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ELABORATO DI LAUREA

Analysis of the effects of different restoration approaches on the structure and functioning of salt marshes in the Venice lagoon

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ABSTRACT:
Salt marshes are coastal ecosystems that provide key services to human population, such as coastal protection and blue carbon sink. Marshes have strongly deteriorated in past decades and, thus, countries worldwide invested for restoring them, mainly aiming at recreating species structural composition. However, if we want to correctly evaluate the success of restoration, both structural and functional aspects must be taken into account. To evaluate restoration success, plants functional traits provide a powerful approach because they allow to link if changes in community species composition are reflected at functional level and, in turn, on the overall functioning of the systems. Here, focusing on extensive salt marsh restoration undertaken in the Venice lagoon, we investigated if two different restoration approaches - one involving the partial removal of structures for protecting the edges (R1) and (R2) without removal - recreated similar taxonomic and functional vegetation composition to natural marshes. Specifically, we investigated if changes in functional composition affected the above- and below- ground primary production. Our results revealed that restored marshes lacked key vegetation in the low shore (i.e., the native *Sporobolus maritimus* was not present in both restoration types). In the mid marsh, vegetation communities of restored marshes differed from natural ones, both in taxonomical composition and in functional traits. Based on the functional traits of resident vegetation we expected higher production in R2, but above- and belowground primary production were not statistically different between natural and restored marshes. Overall, our study found that the type of restoration can have enduring effects on both taxonomic and functional structure of vegetation, but not on the overall functioning of salt marsh ecosystem. Further research on the complex relationships between functional traits, restoration and ecosystem functioning are needed.

Glossary

The following table provides a list of abbreviation used through the text, along with their expanded forms. The intention is the table is to help the unfamiliar readers understand the abbreviations used and to make the text easier to understand.

Abbreviation	Meaning
ABG	Above ground biomass
AC	Alive cover
ANOVA	Analysis of variance
ANPP	Above ground net primary productivity
BLG	Below ground biomass
BNPP	Below ground net primary productivity
CWM	Community weighted mean
GLS	Generalized least squares
LA	Leaf area
LDMC	Leaf dry matter content
MM	Mid marsh
N	Natural marshes
PCA	Principal component analysis
PCoA	Principal coordinates analysis
PERMANOVA	Permutational multivariate analysis of variance
R1	Restored marshes type 1
R2	Restored marshes type 2
SANPP	Above ground specific net primary productivity
SBNPP	Below ground specific net primary productivity
SLA	Specific leaf area
STNPP	Total specific net primary productivity
TC	Total cover
TCA	Total canopy area
TNPP	Total net primary productivity

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1. INTRODUCTION

Coastal ecosystems are complex environments that exhibit great heterogeneity. They are typically classified in mangroves, estuaries, salt marshes, seagrasses, coastal shelf, and coral reefs (Burke et al., 2000). Salt marshes account for 16% of coastal systems at world level, covering an estimated 0.27% in surface area (Ramsar Convention on Wetlands, 2019). For centuries, human population exploited salt marshes for their valuable services and functions, such as fishing and agriculture among other activities (Burke et al., 2000; Brander & Schuyt, 2004). However, this exploitation, along with the effect of sea level rise and other human-related alterations - including land claim, pollution and eutrophication - has threatened these ecosystems (Davy et al.,2009; Airoldi & Beck, 2007). Indeed, it is estimated that at present 25% of the original area of salt marshes has been lost worldwide (Bridgham et al., 2006).

To counter-act this degradation, recent years have seen an increase in restoration actions (Adam, 2019). These projects mainly focused on restoring plant species communities, in terms of taxonomic diversity and abundance, with the underlying assumption that ecosystems services - such as carbon sequestration, habitat provision, and soil stabilization - would be restored along them (Ehrenfeld & Toth,1997; Suding, 2011). However, the connection between plant species diversity and ecosystem functioning is complex and not always predictable (Dìaz & Cabido, 2001). Furthermore, because the climate is changing, it may not always possible to restored communities to the pre-disturbance point (Laughlin et al., 2017). Instead, to understand recovery processes the use of functional traits would be more useful because they are more closely related to ecosystem functioning than species taxonomy and abundance (Dìaz & Cabido, 2001; Laughlin et al., 2017). Additionally, ecosystems with plants communities taxonomically different but functionally similar may provide similar functions and services as the historical ones (Hobbs et al., 2009). Therefore, functional traits in restoration projects should be used alongside the taxonomic approach (Zirbel et all, 2017; Dìaz & Cabido, 2001). In fact, several studies have already used functional traits to assess the effectiveness of restoration (Carlucci et al., 2020).

In this context, focusing on the salt marshes of the Venice Lagoon (Italy) as a case study, we compared the plant communities and ecosystem functioning among two restoration actions and natural marshes. Specifically, to assess the success of the restoration effort, we investigated: first, if restored sites exhibited plant communities similar to natural marshes both in terms of taxonomic and functional traits composition, as well as vegetation cover; second, if restored communities provided net above-and below ground primary production (ecosystem functioning level) similar to natural marshes. Our study could potentially allow for the use of only functional traits to investigate the success of restoration action, rather than relying only on taxonomic composition.

1.1 SALT MARSHES

Salt marshes provide multiple important functions and services for human well-being, including coastal protection, nutrient cycling, sediments filtration and deposition, and carbon sedimentation (Irlandi & Crawford, 1997; Morgan et al., 2009; Valiela et al., 2002, Nellemann et al., 2010). These ecosystems have a global distribution except for the tropics and subtropics, where they tend to be replaced by mangroves (Roman, 2001). Salt marshes develop in coastal areas regularly flooded by salt water and with a low-energy intertidal zone. The morphology of salt marshes is shaped by sediment supply from rivers, tidal action, and changes in sea level, which bring mineral nutrients, organic matter, and salt (Boorman, 2003). The tidal range can greatly vary between salt marshes around the world. These different forces create complex habitats, with various vegetation zones, and a surface criss-crossed by creeks, mudflats, and banks.

1.1.1 ZONATION OF THE PLANT COMMUNITY

Salt marshes, due to the periodic immersion that varies with the height of the marshes, can have high salinity level and an anoxic soil, often low in nutrients. This leads to plant communities limited in species diversity and composed of halophytes, obligate and non-obligate, typically shrubs, grasses and herbs that are well adapted to this challenging conditions (Adam, 1990). In general, three main different zones dominated by different plant communities can be distinguished: high marsh, mid marsh, and low marsh. The low marsh is situated between mid marsh and submerged mudflats and typically consist of one or few species (Ewanchuk & Bertness, 2004) that require a certain degree of salinity to thrive (Boorman, 2003) or where abiotic stress suppress the growth of more competitive species (Bertness & Pennings, 2000). The size of the low marsh area can vary greatly from year to year and season to season, depending on tidal regime and climate (Boorman, 2003).

