# MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS AS INDICATORS OF DROUGHT TOLERANCE IN TALLGRASS PRAIRIE PLANTS

by

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# Abstract

The Konza Prairie in northern Kansas, USA contains over 550 vascular plant species; of which, few have been closely studied. These species are adapted to environmental stress as imposed by variable temperature, precipitation, fire, and grazing. Understanding which plant traits relate to drought responses will allow us to both predict drought tolerance and potential future shifts in plant community composition from changes in local climate. Morphological and physiological measurements were taken on 121 species of herbaceous tallgrass prairie plants grown from seed in a growth chamber. Gas exchange measurements including maximum photosynthetic rate, stomatal conductance to water vapor, and intercellular $CO_2$ concentration were measured. All plants were exposed to a drought treatment and were monitored daily until stomatal conductance was zero. At this point, critical leaf water potential ($\Psi_{crit}$), an indicator of physiological drought tolerance was assessed. Other measurements include root length, diameter, volume, and mass, leaf area, leaf tissue density, root tissue density, and root to shoot ratio. Traits were compared using pair-wise bivariate analysis and principal component analysis (PCA). A dichotomy was found between dry-adapted plants with thin, dense leaves and roots, high leaf angle, and highly negative $\Psi_{crit}$ and hydrophiles which have the opposite profile. A second axis offers more separation based on high photosynthetic rate, high conductance rate, and leaf angle, but fails to provide a distinction between $C_3$ and $C_4$ species. When tested independently, grasses and forbs both showed drought tolerance strategies similar to the primary analysis. Matching up these axes with long term abundance data suggests that species with drought tolerance traits have increased abundance on Konza, especially in upland habitats. However, traits that relate to drought tolerance mirror relationships with nutrient stress, confounding separation of low water versus low nutrient strategies. My results not only illustrate the utility of morphological and physiological plant traits in classifying drought responses across a range of species, but as functional traits in predicting both drought tolerance in individual species and relative abundance across environmental gradients of water availability.

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# Dedication

*For my Dad,*
*You instilled in me every tool I would need to achieve my goals.*
*A fascination with nature*
*The desire to learn*
*Determination*
*Compassion*
*Integrity*
*You knew I could. I knew I could.*

# CHAPTER 1 - Introduction

## Evolution of tallgrass prairie

An ecosystem that once stretched 162 million hectares from western Indiana in the east to the Colorado Rocky Mountains in the west, the North American prairie has undergone a multitude of changes in the last 150 years (Samson and Knopf, 1994). Historically, homesteading and subsistence farming supported development in the Midwest. This was followed by increasing conversion of virgin prairie to agricultural fields, fencing and seeding of pastureland, and intense fragmentation due to road building, and urban development and expansion. As much as 99.9% of the historic range of tallgrass prairie has been lost or modified in some way (Samson and Knopf, 1994). In Kansas, the number is lower (82.6%, Samson and Knopf, 1994), due in part to the natural topography that prevents plowing and other commercial use. The Flint Hills region is a prime example of land protected from the plow by thin rocky soils. Agriculture is still ubiquitous, but well-managed grazing operations have helped preserve invaluable tracts of native tallgrass prairie.

Although grasslands are found all over the world, the tallgrass prairie evolved and was maintained in North America by the complex movements of the continent’s air masses (Borchert, 1950). It is a mesic system dominated by herbaceous vegetation, particularly warm season grasses. Situated in the middle of several other biomes, its central location becomes evident in the conglomeration of species that make up the plant community (Axelrod, 1985; Freeman, 1998). To the east, increased precipitation results in the eastern deciduous forests. In the north, temperature allows a shift to boreal forest. Precipitation again causes a change in the west as the rain shadow of the Rocky Mountains leads to a dry zone just east of the mountain chain (Borchert, 1950). Plants migrate readily and establish indiscriminately where conditions permit.

As a result, species from all of these biomes are found in the tallgrass flora, making it a cosmopolitan assemblage (Freeman, 1998). Even so, prairie communities are not static. The composition has changed many times in the past and current and future climate change may spur another shift in the native plant community.

## Climate Change

While the Midwestern prairies are characterized by high inter- and intra-annual climate variability for both temperature and precipitation (Borchert, 1950), human-influenced global warming increases the probability of alterations in climate and more frequent extreme events for key environmental drivers like precipitation and temperature (Easterling et al., 2000; Houghton et al., 2001; Alley et al., 2003; Alley et al., 2007). The Intergovernmental Panel on Climate Change models a much warmer United States by 2099 (IPCC, 2007). Predictions for the Midwest and Kansas in particular suggest a 3-4 degree Celsius increase in mean annual temperature over this time period. Predictions of the scope of future changes in precipitation vary among climate models, but there is a growing consensus that annual net precipitation for the Great Plains is likely to remain similar to present amounts, but the seasonal distribution and magnitude of rainfall events are likely to change (Gordon et al., 1992; Easterling et al., 2000; Meehl et al., 2005; Christensen et al., 2007). Alterations in precipitation regimes can occur in several ways. First, a reduction in small and intermediate size rain events, and an increase in the frequency of large rain events increases variability as the events become less frequent. This change in timing does not affect the total annual volume of rainfall received, but alters the distribution and amount of precipitation received during rainfall events (Karl and Trenberth, 2003). Secondly, seasonal changes in precipitation can result in more rainfall during the winter months, and reduced rainfall during the summer months (Christensen et al., 2007). If the total amount of rainfall received during the growing season is reduced and the growing season precipitation pattern becomes more variable, the result would likely be greatly reduced water availability for plants, even in the absence of total changes in net annual precipitation (Knapp et al., 2002). Furthermore, the increased frequency of large rain events could further diminish available water as precipitation falling faster than the maximum soil infiltration rate or exceeding field capacity would be lost as runoff. Evapotranspiration losses from the soil will necessarily accelerate under increased temperatures, also leading to less available water in the soil. All told, the consequences for the tallgrass prairie region would be increased soil drying coupled with longer periods of drought.

The variable and complex responses of grasslands to climatic variability present a significant challenge for forecasting responses to future climate change (Nippert et al., 2006). Altered timing of rainfall events, with no change in total rainfall amount, has significant consequences from the physiology of individual plants to ecosystem carbon fluxes (Knapp et al., 2002; Fay et al., 2003; Harper et al., 2005; Fay et al., 2008). The effects of multiple climate changes (e.g., multiple forms of precipitation variability) are predicted to be additive, but more complex interactions are likely for several key processes such as decomposition and soil $CO_2$ flux (Luo et al., 2001). The responses of key plant physiological processes and morphological traits are integral for relating community and ecosystem responses to climate changes that include both directional changes and greater rainfall variability. Extensive work is currently focused on the dominant species responses in this ecosystem in an attempt to predict and understand potential changes (Nippert et al., 2009). Predicting changes in population growth, community structure, and ecosystem energy balance, however, becomes very difficult when little is known mechanistically about the sub-dominant plant community in tallgrass prairies.

Due to their importance in ecosystem function and economic viability, native $C_4$ grasses have consistently been well studied (Knapp et al, 1994; Smith and Knapp, 2003), leaving the physiological responses and morphological characteristics of tallgrass prairie forbs and $C_3$ grasses relatively unexplored. Even with a solid understanding of phylogeny and general function (i.e. nitrogen fixers, $C_3$ grasses, $C_3$ forbs, $C_4$ grasses), a closer examination of the morphology and physiology of many lesser-known tallgrass species is a novel endeavor. These previously unmeasured traits may elucidate complex or previously unknown relationships between physiological processes and anatomical structures. For example, how do maximum photosynthetic rates relate to root morphology to move great quantities of water during periods of peak performance? Specifically, I want to improve our understanding of patterns of water-use during periods of increased water limitation and understand which traits confer an advantage to plants in dry environments or during drought events.

## Drought Physiology

Plants found in arid environments are known to employ a number of strategies to preserve water and subsist under both mild water limitation and extreme drought stress. Physical leaf traits such as leaf size (Dimmit, 2000), stomatal placement, leaf angle, and root depth (Nippert and Knapp, 2007) have all been shown to be successful adaptations to survive or even avoid drought stress. The creosote bush for example is a well-known desert competitor that employs tiny leaves with silvery hairs and waxy cuticle to reduce heat and prevent evaporative losses and an extensive root system for water acquisition (Dimmitt, 2000). Physiology also plays a role in enabling plants to conserve limiting resources and assimilate carbon while minimizing water loss. Take the $C_4$ and CAM photosynthetic pathways for example; both processes evolved to enable water or heat stressed plants to photosynthesize while conserving water (Dimmit, 2000;

Taiz and Zeiger, 2002). Alternatively, strategies to minimize water stress during periods of low water availability may mirror responses to low nutrient availability. Stress tolerators ( including low water and low nutrient species), as proposed by Grime (1977) should be long-lived perennials with low relative growth rates, low mineral and water turnover, and long-lived leaves and roots. During discrete periods of intense water limitation, do drought tolerators limit growth and physiology to conserve resources? Are the better competitors those that can fix carbon when water is most limiting or those that cease stomatal conductance, mobilizing carbon reserves instead? (Tardieu and Simonneau, 1998; McDowell, et al., 2008). Do species that succeed in low water environments out-compete the other species or simply have a lower tolerance threshold?

Within an ecosystem, individual plant responses to drought may differ. For example, various responses may be seen in plants experiencing drought more slowly, over longer periods, or at different points in the plant's life cycle. As drought responses occur over a variety of timescales, each warrants investigation. Experiments should focus on simulating these different conditions in order to observe variable strategies and innate plasticity. Furthermore, while it is generally accepted that in grasslands resource limitation acts as a strong bottom-up control on plants, biotic factors such as herbivory, pathogens, or parasitism are also influential but will not be specifically considered in this investigation.

## Experimental Investigation

Experiments designed to address these issues must be inclusive of all functional groups, and must take into consideration all players in a plant community. Several studies have already been completed that incorporate the use of both dominant and subdominant species (Grime et al., 1997; Craine et al., 2001). Determining predictive traits that can be applied universally will increase success in answering broadly focused questions without forcing experiments to be exhaustive. Although it was conducted small scale, the following preliminary study using similar methods yielded promising results.

An assessment of traits from 22 species was conducted by Nippert and Craine in 2008 (unpublished data) which showed novel relationships between leaf tissue density and critical water potentials. Low tissue density in leaves corresponded to the highest water potentials before wilting. Those with high tissue density show the opposite tendency and are assumed to be best equipped to withstand drought conditions. It was speculated that thick leaves without a low critical water potential ($\Psi_{crit}$) [water availability at the point conductance ceases], may be an adaptation to a low nutrient environment and may therefore have more to do with leaf retention than drought tolerance. An objective of my study was to investigate this relationship further across a broader range of selected species and explore additional traits through further inquiry. Additionally, I would like to know, are these traits static within a species that has a wide geographic range? The urgency of these questions is amplified when the prospect of global climate change is taken into consideration.

