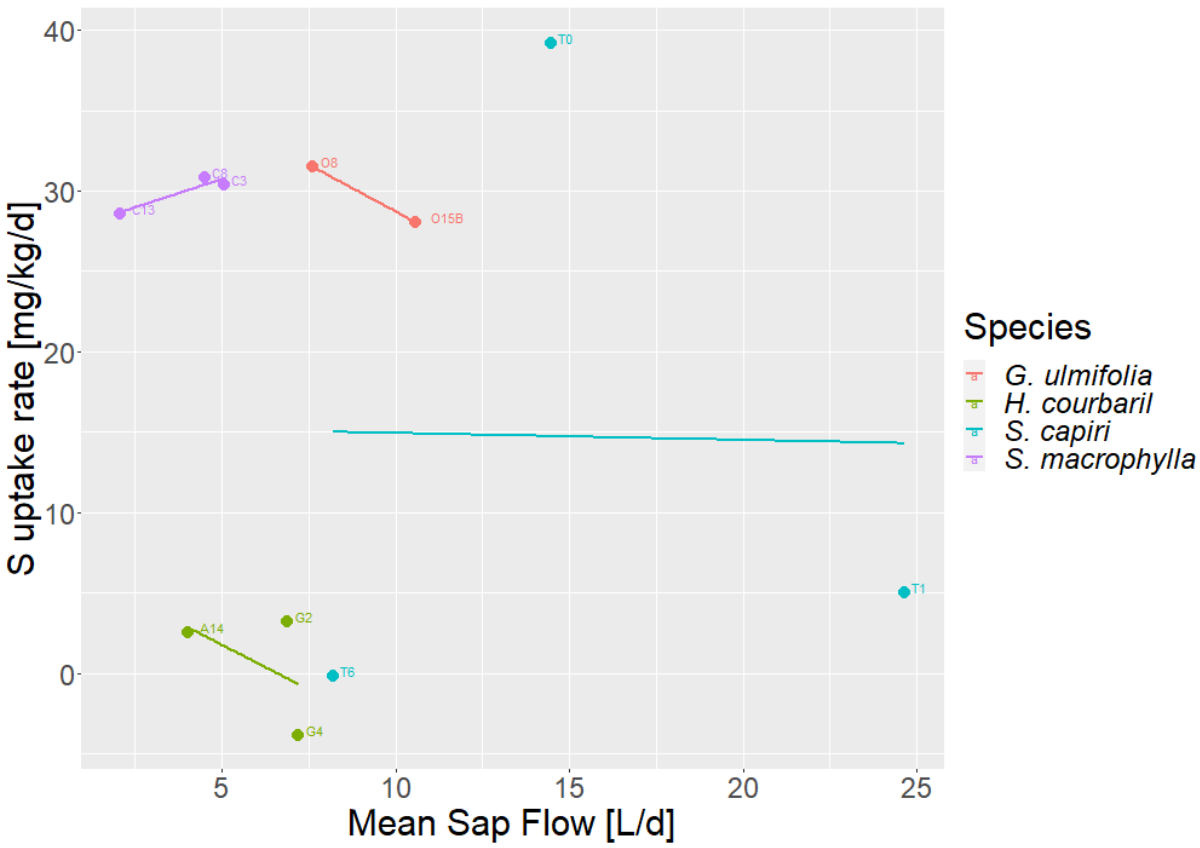

Fig. 41. Scatterplot of daily S uptake in mg/kg/day and mean daily sap flow in L/d.

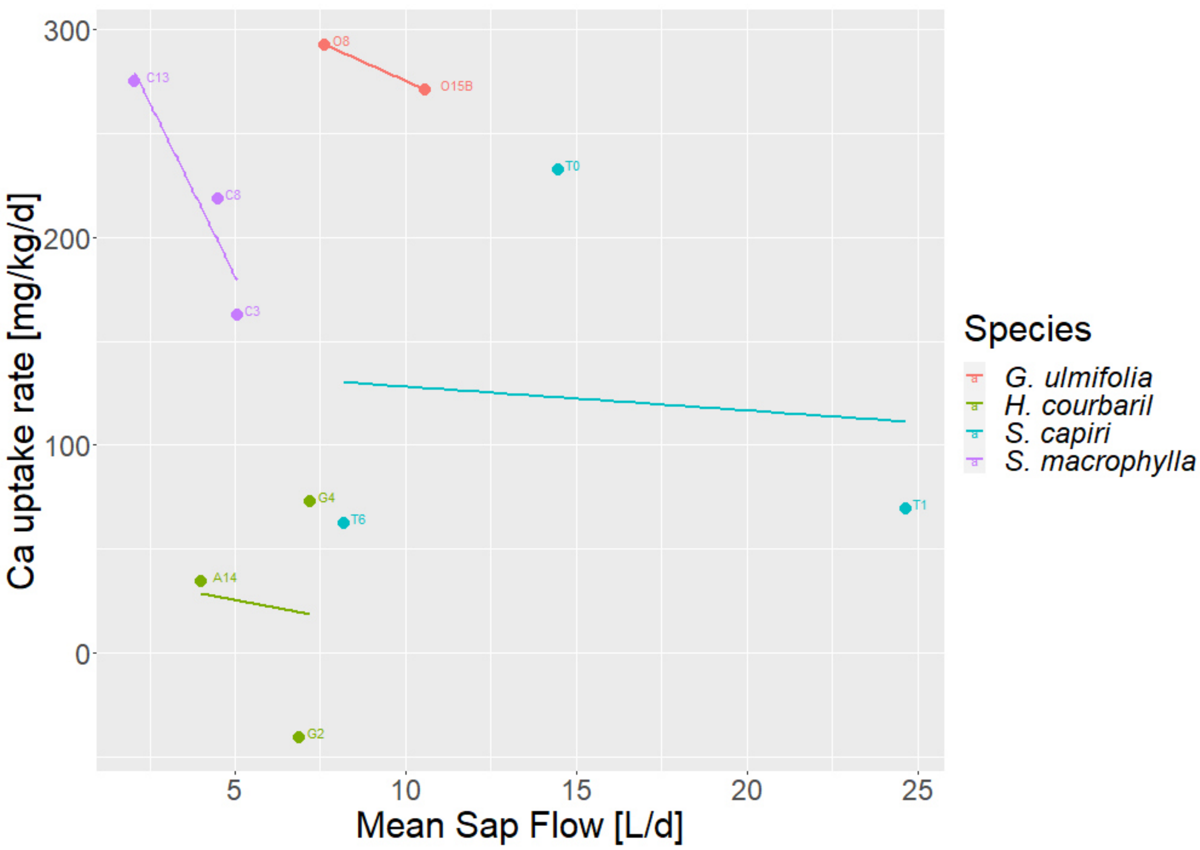

Fig. 42. Scatterplot of daily Ca uptake in mg/kg/d and mean daily sap flow in L/d.