While traditional explanation for the zonation patterns in salt marshes focus on soil elevation, resistance to salinity, and submersion (Nixon, 1982), studies have shown that both biotic and abiotic factors play a key role (Bertness, 1991; Marani et al., 2004; Silvestri et al., 2005). Competition is a key driver in determining the dominance of certain plant species, with those possessing high belowground competitive abilities typically occupying the higher marsh zones in natural condition (Emery et al., 2001). In contrast, species that are less competitive, but possess a higher resistance to stress, are confined to the low marsh (Bertness & Pennings, 2000; Ewanchuk & Bertness, 2004). Studies have shown that low marsh species can successfully colonized the mid and high marsh zone in the absence of competition, while the opposite is not true (Bertness 1991). Facilitation also influences the distribution of species (Bruno, 2000), with certain pioneer species such as *Sporobolus* spp., helping to create conditions suitable for other plants (Castellanos et al., 1994). For example, *Sporobolus* spp. can increase oxygen in the soil thanks to their aerenchyma (Castellanos et al., 1994) or reduce salinity (Callaway 1994). Furthermore, the interplay between salt marsh communities and the landscape is complex (Marani et al., 2013), because plants can retain sediments and thus keep peace with sea level rise (Kirwan et al., 2016). These properties have the potential to define not only a vertical zonation but also a horizontal one, where different plants species thrive along creeks, ponds and banks.

1.1.2 THREATS TO SALT MARSHES

Salt marshes have suffered degradation due to pollution, treatment for pest control, exploitation for agriculture, salt production, aquaculture, energy, and conversion to land for centuries (Adam, 2002). It is estimated that these ecosystems have a loss rate 5-10 times higher than rainforest (Nellemann et al., 2010) and projections of sea level rise indicate that marsh ecosystems could suffer a 58% loss by 2100 (Gattuso et al., 2018). This degradation has led to a loss of valuable functions and services. Furthermore, salt marshes can suffer degradation from the invasion of non-native species such as *Sporobolus patens, S. densiflora, S. alterniflora*, *S. townsendii*, and hybrid of the native *S.maritimus* and *S.alterniflora*, resulting *in S. anglica* due to chromosome duplication (Strong & Ayres, 2009) which have been deliberately introduced in various countries (Pringle, 1993; Strong & Ayres, 2009). These highly invasive and competitive species are replacing the natives one (Adam, 2002), thus, potentially representing a threat to the health of salt marshes (Anttila et al., 1998). Overall, giving the ecological importance of salt marshes and threats they face, a series of actions have been taken to restore and protect these precious ecosystems.

1.1.3 RESTORATION OF SALT MARSHES

Restoration is a management system to mitigate human disruption (Cairns, 1995) and aims to re-establish the pre-disturbance functions and related conditions of an ecosystem (National research council, 1992). However, archiving this goal can be difficult because ecosystems are shaped by a series of events, both biological and climatic, and information about pre-disturbance is often scarce (Adam, 2019). Additionally, changes may be so invasive that pristine areas, and/or specific target species, may be no longer be available (Cairns, 1995; Adam, 2019). When full restoration is possible, it often takes over than 12-25 years to re-establish the functions and conditions (Borja et al., 2010). The ultimate restoration goal should be to restore the full range of ecosystems functions and services that existed prior to the disturbance, and to create a self-sustaining ecosystem (Adam, 2019; Abelson et al., 2020).

Typically, researchers evaluate the success of salt marsh restoration projects by using pre-disturbed or unaffected sites as a reference (Howe & Simenstad, 2015; Thom et al.,2002; Mossman et al., 2022). In some cases, the restoration goal has solely focused on the structure of the ecosystems, i.e., the number and type of species, by assuming that an ecosystem with a high range of species must have a high level of functioning. However, this is not necessarily true as functioning depends on a series of complex interactions between species and the environment (Zedler & Lindig-Cisneros, 2000). In fact, salt marsh restoration, and restoration in general, requires a broader approach that consider ecosystem functions as primary production, carrying capacity (i.e., the ability to support population), connectivity, and nutrient dynamics (Sheaves, 2009).

1.1.4 FUNCTIONAL TRAITS

To evaluate the effectiveness of restoration, it is important to assess the functions of the restored ecosystem. Functional traits offer a powerful approach to this evaluation. Functional traits are defined as morphological, chemical, physiological, structural, phenological, or behavioural characteristics, measurable at individual level (Garnier et al., 2016; Violle et al., 2007). Studies in terrestrial systems showed that measuring traits allow researcher to mechanistically link how species in communities respond to changes in environmental factors and, in turn, how traits can affect ecosystem processes and functions (Lavorel & Garnier, 2002; Garnier et al., 2016; Violle et al., 2007, Díaz et al.,2013). For example, the propensity of an ecosystem to experience fire is deeply linked to plant functional traits of species that have evolved to increase their fitness in the aftermath of a fire, but, at the same time, also increasing their susceptibility to fire (Pausas et al., 2016).

Functional traits can be divided in “hard” or “soft”. “Hard” traits are strongly linked to the response and effect on the ecosystem functions, but are more time-consuming and labour-intense measurements. In contrast, “soft” traits have a weaker link, but require simpler measurements and can serve as a proxy for the “hard” traits (Nock et al., 2016). Thus, employing soft traits that have a well-established connection with ecosystem functioning would allow to sample for many species in several sites, which is fundamental for ecological studies. For instance, specific leaf area (i.e., the area of leaf per amount of biomass invested) is linked to the growth rate of a species (Garnier et al., 2016). Additionally, according to the “mass ratio” hypothesis, the functional traits of most abundant species in a community have the greatest impact on defining the level of ecosystems functioning (Grime, 1998). Therefore, evaluating soft traits, such as specific leaf area, would allow researcher to investigate the success of a restoration project across multiple sites. Thus, functional traits could be a practical and efficient way to monitor the progress of ecological recovery.