I will use similar methods to address the following lines of questioning. How will the tallgrass prairie ecosystem respond to climate change? Will species losses be driven by differences in morphology, functional group, phylogenetics, physiology, or competition? In a typically mesic environment, how can I determine which species may be at risk of extinction under a changing temperature- precipitation regime? I expect to see a range of traits in the diverse association of species on Konza Prairie. Using both morphological and physiological traits measured on these plants, I suspect a trait or suite of traits will predict drought tolerance across all species. Once I determine which species are tolerant, I will have a better understanding of the current plant community and how beneficial drought tolerance traits are in the field.

Landscape heterogeneity should dictate differences in species abundance based on land management practices and the soil moisture characteristics associated with specific management regimes. Logic suggests that drought tolerant species will be found in areas that experience periodic to frequent water stress. For example, annually burned areas tend to have warmer soils early in the growth season (Bremer & Ham, 1999) and dryer soils. These locations should be preferentially inhabited by species with the drought tolerance syndrome.

In addition to low water availability, Konza prairie is limited by a number of other resources. Not only can two resources be important limiting factors, these limiting resources can change over space and time (transient maxima hypothesis, Seastedt and Knapp, 1993). Understanding the conditions that lead to various limitations can be made simpler using plant traits as indicators. For example, plants that successfully survive and continue to grow despite a limitation will have traits that make this possible (Reich et al., 2003). The distribution of plants on Konza is determined by both biotic and abiotic factors such as resource limitation, fire and grazing disturbances, and competition which challenge plant survival. Plants must not only be able to attain vital resources but must often compete inter- and intraspecifically to gain them. Plant traits are responsible for this differential performance on tallgrass prairie as the most successful plants possess the most beneficial traits. Expanding the scope to look at abundance on a broad scale should reveal the most successful strategy employed in tallgrass prairie.

Pursuing these questions should help bring together an understanding of traits that contribute to a plant’s ability to survive drought conditions with current knowledge of plant functional traits centered primarily around nutrient limitation. By using a common technique and statistical analysis, my study can be compared to those assessing traits across nutrient gradients.

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# CHAPTER 2 - Plant Traits and Drought Tolerance

## Introduction

Across a wide variety of ecosystems (Watt, 1947), drought reduces productivity (Knapp, 1984; Tilman and Elhaddi, 1992; Ciais et al., 2005), leads to shifts in species abundance (Tilman and Elhaddi, 1992), and can be responsible for local extinction (Tilman and Elhaddi, 1992). The episodic nature of water availability produces drought at multiple scales, from decade-long reductions in precipitation (Weaver, 1954), seasonal dry periods (Abrams and Knapp, 1986), and daily mid-day inductions of plant water stress (Fahnestock and Knapp, 1994).

Grasslands specifically are characterized by drought (Carpenter, 1940). Tropical grasslands and savannas typically have annual dry seasons during which grasses senesce (Lieberman, 1982). Temperate grasslands periodically experience years with low precipitation that help shape the characteristic plant community (Borchert, 1950, Tilman and Elhaddi, 1992). While mild drought elicits species-level responses, severe events can have more dramatic effects on the entire plant community (Coupland, 1958; Fuhlendorf and Smeins, 1998). With projected increases in temperature and reduced water availability during the growing season (IPCC, 2007), drought is likely to remain an ecologically-important driver of grassland structure in the future.

Plants have evolved a range of physiological responses to low water availability (Eggemeyer et al., 2006; McDowell et al., 2008). Stomatal regulation allows fine temporal control of water loss in response to environmental conditions (Franks et al., 1997; Brodribb et al., 2009). Stomatal regulation allows leaves to avoid low water potentials or tolerate low water potentials. Isohydric plants reduce stomatal conductance (and thereby carbon assimilation) to maintain relatively constant water potentials in response to reduced water availability (Bates and Hall, 1981). Anisohydric species maintain rates of stomatal conductance and carbon assimilation at the expense of decreasing leaf water potentials during dry conditions (Larcher, 1973; Franks et al, 2007; McDowell et al., 2008). Species that employ anisohydry are considered to be drought tolerant as they are able to maintain physiological processes during drought events. While isohydric species can survive drought events, they are sensitive to drought cues and are unable to photosynthesize under stress. In this study, species that employ isohydry are considered to be drought intolerant.

Physiological drought tolerance is expected to be linked to other functional traits due to underlying mechanisms resulting from physiological or evolutionary tradeoffs (Reich et al., 2003). For example, due to inherent tradeoffs in plant resource allocation, stress-tolerant species should have low rates of gas exchange and low maximal growth rates (Reich et al., 2003). In a study of 43 UK grassland species, drought insensitive plants were slow-growing and had the highest relative yield under all conditions (Grime et al., 1997). A number of strategies to preserve water and subsist under both mild water limitation and extreme drought stress have been recorded in plants. Small leaves (Reiger et al, 1992), high leaf angle (Medina et al, 1990), and root morphology have all been shown to be successful adaptations to survive or even avoid drought stress. Cavitation-resistant xylem is present in plants occurring in areas of frequent drought (McDowell et al., 2008). The $C_4$ and CAM photosynthetic pathways both evolved to increase photosynthetic efficiency in hot or arid environments (Gibson, 1998; Nelson & Sage, 2005). Differential performance has been shown between various functional groups (WUE, Kocacinar & Sage, 2003;WUE and $A_{net,}$ Eggemeyer et al., 2006), so I also expect that physiological drought tolerance should vary by functional group.

In order to better understand patterns of drought tolerance among grassland species and their relationship to other functional traits, I measured physiological drought tolerance and numerous morphological traits for a wide suite of species present at a mesic prairie in central North America. My goal was to understand the variation in physiological drought tolerance among species. I also aimed to understand how other functional traits such as maximum photosynthetic rates and root system morphology relate to physiological drought tolerance and how these relationships differ among functional groups. I hypothesized that prairie plants would exhibit a range of responses to drought including plants that can tolerate severe drought and those that cannot survive mild water limitation. I also expected responses to differ among functional groups ($C_3$ grass, $C_4$ grass, $C_3$ forb, $C_4$ forb) due to differences in morphology and phenology. Finally, as a stress tolerance strategy I hypothesized that drought tolerant species would show signs of a physiological tradeoff resulting in lower photosynthetic rates.

## Methods

### *Site Description*

Konza Prairie Biological Station (KPBS) is a 3487 ha native tallgrass prairie located in the Flint Hills of northeastern Kansas, USA (39 05'N, 96 35'W). The prairie landscape is dominated by a few species of warm season grasses (*Andropogon gerardii, Sorghastrum nutans, Schizacyrium scoparium,* and *Panicum virgatum*) while cool season grasses and a diverse suite of forbs round out the plant community. KPBS receives an average of 835 mm of precipitation annually, most of which (75%) falls during the growing season. Over the last century at KPBS, mean annual precipitation regularly deviated from the long term mean by about 25% and reached values as high as 184% of the mean in the wettest year (1533 mm in 1951) and 47% in the driest year (392 mm in 1966). While the mean annual temperature for KPBS is 13° C, the mean low for the year is -3 °C in January and the mean high of 27 °C occurs in July.

### *Plant Cultivation*

Of the 477 herbaceous, non-wetland vascular plants found on KPBS (Towne, 2002), 121 species were chosen for this study. Species chosen for the experiment encompass a broad range of attributes. Phylogeny, life history, and seed availability were all considered during the selection process in order to best represent the floral diversity found on KPBS. Seeds were obtained from a variety of sources, including the Kansas Native Plant Society, the National Plant Germplasm System, Chicago Botanic Garden – National Tallgrass Prairie Seed Bank, Taylor Seed Farms (White Cloud, KS), and local collection from the Konza Prairie Biological Station.

Propagules were germinated on damp filter paper in Petri plates at room temperature. Stratified seeds were stored on damp filter paper in a 5° C incubator for at least 30 days while those that required scarification were abraded with sandpaper before being germinated in appropriate conditions. Seedlings were transplanted to 164 mL plastic Cone-tainers (D-40, Stuewe and Sons, Inc. Corvalis, OR) containing standardized, untreated lowland soil from KPBS (silty clay loam). Plants in containers were grown in a Conviron growth chamber (Model PGV 36, Controlled Environments Limited, Winnipeg, Manitoba) with 16 hour days at 25 ˚C and 8 hour nights at 20 ˚C (Table 2.1). Plants were watered daily and treated with a commercial fertilizer (Miracle Grow 24-8-16 All Purpose Fertilizer) biweekly to eliminate nutrient stress. Eight replicates of each species were maintained.

### *Physiological and Morphological Measurement*

Plants were grown in the growth chamber for 8 - 12 weeks before data collection. Gas exchange was measured using a Li-6400 infra-red gas analyzer with red/blue LED light source and $CO_2$ injector (LICOR Biosciences, Lincoln, NE). Light intensity inside the cuvette was 2000 µmol $m^{-2}$ $s^{-1}$, $CO_2$ concentration was 400 ppm, and relative humidity was kept constant at 40%.

Measurements were performed on the newest fully-expanded leaves and included maximum photosynthetic rate ($A_{max}$), stomatal conductance to vapor ($g_s$), and water use efficiency (WUE) which is the ratio $A_{max}/E$.

Leaf thickness was measured in inter-vein tissue for 2-3 newly-expanded, mature leaves on each plant using digital calipers (Thermo Fisher Scientific Inc., Waltham, MA). Leaf angle relative to horizontal was measured by averaging 3-5 protractor measurements per plant following Norman and Campbell (1989).

After 8-12 weeks, plants were divided into sets of 50 and were subjected to a dry-down period with daily monitoring using a steady state diffusion porometer (Model SC-1, Decagon Devices, Inc., Pullman, WA). Stomatal conductance was recorded daily during dry-down until the conductance rate fell below 5% of the maximum. Following stomatal closure, non-senesced leaf tissue was collected and the hydrostatic pressure potential was measured using a Scholander pressure bomb (PMS Instrument Company, Albany, OR). This leaf pressure potential corresponding to stomatal closure is henceforth referred to as the species' critical water potential ($\Psi_{crit}$). A subset of the leaves was used to measure leaf area (LI-COR Leaf Area Meter, Model LI-3100) and subsequently oven dried and weighed to calculate Specific Leaf Area (SLA).

