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Functional groups based on leaf physiology: Are they spatially and temporally robust?

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Abstract

The functional grouping hypothesis, which suggests that complexity in ecosystem function can be simplified by grouping species with similar responses, was tested in the Florida scrub habitat. Functional groups were identified based on how species in fire maintained Florida scrub regulate exchange of carbon and water with the atmosphere as indicated by both instantaneous gas exchange measurements and integrated measures of function ($\%N$, $\delta^{13}C$, $\delta^{15}N$, C:N ratio). Using cluster analysis, five distinct physiologically-based functional groups were identified in the fire maintained scrub. These functional groups were tested to determine if they were robust spatially, temporally, and with management regime. Analysis of Similarities (ANOSIM), a non-parametric multivariate analysis, indicated that these five physiologically-based groupings were not altered by plot differences ($R = -0.115$, $p = 0.893$) or by the three different management regimes; prescribed burn, mechanically treated and burn, and fire-suppressed ($R = 0.018$, $p = 0.349$). The physiological groupings also remained robust between the two climatically different years 1999 and 2000 ($R = -0.027$, $p = 0.725$). Easy-to-measure morphological characteristics indicating functional groups would be more practical for scaling and modeling ecosystem processes than detailed gas-exchange measurements, therefore we tested a variety of morphological characteristics as functional indicators. A combination of non-parametric multivariate techniques (Hierarchical cluster analysis, non-metric Multi-Dimensional Scaling, and ANOSIM) were used to compare the ability of life form, leaf thickness, and specific leaf area classifications to identify the physiologically-based functional groups. Life form classifications (ANOSIM; $R = 0.629$, $p = 0.001$) were able to depict the physiological groupings more adequately than either specific leaf area (ANOSIM; $R = 0.426$, $p = 0.001$) or leaf thickness (ANOSIM; $R = 0.344$, $p = 0.001$). The ability of life forms to depict the physiological groupings

was improved by separating the parasitic *Ximenia americana* from the shrub category (ANOSIM; $R = 0.794$, $p = 0.001$). Therefore, a life form classification including parasites was determined to be a good indicator of the physiological processes of scrub species, and would be a useful method of grouping for scaling physiological processes to the ecosystem level.

Introduction

Current interest in modeling the role vegetation has on ecosystem and larger scale processes (e.g. regional and global) has lead to a need for an adequate method for simplifying complex terrestrial systems. Process-based models that are spatially explicit across landscapes must generalize vegetation and their responses into a few categories rather than represent every species or individual. The current methodology for this simplification is grouping species into a smaller number of functional groups. This concept that the complexity of nature can be reduced in models by treating a smaller number of functional groups is currently the central method for understanding how changes in the terrestrial surface may influence atmospheric dynamics (Steffen et al. 1992). However current methods for grouping species have not been fully tested to see that these functional groups are linked with processes that influence biosphere – atmospheric interactions.

The plant – atmosphere interactions that are of prime interest for regional and global simulations are the cycling of carbon, water, and nitrogen. These ecosystem cycling processes are strongly linked to plant physiology and may be adequately simulated using plant functional types rather than individual species. For example, litter decomposition is an important part of ecosystem nutrient cycling, and plants with higher C:N ratios have less decomposable litter than those with lower C:N ratios (Perez-Harguindeguy et al. 2000). Transpiration and carbon assimilation are an important part of water and carbon cycling within an ecosystem (Law et al.

2002; Thornton et al. 2002). In order to simulate ecosystem cycling processes, functional groups need to be based on physiological functions that are associated with the ecosystem process being modeled. However functional groups are often defined on attributes that are not related to these ecosystem processes. For instance functional types were defined using a combination of demographic, structural, moisture requirements and phenological characteristics for modeling the response of tropical forests to climate change (Condit et al. 1996). While these groupings may prove useful for models simulating succession, these groupings were not specifically tested for differences in processes such as carbon uptake and water loss, and thus may be inadequate for atmosphere-biosphere interaction models.

For adequate simulation of a process, functional groups must be based on physiological traits that are important for that ecosystem process. In the case of carbon and water dynamics between the atmosphere and biosphere, physiological traits related to leaf gas-exchange would be important indicators for basing functional groups. For instance, percent nitrogen and the values obtained from photosynthetic light response curves allow the gas-exchange potential of the leaf to be determined. The carbon isotope ratio ($\delta^{13}\text{C}$) of a leaf is influenced by the interplay between stomatal conductance and photosynthesis (Ehleringer et al. 1993), and has often been related to a plant's intrinsic water-use efficiency. All of these measures are direct indicators of processes that affect the biosphere-atmosphere interactions of carbon and water cycling. Functional groups based on parameters such as these would be more successful in modeling simulations than ones based on reproductive or other strategies. However, measuring large sets of physiological parameters to determine groups for every ecosystem would be tedious and impractical.

1 In order for these physiological groupings to be useful for modeling, there needs to be an
2 easy-to-measure indicator of function. Box (1996) suggested an approach in which structure
3 would be used as a substitute for function. Specifically, Chapin (1993) suggests that
4 ecophysiological traits may be linked to ecosystem processes by using morphological functional
5 types; species of the same growth form had similar physiological characteristics. For example,
6 species that grow rapidly also have high rates of photosynthesis, transpiration and decomposition
7 (Chapin 1993). However it remains to be determined whether a physiological basis to these
8 morphological classifications exists. This connection between the groups and their function is
9 critical for models to accurately predict the role of vegetation in atmosphere-biosphere
10 interaction models.

11 The use of life forms as indicators of functional groups is appealing because
12 classification into trees, shrubs, epiphytes, vines and forbs, as well as distinguishing between
13 deciduous and evergreen, is not only easy but is based on morphological features of a species
14 that are insensitive to environmental change (Schulze 1982). Indeed several studies have found
15 relationships between physiognomic features and function relating to carbon, nitrogen, and water
16 dynamics. Brooks et al. (1997) found that classification of plant species into seven different life
17 forms was successful in accounting for approximately half of the variation in stable carbon
18 isotopes (water and carbon fluxes) among different plant species in each of three boreal forest
19 ecosystems. In the rainforests of French Guiana, Bonal et al. (2000) also found that stable
20 carbon isotope values varied between deciduous-leaved trees and evergreen leaved trees, with
21 the deciduous trees being more water-use efficient than evergreen leaved species. Jackson et al.
22 (1995) found that evergreen tree species accessed deeper water sources than deciduous species in
23 tropical forests. Reich et al. found that forbs have higher respiration (Reich et al. 1998b) and

greater maximum photosynthesis (Reich et al. 1998a) for a given level of leaf N than woody broad leafed species, while needle leafed conifers have the lowest respiration and photosynthesis for a given level of N.

Leaf characteristics may also be another possible indicator of physiological function since leaf morphology and leaf function have been found to be interrelated. Reich et al. (1991) found that longer-lived leaves have lower net photosynthetic rates and nitrogen contents. Koike (1988) found that in temperate ecosystems, leaf thickness and photosynthesis at light saturation were highly correlated for a broad range of tree species. Reich et al. (1997) found that the relationship between leaf lifespan and photosynthetic function was robust even on a global scale. Species with higher specific leaf area were found to have shorter life spans (Reich et al. 1997) as well as higher maximum photosynthesis (Reich et al. 1998a) and higher respiration (Reich et al. 1998b) per unit leaf N accompanied by a steeper slope between photosynthesis and leaf N. This relationship was true at the species, genera, and functional group level of organization. However in a study in Minnesota, Reich et al. (2003) found that leaf area ratio and specific leaf area ratio were not associated with relative growth rate.

These studies collectively suggest a relationship between morphology and physiological function. However, they generally examine only one or two functional parameters and most do not test for robustness of these groupings over time and with changes in land management. Land management practices can alter the composition and abundance of functional groups (Hadar et al. 1999; Landsberg et al. 1999; Lavorel et al. 1999). For instance, Lavorel et al. (1999) found that ploughing favored grasses while grazing excluded large grasses and favored small species with leafy stems. McIntyre and Lavorel (2001) found that different levels of grazing favored different plant functional types. Fire suppression, although it has been found to lead to an

1 increase in carbon storage, causes shifts in abundance and composition of species in the habitat
2 (Tilman et al. 2000). In addition to changes plant functional groups with land management, an
3 equally important question is if a management regime can alter the function of a species or the
4 groupings. However, to our knowledge, no studies have examined this question.

5 This study tests the functional grouping hypothesis for applicability to carbon and water
6 plant-atmosphere interactions by comparing and grouping species based upon responses to a
7 suite of physiological parameters. We test these groupings spatially across management regimes,
8 and temporally in Florida scrub vegetation. The dwarfed and stunted vegetation in Florida scrub
9 is the ideal habitat to test the functional grouping hypothesis, because stress tolerant plants would
10 tend to conserve function over a wide range of conditions compared to plants that grow rapidly
11 in response to resources. If the functional grouping hypothesis is not supported in a stress
12 tolerant community, then it is not likely to be supported in any ecosystem. Specifically, our
13 objectives were (1) to identify functional groups based on how species in fire maintained Florida
14 scrub function in terms of carbon and water gas-exchange with the atmosphere, (2) to determine
15 whether there is an easy-to-measure morphological characteristic (life form, specific leaf area,
16 leaf thickness) that indicates physiological function and (3) to determining whether these
17 functional groups were temporally and spatially robust by comparing functional groups between
18 years and between different management regimes (prescribed burning, mechanical treatment, and
19 fire suppression).