1.2 AIMS OF THE STUDY

This study aimed to investigate the difference between natural and restored salt marshes in the Venice lagoon, specifically focusing on two types of restorations: R1, which involved partial removal of the structure initially containing the sediments and protecting the edges of the restored marsh, and R2, which involved no removal of the edge structure. The goal was to determine if the functions (net primary production both above and below ground) of restored salt marshes are similar to those of natural ones, using functional traits analysis, plant community composition, coverage. Because sediment characteristics differed between natural and restored marshes (Billah et al., unpublished), we hypothesized that also the taxonomic and functional traits composition will differ, leading, in turn, to differences in net primary production. During the study, we compared the mid and low marsh vegetation, paying attention to the presence of the alien plant *Sporobolus* spp. in the low marsh, a competitor of the native *S. maritimus* (Wong et al., 2018).

2.METHODS

2.1 STUDY AREA

The Venice lagoon (northern Adriatic sea) is the largest wetland in Italy, with an area of approximately 550 km² (about 50 km long and 10 km wide) (Smart & Viñals, 2004). The lagoon is separated from the sea by two long islands, and has three inlets for water exchange, Lido, Malamocco and Chioggia. The river inputs in the lagoon are high in agricultural pollutants resulting in an ongoing eutrophication of the ecosystem (Masiol et al.,2018; Facca et al., 2010).The daily exchange with the Adriatic sea is about 400 million m³ of water, with an inflow of about 3.7 million m³ (Bernstein & Montobbio, 2010).

The lagoon has a semi-diurnal microtidal regime. The average tidal range is 0.6±m (Tagliapietra & Ghirardini, 2006), and the mean depth is 1m (Day et al., 1998). Salinity ranges from less than 28 PSU in the northern zone to more than 32 PSU in the southern zone (Zirino et all, 2014). The climate is Mediterranean.

To understanding the current ecology of the lagoon, it is essential to consider its history and evolution. Over the past 2000 years, there has been a gradual transformation from a palustrine ecosystem with strong freshwater influence to its current state (Roner et al., 2017). In the 16th and 17th centuries, significant waterworks diverted the main rivers (Brenta, Bacchiglione, Sile, Piave, Po and others) from the lagoon. This was done to reduce the amount of sediment carried by the rivers, which was gradually transforming the lagoon into a plain-like ecosystem. This operation fundamentally altered the lagoon, creating an artificial ecosystem (Bondesan & Furlanetto, 2012). As a result of this operation, sediment inputs are reduced, and high tides are causing an ongoing erosion process that strongly affect salt marshes (Madricardo & Donnici, 2014; Lo et al., 2017). Currently, there is a loss of one million cubic meters of sediment per year (Saretta etl.,2010)

In the last century, human action has exacerbated this process with factors such as the creation of the Malamocco-Marghera Channel and the passage of ship enhancing the erosion rate (Cavazzoni, 1995; Carniello et al., 2009). Additionally, subsidence caused by groundwater withdrawal and organic soil oxidation, has caused a drop of nearly 23 cm (Carbognin et al.,2005). Ship traffic has also caused different erosion rates in various areas of the lagoon, with the south-central part experiencing higher rates than the north end (Carniello et al., 2009).

To address these issues, following the biggest flood in 1966, the "Legge Speciale di Venezia" was enacted in 1973, as the first law to safeguard the lagoon. This law prompted a series or restoration action. Since 1989, more than 80 salt marshes have been constructed or restored, recovering an area of 11 km² (Cecconi, 2005). This was done using sediment obtained from the dredging of channels to restore water circulation. Salt marshes construction begins with the creation of a containment barrier and pumping sediment inside, creating artificial island that will be naturally colonized by salt marsh plants (Patassini & Magro, 2016). The types of barriers used are timber piles, brushwood fascines, bags, rolls, and mattress made with rocks, fibres, shells or wood. For the study three types of salt marshes were used: the natural ones (N), as control, with no visible human intervention, restored of type 1 (R1) with structures removed in some part to allow the formation of low marshes, and restored of type 2 (R2) with structures still intact and a clear edge. The N marshes had a higher salinity and lower pH compared to the other marshes, while N and R2 marshes had similar sediment grain size (Billah et al., unpublished) (Supplementary material, Table 1).

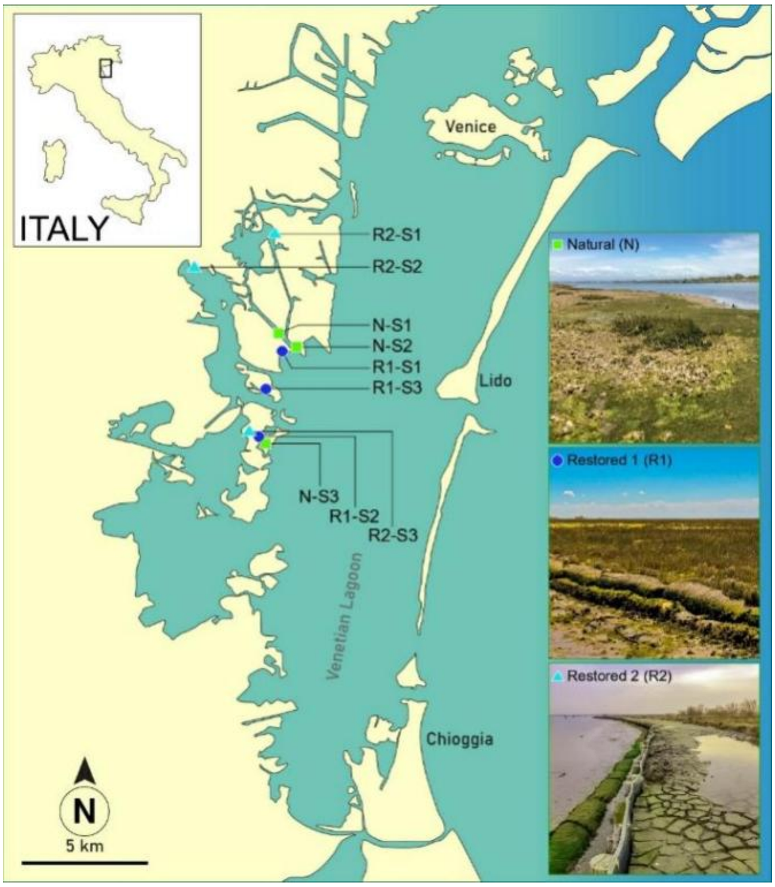

Figure 1- map of the Venice lagoon and the sampling sites.
N-Natural marshes; R1-Restored type 1 with edge barrier removal; R2-Restored type 2 with no removal.