Leaf tissue density ($\rho_{L,}$ g cm$^{-3}$), the ratio of leaf mass to leaf volume was calculated using leaf area and thickness. The remaining biomass was sorted to leaf or stem and dried at 60° C to determine total aboveground biomass. Roots were sorted into coarse (> 2 mm) and fine roots. A representative sample of the fine roots was scanned into a digital root imaging program (Winrhizo; Regents Instruments, Inc., Nepean, Ontario, Canada) which calculated total root length (cm), total root volume (cm$^3$), and average root diameter by length (mm). The remainder of the roots was oven dried, weighed, and used to calculate specific root length (SRL), root tissue density ($\rho_R$, g $cm^{-3}$), and fraction root.

Additional species-level data for a subset of the species included date of first flowering, which is reported as the average first day each year that each species was observed in bloom at KPBS from 2000-2009. Mycorrhizal responsiveness, which is the growth enhancement associated with mycorrhizal inoculation under standardized conditions, and mycorrhizal root length colonization data for my study species were reported by Wilson and Hartnett (1998).

### ***Statistical Analysis***

Ten functional traits were chosen as the primary functional traits of interest. Encompassing tissue and whole plant morphology and physiology, these traits included $\rho_R$, $\rho_L$, average root diameter, leaf thickness, leaf angle, root mass, shoot mass, $\Psi_{crit}$, $A_{max}$, and $g_s$.  The 10 traits were used in pairwise correlations and in principal component analysis (JMP 8.0.2, SAS Institute, Inc., Cary, NC). Multivariate analysis was also performed by functional group (grass v. forb and $C_3$ v. $C_4$) to establish predictive characteristics specific to each group. Correlations between additional traits such as SLA, phenology, and mycorrhizal data and the PCA axes were tested to examine relationships with drought tolerance.

### ***Field Confirmation***

To check for relevance to field-grown plants, I compared my traits data to a field experiment that examined some of my study species. Leaf angle, leaf thickness, specific leaf area, and leaf tissue density were measured on 50 species collected from a range of sites on KPBS. Plants were measured in the summer of 2009 following the same procedures as in the laboratory experiment (Craine and Towne, in review). I employed Welch’s two sample t-tests to test the similarity in sample means due to unequal variances among the traits (R, 2.10.0, Table 2.2). In all traits but leaf angle, no differences were present between laboratory and field-grown plants ($P > 0.05$). Leaf angles did vary significantly but both populations were linearly correlated (Table 2.2**,** $r = 0.58$, $P < 0.0001$).

## Results

### *Univariate Statistics*

Among species, $A_{max}$ varied by a factor of 12.5, ranging from 1.95 µmol $CO_2$ $m^{-2}$ $s^{-1}$ in *Physalis pubescens* to 24.5 µmol $CO_2$ $m^{-2}$ $s^{-1}$ in *Erigeron annuus* (Table 2.3). *Xanthium strumarium* had the least dense leaves (0.10 g $cm^{-2}$) while *Andropogon gerardii* had the most dense (0.86 g $cm^{-2}$). Critical water potential ($\Psi_{crit}$) ranged from -8.9 MPa (*Bouteloua curtipendula*) to -1.1 MPa (*Tradescantia bracteata*). The thinnest leaves belonged to *Chloris verticillata* (0.08 mm) while *Silphium lacinatum* had the thickest (0.57 mm). Root tissue density ($\rho_R$) ranged from 0.11 g $cm^{-1}$ in the $C_3$ forb *Euphorbia marginata* to 0.58 g $cm^{-1}$ in the $C_3$ forb *Amorpha cansecens*. *Psoralidium tenuiflorum* had the largest fraction of belowground biomass (0.84) while the legume *Chamaechrista fasciculata* had the smallest fraction (0.12).

### *Pair-wise Relationships*

Among the 10 main functional traits, 47% of the pairwise correlations were significant. The strongest correlation was between the two gas exchange variables as species with high photosynthetic rates had the highest stomatal conductance (Table 2.4, $r = 0.70$, $P < 0.001$). Correlations among traits extended between roots and leaves. For example, species with thin leaves had thin roots ( $r = 0.42$, $P < 0.001$). Overall, $\Psi_{crit}$ correlated with 4 of the 9 other main functional traits. Species that were more physiologically tolerant of drought (lowest $\Psi_{crit}$) had thin leaves (r = 0.28, $P < 0.001$), thin roots (r = 0.54, $P < 0.001$), dense leaves (r = -0.37, $P < 0.001$), and a high leaf angle (r = -0.39, $P < 0.001$).

### *Multivariate Trait Relationships*

In a multivariate analysis of the 10 main functional traits, the first trait axis separated drought-tolerant species from drought-intolerant species (Table 2.5). Six traits contributed significantly to the axis, accounting for 28.3% of the total variation in all traits among all 121species explained by PCA. Species that were physiologically tolerant of drought (low $\Psi_{crit}$) had: 1.) thin, dense leaves, 2.) thin, dense roots, and 3.) a high leaf angle. For example, *Hesperostipa spartea* which continued to conduct water down to -8.0 MPa had leaves that were 0.62 g cm$^{-3}$ and only 0.12 mm thick. In contrast, *Asclepias speciosa* ceased conducting water at -2.0 MPa. Its leaves had a density of only 0.27 g cm$^{-3}$ and were 0.19 mm thick. Drought-tolerant species did not differ in photosynthetic water use efficiency from drought-intolerant species (Table 2.9). Drought-tolerant species did not flower at different times nor differ in their dependence on mycorrhizal fungi than drought-intolerant species. On average, grasses had a more drought-tolerant strategy than forbs (Table 2.8, $P < 0.001$) and a simple dichotomy of species into grasses and forbs explained 50% of the variation in Axis 1. Neither photosynthetic pathway nor life history was associated with differences in Axis 1 (Table 2.8).

Axis 2 reflected the strong correlation among species in gas exchange rates that were largely independent of drought-tolerance (Table 2.5). As seen in the bivariate relationships, species with high photosynthetic rates also had high rates of stomatal conductance and their leaves were held at a high angle. These species also had a higher fraction of root biomass than those low on the axis (Table 2.9, r = 0.32, $P < 0.001$). On average forbs scored lower than grasses on Axis 2, which reflects their lower rates of gas exchange (Table 2.8). The third axis primarily separated species based on their size at the end of the experiment (Table 2.5). Axis 3 did not include any physiological traits and only explained 3.7% more variation than expected by chance.

With differences in grasses and forbs explaining a large proportion of the variation in Axis 1, multivariate analyses for the 10 main functional traits were run separately for the two groups (Table 2.6, Table 2.7). Patterns among functional traits within functional groups were broadly similar to the overall patterns. Morphological traits were associated for both groups on one axis, drought tolerance was independent of the morphological traits, and plant size was independent of both morphology and drought tolerance. The major difference in trait relationships between grasses and forbs was that physiological drought tolerance was associated with gas exchange parameters for forbs instead of being grouped with the leaf morphological traits (Table 2.6). In grasses, physiological drought tolerance was still associated with both leaf and root tissue traits but also contributed to a lesser extent to the gas exchange axis (Table 2.7).

## Discussion

Physiological responses to drought have been addressed for species in multiple habitats including wetlands (Touchette et al., 2007), dry rainforest (Curran et al., 2009), tropical forest (Baltzer et al., 2009), and temperate forest (Hallik et al., 2009). Assessment of these characteristics is common in dominant forest assemblages, but much less common for herbaceous species and subdominant or rare community members. Across the 121 Konza grassland species that I measured, physiological drought tolerance ($\Psi_{crit}$) ranged from -1 to -8.9 MPa, a range that nearly encompasses the global range of drought tolerance. Grassland species measured by Knapp during the 1983 drought reflected field water potentials much closer to the range I recorded than any measured on KPBS in recent years (Knapp, 1984). For example, I routinely measured $\Psi_{crit}$ at water potentials as low as -8 MPa, but field measurements performed on species coinciding with my study species on Konza prairie were frequently much higher (~ -2 MPa) during average growing season conditions (Nippert and Knapp, 2007).

Physiological drought tolerance is not an isolated trait. Low $\Psi_{crit}$ is associated with a suite of morphological traits that enables plants to withstand the physical stress imposed by very low water potentials experienced as a result of the driving atmospheric force and low water availability. For the Konza flora, drought-tolerant species had thin, dense leaves held at a high angle and thin, dense roots. The direct and indirect advantages of these traits for drought tolerance still remain to be investigated. Yet, a high leaf tissue density is likely associated with either thicker cell walls or smaller cells, which would confer greater physical resistance to negative cellular pressures. The low average root diameter may be a product of thinner xylem elements to prevent cavitation even under very high tension, but could also be indirectly associated with the need to compete for water or nutrients. The inclusion of thin leaves, thin roots, and leaf angle as traits associated with drought tolerance likely reflects a higher prevalence of drought tolerance in grasses which were on average, more drought tolerant than forbs.

Current understanding of stress tolerance strategies and physiological tradeoffs led me to expect that drought-tolerant species would have lower rates of leaf gas exchange. Contrary to this prediction, physiological drought tolerance and gas exchange proved to be orthogonal. The lack of relationship between drought tolerance and gas exchange was not due to bias from photosynthetic pathway. $C_4$ species were not more or less likely to tolerate drought than $C_3$ species, despite the inherent differences that exist between the two pathways. It is possible that the two would be inversely related over a broader set of species or under different conditions. The highest photosynthetic rate that I observed was less than half of the global maximum (24.5

vs. 66 µmol $m^{-2}$ $s^{-1}$, respectively; see Wright, 2004) and was lower than photosynthetic rates previously measured on the same species in situ at Konza (Nippert et al., 2007). Alternatively, drought stress tolerance may differ mechanistically from nutrient stress especially when water stress is only periodic.

As much as drought is an important structuring force in grasslands, many of the species that I examined were physiologically intolerant of drought. Physiologically intolerant species subsisting in this drought-prone ecosystem survive by either escaping drought or avoiding it. Although I was not able to empirically differentiate the two, there seem to be some ecological patterns to the drought intolerant species. First, some drought-intolerant species escape drought by occupying microsites where drought is less important. For example, *Tradescantia ohiensis* is often found in wet microsites which are readily available in deep lowland soil or near hillside seeps which occur commonly at KPBS. Phenological escape allows cool-season species to complete their lifecycles in the wetter, milder spring and fall seasons, eluding water limitation altogether (Taiz and Zeiger, 2002). Alternatively, species employing phenological avoidance, primarily annuals, respond to environmental stimuli during unfavorable conditions by rapidly flowering and setting seed. Completion of the life cycle occurs at an accelerated pace before severe drought occurs. In perennial species, a common avoidance reaction is senescence for the duration of the drought period; plants re-grow leaves and resume their life cycles once conditions improve (*Schizachyrium scoparium*). The last class of avoiders is made up of deeply rooted species, such as *Lespedeza capitata*, that avoid drought stress by accessing deep soil water (Canadell et al, 1996). For example, previous work has shown that soil water is relatively available at depths greater than 1 meter (Briggs and Knapp, 1995; Nippert and Knapp, 2007) on KPBS despite antecedent precipitation patterns. All of these processes have been recorded in field situations (Taiz and Zeiger, 2002), but further characterization of these mechanisms of persistence in prairie species is needed. The drought simulated in my study is likely more comparable to severe drought than episodic seasonal drought; but plant responses occurring over additional timescales warrant investigation as well.

