Abiotic factors related to hydrology and soil have an effect on local spatial distribution of tropical tree species in Paracou, French Guiana

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Despite the fact that several recent studies have focused on tree-habitat associations at a species community scale (Shmitt et al. 2021, Allié et al. 2015), very few have explored how it may vary at a species level. Here, we explore the correlation between 5 different environmental variables (available water capacity (AWC), topographic wetness index (TWI), topography, type of hydric drainage and percentage of iron traces) and the individual spatial distribution of *Symphonia sp.1*, *Oxandra asbeckii* and *Iryanthera hostmanii*. We employed a statistical test of correlations based on the random walk exploration method. Raster files were created for each environmental variable to test for specific associations with the three mentioned tree species. We found effects of biotic factors related to hydrology and soil on local spatial distribution of the three tree species in Paracou. The 5 environmental variables chosen for this study have in some way an influence on the spatial distribution of *Symphonia sp.1*, *Oxandra asbeckii* and *Iryanthera hostmanii*. These results coincide with information found in the literature.

Additional Key Words and Phrases: spatial distribution, hydrological factors, pedology, shar package, Paracou, French Guyana

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1 INTRODUCTION

It is known that chance, seed dispersal limitation and species ecological niche are some of the key drivers in shaping local assemblage of species in neotropical humid forests (Traissac, 2003). Many studies have provided evidence of positive relationships in species-habitat associations (Allié et al. 2015, Shmitt et al. 2021), but they don't explore whether further relationships may exist between the environmental variables and soil characterisation. In a review of 18 scientific articles, Sollins (1998) highlighted soil hydro-morphology as one of the main factors influencing floristic composition in tropical forests. Furthermore, recent studies (Ferry et al 2010, Morneau 2007) have also provided evidence for the significant effect of soil hydrology on forest vegetation dynamics. For this reason, further study on the effect of hydrology-related abiotic variables on local tree spatial distribution dynamics is needed.

In French Guiana, the local hydrological, physical, and geochemical soil features resulting from the weathering process along topographic gradients have been recognized as predominant ecological factors acting on the tree community (Baraloto C, 2007). For example, the presence of red spotted aloterite may be an indicator of a biotic constraint as it is related to the iron fluctuations happening in the soil (Ferry et al. 2003). However, there are no studies to conclude if a higher presence of aloterite would limit the dispersion of tree species. The Paracou field station, located in the north of French Guiana, is a 125-ha tropical forest that has been extensively studied for many years, however, the soil science in some of its biggest plots, and its effects on the vegetation community remain unknown.

This study presents the spatial correlation analysis of 3 specialised tree species (*Symphonia sp.1*, *Oxandra asbeckii* and *Iryanthera hostmanii*) with five environmental variables related to topography and water dynamics: available water capacity (AWC), topographic wetness index (TWI), topography and type of water drainage. Comparing our results with the literature, we aim to explore 1) if these five variables can explain the spatial distribution of *Symphonia sp. 1*, *Oxandra asbeckii* and *Iryanthera hostmanii* at a local scale and 2) if the presence of red aloterite can be considered as a biotic constraint for the distribution of *Symphonia sp. 1* and *Oxandra asbeckii.*

2 MATERIAL AND METHODS

2.1 Study site

The study site comprises four hectares of experimental forest located within the Paracou field station in French Guiana (Fig.1).