2.2 SAMPLING METHODS

Sampling was conducted at the start and end of the growing season, in April and September 2022 respectively. In the low marsh, we stratified the sampling for the presence of *Sporobolus maritimus* and *Sporobolus* spp. For each of the three restoration types (N, R1, R2), we sampled eight plots in the mid marsh, eight plots in *Sporobolus* spp. stands, and eight plots of *Sporobolus maritimus* stands in the low marsh. Plots (quadrats of 50x50 cm) where randomly placed within the marsh zone, about 20 meters apart. In each quadrat, we visually recorded the living and dead coverage of plants, and used a 25x25 cm quadrat to collect the above-ground biomass (ABG) by clipping it at soil level. We also used a corer with a depth of 9 cm to sample the sediments for analyse the below ground biomass (BLG). However, due to logistic constrains we could not sample three quadrats in a natural low marsh.

In the mid marsh area, we found *Salicornia veneta, Puccinellia palustris, Limonium narbonense, Sarcocornia fruticosa, Juncus maritimus, Suaeda* *maritima, Aster tripolium*. While in low marshes, other than *Sporobolus* spp., we only found *Salicornia veneta.* The R2 marshes did not have a low marsh due to their construction, while in R1 *S. maritimus* was lacking. However, subsequent experiment conducted at a later timer revealed the presence of *S. maritimus* in R1. Although we were not able to include this plant in our initial sampling, we acknowledge its existence in the area and its potential significance in future research.

2.2.1 LABORATORY ANALYSIS

We first sorted the ABG between dead and alive plants. We removed the dead plants and retained and separated the alive plants by species. Then, we oven-dried the samples at 70°C for 48h and weighed them.

We cleaned the BLG to separate most of the soil and the debris by using a 0.5 mm sieve. However, roots were not divided by species due to difficulty in identifying them. We then dried and weighed the cleaned BLG samples by using the same procedure as the ABG. It is important to note that, despite the meticulous cleaning, debris, such as shells and pebbles, were still present in the BLG samples.

2.3 FUNCTIONAL TRAITS

We have chosen traits that are commonly measured in ecological studies because they are known to be related to ecosystem functioning (Table 1). We collected three plants for each available species at each site and then measured the functional traits. Plant height was measured in the field as the distance from the soil surface to the highest point in the plant. In the lab, three random leaves, free of damage, from each individual for each species were chosen and photographed; then, we measured their area by using an image analysis software (ImageJ). Leaves were then weighted, dried in the oven for 48 hours at 70°, and weighted again. Afterwards, the leaves area was divided by the dry weights to obtain the specific leaf area (SLA); we than averaged the SLA of the three leaves form each individual plants for each species. To calculate leaf dry matter content (LDMC), we divided the leaves dry weights by their fresh weights; similarly to SLA, we then obtained the averaged LDMC for each individual for each species. Furthermore, we counted the total number of leaves in each individual for each species. Then we computed the average leaf number at species level and we multiplied it to the average leaf area (at species level) to obtain the total canopy area (TCA).

Table 1- Key Functional Traits measured
The table summarizes the key functional traits that were measured as well as their significance for ecosystem functioning in salt marshes.

TRAITS USED	DESCRIPTION	FUNCTION	SOURCE
Height	Measure from the base of the plant to the top	Resources acquisition and competitive abilities.	Gaudett & Keddy, 1988 Westoby, 1998 Westoby et al., 2002
SLA (specific leaf area)	Area of leaf per unit of dry weight.	Reflects the ability to capture light,	Westoby, 1998

		species with high SLA have thin leaves and high photosynthesis rate and growth rate	
LA (leaf area)	Size of an individual leaf	Leaf energy and water balance	Farquhar et al.,2002 Díaz et al., 2016
LDMC (leaf dry matter content)	Leaf dry mass per fresh mass	Reflects the stability of the community, growth rate, influences the decomposition rates.	Polley et al., 2013 Fortunel et al., 2009 Májevoka et al., 2014
TCA (total canopy area)	Total leaf area of the plant	Reflects competitive abilities, it's related to stocking and index of growth	Waring, 1983 Gaudet & Keddy, 1988

2.4 STATISTICAL ANALYSIS

We performed all analysis using R Statistical Software v.4.2.2. (R core team, 2022) and visualized our data using the ggplot2 package (Wickham, 2016).

To examine for differences in community species composition in the mid marsh between the three types of marshes, we performed a PERMANOVA using the adonis2 function of the vegan package (Oksanen et al., 2022). The response variables were species percentage cover at the end of the growing season, while the independent variable was Restoration type (three levels: Natural, R1, and R2). The analysis was performed on a matrix of Euclidean distances with 9999 permutations. The strata argument was used to account for that sites were nested within Restoration type. To assess the assumption of homogeneity of variance in PERMANOVA, we tested for multivariate dispersion using Vegdist and Betadisper (vegan package). To visualize the results, we performed a principal coordinates analysis (PCoA) using the Betadisper function.

We compared above- and below ground specific net primary production (SANPP and SBNPP, respectively) between natural and restored sites, as net primary productivity strongly depends on the amount of biomass present in the system (e.g., bigger plants produce more biomass) (Garnier et al., 2004). To obtain SNAPP and SBNPP, we measured the weight at the start (time 0) and end (time 1) of the growing season for each site. We then determined the ANPP and BNPP at site level by subtracting the living biomass of time 0 to time 1. We repeated this process for each species. And then we standardized net primary production for the initial value of biomass present; therefore, we divided ANPP and BNPP with the ABG or BLG values at time 0 respectively, obtaining SANPP and SBNPP. For the cover we tested the difference in total and living cover at time 1. Additionally, we compared the total and living cover between restored and natural marshes.

To test the influences of restoration approach on total cover, total living cover, and biomass, we conducted ANOVAs with the type of restoration as an independent variable (three levels: N, R1 and R2). Due to the absence of *S. maritimus* in both type of restored sites and the absence of *S. anglicus* from R2 sites, we performed separate tests for the mid marsh (MM) and low marsh. The tests for the low marsh were carried out only for *Sporobolus.* spp.. In addition, an ANOVA was done to compare *S. maritimus* and *Sporobolus* spp. production (SNAPP, SBNPP, TNPP) at time 1. Species (*S. maritimus, Sporobolus* spp.) was the independent variable.

To analyse the difference in functional traits between plant species, we performed a principal component analysis (PCA) and used a scree plot graph to determine the number of principal components to include in our analysis. For the mid marsh, we then calculated the community weighted mean (CWM) for each trait using dbFD, from the FD package (Laliberté et al., 2014), across restoration types. To investigate the difference of functional traits CWM between restoration types, we used ANOVAs. We then conducted a Tukey HSD test to identify between which group there was a statistically significant difference. For TCA, we used the generalized least square, GLS, gls function of the nlme package (Pinheiro & Bates, 2000) to account for heterogeneity in variance across factors.