Natural populations can be used in other ways to validate the findings of this study. For example, landscape heterogeneity should dictate differences in species abundance based on land management practices and the soil moisture characteristics associated with specific management regimes. Drought tolerant species logically should be found in areas with less available water. For example, annually burned areas tend to have warmer soils early in the growth season (Bremer & Ham, 1999) leading to higher evapotranspiration and dryer soils which should preferentially be inhabited by species with my drought tolerance syndrome. Expanding the scope of my questions to look at abundance on a broad scale should reveal the most successful strategy employed in tallgrass prairie overall. Further extrapolation of my results could potentially predict tolerance in other grassland and savanna ecosystems.

In ecosystems that experience unpredictable periodic drought, drought tolerance may be a morphological syndrome. In this study using a large species set of prairie plants, physiological drought tolerance was correlated with morphology but had a negligible relationship with instantaneous gas exchange rates and biomass allocation above or belowground. Thus, plants are built to physically withstand low water potentials via thin, dense leaf and root tissues and high leaf angle without discernible leaf-level costs for reduced photosynthetic rates when water is available. This is contrary to current ideas about stress tolerance in plants where nutrient conservation comes at a physiological cost (Grime et al., 1997; Reich et al, 2003; Craine, 2009). Additionally, traits previously considered to be adaptive to low nutrient environments may actually be beneficial in other capacities. For example, root tissue density may play a role in preventing cavitation or improving refill rates (Wahl and Ryser, 2000). Future incorporation of additional morphological traits may improve the resolution of my tolerance predictions. Differences in vascular structure of herbaceous species is largely unknown (except see: Wahl and Ryser, 2000), and a detailed examination of leaf and root xylem, including assessment of resistances to water flux from roots to leaf mesophyll may improve understanding of the tradeoffs associated with drought tolerance in grassland species.

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# Tables and Figures

**Table 2.1 Controlled environment schedule for lighting and temperature. Bulbs are a combination of fluorescence and actinic light representing the natural spectrum. Each chamber contains 4 each 1000 Watt high pressure sodium lamps and 1000 Watt metal halide lamps.**

| **Time** | 0:00 – 5:59 | 06:00 – 21:59 | 22:00-23:59 |
|---|---|---|---|
| **Temperature** | 20 C | 25 C | 20 C |
| **Lights** | 0 Lamps | 8 Lamps | 0 Lamps |
| **Light Intensity** | 0 | 1200 µmol/m$^2$/s | 0 |

**Table 2.2 Field and laboratory leaf tissue measurements.**
**Means reported with standard deviations; *P* values calculated using Welch two-sample t-tests (α = 0.05). n = 50**

| | **Leaf Angle** | **Leaf Thickness** | **$\rho_L$** | **SLA** |
|---|---|---|---|---|
| **Lab** | 38.6 ±27 | 0.22 ± 0.097 | 0.41 ± 0.145 | 156 ± 54.1 |
| **Field** | 51.8 ± 23 | 0.22± 0.133 | 0.44 ± 0.180 | 138 ± 59.3 |
| ***P*** | **<0.0001** | 0.86 | 0.22 | 0.05 |

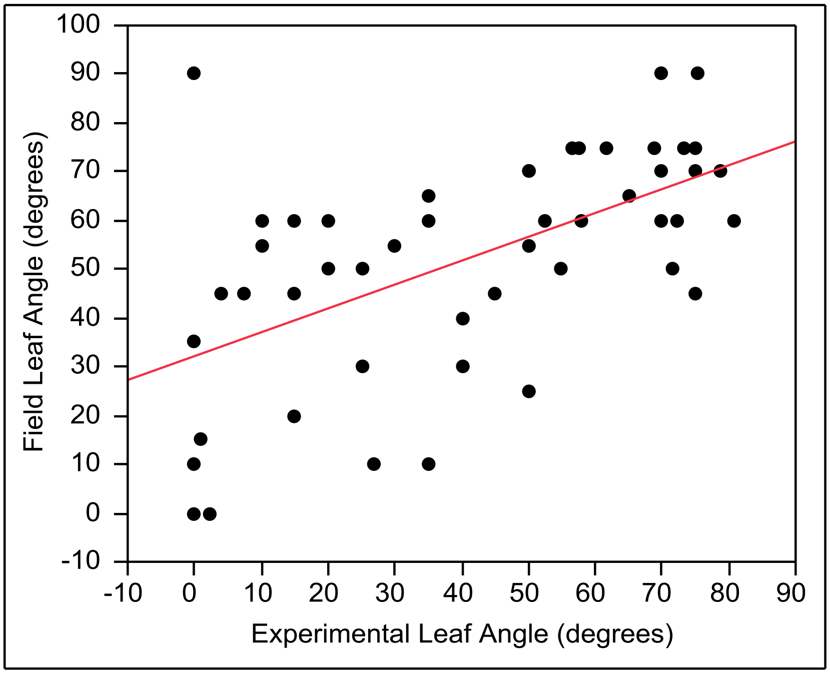

**Figure 2.1 Linear correlation of experimental leaf angle and field leaf angle measurements. (n = 50, r = 0.58, *P <0.0001*)**

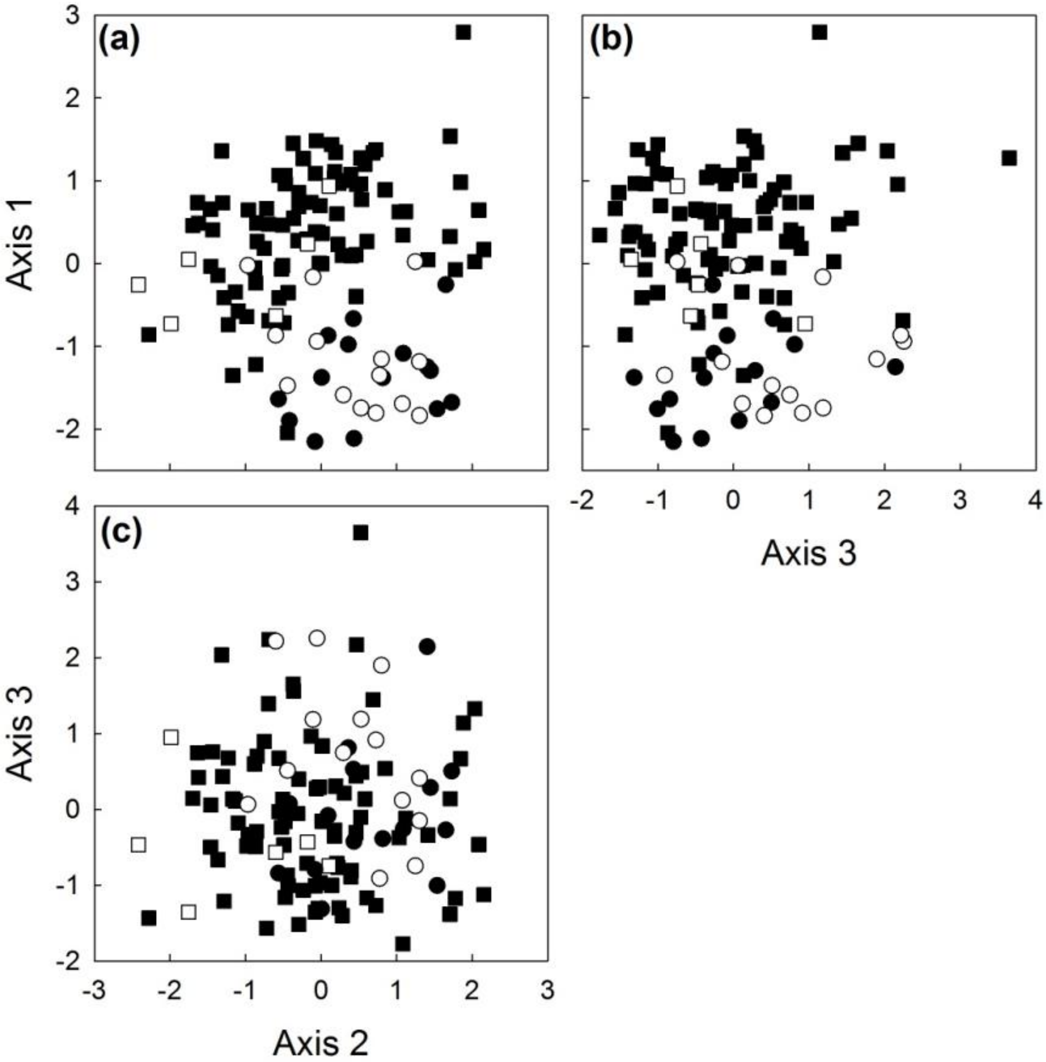

**Figure 2.2 PCA axes. Graminoids are represented by circles; forbs are represented by squares. Open symbols represent $C_4$ photosynthesis; closed represent $C_3$ photosynthesis. n = 121**