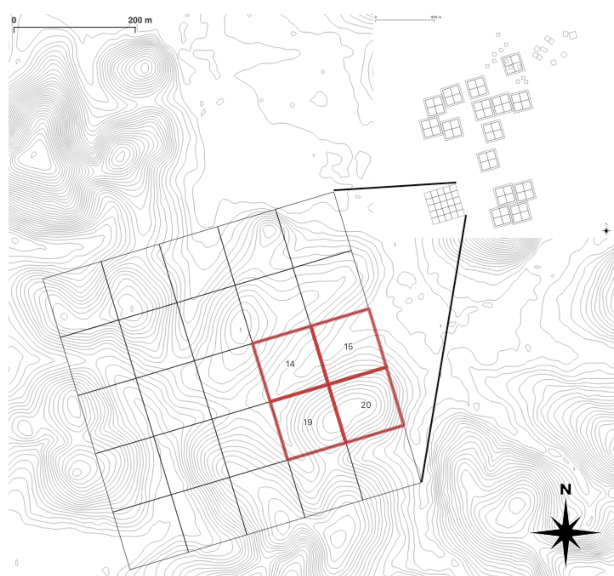

Fig. 1. Map of the parcel 16 at Paracou

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Elevation ranges from 5 and 50 m, and the mean annual temperature is 26 °C, with an annual range of 1–1.5 °C. Rainfall averages 2980 mm.a^{-1} (30-year period) with a 3-month dry season (< 100 mm month) from mid-August to mid-November. The landscape is characterized by a patchwork of hills (100–300 m wide and 20–35 m high) separated by narrow streams. Soils are mostly acrisols (Epron et al., 2006), limited in depth by a transformed loamy saprolite (found at about 1 m deep), which has a low permeability and has a key role at the time of determining the type of water drainage along the topography of the site (Ferry et al, 2003). Upper permeable horizons are usually thickest on hilltops and shallowest in upper or mid-position along slopes (Barthes, 1991). The trees presenting a diameter from base height >10cm of the subplots studied in this report (4 ha) have been inventoried bi-annually since the mid-1990s.

2.2 Soil sampling

The 36 soil sampling points were grouped in four contiguous 1 ha subplots of Parcel 16. Each subplot is delimited by a path on all sides. At each subplot, we mapped out nine equidistant points, at 33 m intervals, with the exterior points 16.5 m from the edges of the subplots. The location of each sampling point was noted using the coordinates of the nearest tagged tree extracted from Guyafor[1] tree database. Using a stainless-steel auger, we dug 1 m deep soil pits at each sampling point. We extracted a soil sample every 20 cm and stored it for analysis. Each change of colour and texture in the soil is an indicator of a change of horizon (Ferry et al, 2003). The different horizons were characterised by describing different qualitative variables in-situ. For example, soil components were described using the soil texture diagram, from which we could extract a proxy of the real percentage of sand, clay and silt of each horizon (Jamagne M., 1977). We also defined the percentage of red hematite spots in the different horizons to explore a hypoxia-related constraint later on.

2.3 Botanical data

We used the tree inventory with the trees presenting <10cm diameter from base height (DBH) from the 2020 inventory of the Guyafor tree database. The area studied presented a total of 264 species with 1900 individuals. Based on cluster classifications (Shmitt et al. 2021), we chose two tree species that have contrasting habitat preferences according to the topography gradient and more than 20 individuals identified in our study area. *Symphonia sp.1* (Clusiaceae) is the most representative species of the *Symphonia* genre in our dataset with 36 individuals and a known species for its preference for the high hill areas (Moreno L. 2022, Schmitt et al. 2021). *Iryanthera hostmanii* (Myristicaceae) shows a high tolerance in waterlogged soils and it is also present in our study site with 34 individuals. The third species we chose to study is *Oxandra asbeckii* (Annonaceae), the most common species in the site with 200 individuals.

2.4 Environmental variables

Considering that species distribution depends on biotic and abiotic factors, we chose four abiotic factors related to topography and hydrology and the presence of spotted aloterite as a biotic constraint.