To test the relationship between specific net above ground primary production (SNAPP), specific net below ground primary production (SNBPP), total net primary production (TNPP) with functional traits for habitat and type of restoration, we used a simple linear regression. To assess the normality of the residual we used a Shapiro-Wilk test (Shapiro & Wilk, 1965).

3.RESULTS

3.1 COMMUNITY SPECIES COMPOSITION

By plotting the data we could see a different species cover between restoration type (Supplementary material, figure 1). For instance, in the mid marsh of R2 marshes there was more *Aster tripolium* but less *Sarcocornia perennis*. Indeed, PERMANOVA revealed that restoration type had a significant effect on species cover composition in the mid marsh (Table 2). Specifically, R2 was different from both N and R1, while N did not differ from R1 (Table 2; Figure 2). The ANOVA on the dispersion around the centroid indicated homogeneity of variance between groups ($F=0.973$; $p=0.3811$) and thus that PERMANOVA results are reliable.

Table 2 - Results of t test with Bonferroni correction for multiple comparisons Pairwise comparisons in species composition. The test indicates dissimilarities between R1, R2 and N marshes.

Pairs	F.model	R2	p-value adjusted
N vs R1	3.0680	0.063	0.093
N vs R2	17.9058	0.280	0.003
R2 vs R1	6.4230	0.123	0.006

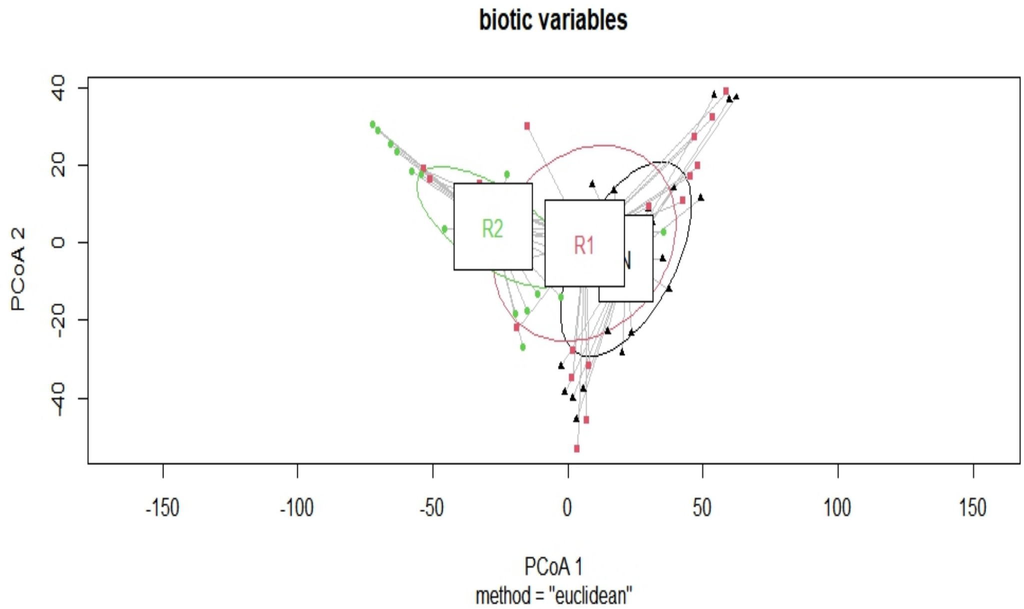

Figure 2 - PCoA graphs scatter plot of species percentage cover in the mid marsh among restoration types. PCoA1 axis explains the most variation in the data, and each point represent a sample.

3.2 COVER

We did not find any significant difference in total and alive plant cover among restoration types, either in the mid marsh or *Sporobolus* spp. stands (Table 3).

Table 3-ANOVAs' result for time 1 for total and living cover.
The test was done for MM and *Sporobolus* spp..

Habitat	Dependent variable	Df	Mean square	F value	p-value
MM	TC	2	155.600	0.675	0.544
MM	AC	2	222.100	1.153	0.377
Sporobolus spp.	TC	1	107.320	1.787	0.252
Sporobolus spp.	AC	1	108.370	1.807	0.250

3.3 NET PRIMARY PRODUCTIVITY

There were no significant relationships between specific net primary productivity and restoration type (Table 4 and Table 5). In addition, no significant relationship was found between the N low marsh patch of *S.maritimus* and *Sporobolus* spp. (Table 7).

Table 4- ANOVAs' results for standardized biomass
ANOVA results of the difference in SANPP, SBNPP, and STNPP among restoration type. The test was done for MM and *Sporobolus* spp..

Habitat	Dependent variable	Df	Mean square	F value	p-value
MM	SANPP	2	120.700	0.582	0.588

MM	SBNPP	2	0.169	0.809	0.408
MM	STNPP	2	1.112	1.112	0.388
Sporobolus spp.	SANPP	1	1706.000	1.696	0.263
Sporobolus spp.	SBNPP	1	0.028	0.103	0.764
Sporobolus spp.	STNPP	1	0.506	1.741	0.258

Table 5- ANOVA for *S. maritimus* and *Sporobolus* spp.
The table shows the results of the ANOVAs, the test was done for the N low marsh.

Dependent variable	Df	Mean square	F value	p-value
SNAPP	1	299.0000	0.1910	0.6850
BLG	1	308.1000	1.1230	0.3490
TB	1	0.1000	0	0.996
SBNPP	1	0.2319	1.4980	0.2880
TNPP	1	0.3786	0.3690	0.5760

3.4 FUNCTIONAL TRAITS

In the PCA, the first two axes were enough to capture much of the variability in the dataset (see scree plot in Supplementary material, Figure 2). Together, these two axes accounted for 73.01% of the variance (45.31% and 23.20% respectively for PCA1 and PCA2). The traits loading on the axes are reported on table 8.

Table 6- PCA loadings for PCA1, PCA2.
The loading of the PCA for PC1 and PC2, showing the contribution of each functional trait to these principal components.

	PC1	PC2
Height	0.461	-0.394
SLA	-0.051	-0.550
LA	-0.524	-0.422
LDMC	0.463	-0.515
TCA	-0.544	-0.315

By using a scatter plot, we can see how the functional traits composition of different plant species relates to the PCA (Figure 3). We can see how *S. maritimus*, *Puccinellia* and *Juncus* are a cluster, indicating a similar height and LDMC, while *Salicornia* spp. and *Salicornia fruticosa* have a similar low SLA; *Limonium* and *Aster* have similar high TCA and LA.