20 Methods and Materials

21 Site Description

22 This study was conducted at the John F. Kennedy Space Center (KSC), Merritt Island
23 National Wildlife Refuge (MINWR) in east central Florida (28° 37'N, 80° 43'W). The climate at

KSC is warm and humid. Mean annual air temperature is 22.8°C with the annual low temperatures occurring in January (15.6°C) and the annual high temperatures in July (27.8 °C). Annual precipitation averages 1394 mm with 66% occurring during the wet season between the months of May and October. Relative humidity during the wet season averages 93% in the early morning and 65% in the early afternoon (data obtained from the Air Force Combat Climatology Center).

Experimental Design

Three sites were selected in the oak – saw palmetto scrub on KSC/MINWR; the Camera Pad Site (28°37.676'N; 80°39.305' W), the Kennedy Parkway Site (28°36.957'N; 80°40.826' W), and the Happy Creek Site (28°37.983'N; 80°39.904' W). Each site had three land management regimes in close proximity (fire suppressed scrub, mechanically treated and burned scrub, and burned scrub) for a total of nine plots. The plots were 30 m by 30 m when possible, however size limitations existed for three plots due to either patchy burns or management strategy. All plots were located on well-drained Pomello soils (Huckle et al. 1974), with the exception of the burn plot in the Kennedy Parkway site that occurs on Immokalee. Both soils are Spodosols with the main difference being that Immokalee tends to have a shallower water table than Pomello (Huckle et al. 1974).

The nine plots vary in three respects; time since burn, management regime, and distance to the water table (Table 1). Since oak - saw palmetto scrub recovers rapidly after fire exhibiting little change in composition or species richness (Schmalzer and Hinkle 1992b), the short variation between time since burn for the recently burned and mechanically treated plots should not exhibit much of an influence on species responses. Fire-suppressed scrub may differ in species composition and cover compared to fire-maintained scrub (Schmalzer and Adrian 2001;

Schmalzer et al. 1994), and is more likely to exert influence on species response. Aside from land management regimes the main difference is the distance to the water table, with a range of a half-meter between the three sites (Table 1). This is particularly important since the composition of oak - saw palmetto scrub is closely related to water table depth with oak dominated scrub on the drier sites and saw palmetto dominating the wetter sites (Schmalzer and Hinkle 1992b), thus the site differences in water table depth will be a further test of the spatial robustness of functional groupings.

Twelve of the dominant scrub species present on KSC/MINWR, that covered the range of life forms (Table 1) and leaf characteristics, were selected for inclusion in this study. Not all species were present in each plot (Table 1). The physiological function of these species was examined using a suite of instantaneous and integrated indicators of carbon, water, and nitrogen dynamic: photosynthetic response curves to light, leaf carbon isotope ratio ($\delta^{13}\text{C}$), leaf nitrogen isotope ratio ($\delta^{15}\text{N}$), leaf %C, leaf %N, and leaf C/N.

Physiological Measurements

Instantaneous Gas Exchange Measurements

Instantaneous gas exchange was measured using a portable photosynthesis system (Li-Cor 6400, LI-COR, Lincoln, NE) under controlled levels of CO_2 ($400 \mu\text{mol} \text{CO}_2 \text{mol}^{-1}$), flow ($500 \mu\text{mol} \text{s}^{-1}$), and light. All other conditions were maintained at ambient levels. If the air or leaf temperature exceeded 35°C , the cooling fan was set to maintain the temperature at 35°C . Measurements were made on spatially segregated individuals within the plot to decrease the likelihood of sampling the same clone. Ainsworth et al. (2003) found that within a 2-ha research site numerous *Quercus geminata* genotypes were present, and the presumable clones (the individuals expressing the same genotype on seven microsatellite loci) were always within a

radius of 18 m. Therefore plot size and the segregated sampling of plants distant from one another, should have decreased the probability of sampling clones

Photosynthetic light response curves were measured on mature sunlit leaves during the summers of 1999 and 2000. In 1999, light response curves were measured on two mature individuals of each species present at all three of the Camera Pad plots (Table 1), and on selected species in the other plots. Measurements were taken at six light levels (2000, 1500, 1000, 500, 200, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and were collected throughout the day (9am – 3 pm EST). In addition to the light curves, measurements of photosynthesis at light saturation (A_{max}) were taken on three mature sunlit leaves of three additional individuals for each species present in the Camera Pad plots (Table 1) as well as some species present in the remaining plots. The saturating light level for each species was determined from the light response curves.

During the summer of 2000, light response curves were collected on 3 mature individuals per species at each plot sampled between 9 am and noon (because of dryer conditions in 2000), at seven light levels (2000, 1500, 1000, 500, 200, 100, 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$). *Lyonia ferruginea* and *L. fruticosa* were excluded from the instantaneous analysis in 2000 because the rust colored scales from these species collected in the Li-Cor 6400 infrared gas analyzer, causing a substantial differential in carbon dioxide between the sample and reference cells when no leaf was present in the chamber.

Six physiological traits were obtained from the light response curves: photosynthesis at light saturation (A_{max}), conductance at light saturation (g_{max}), dark respiration (R_d), intrinsic water use efficiency ($A_{\text{max}}/g_{\text{max}}$), quantum yield (Φ), and the compensation point (I_c). Quantum yield was estimated from the slope of the change in carbon dioxide uptake as the available light

changed from 0 to 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The y - intercept of the line (where net CO_2 uptake = 0) is the compensation point.

Tissue Analysis for Integrated Variables

Several mature leaves were collected from the upper canopy of three spatially segregated individuals for all selected species present in each of the nine plots at the end of both summers, with the exception of the Happy Creek mechanically treated plot in 1999. The leaves from each individual were clumped together into a single sample, and were dried and ground. Subsamples were weighed on a microbalance (Cahn C-33, Cahn Instruments Inc. Cerritos, CA in 1999, and Perkin-Elmer AD 6 Autobalance, Norwalk, CT in 2000) and analyzed for the carbon isotope ratio ($\delta^{13}\text{C}$), percent carbon (%C), nitrogen isotope ratio ($\delta^{15}\text{N}$), and percent nitrogen (%N) on a light stable isotope mass spectrometer (Delta Plus, Finnigan, Bremen, Germany) at the Environmental Protection Agency's Integrated Stable Isotope Research Facility (ISIRF; Corvallis, OR). Due to a balance malfunction in 2000, a small subset of 2000 %N values were suspect. However, the remaining percent nitrogen and C:N values taken in 2000 were highly correlated with the corresponding values in 1999 ($R^2 = 0.832$, $p = <0.0001$; $R^2 = 0.898$, $p = <0.0001$ respectively), thus the 1999 %N values were substituted in all spatial analyses with 2000 data. However for temporal analysis, the 2000 %N data was used, with the assumption that if there was any effect of using the suspect data, it would be in making the two years more dissimilar.

Morphological Measurements

The twelve species were classified into four life form groupings; trees, shrubs, vines, and palmetto based on descriptions by Nelson (1994; 1996) and Lakela and Wunderlin (1980) (Table 1). *Ximenia americana* is a hemiparasite on the roots of other plants, however this parasitism

1 does not appear to be host-specific or mandatory for survival (Nelson 1994). *Galactia elliottii*
2 and *Smilax auriculata* are vines, and *Serenoa repens* is the only palmetto. All of the scrub
3 species are either evergreen or semi-evergreen, so comparisons between evergreen and
4 deciduous species were not possible.

5 The specific leaf area (SLA), or leaf area per leaf mass, was calculated for one mature
6 leaf from 20 individuals for each species at the Camera Pad burn plot. The area of each leaf was
7 obtained using a leaf area meter (Li-Cor 3100, Li-Cor, Lincoln, NE). The leaves were then dried
8 for 48 hours and weighed (± 0.0001 g; SA120, Scientech). ANOVA and multiple comparisons
9 were used to determine significant species differences (SPSS v. 10.1). The species were then
10 grouped into two categories based on their SLA; high SLA ($>6.5 \text{ m}^2 \text{ kg}^{-1}$) or low SLA ($<6.5 \text{ m}^2$
11 kg^{-1}).

12 Leaf thickness (LT) was obtained for one mature leaf from 11 individuals for each
13 species present at the Camera Pad burn plot using a thickness gauge (± 0.001 in [0.0025 cm];
14 Teclock Corporation, Japan). ANOVA and multiple comparisons were used to determine
15 significant species differences (SPSS v. 10.1). The species were grouped into three categories
16 based on leaf thickness; thick leaves ($> 0.5 \text{ mm}$), intermediate leaves ($>0.32\text{mm}$ and $<0.5 \text{ mm}$),
17 and thin leaves ($<0.32 \text{ mm}$).

18 Analysis of Functional Groups

19 Initially, functional groups of species were identified at only the fire-maintained Florida
20 scrub plot, the Camera Pad burn plot, based on common physiological traits measured during the
21 summer of 1999 (May – August). Data from 1999 in the other plots and the 2000 data were used
22 in testing the spatial and temporal robustness of this initial grouping. A fire-maintained plot was

used for this initial determination because typical scrub characteristics were exhibited, such as vegetation composition, vegetation cover, and presence of openings.

The physiological functional groups were identified using hierarchical cluster analysis (PC-ORD v. 4.0, SPSS v. 10.1) with the average linkage method and the Euclidean distance (ED) measure. Due to large differences in the scales of the ten physiological parameters, data was transformed into standard deviation units above or below the mean (Z scores) (Pagano 1994). To test for bias of the clusters, these results were compared to results from analyses using a variety of linkage methods and distance measures. In general the groupings obtained by the various methods were in agreement. The Mantel test was used to determine whether the clusters were significantly different from clusters obtained by chance (PC-ORD v. 4.0).