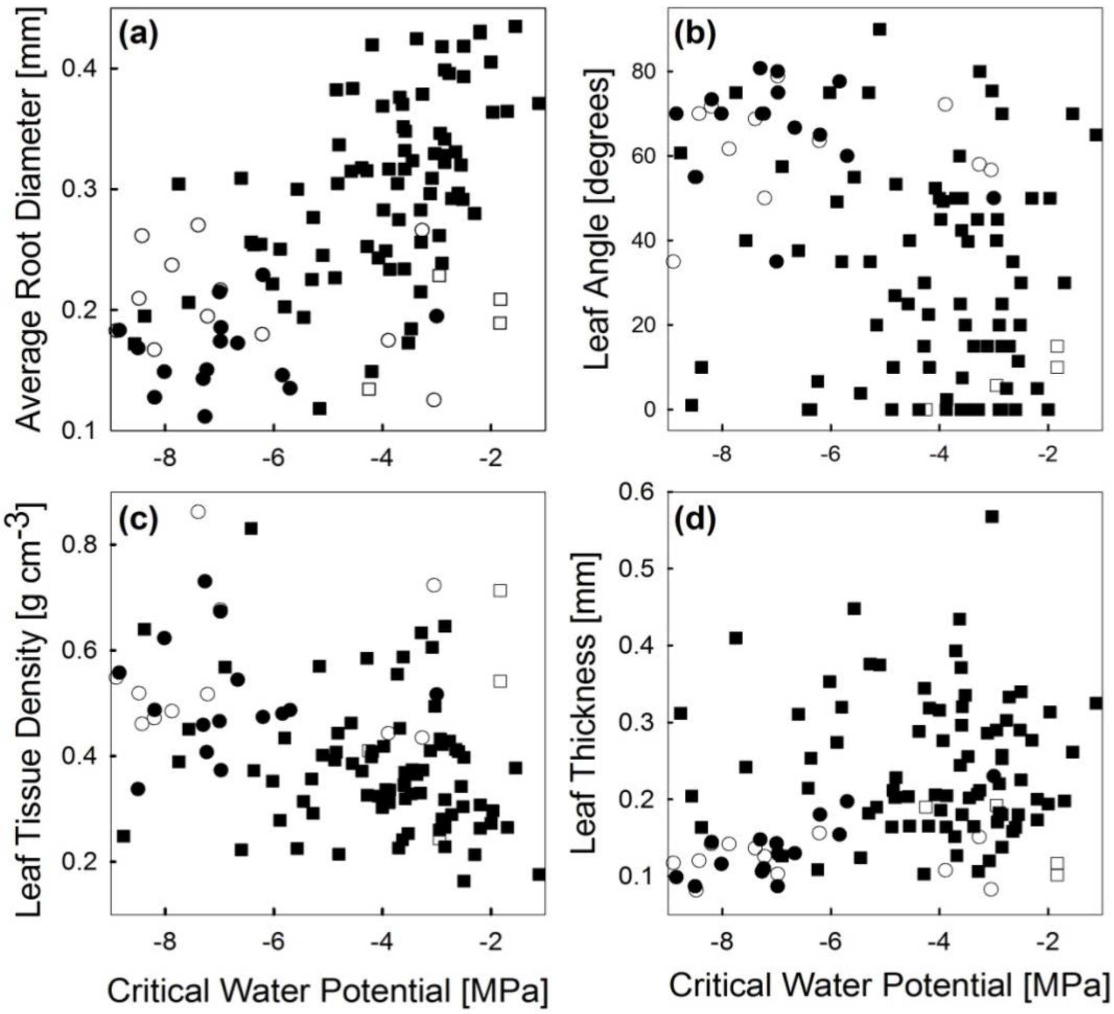

**Figure 2.3 Pairwise correlations. Graminoids are represented by circles; forbs are represented by squares. Open symbols represent $C_4$ photosynthesis; closed represent $C_3$ photosynthesis. (A) n = 111, $R^2$= 0.29, *$P < 0.0001$* (B) n = 105, $R^2$ = 0.15, *$P < 0.0001$* (C) n = 107, $R^2$= 0.14, *$P < 0.0001$* (D) n = 110, $R^2$= 0.08, *$P = 0.0034$***

**Table 2.3 Univariate statistics. n = 121**

| | $A_{max}$ (μmol $CO_2$ $m^{-2}$ $s^{-1}$) | $g_s$ (mol $H_2O$ $m^{-2}s^{-1}$) | $\Psi_{crit}$ (bars) | Leaf Thickness (mm) | Leaf Angle (degrees) | Avg. Root Diameter (mm) | SLA ($cm^2$ $g^{-1}$) | $\rho_L$ ($g/cm^{-3}$) | SRL (m $g^{-1}$) | $\rho_R$ (g $cm^{-3}$) | Fraction Root |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Mean** | 10.3 | 0.131 | -46.7 | 0.216 | 38.6 | 0.273 | 156.1 | 0.406 | 99.1 | 0.304 | 0.391 |
| **Standard Deviation** | 4.3 | 0.062 | 20.6 | 0.097 | 27.2 | 0.088 | 54.1 | 0.145 | 70.6 | 0.097 | 0.148 |
| **Max** | 24.5 | 0.303 | -11.2 | 0.568 | 90.0 | 0.455 | 315.5 | 0.862 | 437.4 | 0.586 | 0.835 |
| **Median** | 10.2 | 0.124 | -40.0 | 0.196 | 40.0 | 0.268 | 152.9 | 0.391 | 81.9 | 0.295 | 0.362 |
| **Min** | 2.0 | 0.028 | -89.0 | 0.081 | 0.0 | 0.097 | 54.9 | 0.100 | 17.1 | 0.105 | 0.122 |

**Table 2.4 Pair-wise correlations and *P*-values for ten primary traits. *P*-values in the upper right and correlation coefficients in the lower left are bolded for statistical significance ($\alpha = 0.05$).**

| | $A_{max}$ | $g_s$ | $\Psi_{crit}$ | Leaf Thickness | Leaf Angle | Avg. Root Diameter | $\rho_L$ | $\rho_R$ | Shoot Mass | Root Mass |
|---|---|---|---|---|---|---|---|---|---|---|
| **$A_{max}$** | --- | **0.001** | 0.88 | 0.10 | 0.45 | 0.18 | 0.30 | 0.41 | 0.60 | 0.82 |
| **$g_s$** | **0.70** | --- | 0.90 | **0.001** | 0.43 | 0.07 | **0.02** | **<0.01** | **<0.001** | **0.02** |
| **$\Psi_{crit}$** | -0.01 | 0.01 | --- | **<0.01** | **<0.001** | **<0.001** | **<0.001** | 0.09 | 0.23 | 0.43 |
| **Leaf Thickness** | 0.15 | **0.30** | **0.28** | --- | 0.72 | **<0.001** | **<0.001** | **<0.01** | 0.19 | 0.24 |
| **Leaf Angle** | 0.07 | 0.08 | **-0.39** | -0.04 | --- | **<0.01** | 0.21 | 0.74 | 0.18 | 0.08 |
| **Avg. Root Diameter** | 0.12 | 0.17 | **0.54** | **0.42** | **-0.26** | --- | **<0.001** | **<0.001** | **<0.01** | 0.62 |
| **$\rho_L$** | -0.10 | **-0.22** | **-0.37** | **-0.53** | 0.13 | **-0.44** | --- | **0.05** | **<0.001** | 0.61 |
| **$\rho_R$** | -0.08 | **-0.26** | -0.16 | **-0.24** | 0.03 | **-0.30** | **0.18** | --- | 0.83 | 0.11 |
| **Shoot Mass** | -0.05 | **-0.33** | -0.12 | -0.12 | -0.13 | **-0.25** | **0.36** | 0.02 | --- | **<0.001** |
| **Root Mass** | -0.02 | **-0.21** | -0.08 | 0.11 | 0.17 | -0.05 | 0.05 | 0.15 | **0.45** | --- |

**Table 2.5 Eigenvectors and eigenvalues resulting from rotation in Principal Component Analysis. Bold values represent a significant contribution to the axis. Eigenvalues are listed for each axis with the cumulative percentage of variation explained. n=121**

| Eigenvectors | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|
| Avg. Root Diameter | **0.80** | -0.02 | -0.10 |
| Leaf Thickness | **0.71** | -0.31 | -0.10 |
| $\rho_L$ | **-0.71** | -0.13 | 0.12 |
| $\Psi_{crit}$ | **0.70** | 0.30 | 0.19 |
| $\rho_R$ | **-0.41** | -0.20 | 0.08 |
| Leaf Angle | **-0.40** | **0.47** | 0.12 |
| $g_s$ | 0.24 | **0.82** | -0.29 |
| $A_{max}$ | 0.12 | **0.80** | -0.02 |
| Root Mass | 0.02 | 0.05 | **0.89** |
| Shoot Mass | -0.18 | -0.19 | **0.76** |
| **Eigenvalues** | **2.8 (28.3%)** | **1.7 (45.7%)** | **1.4 (59.3%)** |

**Table 2.6 Forbs: eigenvectors and eigenvalues resulting from the rotated PCA axes containing forb species. Bold values represent a significant contribution to the axis. Eigenvalues are listed for each axis with the cumulative percentage of variation explained. n = 92**

| **Eigenvector** | **Axis 1** | **Axis 2** | **Axis 3** |
|---|---|---|---|
| $A_{max}$ | **0.80** | 0.12 | -0.14 |
| $g_s$ | **0.71** | 0.25 | **-0.36** |
| Avg. Root Diameter | **0.63** | 0.17 | 0.02 |
| $\Psi_{crit}$ | **0.47** | -0.24 | -0.04 |
| $\rho_R$ | **-0.47** | -0.09 | -0.11 |
| $\rho_L$ | -0.32 | **-0.62** | 0.08 |
| Leaf Thickness | 0.31 | **0.74** | 0.28 |
| Leaf Angle | -0.15 | **0.76** | -0.15 |
| Shoot Mass | -0.06 | **-0.39** | **0.80** |
| Root Mass | -0.05 | 0.24 | **0.83** |
| **Eigenvalue** | **2.8 (28.2%)** | **1.5 (43.5%)** | **1.4 (57.2%)** |

**Table 2.7 Graminoids: Resulting eigenvectors and eigenvalues from the rotated PCA axes containing graminoid species. Bold values represent a significant contribution to the axis. Eigenvalues are listed for each axis with the cumulative percentage of variation explained. n = 29**

| **Eigenvector** | **Axis 1** | **Axis 2** | **Axis 3** |
|---|---|---|---|
| Leaf Thickness | **0.76** | -0.03 | 0.05 |
| Leaf Angle | **0.67** | 0.12 | -0.18 |
| $\Psi_{crit}$ | **0.63** | 0.11 | **-0.44** |
| $\rho_L$ | **0.51** | **0.35** | -0.02 |
| Avg. Root Diameter | **0.48** | 0.25 | 0.09 |
| $A_{max}$ | **0.37** | 0.19 | **0.77** |
| $\rho_R$ | -0.30 | **0.64** | 0.29 |
| Root Mass | 0.05 | **0.82** | -0.08 |
| Shoot Mass | 0.12 | **0.68** | **-0.38** |
| $g_s$ | 0.00 | -0.20 | **0.77** |
| **Eigenvalue** | **2.2 (22%)** | **1.9 (41.1%)** | **1.5 (56.4%)** |