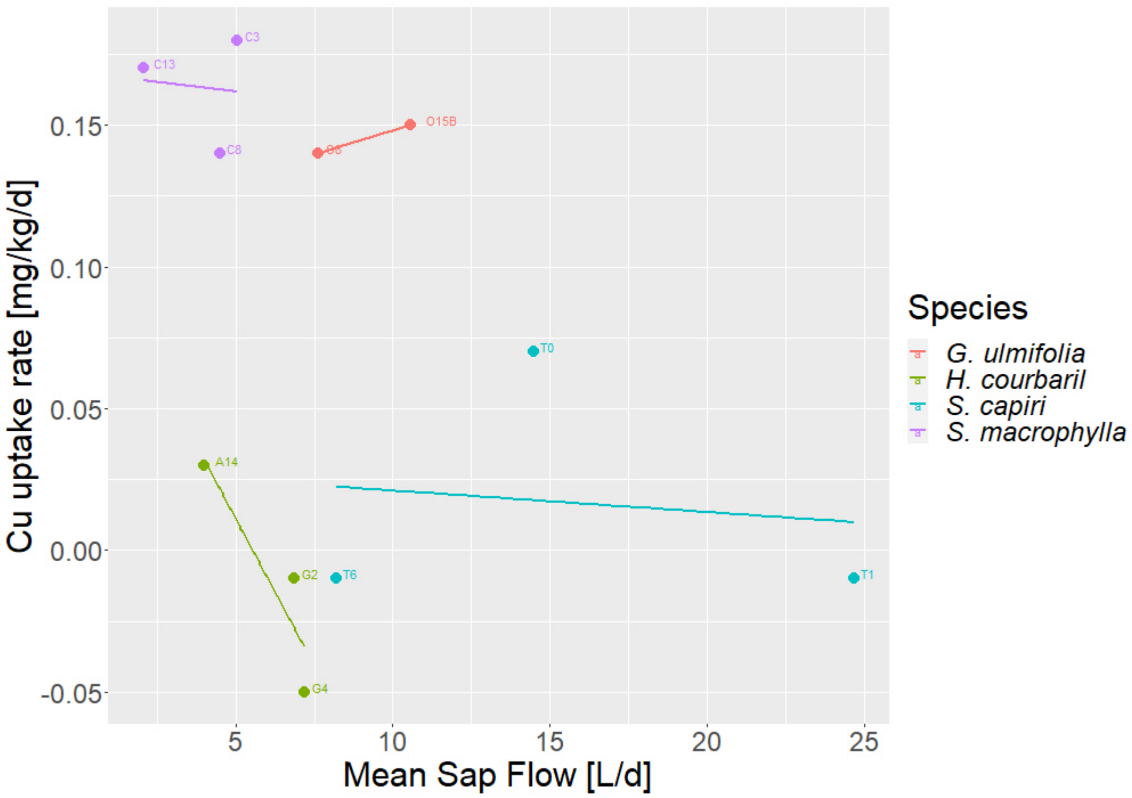

Fig. 43. Scatterplot of daily Cu uptake in mg/kg/d and mean daily sap flow in L/d.

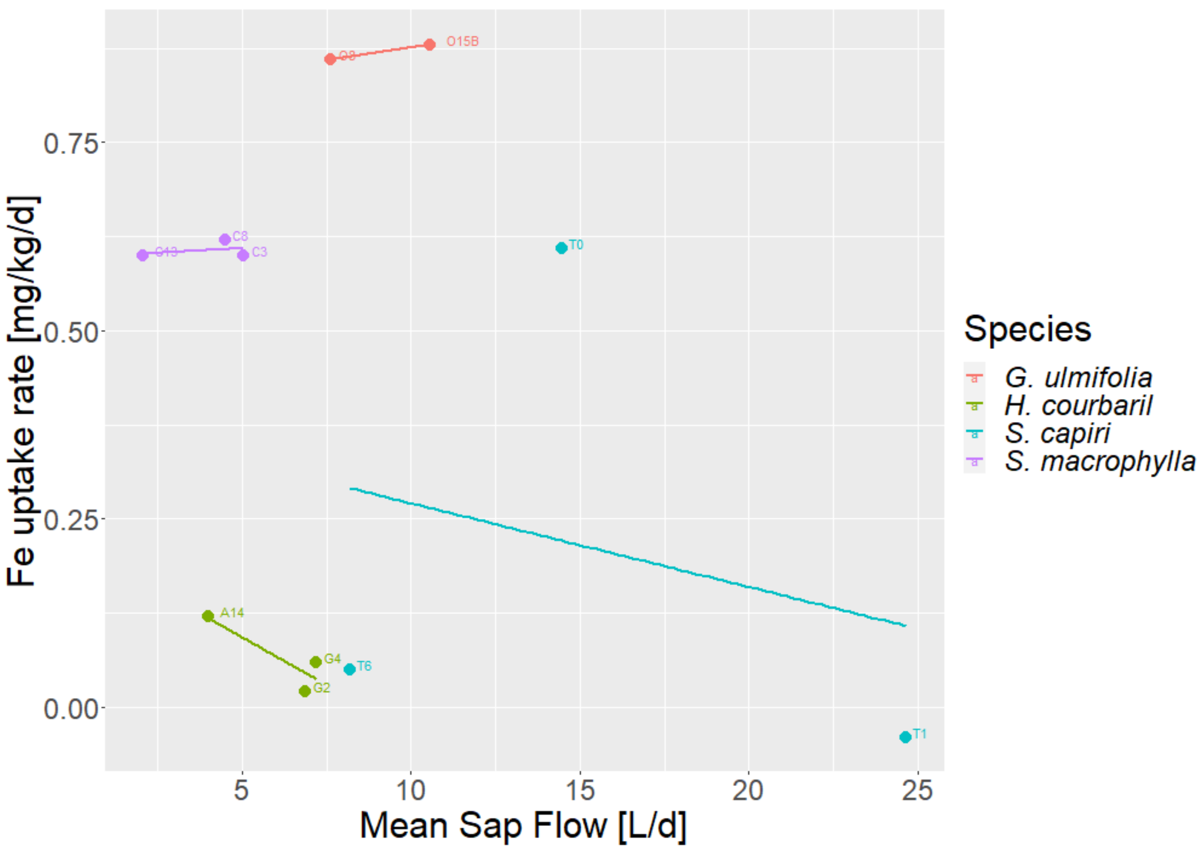

Fig. 44. Scatterplot of daily Fe uptake in mg/kg/d and mean daily sap flow in L/d.