Statistics for Spatial Robustness

Analysis of Similarities (ANOSIM) was used to determine whether the physiological functional groups were robust across plots and management regimes in 2000 (PRIMER-E v. 5; PRIMER-E Ltd, Plymouth Marine Laboratory, UK). The 2-way cross layout of the ANOSIM is a non-parametric permutation procedure similar to the parametric MANOVA that addresses two null hypotheses simultaneously. Non-parametric tests were used instead of a parametric analysis because data sets are not required to adhere to the assumptions of parametric tests (normality and homogeneity of variances) (McCune and Mefford 1999). The test statistic, R, compares the degree of separation of the treatments by comparing the differences between treatments to the differences among the replicates for each treatment using the average rank similarities. R near zero indicates that there is little to no separation among the *a priori* groups accepting the null hypothesis, whereas an R near 1 indicates complete separation among the groups (see Clarke and Warwick (2001) for further details on the procedure).

1 The first null hypothesis was that there were no spatial effects (plot or treatment
2 depending on test) allowing for the fact that there may be differences between physiological
3 functional groups. The second null hypothesis was that there were no differences in
4 physiological functional groups allowing for spatial differences. These analyses were conducted
5 on two different subsets of the Z-score transformed 2000 data with the 1999 %N and C:N ratios
6 (see details above) for both plot and management regime. The two subsets maximized either the
7 number of species by plot combinations or the number of physiological parameters that could be
8 included (Table 2).

9 Statistics for Temporal Robustness

10 Robustness of the physiological functional groups temporally between 1999 and 2000
11 was addressed using a 2-way ANOSIM. The two null hypotheses were no effect of year, or no
12 difference in physiological functional group while allowing for differences in the other. This
13 analysis was conducted on two Z-score transformed data sets: one in order to maximize the
14 number of species by plot combinations, and the other to maximize the number of physiological
15 parameters (Table 2).

16 Statistics for Robustness of Morphological Indicators of Function

17 Hierarchical Cluster analysis and non-metric Multi-Dimensional Scaling (MDS) were
18 used to assess which morphological indicator best represented the species clusters based on
19 physiological function across all the plots using 2000 data with the 1999 %N and C:N ratios (see
20 details above). All plot by species combination of data were included for this analysis (Table 2).
21 The Hierarchical Cluster Analysis and the MDS were computed from the same distance matrices,
22 in which the physiological variables were transformed with the Z-score (see above for details)
23 and the Euclidean distance measure was used. A hierarchal cluster analysis and MDS were

1 computed using all ten of the physiological parameters for 48 species by plot combinations.

2 Another hierarchical cluster analysis was also computed using only the integrated measures for 64
3 species by plot combinations.

4 To examine which morphological indicator was more adequate for depicting the
5 physiologically based functional groups, the MDS ordination output was examined in 3-
6 dimensional space, with the different morphological groupings (life form, life form + *Ximenia*
7 *americana*, SLA, and leaf thickness) superimposed on the ordination. ANOSIM was used to
8 determine whether differences existed between the groups of each morphological indicator. The
9 best indicator of physiological function was determined based on the value of the R statistic from
10 the ANOSIM. The closer R is to 1 the more complete the separation between the groups, thus a
11 better indicator of physiological function.

12 Results

13 Functional Groups

14 The 1999 physiological data from the camera pad burn site separated the species into five
15 physiologically-based functional groups from the cluster analysis at a similarity distance of
16 approximately 24 (Figure 1). *Galactia elliotii* and *Smilax auriculata*, both vines, were members
17 of the first functional group. *Myrica cerifera* and the three oaks were members of a second
18 functional group. Two of the oaks, *Quercus geminata* and *Quercus myrtifolia*, were the species
19 that were the most similar in their physiological responses. All four of these species are trees.
20 The palmetto, *Serenoa repens*, and the hemi-parasitic shrub *Ximenia americana* were not
21 clustered with any other species. The shrubs *Lyonia lucida* and *Vaccinium myrsinites* differed
22 the most from the other eight species, however since they had similar physiological responses
23 they were placed together in another functional group.

Morphological Indicators of Function

Many of the differences between the five physiologically-based functional groups could be explained by the physiological differences between life forms (Table 1, Figure 1). For example, trees and vines had higher maximum photosynthesis at light saturation (A_{\max}) on an area basis ($p \leq 0.017$) and intrinsic water-use efficiencies ($p \leq 0.002$) than did evergreen shrubs and palmetto (Table 3). A_{\max} on a mass basis further separated the life forms, with the vines having higher maximum carbon assimilation than the evergreen trees ($p < 0.001$) (Figure 2a). As expected, A_{\max} was correlated with %N in the leaves ($r=0.830$, $p=0.003$), thus shrubs and palmetto had lower values than trees and vines. Leaf nitrogen concentrations were also correlated with leaf carbon concentrations ($r = 0.655$, $p = 0.040$) (Figure 2b), with shrubs having the highest C:N ratio and the vines having the lowest (Table 3). Plant functional types with high leaf nitrogen, such as vines, also had higher $\delta^{15}\text{N}$ with values near zero (Figure 2c). The palmetto and trees both had intermediate nitrogen concentrations; however, the trees had a similar $\delta^{15}\text{N}$ signal to the shrubs while the palmettos signal was similar to the vines.

For several of the physiological parameters *Ximenia americana*, the hemi-parasitic shrub, responded differently than the other shrubs (Table 3). For instance, it had a higher maximum conductance at light saturation and was less efficient in its water use. *Ximenia americana* also had a higher leaf nitrogen concentration and more enriched $\delta^{15}\text{N}$ than the other shrubs (Figure 2, Table 3).

Few relationships existed between the other two morphological characteristics and the physiological parameters. Specific leaf area (SLA) was positively associated with leaf nitrogen concentration as well as photosynthesis at light saturation on a mass basis (Figure 3). Leaf thickness was positively associated with $\delta^{13}\text{C}$ and photosynthesis at light saturation on an area

basis (data not shown). No other associations were identified.

Of the three morphological characteristics, only life form classifications were able to adequately depict membership in the physiologically based functional groups (Figure 1). Groupings based on specific leaf area and leaf thickness contained physiologically dissimilar species. For instance, specific leaf area grouped *Galactia elliottii* and *Vaccinium myrsinites* together, yet these are two of the most dissimilar species in their physiological responses.

Spatial Robustness

Management regime did not alter species responses in the Florida scrub. For instance, the species at the burn and mechanically treated Camera Pad plots exhibited similar physiological responses (Figure 4). Similar trends were also observed between the Camera Pad burn and fire-suppressed plots (data not shown). Neither plot location (water table depth) nor management regime effected the relative species ranking when all physiological parameters were considered, ($p=0.89$ and 0.34 respectively, Table 4), or when just the integrated measures were considered ($p=0.48$ and 0.10 respectively). In addition, species still clustered into the same five physiological groupings regardless of plot location or management regime, and these groups are statistically different from each other with either dataset (all physiological variables or just the integrated measures, Table 4). One exception was groups 1 (*S. repens*) and 3 (*Quercus* group), which did not cluster separately in the plot test using only the integrated measures ($p=0.079$), but did when considering management regime ($p=0.007$).

Temporal Robustness

Species exhibited similar physiological responses (Figure 4) and clustered into the same five functional groups in two climatically different years. Species were ranked in the same

relative order in both 1999 and 2000 when all physiological parameters were considered ($p=0.72$, Table 4), or when just the integrated measures were considered ($p=0.71$). The physiological functional groups were temporally robust since each of these five functional groups was significantly different from each other in both years (Table 4).

Robustness of Morphological Indicators of Function

As noted above, life forms adequately described the initial five physiologically-based functional groups, and these initial groupings of scrub species were spatially and temporally robust. However, do the life form categories still adequately describe these functional groups across all management regimes and plots? Using the 2000 data at all the plots, species still clustered into distinct life form categories as had previously been shown for 1999 in the Camera pad burn plot (Figure 5). The trees, shrubs, vines, and palmettos did cluster differently based on their physiology, and the parasitic shrub also clustered into its own group. Interestingly, the life form classifications were able to depict the functional groups not only using both the instantaneous and integrated variables (Figure 5a) but also when only the integrated variables were used (Figure 5b). Occasionally, a species on a particular plot would cluster outside its life form group, but in general, all species observed on the different plots clustered together surprisingly well within the correct life form. Spatial separation of species between the various plots did not alter the physiological functional groups or the ability of the life form classifications to depict the groupings.

The life form classifications remained the most useful morphological indicator of physiological function for the scrub species regardless of temporal and spatial differences (Figure 6). Neither specific leaf area (Figure 6a) nor leaf thickness (Figure 6c) had as good of separation between groups as did life form. In all cases the groupings were stronger using all ten

1 physiological parameters over just the integrated measures (Table 5). The degree of separation
2 for SLA groupings was higher than for leaf thickness (ANOSIM; $R = 0.426$ and $R = 0.344$
3 respectively). However, the degree of separation for life form was much larger than for either
4 SLA or leaf thickness ($R = 0.629$). A high degree of separation is indicative of complete
5 separation between the groups, whereas small values imply little separation. Thus the life form
6 groupings adequately explained the variation in the physiological parameters.