**Table 2.8 Multiple regression with categorical variables, general linear model. For each contrast I report least squares means (LSM) and partial $R^2$, each contrast's proportion of the total variation explained by the model ($\alpha = 0.05$).**

| | **Axis 1** | | | **Axis 2** | | | **Axis 3** | | |
|---|---|---|---|---|---|---|---|---|---|
| | ***P*** | **Partial $R^2$** | **LSM** | ***P*** | **Partial $R^2$** | **LSM** | ***P*** | **Partial $R^2$** | **LSM** |
| **Growth Form** | **<0.0001*** | **0.50** | | **0.0002*** | **0.10** | | **0.02** | **0.04** | |
| **Grass** | | | -1.27 | | | 0.55 | | | 0.39 |
| **Forb** | | | 0.35 | | | -0.36 | | | -0.26 |
| **Photosynthetic Type** | 0.79 | 4.06E-04 | | **0.02** | **0.04** | | 0.82 | 3.66E-04 | |
| **C3** | | | -0.43 | | | 0.42 | | | 0.03 |
| **C4** | | | -0.49 | | | -0.23 | | | 0.10 |
| **Life History** | 0.64 | 0.001 | | 0.45 | 0.004 | | 0.15 | 0.01 | |
| **Annual** | | | -0.49 | | | 0.003 | | | 0.22 |
| **Perennial** | | | -0.42 | | | 0.19 | | | -0.09 |
| **Growth Form x PS Type** | | | | | | | **0.03** | **0.03** | |
| **Life History x PS Type** | | | | **0.04** | **0.03** | | | | |
| **Model $R^2$** | 0.50 | | | 0.16 | | | 0.09 | | |

**Table 2.9 Pair-wise correlations between PCA axes and secondary plant traits. Bold values represent statistically significant *P* values ($\alpha$=0.05).**

| | Axis 1 | | Axis 2 | | Axis 3 | |
|---|---|---|---|---|---|---|
| | *r* | *P* | *R* | *P* | *r* | *P* |
| SLA | **-0.27** | **<0.01** | -0.08 | 0.40 | **-0.23** | **0.01** |
| SRL | **-0.60** | **<0.001** | 0.10 | 0.28 | 0.01 | 0.87 |
| Fraction Root | **0.22** | **0.02** | **0.32** | **<0.001** | 0.08 | 0.37 |
| Myc. Responsiveness | 0.32 | 0.13 | -0.25 | 0.24 | 0.04 | 0.84 |
| Myc. Colonization | 0.09 | 0.68 | -0.20 | 0.34 | 0.22 | 0.31 |
| Water Use Efficiency | -0.05 | 0.63 | 0.09 | 0.35 | **0.23** | **0.01** |
| Date of First Bloom | -0.06 | 0.60 | -0.09 | 0.44 | 0.13 | 0.27 |

# CHAPTER 3 - Predicting Abundance across Multiple Scales Using Plant Functional Traits

## Introduction

Environmental stress is a key regulator of plant growth, as plants are impacted by a range of stresses during their lifetime. Often plants are well-adapted to a distinct set of stresses while being negatively impacted by others. Resource limitation is a prominent stress that plays a role in structuring plant communities and restraining fecundity. For example water, light, and nutrients are critical for plant growth and maintenance. Lacking one would result in plant death while low levels limit growth rates and other physiological processes. While all of these other biotic and abiotic factors such as disturbance, competition, pathogens, and herbivory also factor into plant community structure, the critical role of resource limitation is addressed as the primary control . Natural selection under many conditions has led to variation in traits that increase fitness in response to these stresses. Disparity in plant performance within a stressed environment is due primarily to differences in plant characteristics or traits.

Species fitness is influenced by adaptive traits in a given environment. All living plants must be suited to some degree to their local environment to initially germinate and become established. Further survival is contingent on the traits possessed by a plant for resource acquisition, competition, and defense. The most successful plants should be those that are well adapted to the stresses of a given environment, a result of beneficial traits. Traits have been used to understand community structure (Tilman and Elhaddi, 1992; Diaz et al., 1998) and ecosystem function (Craine et al., 2002; Craine and Lee, 2003) as well as possible changes imposed by biotic and abiotic factors (light environment (Reich et al., 2002), climate change (Diaz et al., 1998), invasive species (Craine and Lee, 2003), disturbance (Craine et al., 2001), and nutrient availability (Craine et al., 2001)). As plant traits are found to consistently correlate with a specific stress or environment, these predictive characteristics are called functional traits.

Plant functional traits are often correlated with each other leading to the formation of discrete groups that describe particular survival strategies (Grime, 1977; Chapin, 1980; Grime et al., 1997; Diaz et al, 1998; Craine et al, 2001; Tjoelker et al., 2005). These suites of traits are responsible for the performance of a plant in its environment. For example, species in low nutrient environments often have dense root and leaf tissues, high leaf longevity, high nitrogen use efficiency (NUE), and high root: shoot ratios; all traits that allow the preservation of nutrient-rich tissues (Chapin, 1980; Grime et al., 1997; Craine et al, 2001; Craine et al, 2002). Species successful in high nutrient environments have the reverse; high relative growth rates, low leaf and root tissue density, and low root: shoot ratios that allow rapid growth to take advantage of the available resources. In water-stressed environments there is less agreement about the traits that make up the survival strategy. Reich et al. (2003) suggests that plants should have high water use efficiency, thick leaves and cuticles, thick-walled cells, and low SLA while Tucker shows that a drought tolerance strategy in response to pulsed water availability contains thin, dense roots and leaves, high physiological drought tolerance, and high leaf angles (Chapter 2, this volume). These strategies should reflect traits that overcome the most prominent local environmental stress or resource limitation.

Further improving the utility of functional trait strategies would allow one to use simple measurements of a single or a few traits to establish the strategy being employed rather than performing a full profile or experimental assessment. In this way, plant functional traits or groups of traits should also be useful as predictors of relative abundance or growth at multiple scales, as the plants with the most beneficial attributes should be the most abundant. Ecological gradients are useful for comparing differences in limiting resources that should result in trait differences (Diaz et al., 1998; Craine et al., 2001; Craine and Lee, 2003) and variable abundance. Although plant survival occurs at the microhabitat scale, functional trait success should be evaluated at various scales. Plot-level or watershed-level assessments should average across all microhabitats or a representative sample within that physical space to yield the sum of all successful strategies within the space. Landscape scale assessments amplify this process. The traits that best predict abundance at this scale are those that overcome or are well-adapted for the most common or most limiting stressor across all microsites.

In the North American tallgrass prairie stresses may be natural or anthropogenic. As primary drivers of the tallgrass prairie climate, grazing, and fire influence plants directly as well as impacting soil characteristics (Hulbert, 1969), nutrient availability (Blair, 1997), and the entire biotic community. This ecosystem is characterized by extremes and unpredictability. Both rainfall and temperature are variable and drought and excess rainfall are both relatively common. Historically bison grazed throughout the Great Plains. Their grazing behaviors cause marked changes in the plant community (Towne et al., 2005) by increasing the abundance of forbs and reducing that of grasses (Hartnett et al., 1996; Collins et al., 1998; Towne et al., 2005). Nutrient availability is also impacted, as digested plant matter is re-deposited and feeds back into the nitrogen cycle, ultimately leading to greater nitrogen availability in grazed areas (Blair, 1997; Johnson and Matchett, 2001). Predicting the responses of plants to grazing conditions may lead one to look for plants that grow rapidly to take advantage of the nutrient availability and result in low tissue density and high specific leaf area (Grime et al., 1997; Wahl and Ryser, 2000; Craine and Lee, 2003). Fire affects  nutrient availability and plant communities as well, typically decreasing nutrient availability and increasing cover of grasses when burned annually. Testing a variety of scales should take all of these drivers into consideration.

My primary interest is finding traits that best predict relative abundance in tallgrass prairie. A study conducted on 76 species in Minnesota grasslands was able to explain up to 80% of the variation in relative abundance in fertilized plots using plant traits (Craine et al., 2001). Drought tolerance traits should be significant predictors of relative abundance across a landscape where drought is ubiquitous. The importance of these traits is hypothesized to vary across burned, unburned, grazed and ungrazed watersheds, as water stress is likely to vary among them (Seastedt et al., 1991; Blair, 1997; Johnson and Matchett, 2001). I hypothesized that drought tolerance traits should be the best predictors of drought tolerance in upland, ungrazed, and burned sites where water is frequently less available than in lowland, grazed, and unburned sites (Seastedt et al., 1991; Johnson and Matchett, 2001). Nutrients are also limiting in this ecosystem and are hypothesized to be less available in upland, ungrazed, and burned sites. Low nutrient traits will likely be prevalent in these sites. Finally, mycorrhizal root colonization and mycorrhizal responsiveness should be important in all treatments as many prairie grasses and forbs are obligate mycotrophs and the association often improves resource acquisition and competitive ability (Wilson and Hartnett, 1997). Determining which traits best correlate to abundance under specific conditions can give me insight into the survival strategies present in abundant species in prairie communities.

## Methods

### *Site Description*

Konza Prairie Biological Station (KPBS) is a 3487 ha native tallgrass prairie located in the Flint Hills of northeastern Kansas, USA (39 05'N, 96 35'W). The landscape is dominated by low rolling hills composed of alternating layers of shale and limestone. The flat tops of these hills often have thin rocky soil (Florence, cherty clay loam soils) that drains rapidly while the lowland soils (Tully, silty clay loam soils) have deep fertile soils with more available moisture (Nippert and Knapp, 2007). Considered a mesic prairie, Konza supports over 550 vascular plant species (Towne, 2002). The plant community is primarily herbaceous with dominant warm season grasses and a diverse suite of forbs. KPBS receives an average of 835 mm of precipitation annually, most of which (75%) falls during the growing season. The mean annual temperature for KPBS is 13° C. The average low for the year is -3 °C in January and the average high of 27 °C occurs in July.

KPBS has been studying the ecological effects of various land management practices for 27 years by assigning over 60 watersheds an experimental fire and grazing treatment. The site-level experimental design at KPBS was set up by Hulbert in 1983 (Hulbert and Wilson, 1983) and treatments in many of the plots have been continued to present day. Prescribed burns are assigned to each watershed at one, two, four, or twenty year intervals. Four watersheds are grazed by cattle while 10 more are grazed by the native ungulates *Bos bison* (bison). Controlled burns take place in the spring (mid March–late April).

### *Abundance Measurements*

As part of the long term research at KPBS, plant composition has been sampled twice annually (late May-June and mid-August - September) since 1983, to capture canopy cover and frequency values for both early- and late-season species. Twenty watersheds were chosen to represent the six land management treatments; grazed and ungrazed watersheds that are burned annually or infrequently (every 20 years) in the uplands or lowlands. In each watershed there are eight 50-meter permanent transects; half of which are located in shallow, rocky upland soil while the other half are located in deep, fertile lowland soil. Relative abundance was sampled in five permanently marked circular plots (10 $m^2$) that are evenly spaced along each transect. A modified Daubenmeier cover scale (Bailey and Poulton, 1968) was used to visually estimate species cover.