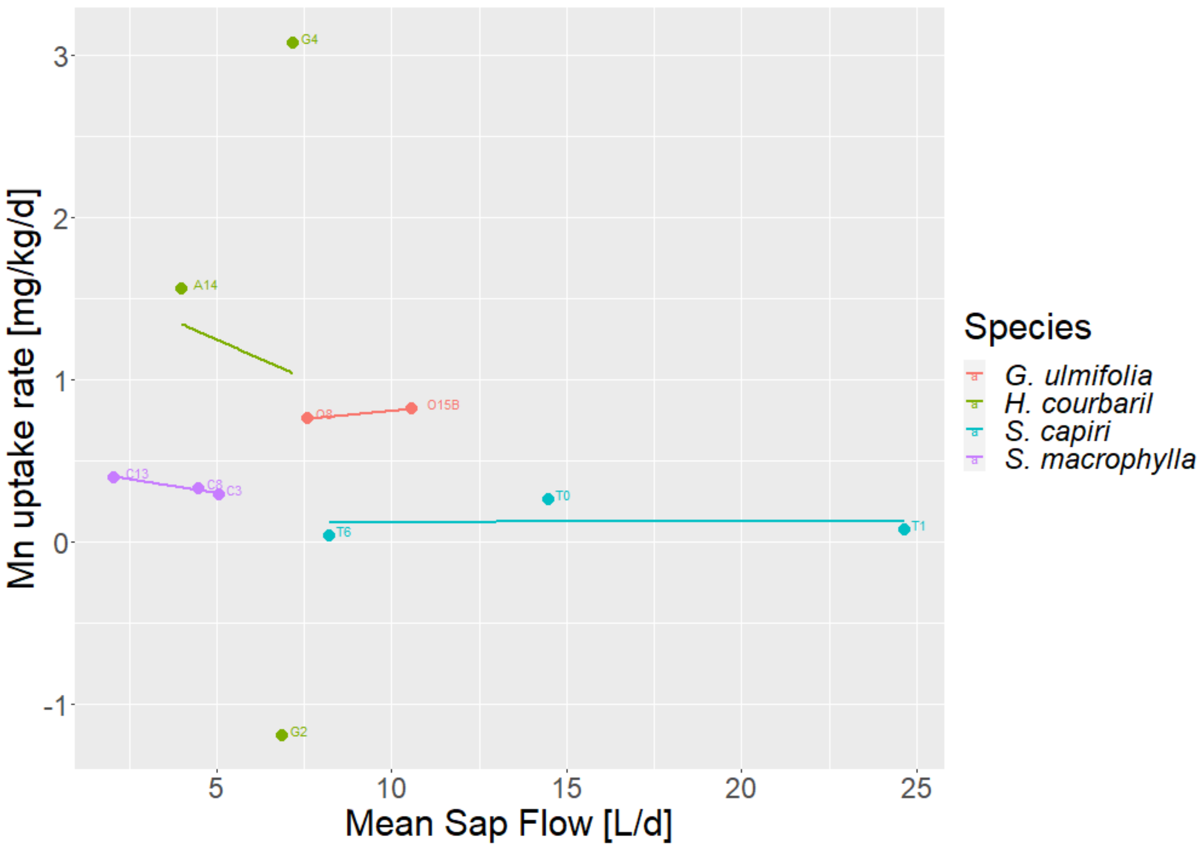

Fig. 45. Scatterplot of daily Mn uptake in mg/kg/d and mean daily sap flow in L/d.

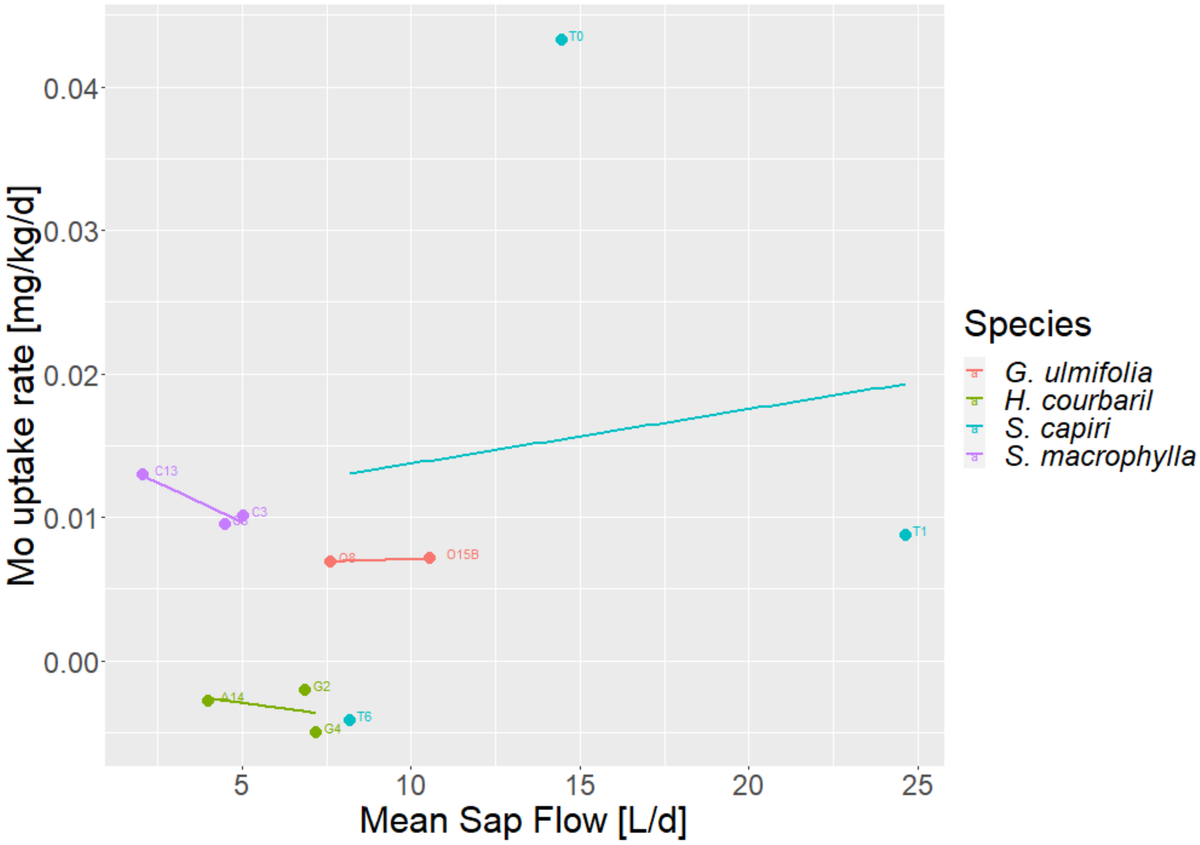

Fig. 46. Scatterplot of daily Mo uptake in mg/kg/d and mean daily sap flow in L/d.