7 The parasite *Ximenia americana* differed in physiological response when compared to the
8 other shrubs (see above for details). By removing *X. americana* from the shrubs and placing it in
9 its own category, which might be considered a parasitic life form (Figure 6d), the degree of
10 separation between the groups increased ($R = 0.794$). Whereas under the four life form
11 classification, the shrubs and the palmettos were not found to differ in their physiological
12 responses (ANOSIM; $R = 0.16$, $p = 0.064$), by separating the *X. americana* from the shrubs all
13 five groups differ from one another. Thus separation into trees, shrubs, vines, palmetto, and *X.*
14 *americana* adequately describes physiological function.

15 Discussion

16 In the fire maintained Florida scrub habitat, species were not unique in physiological
17 characteristics, instead discreet groups of species contained similar characteristics. Based on
18 these similarities, five distinct physiologically based functional groups were formed (Figure 1).
19 *Serenoa repens* comprises a single species category. It is the only palmetto found in the oak –
20 saw palmetto scrub at KSC/MINWR, but comprises between 30 – 40% of the ground cover
21 (Schmalzer and Hinkle 1992b). The other single species category is the shrub *Ximenia*
22 *americana*, which is the only parasitic plant common to this area of scrub. Each of the
23 remaining three physiological groupings consisted of two or more species. *Quercus chapmanii*,

1 *Q. geminata*, *Q. myrtifolia*, and *Myrica cerifera* were grouped together based on similar
2 responses, and this group typically comprises approximately 40% of the ground cover
3 (Schmalzer and Hinkle 1992b). *Lyonia lucida*, *L. ferruginea*, *L. fruticosa*, and *Vaccinium*
4 *myrsinites* were grouped together, whereas *Smilax auriculata* and *Galactia elliottii* made up the
5 final group.

6 These scrub species continued to group into the five physiologically based groups when
7 examined across a broader temporal and spatial scale (Table 4). Spatially, the groups were
8 consistent across fire management regimes and with varying water table depth. Temporally, the
9 species formed similar groups in two climatically different years (1999 and 2000), even though
10 precipitation during the summer of 2000 was only 43% of that in 1999. Thus, these five groups
11 appear to adequately represent the diversity of physiology in Florida scrub at the KSC/MINWR
12 even in climatically different years, changing management regimes and spatial variations in the
13 water table. Interestingly, these same groupings were established whether one use detailed
14 instantaneous gas-exchange data or integrated measures of function determined from leaf
15 samples. Brooks et al. (1997) also found that life form groupings derived from $\delta^{13}\text{C}$ remained
16 stable temporally and spatially. For modeling or extrapolation purposes, this grouping simplifies
17 the system from twelve species to five physiological groupings; however, such simplification
18 would be easier if morphological features rather than physiological measurements could identify
19 these groups.

20 Leaf characteristics were not able to adequately depict the physiological responses of
21 scrub species (Figures 1, 6, Table 5). In some studies, these variables are adequate indicators of
22 function (Ackerly 1999; Reich et al. 1998a; Reich et al. 1997; Reich et al. 1998b); however,
23 these studies cross a much wider geographical area, or are from ecosystems with a deep and

1 complex canopy cover. Florida scrub does not have distinct canopy strata, instead, all species
2 develop in high light environments with the exception of fire-suppressed scrub in which the trees
3 become the overstory and the shrubs and palmetto the understory. The leaf adaptations of scrub
4 plants are most likely due to the xeric nature of the system. Thus the variation of these
5 characteristics within the ecosystem does not appear to follow the typical pattern of more
6 complex canopies. Some typical patterns of leaf morphology and physiology did exist such as a
7 positive correlation between SLA and photosynthesis on a mass basis and SLA and nitrogen
8 concentration (Figure 3), but overall these variables did not adequately describe the variation of
9 scrub physiological types (Figure 1). For instance *Vaccinium myrsinites* and *Galactia elliottii*
10 both had high specific leaf areas but were very dissimilar in physiological responses. *Ximenia*
11 *americana* and *Galactia elliottii* both had thin leaves yet these species were also dissimilar in
12 physiological response. There was not good separation in the physiological responses of scrub
13 species that possessed thin or thick leaves or had high or low SLA (Figure 6, Table 5).

14 Life form classifications proved to be a powerful predictor of the physiology of scrub
15 species (Figures 1, 5, and 6; Table 5). Previous research has shown that although life forms are
16 based on a morphological and structural basis they serve as a good indicator of physiological
17 processes. For instance, Chapin et al. (1996) found that in the arctic traits associated with
18 resource acquisition and growth rate were important for separating eight growth form categories
19 (evergreen trees, deciduous trees, evergreen shrubs, deciduous shrubs, sedges, grasses, forbs,
20 mosses, and lichens). Plants with high relative growth rates in the arctic were also found to have
21 short-lived thin leaves, with high Nitrogen concentrations and photosynthetic rates. In Florida
22 scrub the life form categories (trees, shrubs, vines and palmetto) agreed well (ANOSIM; $R =$
23 0.629) with their physiological groupings (Figures 1, 4, and 5). Separating the parasitic plant

1 *Ximenia americana* from the shrubs category makes an improvement (ANOSIM; $R = 0.794$) on
2 the ability of distinguishing the functional groups based on the suite of physiological parameters
3 (Figures 1, 5, and 6; Table 5), and is a more accurate representation of the original five
4 physiological groups we found in the fire-maintained scrub. *Ximenia* is a facultative
5 hemiparasite that attaches to the roots of its host plant, from which it obtains water and nutrients,
6 and thus would function differently from the other shrubs. Hemiparasites generally have high
7 stomatal conductances, high rates of transpiration and low water-use efficiencies thus
8 maintaining a steeper water potential gradient between the roots and the leaves of the parasite
9 than the host plant (Ducharme and Ehleringer 1996; Goldstein et al. 1989). This steep water
10 potential gradient is responsible for the import of water and nutrients from the host plant, and
11 may lead to a high nitrogen concentration in the leaves of the parasite (Lambers et al. 1998).
12 Separating parasites into a separate group is problematic because hemiparasites are difficult to
13 identify visually as they are diverse in taxa as well as morphology (Lambers et al. 1998).
14 However, if *a priori* knowledge of parasitism is available, then parasitic species should not be
15 included in its respective life form group, but together with other parasites.

16 The physiological similarities of species within a life form grouping might have been due
17 to members being closely related taxonomically. Indeed, taxonomic relatedness within a
18 functional group is not at all unusual. In Argentina, Diaz and Cabido (1997) found that a single
19 plant family dominated some plant functional types. In this study, two of the functional groups
20 identified included species that are closely related on a taxonomic basis. The shrubs, *Lyonia*
21 *ferruginea*, *L. fruticosa*, *L. lucida*, and *Vaccinium myrsinites*, not only include species that
22 belong to the same genera, but all species included in this group belong to the Ericaceae family
23 (Wunderlin 1982). Members classified as trees (*Quercus chapmanii*, *Q. geminata*, *Q. myrtifolia*,

1 and *Myrica cerifera*) were also closely related taxonomically with all species belonging to the
2 same subclass Hamamelidae (Cronquist 1981). However, little ecological information is usually
3 contained in the family or higher levels of taxonomy (Scholes et al. 1997), since traditional
4 taxonomy depends strongly on morphological similarities which is presumed to represent
5 evolutionary relatedness rather than any ecological similarities.

6 Taxonomy does not explain similarities between all species as it misses similarities due
7 to convergent evolution (Bond 1997). For example, the C₄ photosynthetic pathway has evolved
8 multiple times in different taxonomic groups (Ehleringer and Monson 1993). Plant
9 classifications based on functional attributes may cross taxonomic classifications (Woodward
10 and Kelly 1997). In fact, the vines in this study contain two species that although similar in
11 growth form and physiology belong to different taxonomic classes. *Smilax auriculata* is a
12 monocot (class Liliopsida) whereas *Galactia elliottii* is a dicot (class Magnoliopsida) (Cronquist
13 1981). The remaining two functional groups each consisted of only one species, the palmetto
14 *Serenoa repens* is a monocot (Cronquist 1981) along with the parasite *Ximenia americana*.
15 Interestingly, *Ximenia americana* and *Galactia elliottii* which were found to be extremely
16 dissimilar on a physiological basis, are more closely related to each other taxonomically than to
17 any of the other species; they both belong to the subclass Rosidae (Cronquist 1981). Although
18 taxonomic relatedness could play a role in determining two of the functional groups, the low
19 diversity of this system does not lend itself to teasing out taxonomic relatedness from the
20 functional groupings. Further studies of more diverse scrub systems in Florida would be needed
21 for addressing the issue of the importance of taxonomic relatedness in species functioning.

22 Because functional grouping of plants adequately described the diversity of plant
23 physiology within the Florida scrub and these groups remained stable spatially and temporally,

1 changes in ecosystem processes can be inferred from data on changes in species composition or
2 leaf area. For example, composition of scrub is closely related to water table depth (Schmalzer
3 and Hinkle 1992b). At KSC/MINWR, as the depth to the water table decreases species
4 composition shifts towards lower trees abundance and a doubling of saw palmetto abundance,
5 but total plant cover remains about the same (Schmalzer and Hinkle 1992b). This shift in
6 composition might be associated with less carbon assimilation because *S. repens* has a lower
7 photosynthetic rate than the trees. Composition changes may also occur with management
8 regime, which often acts as a disturbance on the system. In mechanically treated scrub, *S. repens*
9 returns to only about 50% of its pre-burn cover (Schmalzer and Boyle 1998) whereas the
10 regrowth of trees and shrubs is similar to that of burned scrub (Schmalzer and Adrian 2001).
11 *Serenoa repens* is unique among the scrub species in its physiological response in that although
12 it has a moderate rate of photosynthesis it is efficient in water use, and a change in abundance
13 could have a significant impact on ecosystem processes. Loss of a large percentage of *S. repens*
14 may lower the amount of carbon gained per water lost for the system, particularly if the loss of *S.*
15 *repens* is not associated with a change in cover of the other functional groups.