[1]Guyafor, DataBase of the French guiana Permanent Plot Network, Cirad-CNRS-ONF

Based on the literature, we considered the Topography Wetness Index (TWI), the available water capacity (AWC), the topography and the type of hydric drainage as the most studied abiotic variables to determine the hydric constraints related to the slope of terrain. The topographic wetness index identifies the areas where water accumulates and it is thus crucial for the study of local spatial distribution (Allié et al., 2015). TWI was obtained from the dataset created by Schmitt et al., 2021. The data was derived from a 1-m resolution digital elevation model built based on data from a LiDAR campaign done in 2015 using SAGA-GIS (Conrad et al., 2015). The available water capacity (AWC) estimates the amount of water retained by the soil using the type of soil texture. It was estimated using the soil texture data that we collected from each soil horizon in the field and the following equation from the 'Modèle de bilan hydrique forestier' (INRAE - UMR Silva):

$$\alpha \times \beta \times (100 - \epsilon)/100 \tag{1}$$

Where α stands for the available water in the soil, β represents the bulk soil density, and ϵ the percentage of coarse elements.

To determine the available water and bulk density variables, we used the table issued by the 'Service de cartographie des sols de l'Aisne' ((Jamagne M., 1977); in Baize and Jabiol, 1995). It presents standardised hydrological values such as the available water in the soil (g of water for every 100g of soil) and the bulk soil density, used as an indicator for soil compaction (Annex 1). Topography was defined in-situ by identifying three main positions in the slope: hilltop, slope or lowlands. The type of water drainage was described for every sampling point based on the classification presented by Ferry et al. (2003). Finally, the presence of spotted aloterite was determined by the percentage of spots related to iron fluctuations in our soil samples. An approximation of red spots was made by comparing the total spots coverage to the total surface of the sample. Low hill locations were excluded for this variable as the iron traces could not be observed as a consequence of the permanent waterlogging occurring on site.

2.5 Data analysis

We chose the 'shar' package in R to test if the random walk algorithm used in calculating the habitat-species correlations would provide us similar results on the distribution of species than the torus translation algorithm, widely used in ecology for this kind of associations (Velazquez et al., 2016).

We examined the habitat-association patterns of trees in the four subplots of the P16. To do this we used the 'shar' package from Rstudio. This package was developed to provide a tool set to analyse species-habitat associations of spatial point patterns, it is designed for discrete environmental data (Hesselbarth, 2021). In order to make the shar package accessible for as many people as possible, it uses two R packages used for spatial data, the 'raster' and 'spatstat' packages (Hijmans, 2019). To be able to use this methodology we need one raster file presenting the environmental conditions and the individual spatial location of the different species or individuals selected.

Having only the data for the holes made in the field we had to interpolate our data using the kriging method in order to create a raster representing all the surface of our 4 subplots.

As the package only works with discrete data we had to create classes for each variable. The class system is named habitat in the package 'shar'. For the rest of this article we will talk about habitat to make it easier to understand. The different habitat are described in the table 1 below.

To analyse species-habitat associations, the potential interdependence between species locations and environmental conditions must be broken by randomising the data. There are different possibilities to break this interdependence, here we decided to randomise the environmental data while keeping the locations of our species stable (Harms et al., 2001; Plotkin et al., 2000).

This randomization will be done by moving the raster with our environmental data using a random walk algorithm. If we find our species more often in the initial model than in the randomised one then we can say that species-habitat associations are present. From the method we use if a positive association is found to an environment, generally a negative association will be present too. We used $\alpha = 0.05$ to determine statistical significance throughout this study.

3 RESULTS

Concerning the results of our associations, we can observe in Table 2 that *Symphonia sp.1* has a positive relationship with a low TWI between 1 and 1,99. A similar result is observed for *Oxandra asbeckii* except that there is also a negative correlation with a high TWI of 6 to 6,99. For *Iryanthera hostmanii*, the topographic wetness index is positively associated with a high TWI (0 to 1,99) and negatively associated with a low TWI with values between 5 and 6,99.