Average relative abundance in the watershed for each year was calculated by selecting the larger abundance for each species from the two sample periods and using the midpoint of the cover class to average across all upland or lowland plots in the watershed. I averaged across 17 years (1993-2009) to yield a single relative abundance value for each prairie species. Relative abundance for each watershed was combined across similar treatments to gain average values for each treatment combination as well as values of maximum contrast. For example, abundance was averaged across all grazed watersheds to gain a value of single relative abundance for the grazed treatment that could be compared to the ungrazed treatment. This was done for grazed, ungrazed, annual burns (burned), 20 year burns (unburned), upland, and lowland treatments. These categories will be referred to as contrasts. Finally, I averaged across all treatments to get a single abundance value for each species across all of Konza.

Throughout the remainder of the paper, watershed treatments will be named using a three character code. The first place designates grazed (G) or ungrazed (U). The second character describes the burn frequency, 1 for frequent and 20 for infrequent. The third character refers to the topographic position, upland Florence soils (f) or lowland Tully soils (t). For example the code U20f refers to the average value of all sample plots that were ungrazed, burned infrequently, and found in the uplands.

### *Plant Traits Measurements*

Of the 304 species recorded over the 17 years of abundance sampling, 84 of these were examined for drought tolerance traits by Tucker (Chapter 2, this volume). Tallgrass prairie species were grown from seed in a growth chamber for at least 8-12 weeks. Upon flowering or reaching a size sufficient for measurement, maximum physiological measurements were taken using a Li-6400 portable photosynthesis machine (LICOR Biosciences, Lincoln, NE). Plants were exposed to a drought period during which they were monitored for leaf stomatal conductance until the plant stopped conducting. At this point the critical water potential ($\Psi_{crit}$) was measured, an indicator of physiological tolerance to drought. Morphological leaf and root traits including leaf angle, leaf thickness, leaf tissue density, average root diameter, root tissue density, root mass, shoot mass, and fraction root were also measured. Average date of first bloom for many of the study species was obtained from KPBS and mycorrhizal responsiveness and mycorrhizal root colonization data was reported by Wilson and Hartnett (1998).

JMP (JMP 8.0.2, SAS Institute, Inc., Cary, NC) was used in all analyses. Missing traits data values were first filled using an average for the trait to eliminate instability in the models. All abundance values were log transformed prior to analysis. Stepwise multiple linear regressions were performed for each treatment and each contrast using AIC to determine best fit.

## Results

Critical water potential did not predict relative abundance on Konza. Its effectiveness was limited to upland and infrequent contrasts and three treatment combinations (Tables and Figures

Table 3.1). Two other drought tolerance traits, root tissue density and leaf angle were significant predictors of relative abundance across all of KPBS ($R^2 = 0.19$, Table 3.2). Root tissue density was also positively related to upland and lowland abundance, frequently burned plots, grazed and ungrazed plots as well as four out of the eight treatment combinations in the multivariate analysis. In pairwise comparisons to all contrasts and treatment combinations, root tissue density was significant in all but one comparison (Tables and Figures

Table 3.1). Surpassing the other traits in frequency and significance, root tissue density was the best single predictor of abundance I measured in this ecosystem.

Contrasting treatments allowed the assessment of individual management components such as presence and absence of grazing and frequency of burns (frequent or infrequent), as well as topographic position (upland or lowland). Root tissue density was the strongest single predictor in the burned, ungrazed, and lowland contrasts (Tables and Figures

Table 3.1). In the upland contrast, critical water potential was the best single predictor and it explained more variation than root tissue density and average root diameter in the model (partial $R^2 = 0.11, 0.07, 0.05$, Table 3.2). Lowland abundance was described by root tissue density alone, but only explained 11% of the variation. In the burned watersheds, root tissue density and leaf angle explain 20% of the total variation. The best model to describe unburned watersheds contained a single variable, leaf tissue density, which only explained 8% of the variation (Table 3.2). However, through linear regression, critical water potential was also shown to be a significant predictor in unburned watersheds ($P = 0.01$, Tables and Figures

Table 3.1). Models for grazed and ungrazed both explained 20% of the variation in abundance, but the component traits shared only one commonality, root tissue density (Table 3.2). Abundant plants in ungrazed watersheds had dense roots, thin leaves, a large allocation to roots and a small allocation to aboveground biomass. Grazed watersheds however, were best described by dense roots and a high leaf angle [very similar to overall abundance]. The best single predictor for each differed as well, in ungrazed watersheds it was root tissue density, while in grazed watersheds leaf angle was most successful (Tables and Figures

Table 3.1).

Both upland grazed treatment combinations had models composed of root and leaf traits. They were both predicted by high leaf angle and dense roots (G20f, $R^2 = 0.30$; G1f, $R^2 = 0.37$; Table 3.2). Both lowland grazed sites were best described by a model with a single parameter, G20t by low conductance rates ( $R^2 = 0.11$) and G1t by dense roots ( $R^2 = 0.11$). Root mass was one of the largest contributing factors in the ungrazed treatments. It was the only parameter describing abundance in U20f ($R^2 = 0.22$). It was a component in the models for U20t and U1t (partial $R^2 = 0.09, 0.06$). Only U1f lacks root mass as a trait, as it is described by root tissue density alone ($R^2 = 0.22$).

The following trends were present among treatment combinations and contrasts in the first multivariate analysis (Table 3.2). Four groups shared the paired traits root tissue density and leaf angle; overall abundance, frequently burned, grazed and G1f. These were all predicted to experience more water stress relative their opposites, but could be nutrient limited as well. Leaf angle, an indication of high light availability was seen in the grazed contrast and 3 out of 4 grazed treatments, overall abundance, the frequent contrast, and an ungrazed treatment (U20t). Root mass was consistent as it appeared in 3 out of 4 ungrazed treatments and the ungrazed contrast.

When mycorrhizal data was incorporated, sample size dropped dramatically ($n < 20$), but in many cases the explanatory power of the models improved (Table 3.3). For example, the model for overall abundance described 19 % of the variation in the first analysis, but with mycorrhizal data added the model changed to include leaf tissue density, low shoot mass, a high percent mycorrhizal root colonization, and explained 64% of the total variation. Again, the sample size dropped dramatically (n = 19). Leaf tissue density also became more significant as a component trait with mycorrhizal traits in many treatments including upland, ungrazed, G1f, G1t, and U1t. Mycorrhizal data was not a component in any of the four 20 year burn combinations, but it was important in all four annually burned combinations.

## Discussion

The plant traits I measured predict species relative abundance on Konza prairie. Several strategies are noted in the trait-abundance contrasts present among the various treatment combinations. I was able to describe up to 37% of the variability found in the G1f combination plots using root tissue density and angle (n = 53, Table 3.3) with the ten primary traits. When mycorrhizal data is incorporated, I can explain up to 70 % in U1f with mycorrhizal root colonization alone (Table 3.3).

Tallgrass prairie has a number of limiting resources that tend to fluctuate based on loss and gain of nutrients and change in physical environments under grazing, burning, or climatic factors. At times there may even be multiple limiting factors in a single location (Seastedt and Knapp, 1993; Blair, 1997). Many of the models identified in this study suggest that plants are adapted to water stress, nutrient stress, or both. For example, low critical water potentials indicate plants that can tolerate high levels of water stress before gas exchange stops (Tucker, Chapter 2, this volume), while high leaf tissue density is often associated with low nutrient environments (Wahl and Ryser, 2000; Craine, 2009). Some of these models contain multiple traits that point to multiple resource strategies or the traits themselves have been shown to be advantageous in response to different limiting resources. Determining the difference is problematic however, due to the limited understanding we currently have about drought tolerance as a resource strategy (Craine, 2009).

Root tissue density ($\rho_R$) appears to be among the most important traits in tallgrass prairie. Overall abundance on Konza and all of the contrasts except infrequent burning were predicted by root tissue density. High root tissue density has often been linked with low nutrient environments and tends to be correlated with high leaf tissue density (Wahl and Ryser, 2000). Dense roots have low turnover rates and are robust due to a high percentage of root stele (Wahl and Ryser, 2000). They also have a larger number of thin xylem elements with reinforced cell walls (Hacke et al., 2001) than less dense roots which could help prevent embolisms and subsequent cavitation as well as increase refill rates (Wahl and Ryser, 2000). The relationship between cavitation resistance and reduced water transport was discussed in the 2003 paper on plant functional trait tradeoffs (Reich et al., 2003). These vascular characteristics may be responsible for its performance as a drought tolerance trait in a recent study by Tucker (Chapter 2, this volume). It is not possible in this study to determine which is the more important function of this trait, but it likely functions to tolerate stress in multiple capacities.

These problematic overlaps in survival strategy leave many of the fire, grazing, and topographic treatments in the balance between water and nutrient limitation. Nearly every trait determined to be related to drought tolerance by Tucker (Chapter 2, this volume) for this species set also falls into the relatively well-defined category of low nutrient traits (Craine, 2009). Critical water potentials in the models help to pull out those areas where drought tolerance is sure to play a role; across upland sites, infrequent sites, and to a lesser degree in U20t. While this result confirms previous results that uplands are more water limited than lowlands (Briggs et al., 1995; Nippert and Knapp, 2007), this trait is unsuccessful in predicting average abundance on Konza and many of the contrasts. It is probable that while water limitation plays a role in structuring all communities on Konza, critical water potential may not the best trait to represent adaptation to low water availability. It may be more successful, however in tolerating discrete drought events in this ecosystem which are most prevalent or severe in areas where water is commonly limiting.

Light limitation is another stress that occurs in some locations on Konza Prairie. While it does occur, light is less likely to be limiting than water or nutrients. Areas that experience high levels of light should exhibit an increase in allocation to belowground parts, as energy will be shifted to increase acquisition of limiting water or mineral resources (Craine, 2009). Maintaining a balance of these limiting factors allows the plant to maximize photosynthetic rates. This could be responsible for the positive correlation between areas of lower plant canopy such as annually burned treatments and root mass or root tissue density. Although grazing should lead to increased available light, Johnson and Matchett (2001) have shown that root mass is still much lower in annually burned grazed areas than ungrazed areas. I report high root mass in three out of four ungrazed treatment combinations except U1f where I see high root tissue density. I would expect to see the opposite resource allocation, allocation to shoots, in light-limited environments such as unburned prairies with thick plant canopies and dense surface litter. As limiting factors are known to shift on Konza, light limitation would be more easily detected by evaluating temporal rather than spatial gradients. While high shoot mass was not included in any of the models, light limitation may be better detected by sampling late in the growing season rather than using the methods employed here.

There are some treatments on Konza Prairie where my traits do not work very well. For example, the lowland and infrequent contrasts have very low $R^2$ values contributed by single traits ($\rho_R$, $R^2 = 0.11$; $\rho_L$ $R^2 = 0.08$,). G1t and G20 t each have models that explain only 11 % of the total variation (with traits root tissue density and conductance respectively), echoing the low descriptive power seen in the lowland contrast. Furthermore, lowland, infrequent, and G20t do not improve with the introduction of mycorrhizal data as many other treatments did. While these traits are likely to be one part of the story, it is clear that the traits driving fitness under these conditions are not present in my traits set. While morphological traits may be important here, only further work can determine the nature of the missing traits. Although the explanatory power of the ten primary traits or trait sets used in the first analysis was often near 20%, the addition of more traits will likely increase the variation described by plant functional traits. For example, if critical water potential was important in a model, another trait that improves drought tolerance such as rooting depth may further improve the model.