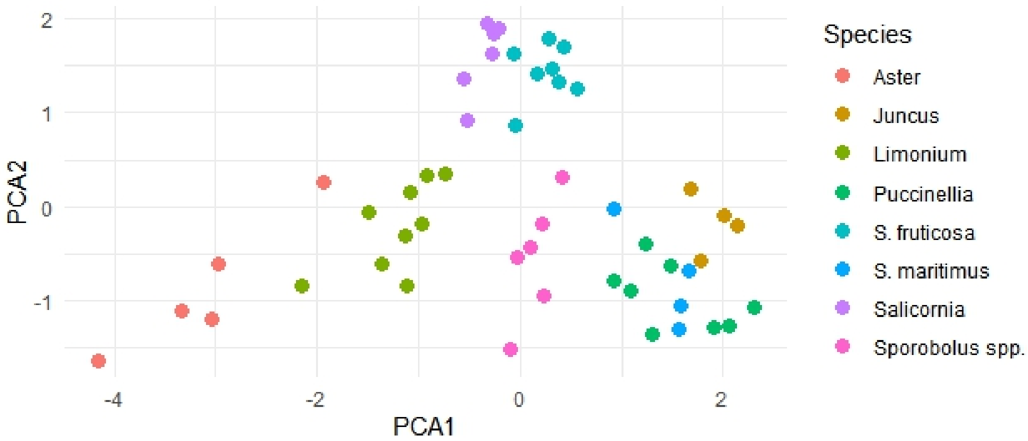

Figure 3- Distribution of species on the PCA scatter plot.
The graph show the distribution of different plant species based on their functional traits in relation with PC1 and PC2. On the lower right angle we can found the species with high LDMC and height, on the lower left angle the species with high TCA and LA, on the central low zone the species with high SLA.

In the mid marsh, ANOVAs analyses found statistical difference for CMW SLA (Mean square=60.22, $F_{2,6}$=6.04, p-value=0.037, Shapiro-Wilk: W=0.891 p-value=0.203) and CWM LDMC (mean square=0.003, $F_{2,6}$=15.94, p=0.004). The TukeyHSD tests indicated that in N marshes the plant community had higher CMW LDMC (Table 8), but lower SLA, than R2 marshes, while no statistical significant differences were found between N and R1, or R1 and R2 (Table 8). No statistical significant differences were found for LA (Mean square=1.81, $F_{2,6}$=0.398, p=0.688, Shapiro-Wilk: W=0.956, p=0.752) and Height (Mean square=11.42, $F_{2,6}$=2.298, p=0.182; Shapiro-Wilk: W=0.939, p=0.570). Also for CWM of TCA, the GLS indicated that CMW TCA did not differ among restoration types ($F_{2,6}$=1.454, p=0.305).

Table 7- Average traits for restoration sites

Traits	N	R1	R2
SLA	53.97	58.75	62.92
Height	26.24	24.18	22.34
LA	6.31	4.94	4.99
LDMC	0.205	0.171	0.138
TCA	40.87	34	65.03

Table 8- Tukey HSD results for LDMC and SLA

TukeyHSD	LDMC		SLA	
	Diff	p-value	Diff	p-value
R1-N	-0.034	0.065	4.79	0.231
R2-N	-0.067	0.003	8.95	0.031
R1-R2	0.033	0.071	4.17	0.310

Figure 5 shows the relationships between CWM of SLA and SANPP and SBNPP (combining the low and mid marsh). The results indicate a strong positive relationship between SLA and SNAPP (β=1.91±0.5, t-value=3.785, p=0.002,

R^2=0.49; Shapiro-Wilk: W=0.912, p=0.108). There was no statistical difference for SLA - SBNPP relationship (β=-0.012, t-value=-1.232, p=0.237, R^2=0.09Shapiro-Wilk: W=0.967, p=0.773).

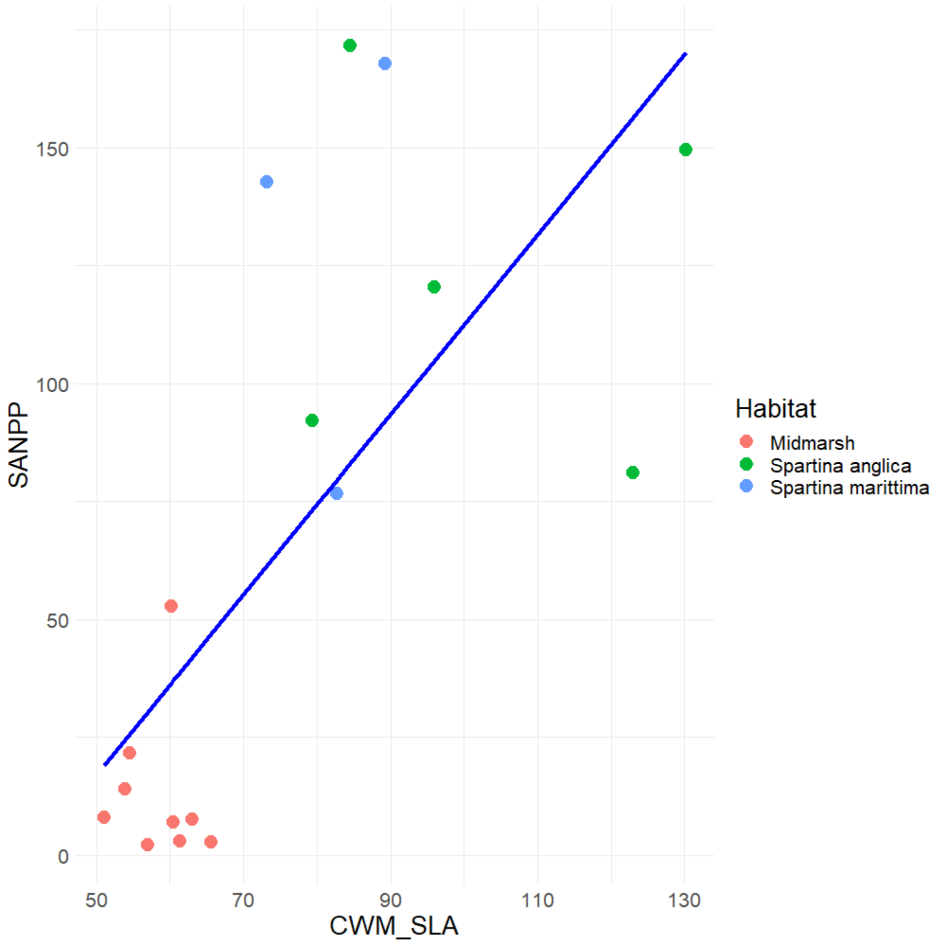

Figure 5- SANPP-SLA relationship across marsh zones
The figure shows the relationship between SANPP and SLA across marsh zones, every point represent a different marsh. The plot shows a clear position of the mid marsh and low marsh. SLA has a positive association with SANP.