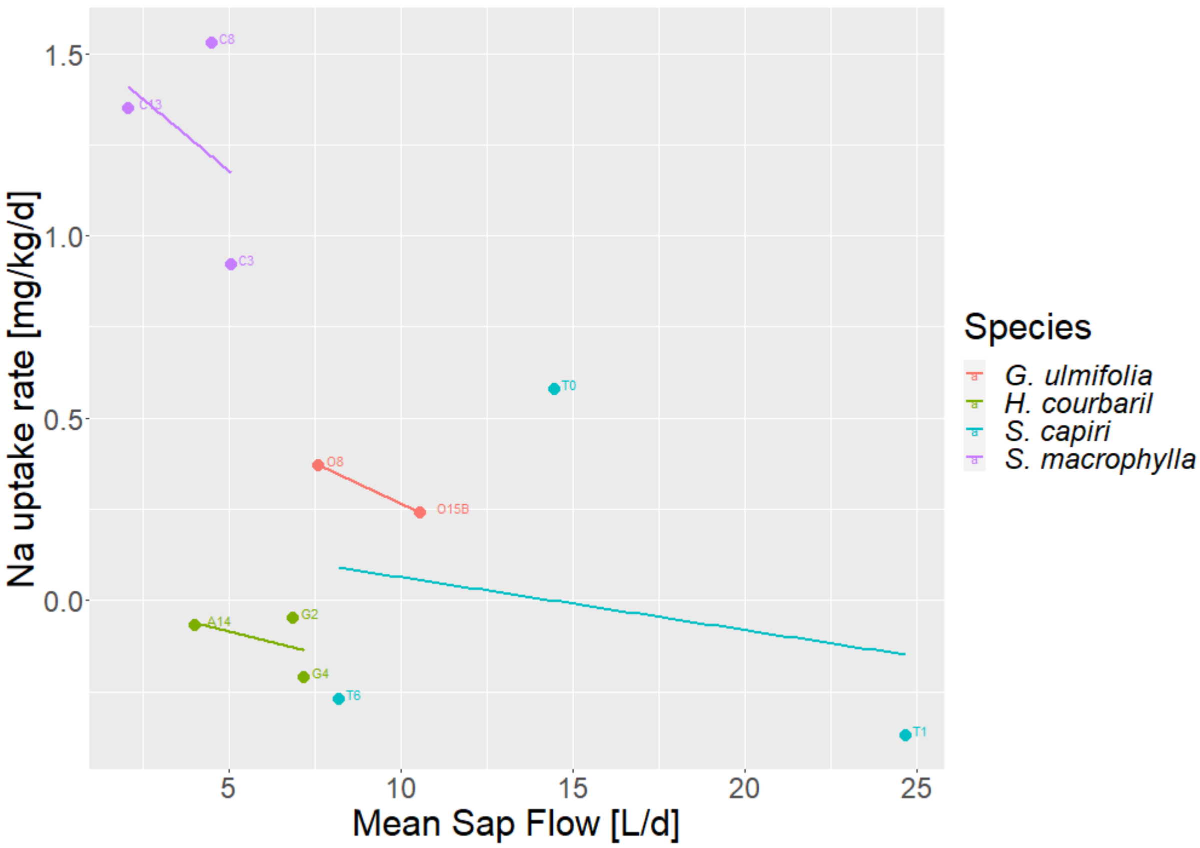

Fig. 47. Scatterplot of daily Na uptake in mg/kg/d and mean daily sap flow in L/d.

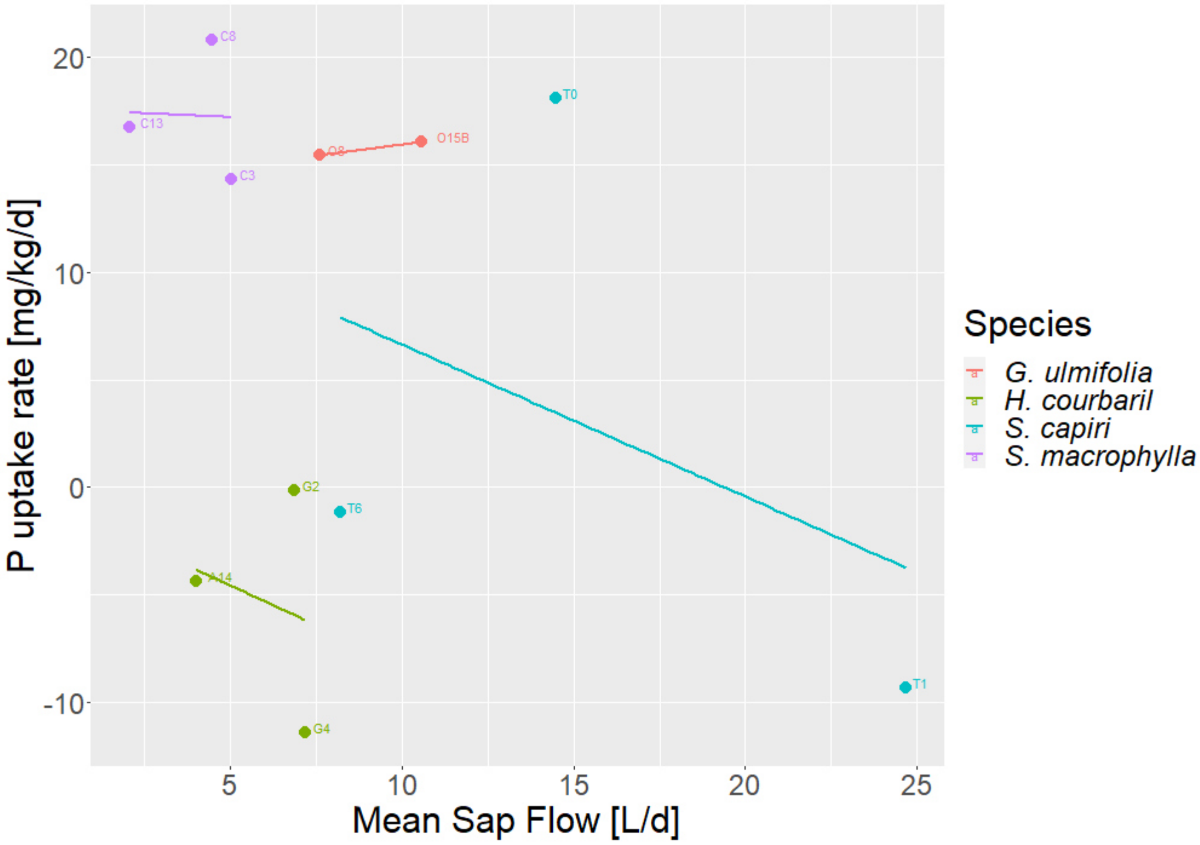

Fig. 48. Scatterplot of daily P uptake in mg/kg/d and mean daily sap flow in L/d.