Table 2. Results of the association between TWI and the three species

TWI			
Habitat	*Symphonia sp.1*	*Iryanthera hostmanii*	*Oxandra asbeckii*
1	n.s.	negative	positive
2	positive	negative	n.s.
3	n.s.	n.s.	n.s.
4	n.s.	n.s.	n.s.
5	n.s.	n.s.	n.s.
6	n.s.	positive	n.s.
7	n.s.	positive	negative

For the variable available water capacity (Table 3), a positive correlation is observed between *Symphonia sp.1* and a high available water capacity, for the other habitats the association is not significant. For *Iryanthera hostmanii*, there seems to be a negative association for an AWC between 121 and 160 mm but a positive association for habitat 4 with an AWC of 101-120 mm. In *Oxandra asbeckii*, a positive correlation is noticed when the AWC is more important as in *Symphonia sp.1*.

Table 3. Results of the association between AWC and the three species

AWC			
Habitat	*Symphonia sp.1*	*Iryanthera hostmanii*	*Oxandra asbeckii*
1	n.s.	n.s.	n.s.
2	n.s.	n.s.	negative
3	n.s.	positive	negative
4	n.s.	negative	n.s.
5	positive	negative	positive

For topography (Table 4), *Symphonia sp.1* has a negative association with habitat number 3, which represents lowlands. *Oxandra asbeckii* also has this negative association with this habitat but in addition has a positive association with the hilltop, habitat number 1. *Iryanthera hostmanii*, on the contrary, has a negative relationship with habitat 1 and positive with habitat 3.

Table 4. Results of the association between topography and the three species

Topography			
Habitat	*Symphonia sp.1*	*Iryanthera hostmanii*	*Oxandra asbeckii*
1	n.s.	negative	positive
2	n.s.	n.s.	n.s.
3	negative	positive	negative

For the variable including the different types of drainages (Table 5), *Iryanthera hostmanii* has a positive relationship with habitat number 5 (SHBF) which corresponds to the hydromorphic lowland system. For *Oxandra asbeckii*, a negative relationship is observed for habitat 1 (DVP) representing deep vertical drainage. Finally *Symphonia sp.1* has a positive correlation with habitat 2 (DLS) and negative with habitat 5 (SHBF) corresponding respectively to superficial lateral drainage and hydromorphic lowland system.

Table 5. Results of the association between the different classes of drainage and the three species

Drainage			
Habitat	*Symphonia sp.1*	*Iryanthera hostmanii*	*Oxandra asbeckii*
1	n.s.	n.s.	negative
2	positive	n.s.	n.s.
3	n.s.	n.s.	n.s.
4	n.s.	n.s.	n.s.
5	negative	positive	n.s.

Finally, the variable of the percentage of iron traces in Table 6, has a positive relationship with *Symphonia sp.1* when it is in habitat number 5 which represents a percentage between 81 and 100%. On the other hand the relationship is negative with habitat number 1 when the iron traces are between 0 and 20%. *Oxandra asbeckii* has

Table 1. Correspondent values to habitat number used in the spatial analysis

Habitat number	AWC	Water drainage	Iron traces	TWI	Topography
1	60-80	DVP	0-20	0-0,99	Hilltop
2	81-100	DLS	21-40	1-1,99	Slope
3	101-120	SHA	41-60	2-2,99	Bas Fond
4	121-140	SHBV	61-80	3-3,99	/
5	141-160	SHBF	81-100	4-4,99	/
6	/	/	/	5-5,99	/
7	/	/	/	6-6,99	/

a positive relationship with habitat 5 as does *Symphonia sp.1* but we observe a negative association with habitat 2, representing a percentage of iron traces between 21 and 40.

Table 6. Results of the association between the percentage of iron traces and the three species

Percentage of iron traces		
Habitat	*Symphonia sp.1*	*Oxandra asbeckii*
1	negative	n.s.
2	n.s.	negative
3	n.s.	n.s.
4	n.s.	n.s.
5	positive	positive

At the end of our results, we observed a negative correlation between the TWI and the AWC. We therefore performed a linear regression to see if a correlation would exist between the TWI and the AWC factors. We also performed a correlation analysis to further confirm the interaction. The results obtained were not significant (p-value=0.8626).