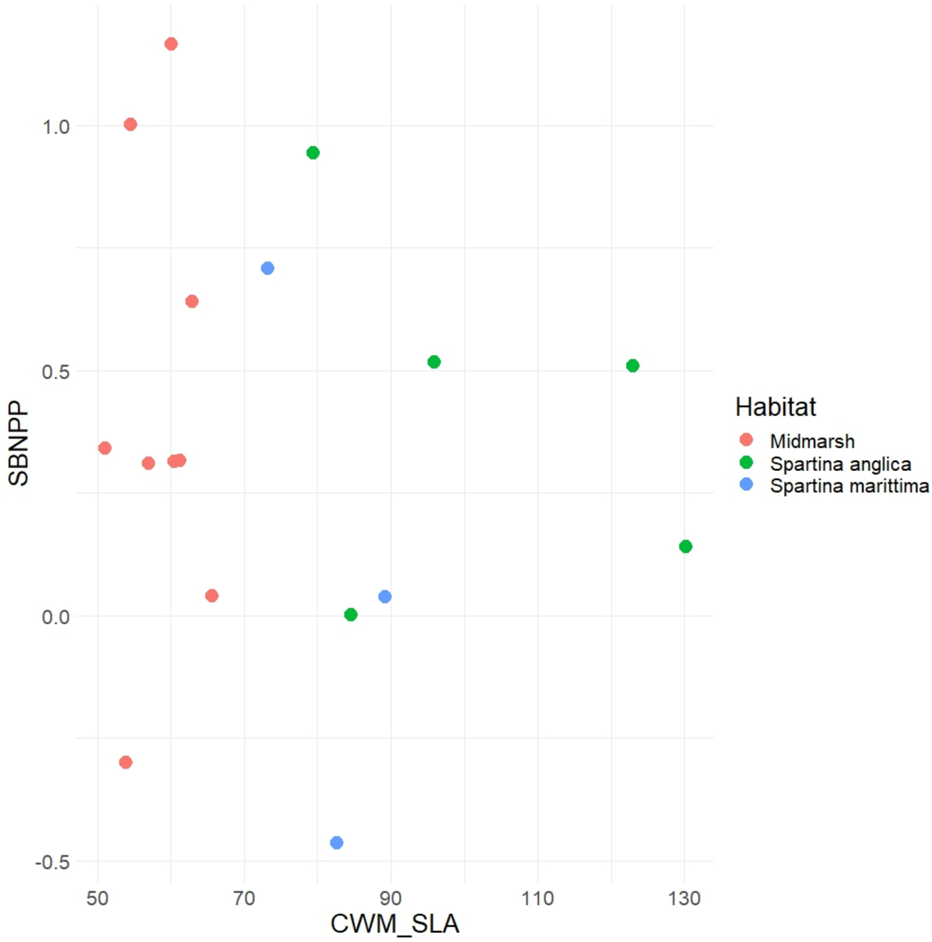

Figure 6- SBNPP-SLA relationship across marsh zones
The figure shows the abscende of relationship between SANPP and SLA across marsh zones, every point represent a different marsh.

4. DISCUSSION

The results of the study indicate a clear difference in plant communities between restored and natural marshes. However, these differences were not reflected by biomass, net primary productivity, nor by total coverage. Analysis of functional traits revealed significant difference between restored marshes. Specifically, natural marshes had lower and higher SLA and LDMC respectively in the mid marsh zone. Additionally, a statistically significant positive relationship was found between SLA and SNAPP, while no relationship was found for SLA and SBNPP.

In our study, we expected similarities between R2 and N marshes in species composition and biomass, but not between these and R1, due to the similar sediments (Billah et al., unpublished). However, our results contradicted this expectation. The cover graph showed that certain species were present only on N, as *Suaeda* and *Juncus,* while other species were more abundant on R2, such as *Puccinelia* and *Aster*. These differences were reflected by the PERMANOVA and the PCoA indicating that the mid marsh of N and R1 were similar, with R1 as a halfway point between N and R2. These results could be explained by the interaction of a series of abiotic factors, such as marsh morphology, and biotic factors. For example, *Suaeda*, more present in the N marshes, may be excluded by *Puccinellia* in certain condition, which is more present in both R1 and R2 (Tessier et al., 2000). Additionally, *Limonium* was more present in N, probably due to higher salinity, as it is more resistant and competitive in that conditions (Hassan et al., 2017). Another explanation for the similarities between R1 and N could be the removal of the artificial structures as they can affect the macro-fauna grazing and the submersion time and the nutrient exchange is different (Rezek et al., 2017). The removal can lead to a different plant succession. Indeed, *Sprobolus* spp., a typical pioneer species (Castellano et al., 1994) was present on R1 marshes but not on R2. Therefore, this operation could lead to changes in plant community composition, potentially favoring the growth of some pioneer species.

While the absence in R2 of *Sprobolus* could be explained by the absence of the low shore, it is interesting to note how *S. maritimus* was largely present only on N. While further study are needed, as *S. maritimus* was acknowledged on R1 on subsequent expeditions, the ANOVA we carried out to confront the patches of *Sporobolus* spp. and *S. maritimus* did not show any significance between these species. Moreover, *Sporobolus* spp. as in other studies shows an absence of difference between restored and natural marshes independent from the sediment type (Rezek et al.,2017). This result rise the point that in this area *Sporobolus* spp. maybe ecological equivalent to the native *S. maritimus*. More studies are needed to elucidate this important point.

The PCA on functional traits revealed that the species investigated had different investment on different competitive abilities and resource acquisition. The PCA indicates a strong influence of LDMC in the variation, with two of the three species with high LDMC more present on the natural marshes, followed by the R1. High presence of these species could suggest a higher stability of the communities, because plants with a higher LDMC have thicker and tougher leaves, which is associated with higher resistance to stressors (Westoby et al., 2002; Polly et al., 2013; Májeková et al., 2014). Additionally, we found a significant difference in CWM SLA between restoration types, with R2 mid marshes having higher SLA. The switch to higher SLA in R2 communities arose from the higher presence of *Aster* in these marshes, a species with higher SLA and TCA. The higher abundance on this species may be related to a difference to soil nutrients or presence of fresh water (Díaz et al, 2016; Clapham et al., 1942).