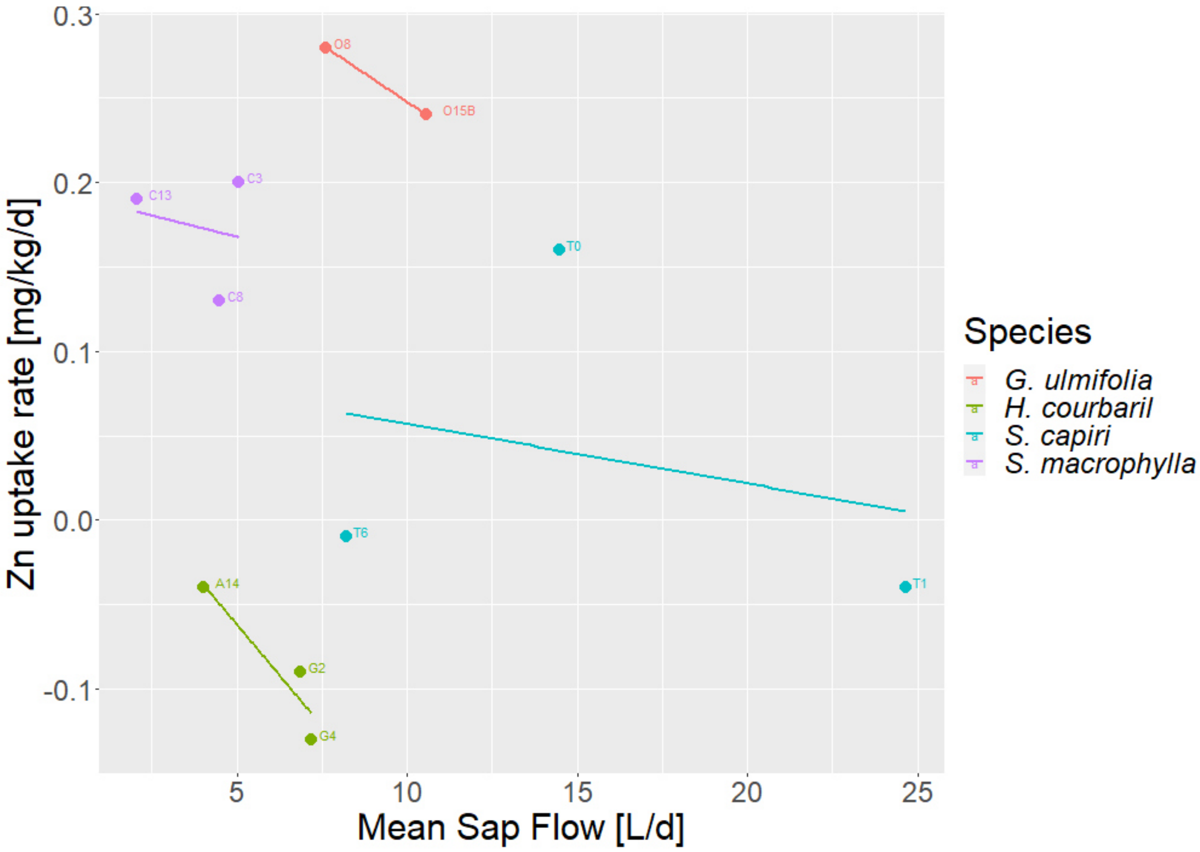

Fig. 49. Scatterplot of daily Zn uptake in mg/kg/d and mean daily sap flow in L/d.