16 Composition differs in fire-suppressed scrub when compared to burned and mechanically
17 treated scrub. The percent cover of the trees more than doubles in fire-suppressed scrub and
18 approaches approximately 80 – 90% of the cover whereas the percent cover of *S. repens* is about
19 a third of that found in burned scrub. Total vegetation cover also doubles (Schmalzer and Hinkle
20 1992b). By doubling the vegetation cover, more water will be lost due to transpiration in the
21 fire-suppressed scrub than the fire-maintained scrub. More carbon may be assimilated in the
22 fire-suppressed scrub than the fire-maintained scrub because of the increase in tree cover, which
23 has high rates of photosynthesis and higher leaf area when compared to *S. repens*.

1 Changes in community composition have been noted to alter ecosystem processes in
2 other systems. For instance, in New Mexico grasslands have less total organic carbon than
3 mesquite shrublands, suggesting a loss of CO₂ to the atmosphere will accompany a shift from
4 grass to shrub-dominated systems (Reynolds et al. 1997). In the Patagonian steppe, the increase
5 in shrub cover that accompanied increased grazing intensity reduced transpiration and annual net
6 primary production but increased water loss due to evaporation and drainage (Aguiar et al.
7 1996). Chapin et al. (1996) found that grouping species into growth form categories was useful
8 not only for capturing regional ecosystem dynamics, but also predicting the effects of vegetation
9 on the environment and responses to climate change in the arctic. For instance, global warming
10 was predicted to increase the abundance of trees. Based on plant function, they predicted that
11 this change would lead to increased carbon storage, higher transpiration, and reduced albedo.
12 However, these types of predictions for climate change must be made cautiously, because they
13 imply that plant physiological processes will not change with the climate. We found both spatial
14 and temporal robustness in our functional groups, but under different stresses such as
15 temperature change or elevated CO₂ the results may have been different. In fact, studies have
16 shown that under elevated CO₂ photosynthetic acclimation differs between the three dominant
17 oaks in Florida scrub. These differences are not only species dependent, but also appear to be
18 dependent on the stage of regrowth. In young scrub, elevated CO₂ stimulated photosynthesis of
19 both *Quercus myrtifolia* and *Quercus geminata*, but decreased the maximum rate of
20 carboxylation and specific leaf area in *Quercus myrtifolia* [Li, 1999 #71]. In mature scrub,
21 elevated CO₂ stimulated photosynthesis at light saturation in *Quercus chapmanii* and *Quercus*
22 *myrtifolia*, but not in *Quercus geminata* [Ainsworth, 2002 #471]. This type of inability to use
23 plant functional groups to generalize responses to and effects of climate changes has also been

1 found in the arctic. Manipulation of fertilization and shading only had a significant effect on one
2 of six functional types, whereas manipulation of water did not affect any of the six functional
3 types. (Dormann and Woodin 2002).

4 Physiologically-based functional groups and life-form based groups will also be limited
5 in their ability address distribution changes with climate change. In order to determine
6 distribution responses to environmental change, the regeneration phase could be important in the
7 development of the functional groups to predict species spread and distribution by inclusion of
8 information such as dispersal rate and spread (Hobbs 1997). Classifications based on life forms
9 and phenology often fails to include information about the dynamics of the community (Noble
10 and Gitay 1996). For instance, in an Australian semi-arid woodland the five main functional
11 types identified by a combination of growth form and life history attributes (perennial forbs,
12 subshrubs, C₄ grasses, trees/shrubs, and annual forbs) do not capture the variation in seed and
13 dispersal biology included for each species (Westoby and Leishman 1997). Information on
14 dispersal and regeneration might need to be incorporated into the suite of parameters before
15 determining if life forms could predict the distribution of Florida scrub in response to global
16 change. However, all twelve scrub species included in this study revegetate by resprouting after
17 stand replacing fires. *Galactia elliottii* and *L. ferruginea* are obligate resprouters, whereas *S.*
18 *repens* and *S. auriculata* may also seed besides resprouting. The remaining seven species
19 revegetate by a combination of resprouting and clonal spread (Menges and Kohfeldt 1995).
20 Although resprouting after fire occurs relatively quickly (Schmalzer and Hinkle 1992a), spread
21 of scrub species into adjacent clearings occurs much more slowly. In fact, oaks and ericads
22 slowly vegetate openings by spreading clonally from the perimeters. There is little establishment
23 of woody species by seeding in the openings (Schmalzer and Adrian 2001). Clonal spread by *S.*

1 *repens* may be incredibly slow with growth rates between 0.6 and 2.2 cm/yr and seedling
2 recruitment is rare (Abrahamson 1995). The dependence on vegetative spread and the slow rates
3 at which these species colonize disturbed areas draws into question the ability of this system to
4 dynamically respond to global changes. However, if species distributions in response to climate
5 change are predicted by other means, then grouping by life form would probably be an adequate
6 means for classifying physiological functional groups for predicting functions such as ecosystem
7 carbon and water dynamics.

8 In spite of the limitations just mentioned, five life forms in the Florida scrub were found
9 to be good predictors of functional groups based on how species regulate carbon and water
10 exchange with the atmosphere. These groupings were stable with changes in management
11 regime, water table depth and in two climatically different years. It is not surprising that life
12 form classifications serve as good indicators of a plants physiological response. Chapin (1993)
13 suggests that plants with high relative growth rate tend to have high rates of photosynthesis,
14 transpiration, tissue turnover, herbivory, and decomposition. Trade-offs exist between growth
15 and allocation to structure, defense, storage, and reproduction; and species of a similar life form
16 tend to have similar allocation strategies. Large plants allocate more to structural biomass rather
17 than photosynthetic biomass and because of their large size have lower relative growth rates
18 (Chapin 1993). This type of connection between life form and physiological strategy was found
19 in the Florida scrub. For instance, while both vines and trees in this study had high rates of
20 carbon assimilation, vines were higher in stomatal conductance and leaf nitrogen, but lower in
21 water use efficiency. These physiological differences were associated with structural
22 differences. The Florida scrub trees allocate carbon to woody biomass and belowground storage
23 and produce leaves with high C:N ratios which are less palatable to herbivores and decomposers,

1 whereas the vines, allocate little to woody structures and storage and produce leaves that have
2 higher nitrogen concentrations indicative of higher leaf turnover due to herbivory and
3 decomposition. This study adds to the accumulating evidence that groupings based on life forms
4 are adequate for explaining function in a variety of systems irrespective of whether
5 physiological, phenological, physiognomic, or a combination of traits are examined.

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Figure 1: Dendrogram depicting physiological based functional groups derived from the 1999 Camera Pad burn plot data and how they relate to the morphological classifications: life form, leaf thickness (LT), and specific leaf area (SLA). The physiological variables used to create the clusters included A_{\max} , g_{\max} , R_d , I_c , Φ , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, and C:N. These clusters are significantly different from random ($p = 0.04$).

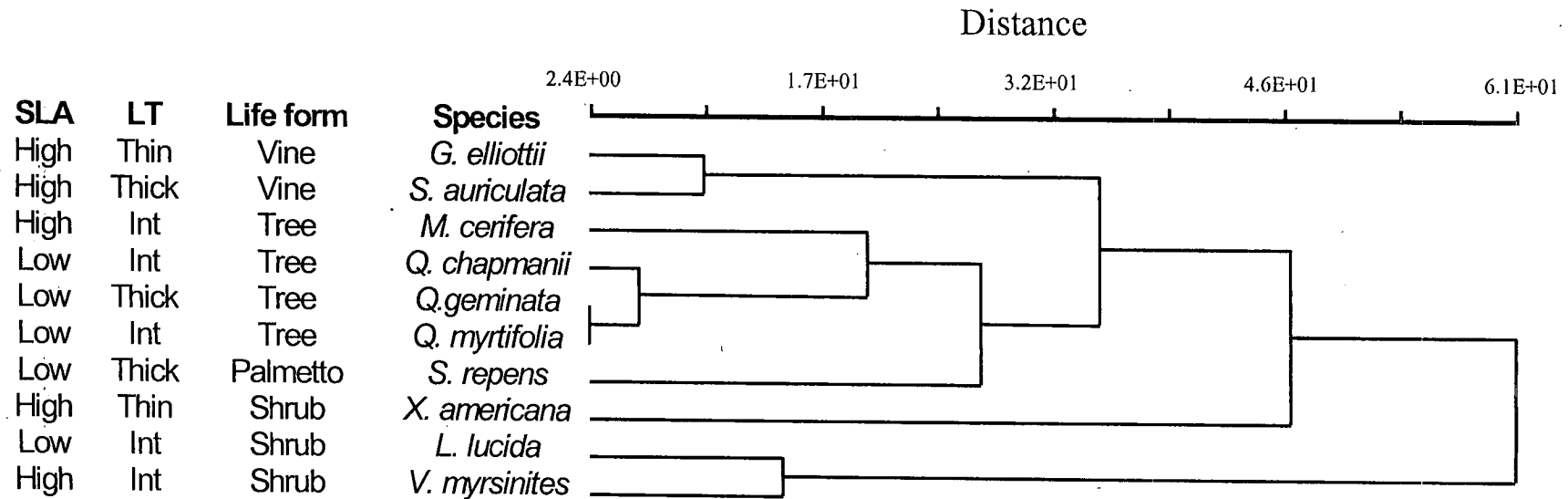


Figure 2: Photosynthesis at light saturation (a), leaf carbon concentration (b), and the nitrogen isotope ratio (c) as a function of leaf nitrogen concentration in 1999 for the Camera Pad burn plot. The data point is the species mean and the error bars indicate the standard error. The life form categories are depicted in the color scheme (palmetto = black triangle with white dot, shrubs = gray, trees = black, and vines = white).