Despite the difference in species composition and functional traits among restoration types, our results showed that natural and restored marshes had similar plant living and total coverage, and specific net primary productivity (SANPP and SBNPP), both in the mid marsh and for *Sporobolus* spp. in the low marsh. Interestingly, our results on the main driver on primary production (combining both the mid and low marsh), indicate that CWM SLA is a strong proxy for SNAPP, as already found in terrestrial systems (Garnier et al., 2016). This positive relationship, however, was driven by both *Sporobolus* species, with much higher SLA and SANPP than any mid marsh community. Thus, it seems that in the mid marsh the significant, but modest, increase in SLA in the community was not enough for leading to a significant increase in SANPP (although it showed a tendency to be higher). Overall, our analysis add to a growing body of research on the capacity of functional traits to inform on changes in ecosystem functioning (Garnier et al., 2016: De Bello et al., 2010, 2019).

Regarding SBNPP, we did not find any difference among restoration types or on the relationship between SLA and SBNPP. It is possible that other factors, or traits, maybe more important in driving these relationships. Alternatively, similarities among restoration types could be due to the variable number of debris present in the samples, which may have increased the variance and thus masked any possible significant differences.

5. CONCLUSIONS

We observed difference in species composition and functional traits between restored and natural sites, which were likely correlated to the restoration action. However, contrary to our hypothesis, these differences did not seem to affect relevant functions such as production, as we did not find significant effects of restoration type on the living and total coverage or specific net primary productivity.

Our results highlight the link between CWM of specific functional traits and specific net primary productivity at broader level, i.e., when considering both the mid and low marsh together. This suggests that functional traits can be employed to investigate the success of a restoration projects, if the breadth in traits variation is large enough. Also, our results further confirm that selecting plants with specific traits could enhance restoration outcomes.

In conclusion, our result support the idea that the success of restoration should be evaluated at a functional level. However, further research is needed to identify the key drivers of the differences in functional trait composition and to understand how salt marsh communities may evolve over time. By combining these approaches we could obtain a better mechanistic understanding of the effect of restoration on the salt marshes ecosystem.

6. LITERATURE CITED

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7. SUPPLEMENTARY MATERIAL

Table 1- Result's of Masum et al.'s unpublished. Main soil characteristics.
The table presents the soil characteristics of N,R1, and R2 for both the low marsh (LW) and the midmarsh (MM). The data presented are unpublished and collected by the authors in 2021. Four soil samples were randomly collected per site.

Marshes:	Salinity	pH	Organic	Bulk	Clay

	(μS/cm):		matter (%)	density g/cm³	fraction (%)
N MM	19214	7.66	21.40	0.88	85.1
N LW	11334	7.92	15.00	1.01	78.9
R1 MM	4780	8.12	11.40	1.36	27.8
R1 LW	6881	8.16	11.10	1.36	44.4
R2 MM	6439	8.09	16.40	0.97	85.1

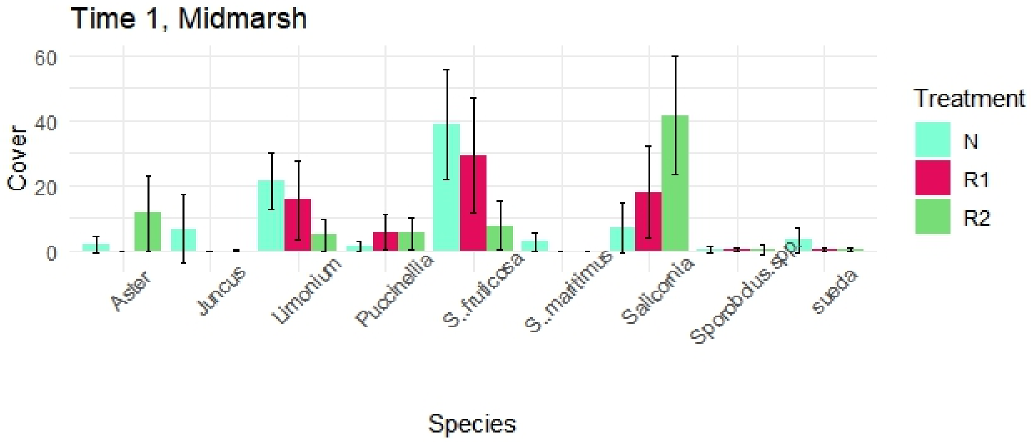

Figure 1- Barplot of midmarsh cover at time 1.

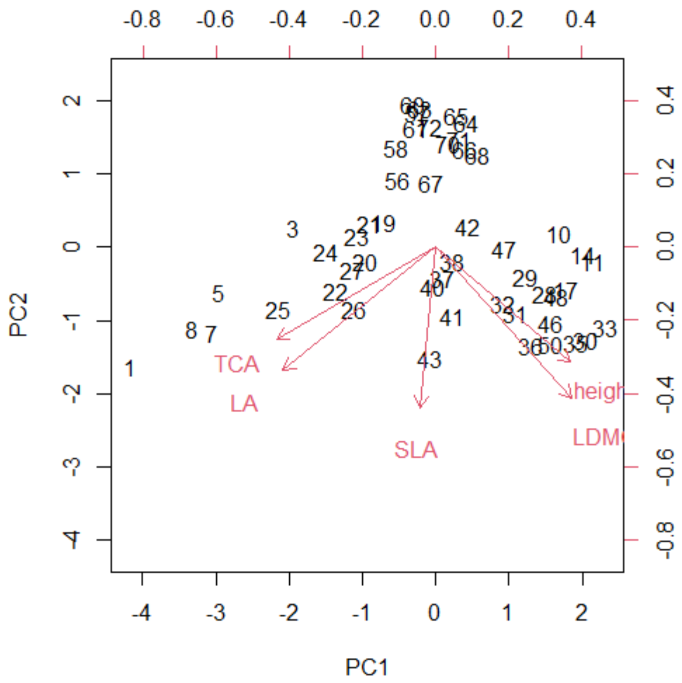

Figure 2- scatter plot of PC1 and PC2.
The arrows indicate the strength and direction of the contribute of each variable to the PC,. TCA, LA, height and LDMC creates a angle of 90° indicating a contrasting relationship.