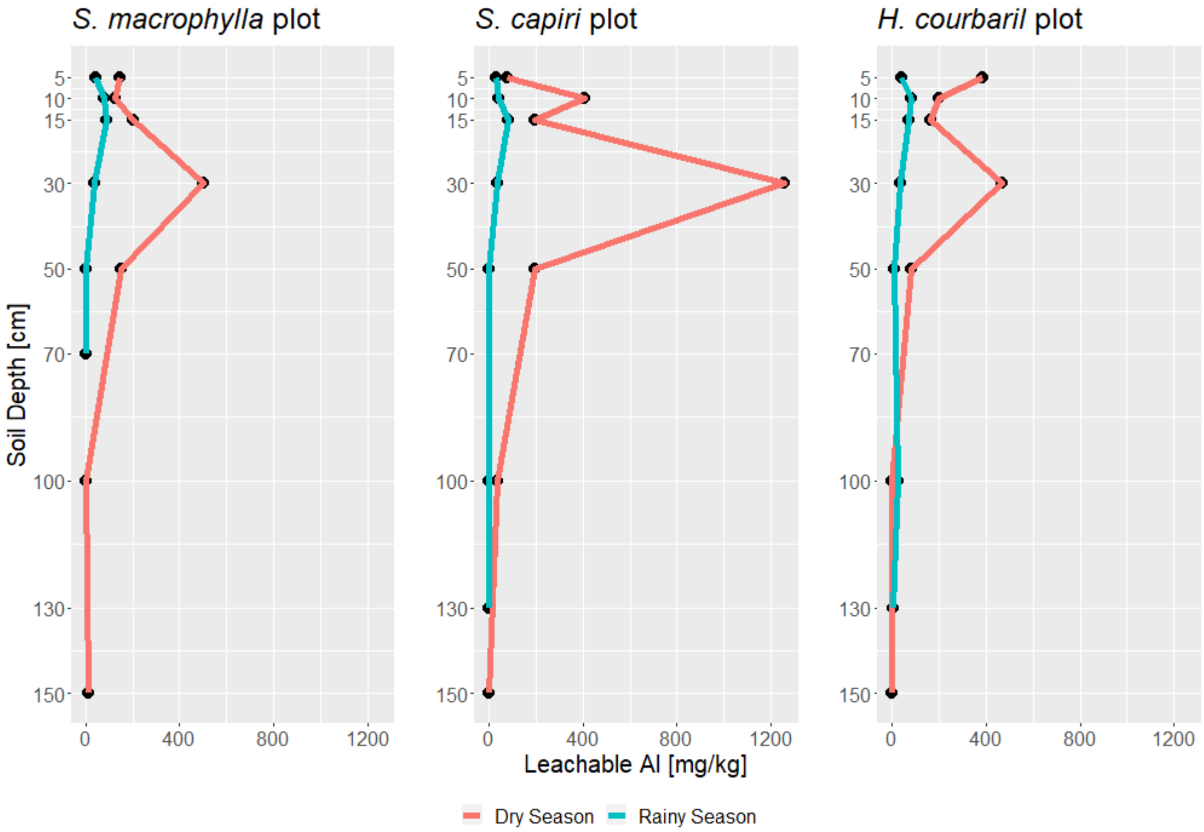

Fig. 50. Course of leachable Al concentrations (± 30.9%) of the three soil plots in dry and rainy season.

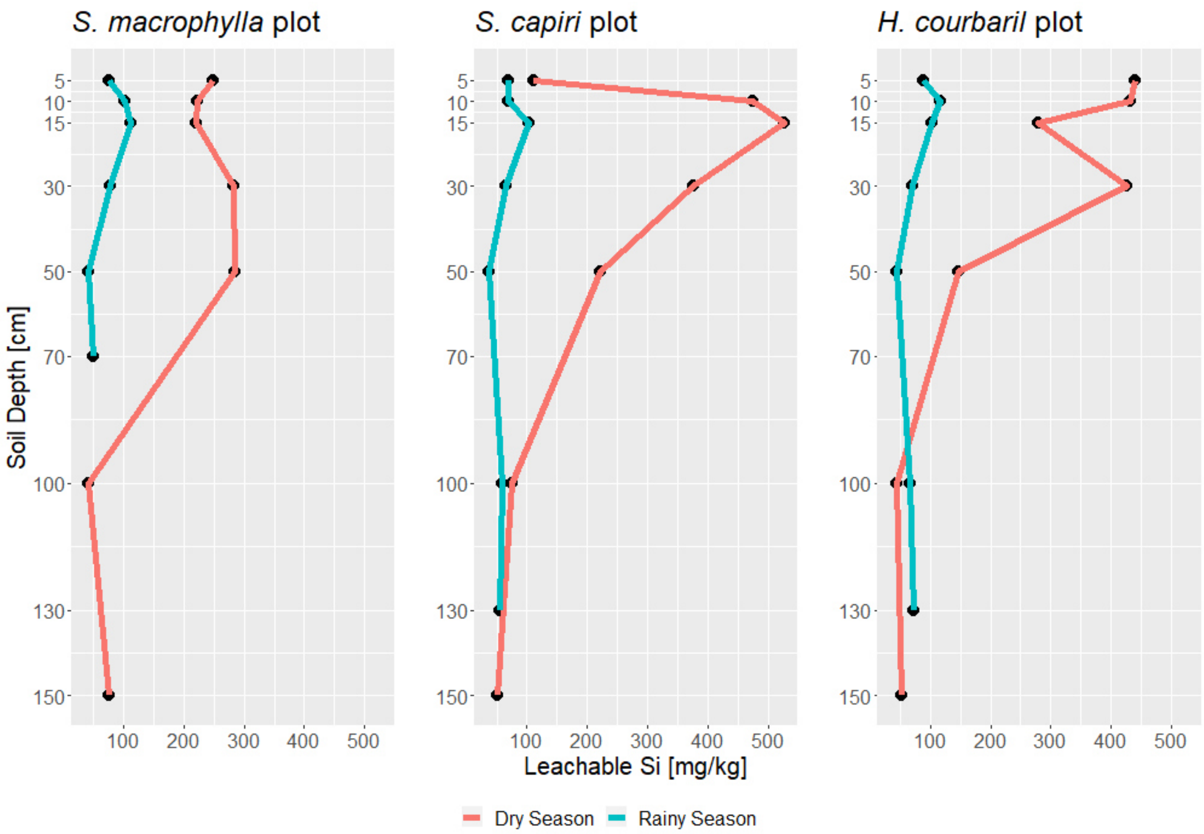

Fig. 51. Course of leachable Si concentrations (± 18%) in the three soil plots in dry and rainy season.

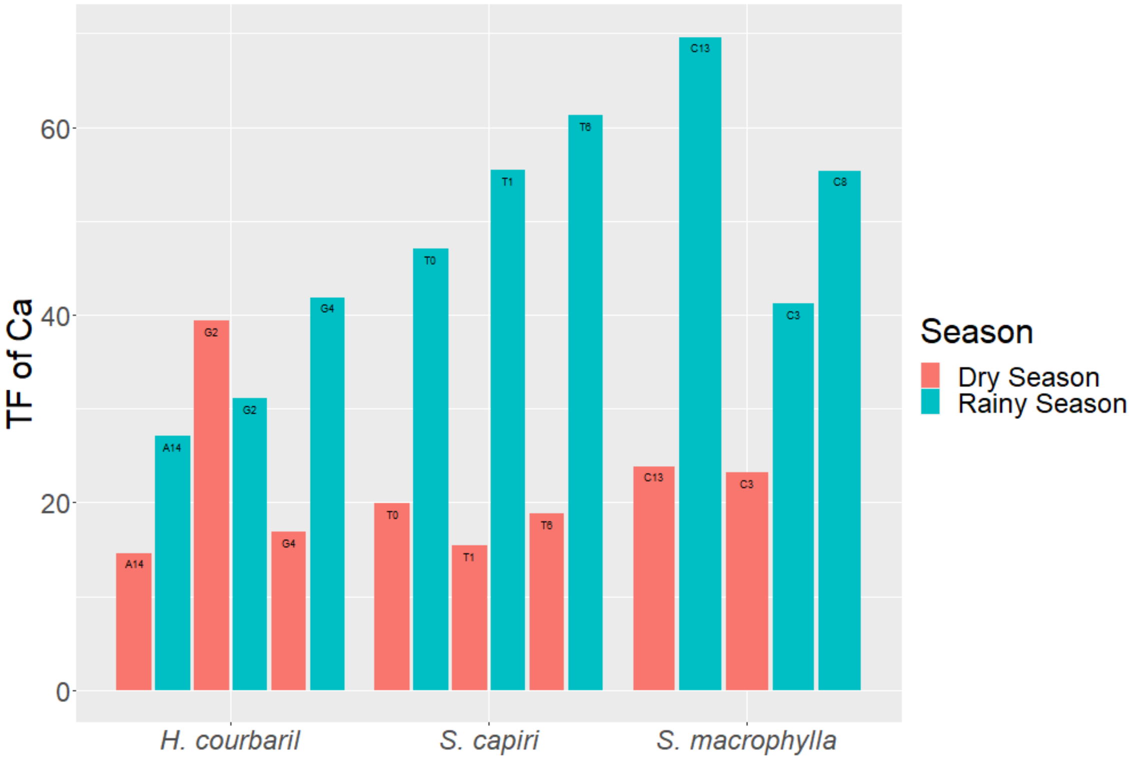

Fig. 52. Soil to plant transfer factor (TF) of Ca in dry and rainy season of H. courbaril, S. capiri and S. macrophylla individuals.