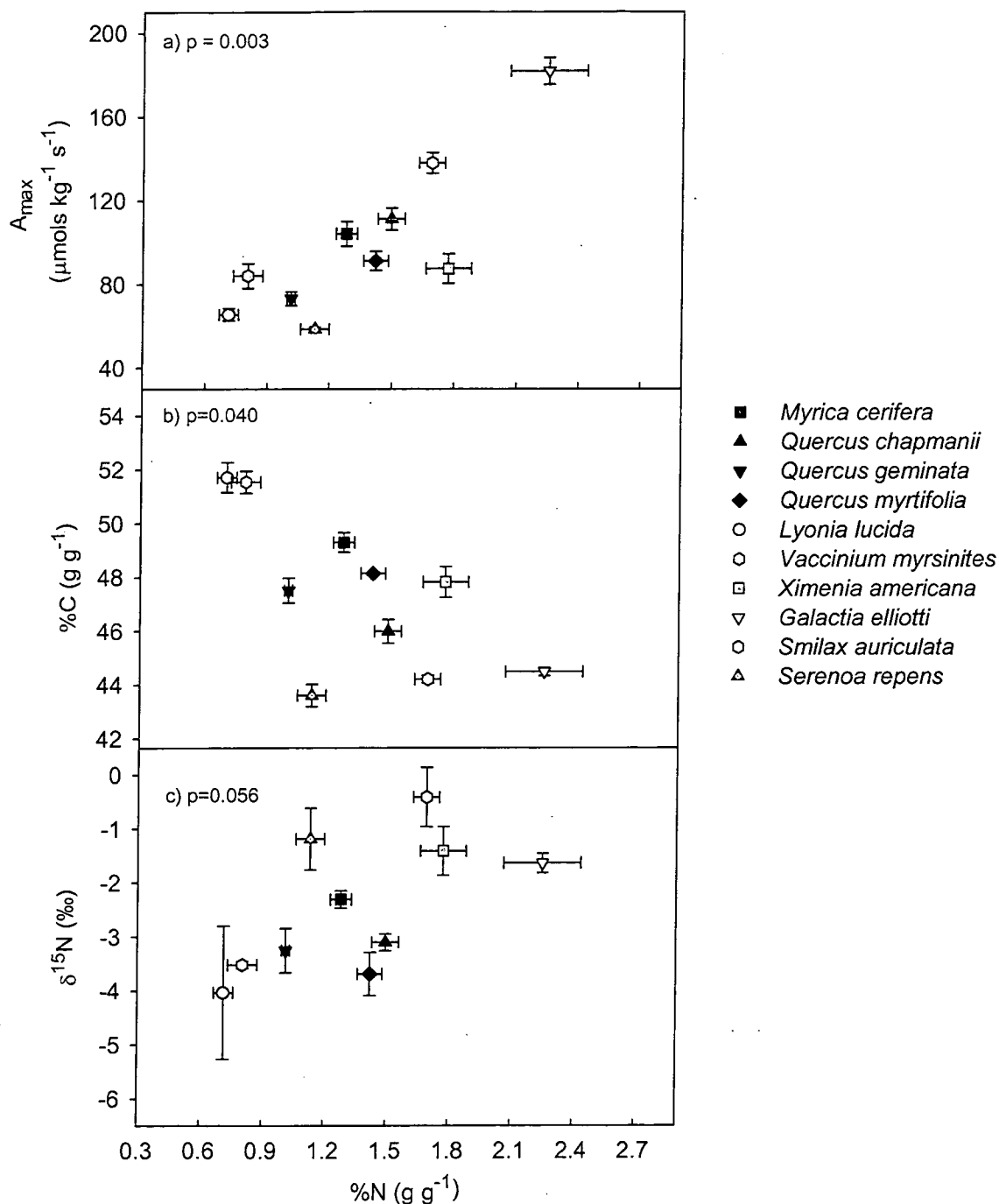


Figure 3: Photosynthesis at light saturation (a) and percent nitrogen (b) as a function of specific leaf area for scrub species in 1999 at the Camera Pad burn plot.

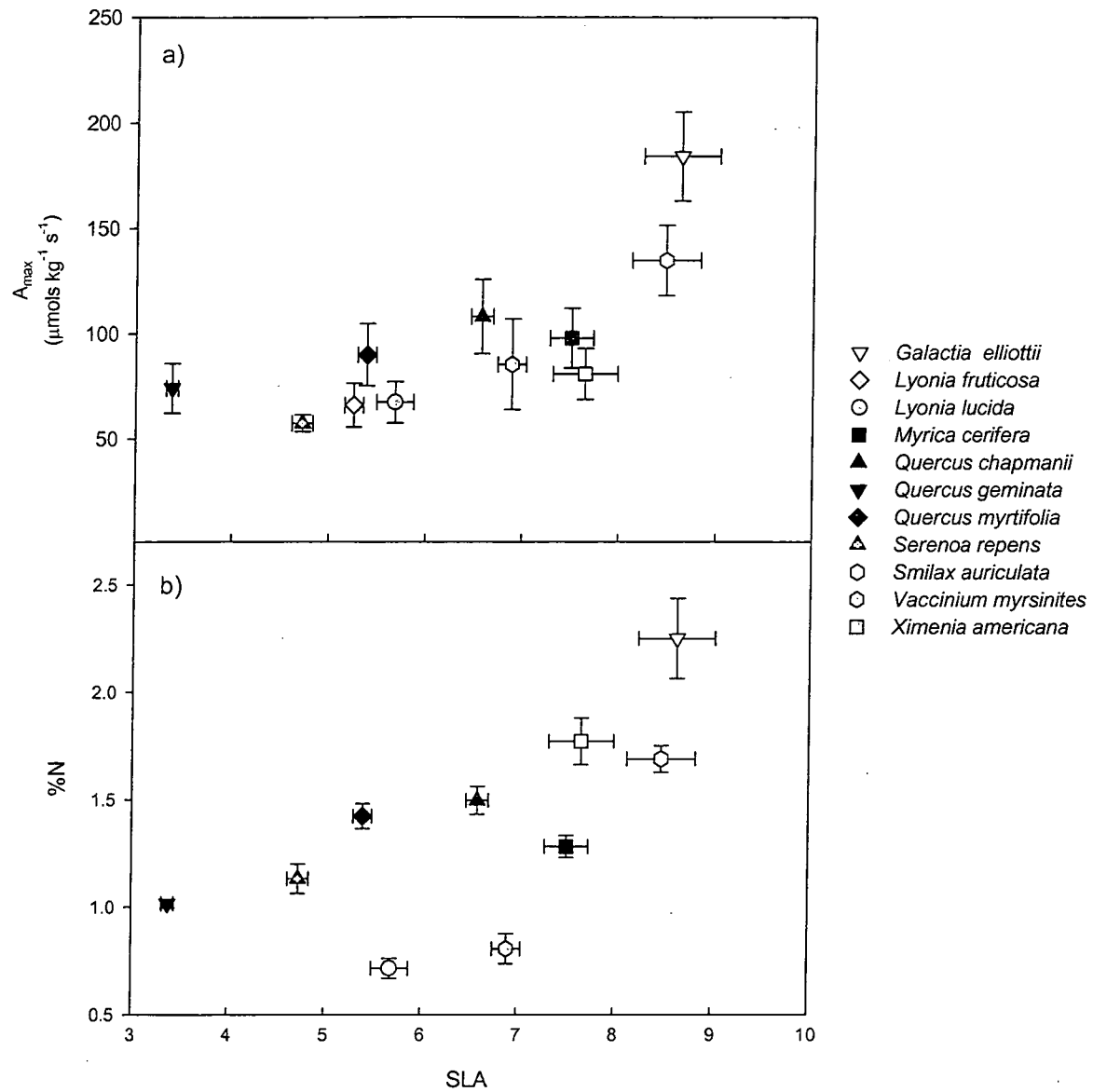


Figure 4: Spatial and temporal robustness of the physiological responses of scrub species. Spatial robustness (a and b) in 2000 between two plots with varying management regimes; the Camera pad burn plot (CPb) and the Camera Pad mechanically treated plot (CPmt). Temporal robustness (c and d) between 1999 and 2000 responses data shown are from the Camera Pad burn plot. Data points are species means and error bars indicate standard error.