Thanks to the interpolation of our points we were able to create a raster for each environmental constraint. Each raster allows us to visualize the distribution of the constraint on our 4 ha. By implanting the three species we selected, we can visually obtain their distribution according to the selected constraint as for example with the raster of the AWC (Fig 2). As we have 5 different constraints we were able to make 5 maps, the one concerning the AWC is shown below and the other four can be found in the Appendix.

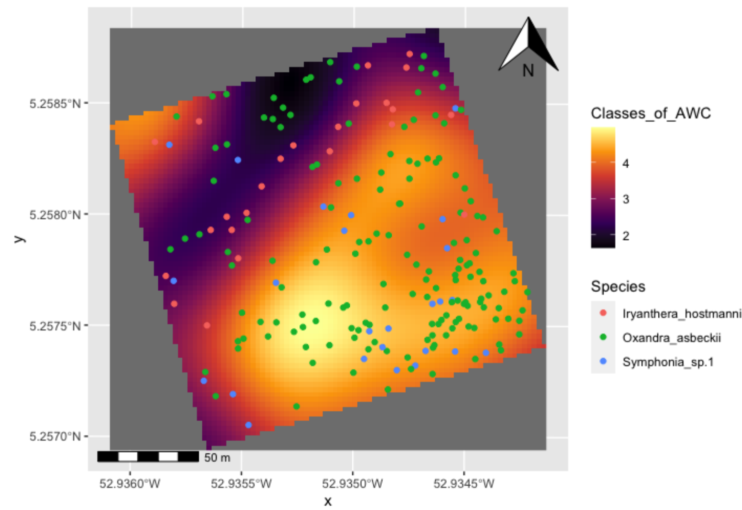

Fig. 2. Map of the distribution of the 3 selected species according to the AWC environmental constraints

4 DISCUSSION

4.1 Species-habitats associations

Based on the null hypothesis that there is no effect of each environmental variable on the spatial distribution of *Symphonia sp.1*, *Oxandra asbeckii* and *Iryanthera hostmanii* along the topographic gradient, we aim to reject or accept this assumption by exploring the results obtained from our spatial correlation analysis.

We found that most of the significative correlations of the environmental variables are consistent with the ones exposed in the literature. Schmitt et al. (2021) showed that the relative probability of occurrence of *Iryanthera hostmanii* increased with the TWI values. We also found a positive correlation for this species between the presence of individuals and an affinity to soils presenting high TWI values (Table 2, values between 5-6,99), strengthening the idea that *Iryanthera hostmanii* is a species with high tolerance in waterlogged environments (Baraloto et al. 2007). On the other hand, *Symphonia sp.1* showed a positive correlation with low TWI values, agreeing with the study of Vincent et al. (2011) about the low tolerance of this species in waterlogged environments. Further studies on the functional traits that allow this species to thrive in such constraining environments should be done to better understand its ecological niche.

Symphonia sp.1 and *Iryanthera hostmanii* (both represented by less than 10 individuals per hectare in this study), show significant spatial associations with the typology of drainage. However, *Oxandra asbeckii*, which is represented in the study with more than 200 individuals, was not significant for any type of drainage. The number of individuals may be an asset to take into account when Superficial lateral drainage (SLD) has been identified in hilltops and slopes (Ferry et al., 2003), which is consistent with the preference of *Symphonia sp.1* to be more present across the slope and on the hilltop (Table 4). SLD was the most common type of drainage across the four subplots, probably explaining the reason why *Oxandra asbeckii* did not turn out significant in any of the types of water drainage.

The random walk algorithm used in the variables-species correlation analysis (Hesselbarth, 2021) provided different results from studies that used the torus translation algorithm, commonly used in ecology for spatial distribution analysis (Velázquez et al., 2016). For example, F. Morneau (2007) presented an extensive spatial analysis report using torus translation on the affinity of species to topography, obtaining non significative results for the topography gradient for *Iryanthera hostmanii*. In contrast, our results show a positive correlation for the low hills and a negative correlation for the hilltop, reinforcing the fact that *Iryanthera hostmanii* is a species with a high tolerance to waterlogged environments. On the other hand, *Symphonia sp 1* was also considered in the study of Morenau and it was significantly related to the slope habitat.