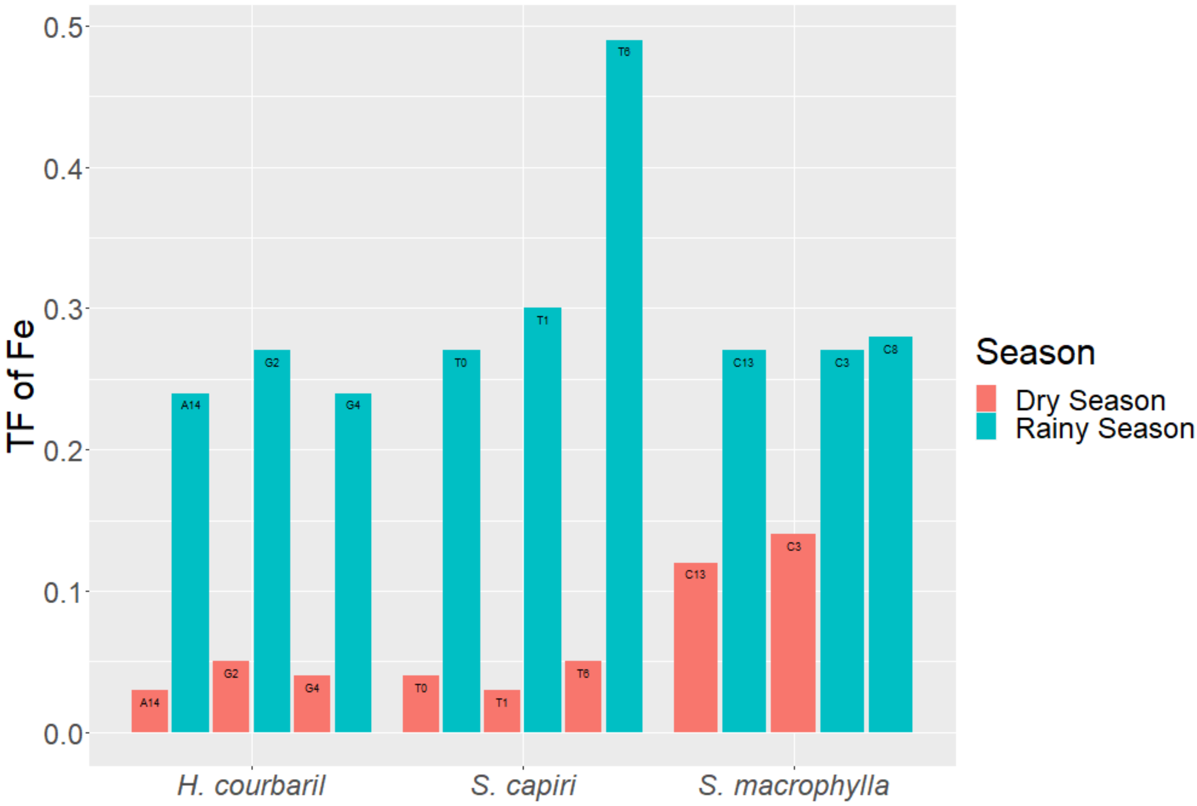

Fig. 53. Soil to plant transfer factor (TF) of Fe in dry and rainy season of H. courbaril, S. capiri and S. macrophylla individuals.

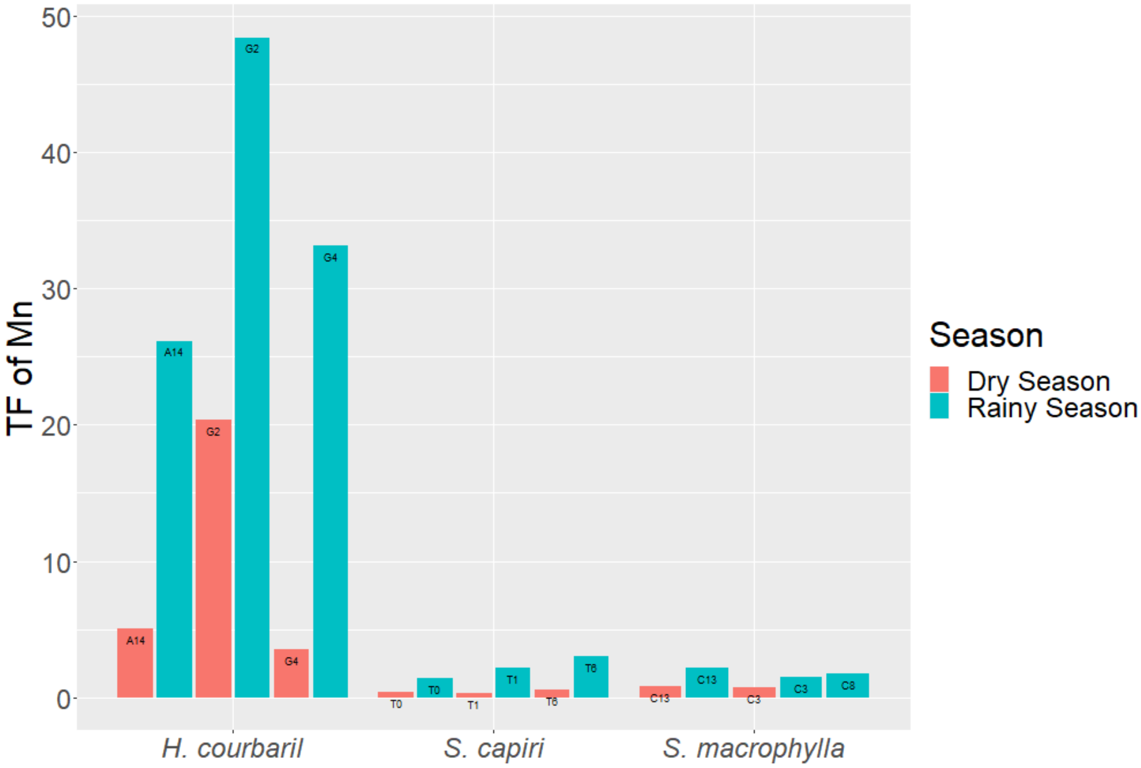

Fig. 54. Soil to plant transfer factor (TF) of Mn in dry and rainy season of H. courbaril, S. capiri and S. macrophylla individuals.