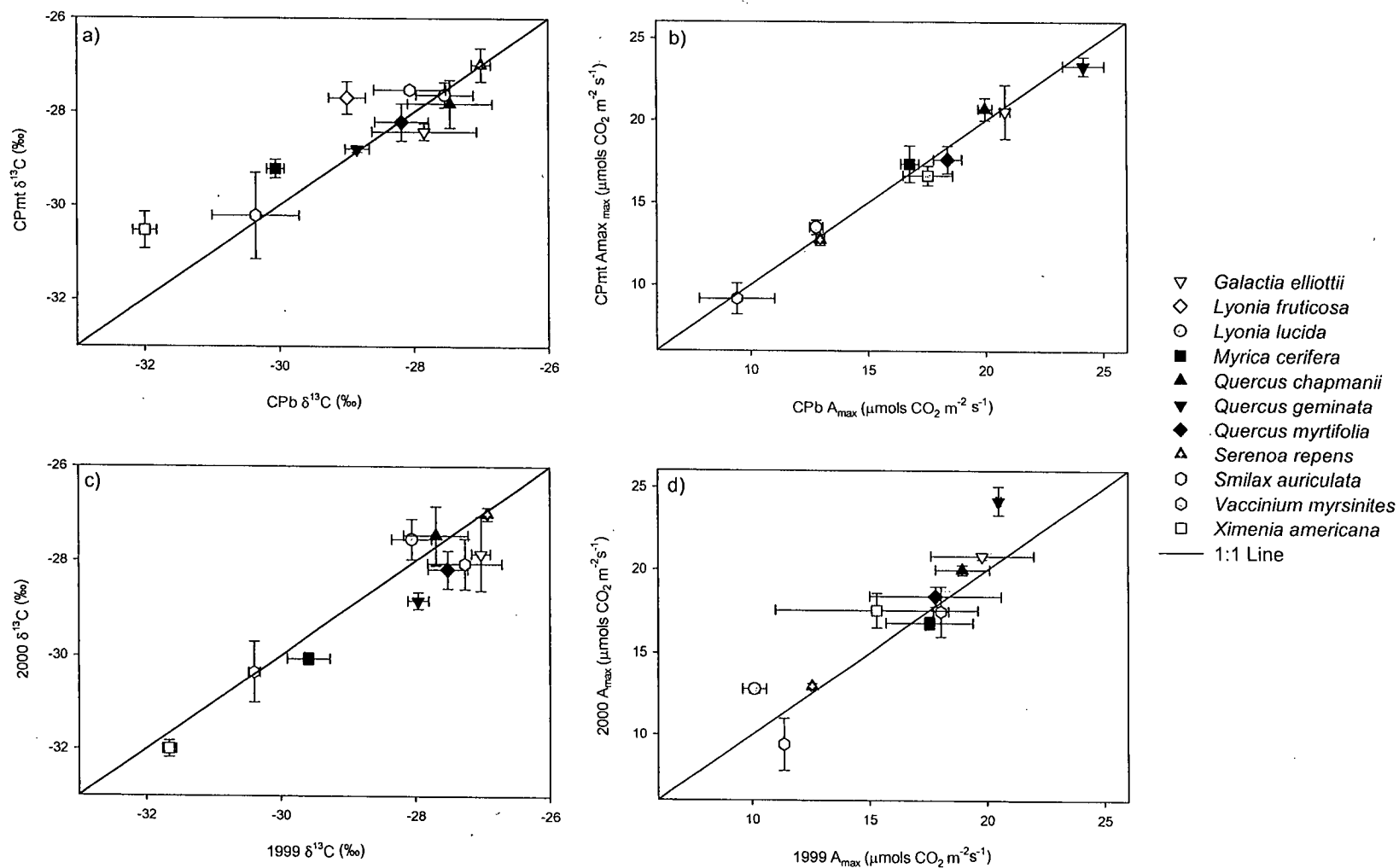


Figure 5: Dendrograms depicting physiological based functional groups in 2000 for life form classifications and species based on (a) 48 species mean values for A_{\max} , g_{\max} , R_d , I_c , Φ , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, and C:N from the nine plots and (b) 64 species mean values for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, and C:N.

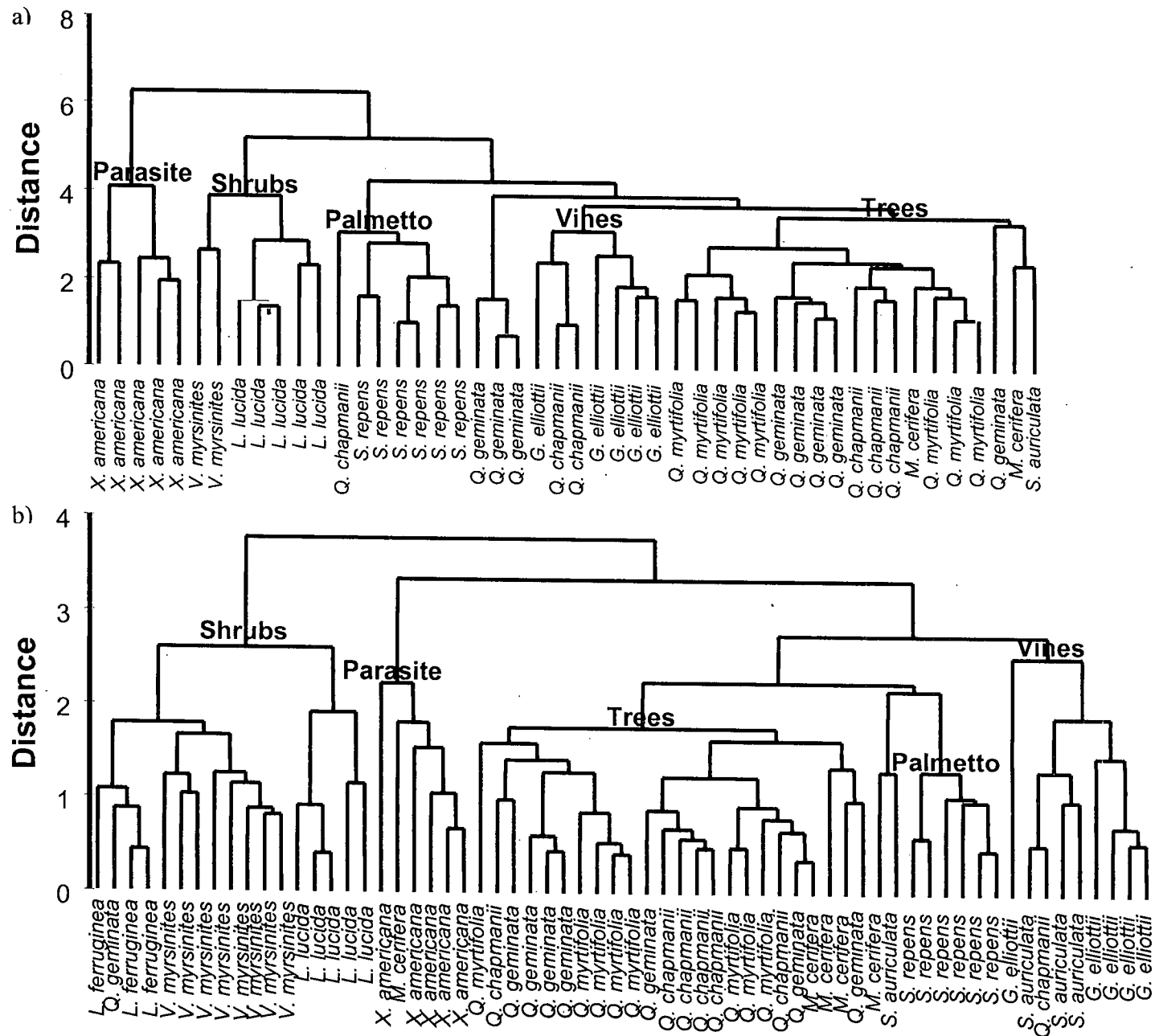


Figure 6: Non-metric multidimensional scaling (MDS) of the physiological functional groups (stress = 0.08) depicted by (a) specific leaf area, (b) life form, (c) leaf thickness, and (d) life forms + *Ximenia americana* as a separate category. Data used were from the 2000 sampling period and included responses for all ten parameters on 48 species means.