4.2 Ferrugination as an indicator of a biotic constraint

Despite the fact that red spotted aloterite has been described as a possible indicator for the water table limit in tropical soils (Ferry et al. 2003), there are no clear results on whether or not it could be an indicator of a biotic constraint for species distribution. The results show a positive correlation between high presence of spotted red alloterite and the presence of *Symphonia sp 1* and *Oxandra asbeckii* (Table 6). These results go against our hypothesis that maybe the high presence of red spotted alloterite may be a constraint for the distribution of tree species. However, it has been evidenced that Fer+ dynamics and its interaction with the soil organic matter will be affected by the raise of temperatures due to climate change (Barcellos et al., 2018; Bhattacharyya et al., 2018). Consequently, a deeper understanding on the specific role of iron in the soil in response to abiotic factors such as temperature or moisture is needed to better predict how it can be an indicator for the distribution of the above ground vegetation. We believe that contrasting information of the roots' structure (their dimensions within the soil column, preferences with more precise quantifications of soil ferrugination would provide more accurate answers on how the location of the water table may be a biotic constraint for the vegetation.

5 CONCLUSION

Soil conditions are known to be heterogeneous at Paracou, and several studies have indicated that many soil physical and chemical properties are correlated with topographic position. This study provides more evidence to highlight topography as a determinant environmental variable when trying to understand the distribution of species in diverse environments such as tropical forests.

Significant correlations were found between the 5 abiotic variables related to topography and soil across the three species studied. Only the hydric drainage was not significative for *Oxandra asbeckii*, most probably as a consequence of interpolation errors due to the very limited number of individuals that were studied.

When trying to consider the presence of red spots as an indicator of a biotic constraint, we found no significative correlation between the high percentage of iron traces and the species local distribution. It is important to highlight that the percentage of red spotted aloterite was collected without a referenced methodology. This may have led to serious bias at the time to quantify the level of ferrugination in the soil to define where the water table limit is found. Fritsch et al. (1986) estimated that the alloterite layer is found in the first 2,5 m of the soil column, which was out of our reach, as this study was limited by the maximum 1m depth for the soil samples.

Even though most of the results have shown an effect of abiotic factors on local distribution species along the topographic gradient, we believe that the statistical correlation test methodology could be improved. Further statistical analysis that explore the correlation between the abiotic variables is encouraged to design models that can better explain the connectivity between the soil and the plant community.

We believe that measuring quantitative variables that can explain the geochemistry of the soil will make a crucial contribution to the understanding of the physical and chemical process occurring in the soil, which may have a direct or indirect impact to the distribution of the species across the forest.

Soil science is still deeply misunderstood in the field station of Paracou. This report presented a preliminary study that we hope will be further developed in the future and provide answers to the existing correlations between tree species and biotic and abiotic factors.

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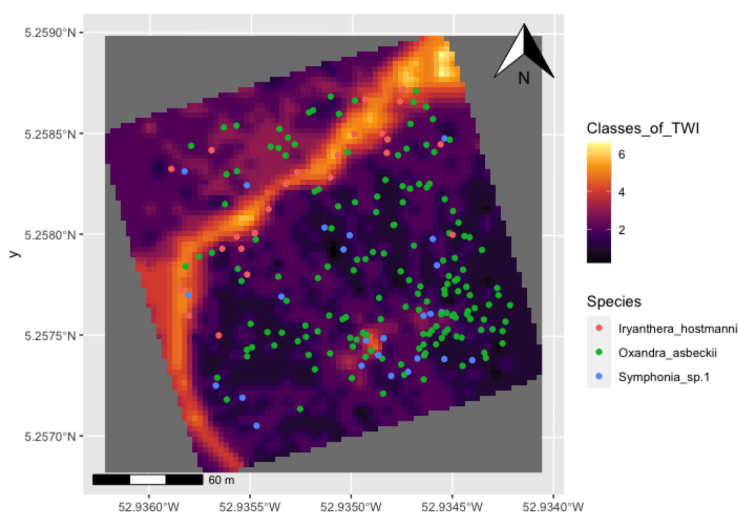
A APPENDIX