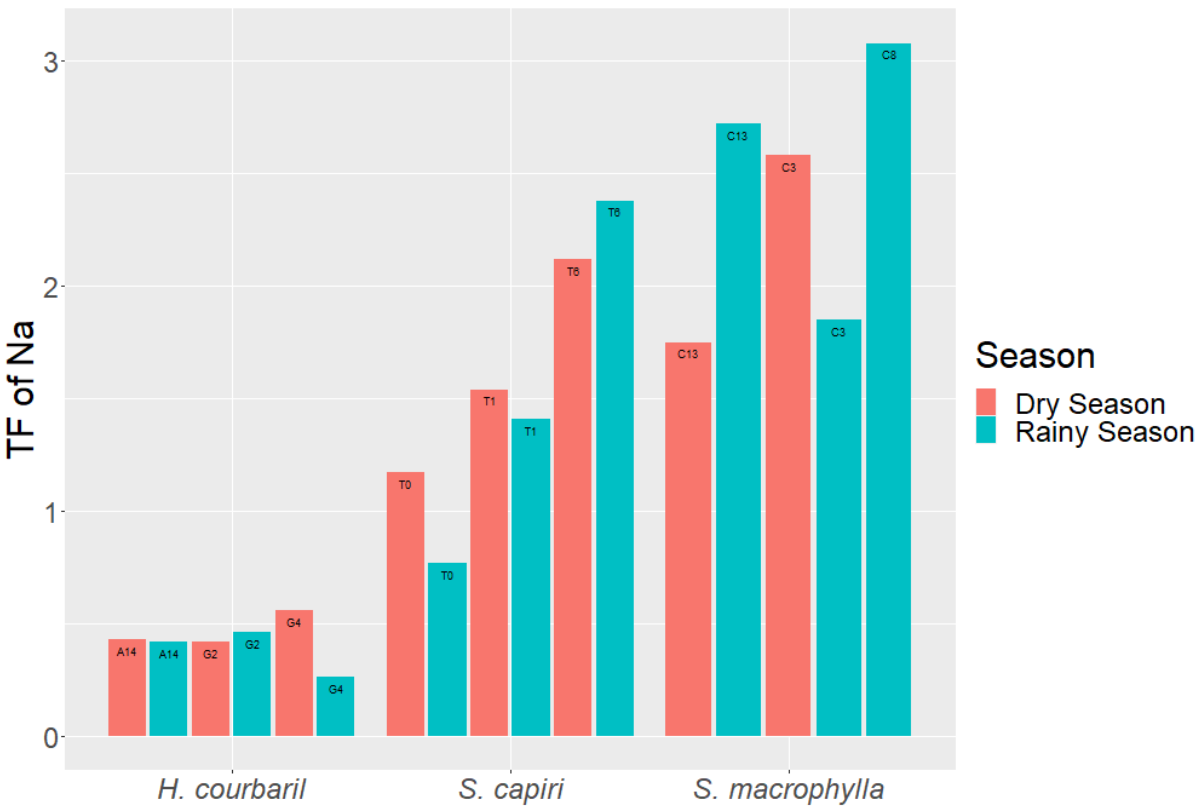

Fig. 55. Soil to plant transfer factor (TF) of Na in dry and rainy season of H. courbaril, S. capiri and S. macrophylla individuals.

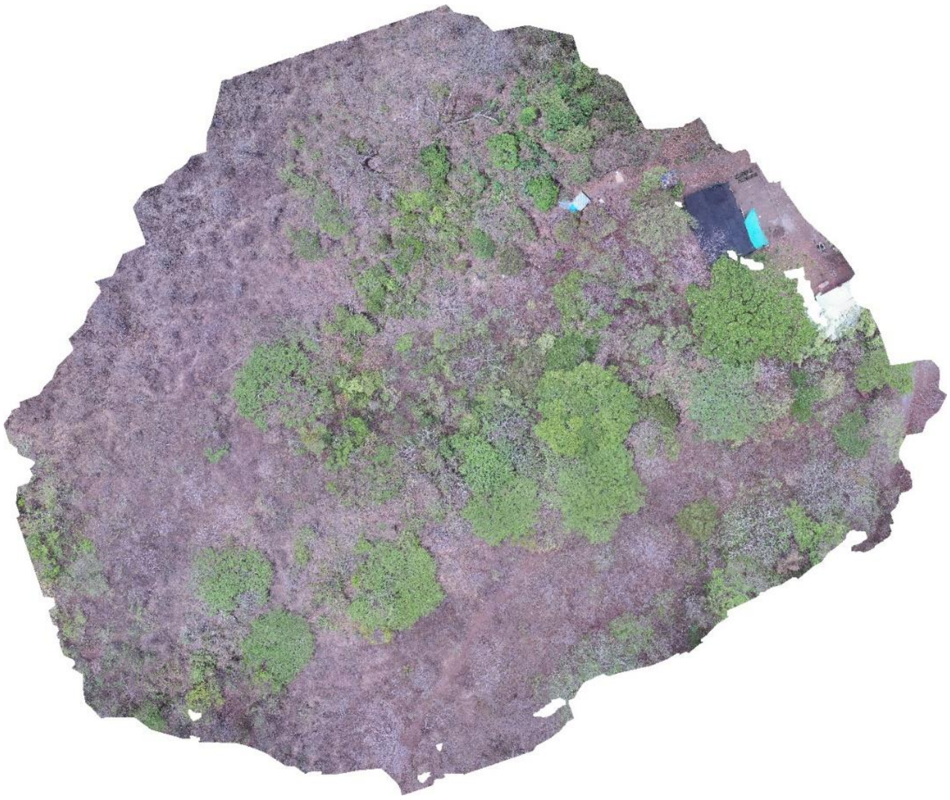

Fig. 56. Drone overflight of the field site at the end of dry season (14.04.2021) by Malkin Gerchow.

Fig. 57. Drone overflight of the field site at the beginning of rainy season (13.06.2021) by Malkin Gerchow.

Fig. 58. Image of H. courbaril leaves showing symptoms of Mn toxicity.