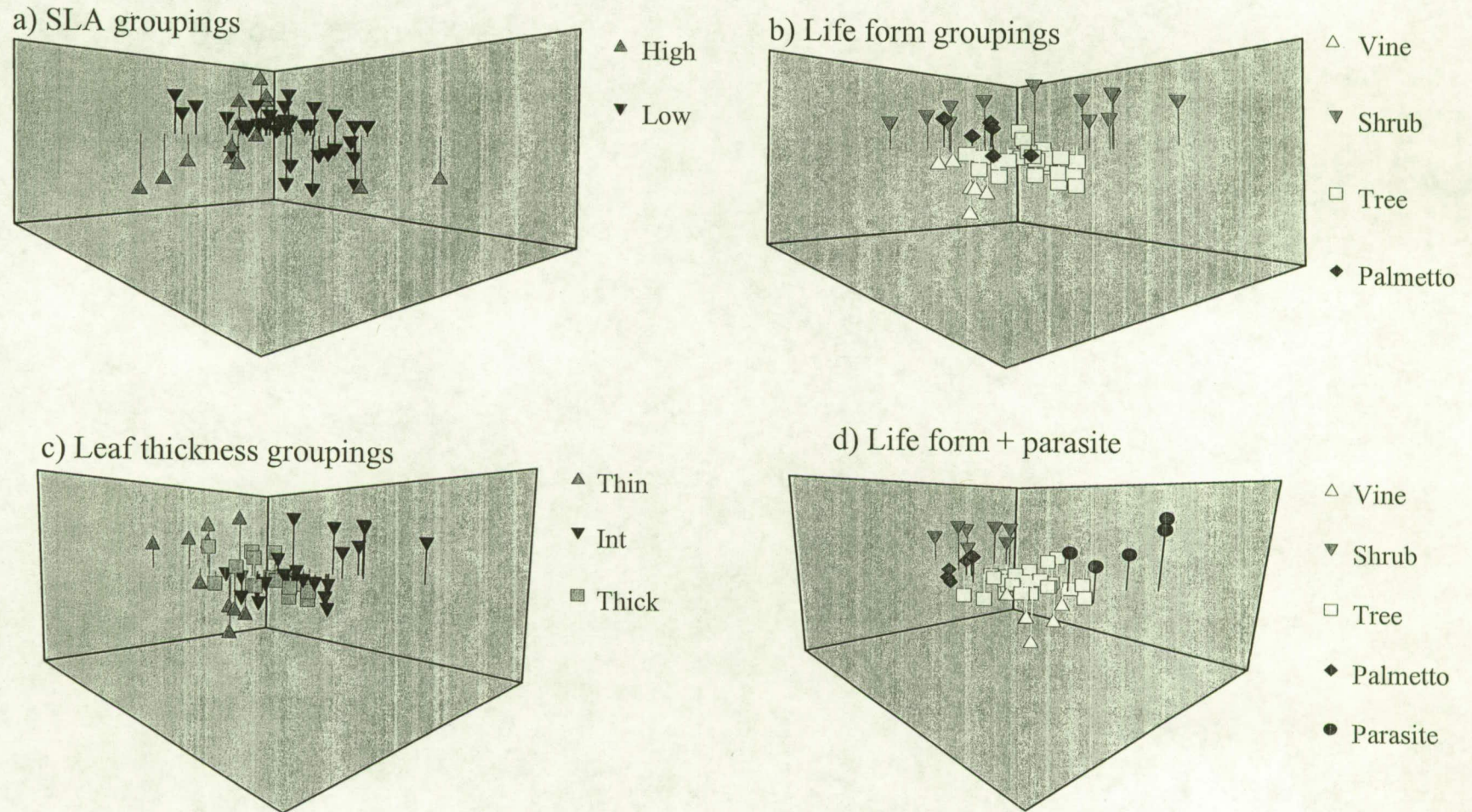


Table 1: Characteristics of the nine study plots.

	Water table depth	Year burned	No. species present	Species and life forms present			
				<i>Trees</i>	<i>Shrubs</i>	<i>Vines</i>	<i>Palmetto</i>
Camera Pad	1.7 m						
Burn		1997	11	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia fruticosa</i> , <i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i> , <i>Ximenia americana</i> *	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	<i>Serenoa repens</i> *
Fire-suppressed		1986	8	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia ferruginea</i> , <i>Vaccinium myrsinites</i>	<i>Galactia elliottii</i> *	<i>Serenoa repens</i> *
Mechanically treated		1997	12	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia ferruginea</i> , <i>Lyonia fruticosa</i> , <i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i> , <i>Ximenia americana</i> *	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	<i>Serenoa repens</i> *
Happy Creek	2.1 m						
Burn		1997	10	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i> , <i>Ximenia americana</i> *	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	<i>Serenoa repens</i> *
Fire-suppressed		1986	10	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia fruticosa</i> , <i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i>	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	<i>Serenoa repens</i> *
Mechanically treated		1997	10	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i> , <i>Ximenia americana</i> *	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	<i>Serenoa repens</i> *
Kennedy Parkway	1.9 m						
Burn		1998	8	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia fruticosa</i> , <i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i>		<i>Serenoa repens</i> *
Fire-suppressed		>20 yrs	9	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia ferruginea</i> , <i>Vaccinium myrsinites</i> , <i>Ximenia americana</i> *	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	
Mechanically treated		1997	12	<i>Quercus chapmanii</i> *, <i>Quercus geminata</i> *, <i>Quercus myrtifolia</i> *, <i>Myrica cerifera</i>	<i>Lyonia ferruginea</i> , <i>Lyonia fruticosa</i> , <i>Lyonia lucida</i> *, <i>Vaccinium myrsinites</i> , <i>Ximenia americana</i> *	<i>Galactia elliottii</i> *, <i>Smilax auriculata</i>	<i>Serenoa repens</i> *

* Indicates species that were included in the subset on which instantaneous measurements were taken to address spatial robustness.

Table 2: Summary of statistical tests used for data analysis. # S x P is the number of species by plot combinations included in the analysis. All plots include data from 8 of the 9 plots, because HCmt was not sampled in 1999.

Robustness	Analysis	# S x P	Plots	Parameters	Effects
Spatial	ANOSIM	48	All	A_{\max} , g_{\max} , R_d , I_c , Φ , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	Plot, Management regime, Functional Groups
	ANOSIM	64	All	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	Plot, Management regime, Functional Groups
Temporal	ANOSIM	25	CPb, CPmt, HCb	A_{\max} , g_{\max} , R_d , I_c , Φ , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	Year, Functional Groups
		58	All	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	Year, Functional Groups
Morphological Indicator	Cluster	48	All	A_{\max} , g_{\max} , R_d , I_c , Φ , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	Functional Groups, Life forms
		64	All	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	Functional Groups, Life forms
	ANOSIM	48	All	A_{\max} , g_{\max} , R_d , I_c , Φ , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	SLA, Leaf thickness, Life form
		64	All	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %N, %C, C:N	SLA, Leaf thickness, Life form

Table 3: Physiological measures for the functional groups from the 1999 data in the Camera Pad burn plot.

	Tree	Shrub	Parasite	Palmetto	Vine
A_{max}	17.01 (0.69)	12.13 (0.58)	10.57 (0.53)	12.13 (0.58)	18.62 (0.83)
g	0.27 (0.01)	0.27 (0.02)	0.63 (0.04)	0.32 (0.02)	0.34 (0.002)
WUE	64.91 (1.91)	45.22 (1.54)	16.85 (0.72)	39.63 (2.7)	55.66 (2.71)
%C ($g\ g^{-1}$)	48.52 (0.53)	50.07 (0.71)	47.82 (0.57)	43.60 (0.42)	44.37 (0.12)
%N ($g\ g^{-1}$)	1.22 (0.08)	1.15 (0.19)	1.77 (0.11)	1.13 (0.07)	2.03 (0.17)
C:N	42.47 (3.76)	52.58 (7.84)	27.18 (1.58)	38.83 (2.41)	22.51 (1.80)
$\delta^{15}N$ (‰)	-3.22 (0.23)	-2.86 (0.51)	-1.42 (0.45)	-1.19 (0.57)	-1.15 (0.36)
$\delta^{13}C$ (‰)	-28.16 (0.23)	-30.21 (0.57)	-31.66 (0.10)	-26.93 (0.02)	-27.12 (0.20)

Table 4: Summary of analysis of similarities (ANOSIM) for determination of spatial and temporal robustness between treatments (plot, management regime, and year) of the physiologically based functional groups (PFG). See methods for details on the dual hypothesis testing for treatments and PFG with the ANOSIM test. Pairwise comparison numbers indicate differences between the physiological functional groups: Group 1 (*Serenoa repens*), Group 2 (*Lyonia lucida* and *Vaccinium myrsinites*), Group 3 (*Myrica cerifera*, *Quercus chapmanii*, *Quercus geminata*, and *Quercus myrtifolia*), Group 4 (*Galactia elliottii* and *Smilax auriculata*), Group 5 (*Ximenia americana*).

Grouping Variable	Parameters Used	Pairwise comparison	Plot		Management Regime		Year	
			R	P	R	P	R	P
Treatment	Instantaneous and Integrated	Instantaneous	-0.115	0.893	0.018	0.340	-0.027	0.725
		Integrated	0.075	0.476	0.059	0.099	-0.014	0.708
PFG	Instantaneous and Integrated		0.796	0.001	0.724	0.001	0.682	0.001
		1-2	1.00	0.111 ^a	0.876	0.006	0.841	0.002
		1-3	0.667	0.009	0.594	0.001	0.562	0.002
		1-4	1.00	0.333 ^a	1.00	0.033	0.861	0.002
		1-5	---	---	1.00	0.033	1.0	0.010
		2-3	0.902	0.001	0.908	0.001	0.708	0.001
		2-4	1.00	0.111 ^a	1.00	0.003	0.997	0.001
		2-5	1.00	0.111 ^a	1.00	0.007	0.985	0.001
		3-4	0.629	0.006	0.508	0.001	0.307	0.006
		3-5	1.00	0.003	0.935	0.001	0.774	0.001
		4-5	1.00	0.333 ^a	0.690	0.100 ^a	0.972	0.001
	Integrated		0.800	0.001	0.816	0.001	0.776	0.001
		1-2	0.932	0.002	0.900	0.001	0.895	0.001
		1-3	0.282	0.079	0.424	0.007	0.424	0.001
		1-4	0.667	0.148 ^a	0.707	0.005	0.428	0.001
		1-5	---	---	1.00	0.033	1.00	0.001
		2-3	0.917	0.001	0.902	0.001	0.875	0.001
		2-4	1.00	0.003	1.00	0.001	0.979	0.001
		2-5	1.00	0.007	1.00	0.001	0.987	0.001
		3-4	0.768	0.001	0.713	0.001	0.650	0.001
		3-5	0.926	0.001	0.907	0.001	0.946	0.001
		4-5	1.00	0.037	0.819	0.009	0.769	0.001

^a = the sample size is too small to deliver a significant p value. However the R statistic indicates that there is good separation for all pairwise comparisons.

Table 5: Summary of analysis of similarity (ANOSIM) to determine the acceptable morphological indicator of physiological function.

Morphological Indicator	Parameters	R	p
Lifeform	Instantaneous & Integrated	0.629	0.001
	Integrated	0.598	0.001
Lifeform + <i>Ximenia americana</i>	Instantaneous & Integrated	0.794	0.001
	Integrated	0.789	0.001
Specific leaf area	Instantaneous & Integrated	0.426	0.001
	Integrated	0.275	0.001
Leaf thickness	Instantaneous & Integrated	0.344	0.001
	Integrated	0.250	0.001