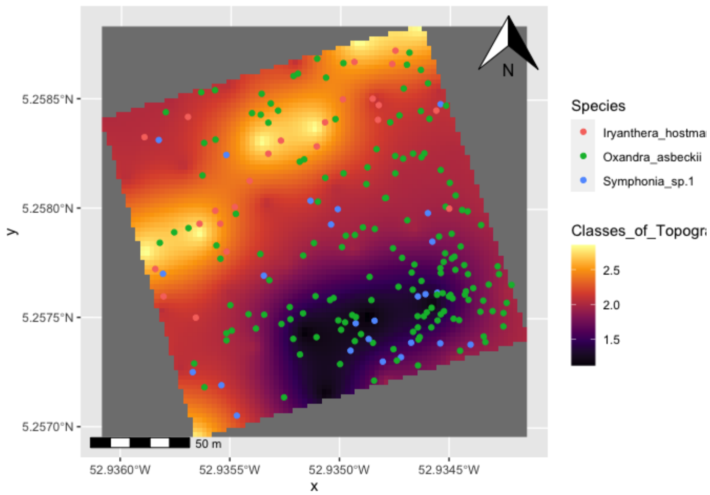
A.1 Appendix 1 : Table for the determination of AWC

Classe de texture (selon le triangle de Jamagne)	Humidité % à la capacité au champ (pF=2.5)	Huminité % au point de flétrissement permanent(pF=4.2)	Eau utile (g d'eau pour 100 g de sol)	Densité apparente (sans dimension)	Réservoir utilisable (mm d'eau par cm de sol)
S	8	3	5	1.35	0.7
SL	12	5	7	1.40	1.0
SA	19	10	9	1.50	1.35
LlS	15	7	8	1.50	1.20
LS	19	9	10	1.45	1.45
LmS	20	9	11	1.45	1.60
LSA	22	11	11	1.50	1.65
LAS	24	12	12	1.45	1.75
Ll	17	8	9	1.45	1.30
Lm	23	10	13	1.35	1.75
LA	27	13	14	1.40	1.95
AS	33	22	11	1.55	1.70
A	37	25	12	1.45	1.75
AL	32	19	13	1.40	1.80
A lourde	29	18	11	1.50	1.65

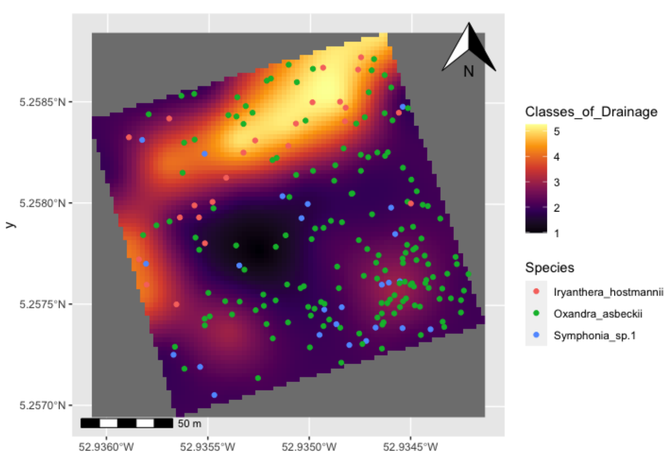
A.2 Appendix 2 : Map of the distribution of the 3 selected species according to the TWI environmental constraints



A.3 Appendix 3 : Map of the distribution of the 3 selected species according to the topography environmental constraints



A.4 Appendix 4 : Map of the distribution of the 3 selected species according to the drainage environmental constraints



A.5 Appendix 5 : Map of the distribution of the 3 selected species according to the percent of iron traces environmental constraints