The incorporation of mycorrhizal data added tremendous explanatory power to many of the treatments in the second multiple regression analysis; however, this was at the expense of sample size. This suggests two distinct possibilities. First, percent mycorrhizal colonization and percent mycorrhizal responsiveness as plant traits are likely very important in this ecosystem where many species are known to be obligate or facultative mycotrophs (Wilson and Hartnett, 2008). Naturally, in a system where mycorrhizal symbiosis confers a competitive advantage, traits involving this relationship should strongly influence relative abundance. Therefore, collecting data for mycorrhizal root colonization and mycorrhizal responsiveness on a broader species set should add descriptive power to whole communities of prairie plants.

Alternatively, the increased $R^2$'s may be due to the fact that the species with mycorrhizal data were primarily common species and lacked the rare and subdominant component included in the remainder of the plant trait measurements. Furthermore, reducing the sample size is likely to reduce sampling of functional groups or guilds that may also respond differentially to mycorrhizae. Therefore, mycorrhizal colonization may be a good descriptor of these common species, but I am unable to compare the effect on non-dominant species. It is possible that mycorrhizae are responsible for maintaining high abundance in common species but are not responsible for the success of rare species. Either way, these mycorrhizal trait relationships in tallgrass prairie ecosystems are important because ecosystem function is likely much more dependent on the success and dynamics of these common species than the less common ones.

A trend in this data is the repeated pairing of mycorrhizal root colonization to leaf tissue density. There is also a single relationship with mycorrhizal responsiveness. Although this relationship is unlikely to be causal, the traits may be indirectly related. Leaf tissue density is commonly measured in the functional trait literature and is associated with low relative growth rates, long leaf life span, and low rates of nutrient turnover (Ryser, 1996; Craine and Lee, 2003); all of which are beneficial in low productivity environments. Additionally, dense leaves have high tensile strength and are thought to be more resistant to damage and herbivory, making this adaptation potentially beneficial in grazed areas. Mycorrhizae are also commonly adapted to low-nutrient plants, but more work will have to be done to determine the source of this link between functional traits.

Although the thirteen traits I chose as predictors of relative abundance did not explain all of the variation in the data set, there was a relatively high degree of descriptive power especially when the range of species and other possible sources of variation are taken into consideration.

This work confirms that adaptive plant traits are employed in areas where water and nutrients are the limiting factors. These two survival strategies share several traits including root tissue density, leaf tissue density, and leaf thickness. Understanding the nuances of the two strategies will require a more elegant experiment to parse the relative contribution to each, but a few clues can be found in this experiment. For example, I saw that morphological traits were seen in nearly every treatment instead of the physiological responses predicted by the low nutrient plant strategy. This fits closely with the drought tolerance strategy assembled by Tucker (Chapter 2, this volume), where drought tolerance was composed of critical water potential and leaf and root morphological traits. Critical water potential did not strongly predict abundance across all of Konza as expected, suggesting that it may not be the best trait to represent drought tolerance or that nutrient stress may be more important in some areas. Despite my uncertainty about Konza’s primary stressors, I know that the most prominent traits to use to predict success on Konza include root tissue density, mycorrhizal colonization and leaf tissue density. Furthermore, these traits can be used as tools to predict species success, invasibility, or likelihood of establishment in prairie restoration situations. The next step is to fill in the gaps in my models both by improving mycorrhizal data and incorporating additional hydraulic traits. The development of a strong drought tolerance strategy will require more experimentation and testing in other ecosystems, but will fill a critical niche in scientific understanding of plant functional traits.

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# Tables and Figures

**Table 3.1 Pairwise regressions for all traits and all treatments. Bold values indicate statistical significance. Estimate abbreviated “Est”. ( $\alpha = 0.05$)**

| | $A_{max}$ | | Cond. | | $\Psi_{crit}$ | | Leaf Angle | | Leaf Thickness | | $\rho_L$ | | $\rho_R$ | | Avg Root Diameter | | Root Mass | | Shoot Mass | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Est | *P* | Est | *P* | Est | *P* | Est | *P* | Est | *P* | Est | *P* | Est | *P* | Est | *P* | Est | *P* | Est | *P* |
| Abundance | -0.01 | 0.78 | -2.3 | 0.43 | -0.01 | 0.12 | 0.02 | **0.01** | -3.4 | 0.06 | 2.0 | 0.09 | 5.4 | **0.003** | -0.6 | 0.78 | 0.001 | **0.03** | -0.0002 | 0.57 |
| Upland | -0.04 | 0.34 | -0.8 | 0.78 | -0.02 | **0.01** | 0.01 | **0.04** | -3.0 | 0.11 | 1.5 | 0.26 | 4.9 | **0.01** | -0.9 | 0.66 | 0.001 | 0.20 | -0.0003 | 0.43 |
| Lowland | -0.03 | 0.46 | -4.6 | 0.12 | -0.003 | 0.76 | 0.01 | 0.10 | -3.0 | 0.10 | 1.4 | 0.24 | 5.3 | **0.004** | -0.3 | 0.88 | 0.001 | **0.03** | -0.0001 | 0.85 |
| Grazed | -0.02 | 0.53 | -2.2 | 0.42 | -0.01 | 0.06 | 0.02 | **0.001** | -3.2 | **0.05** | 2.2 | **0.04** | 4.4 | **0.01** | -1.6 | 0.39 | 0.001 | 0.05 | 0.0000 | 0.95 |
| Ungrazed | -0.03 | 0.47 | -4.8 | 0.13 | -0.01 | 0.43 | -0.001 | 0.92 | -4.4 | **0.04** | 1.5 | 0.32 | 6.1 | **0.004** | -0.4 | 0.87 | 0.001 | 0.18 | -0.0002 | 0.55 |
| Frequent | 0.01 | 0.87 | -2.4 | 0.39 | -0.01 | 0.22 | 0.01 | 0.06 | -3.6 | 0.06 | 1.3 | 0.29 | 6.3 | **0.001** | -0.5 | 0.80 | 0.001 | **0.05** | -0.0003 | 0.44 |
| Infrequent | -0.03 | 0.48 | -1.4 | 0.61 | -0.02 | **0.01** | 0.01 | 0.06 | -3.0 | 0.08 | 2.7 | **0.02** | 3.5 | **0.04** | -1.3 | 0.48 | 0.001 | 0.06 | -0.0001 | 0.82 |
| G1f | -0.03 | 0.44 | -3.0 | 0.31 | -0.02 | **0.02** | 0.02 | **0.004** | -3.9 | 0.08 | 1.6 | 0.21 | 7.1 | **.0002** | -2.7 | 0.21 | 0.001 | 0.12 | -0.0002 | 0.54 |
| G1t | 0.004 | 0.92 | -3.6 | 0.18 | -0.002 | 0.80 | 0.01 | 0.31 | -2.5 | 0.16 | 1.1 | 0.33 | 4.4 | **0.01** | -0.8 | 0.67 | 0.001 | 0.09 | 0.0003 | 0.40 |
| G20f | 0.001 | 0.99 | 1.4 | 0.65 | -0.02 | **0.01** | 0.02 | **0.002** | -0.9 | 0.71 | 1.8 | 0.17 | 4.3 | **0.02** | -0.5 | 0.81 | 0.001 | **0.02** | 0.0001 | 0.79 |
| G20t | -0.06 | 0.10 | -6.7 | **0.01** | -0.01 | 0.16 | 0.01 | 0.14 | -2.1 | 0.21 | 2.4 | **0.03** | 3.4 | **0.04** | -1.6 | 0.41 | 0.001 | **0.04** | 0.0004 | 0.19 |
| U1f | 0.01 | 0.90 | -3.0 | 0.34 | -0.01 | 0.32 | 0.01 | 0.51 | -3.2 | 0.11 | 0.9 | 0.54 | 7.3 | **.0003** | -0.2 | 0.93 | 0.001 | 0.27 | -0.0003 | 0.37 |
| U1t | -0.07 | 0.17 | -8.7 | **0.01** | 0.003 | 0.77 | -0.01 | 0.46 | -3.6 | 0.26 | 2.1 | 0.20 | 6.0 | **0.01** | 0.7 | 0.78 | 0.001 | 0.11 | 0.00004 | 0.92 |
| U20f | 0.03 | 0.57 | -0.2 | 0.94 | -0.02 | 0.06 | 0.01 | 0.13 | 0.5 | 0.85 | -0.1 | 0.93 | 3.3 | 0.12 | -1.2 | 0.59 | 0.002 | 0.001 | 0.001 | 0.18 |
| U20t | 0.01 | 0.87 | -3.6 | 0.33 | -0.02 | **0.05** | -0.005 | 0.58 | -3.9 | 0.22 | 2.6 | 0.07 | 4.4 | **0.04** | -0.8 | 0.75 | 0.001 | **0.03** | 0.0004 | 0.42 |

**Table 3.2 Stepwise multiple linear regression, containing 10 primary traits. Partial $R^2$ is the proportion of model $R^2$ contributed by each trait. Sum of Squares represented by SS. ($\alpha = 0.05$)**

| Treatment | $R^2$ | n | Trait | Partial $R^2$ | P value | Estimate | SS |
|---|---|---|---|---|---|---|---|
| **Abundance** | 0.19 | 78 | $\rho_R$ | 0.10 | 0.004 | 5.1 | 17.4 |
| | | | Leaf Angle | 0.09 | 0.01 | 0.02 | 15.2 |
| **Upland (f)** | 0.23 | 65 | $\Psi_{crit}$ | 0.11 | 0.003 | -0.03 | 15.3 |
| | | | $\rho_R$ | 0.07 | 0.01 | 4.7 | 10.3 |
| | | | Avg Root Diameter | 0.05 | 0.04 | 5.1 | 6.9 |
| **Lowland (t)** | 0.11 | 73 | $\rho_R$ | - | 0.004 | 5.3 | 17.7 |
| **Frequent (1)** | 0.20 | 72 | $\rho_R$ | 0.15 | 0.00 | 6.251 | 22.1 |
| | | | Leaf Angle | 0.05 | 0.047 | 0.013 | 6.9 |
| **Infrequent (20)** | 0.08 | 72 | $\rho_L$ | - | 0.02 | 2.7 | 10.4 |
| **Grazed (G)** | 0.20 | 75 | Leaf Angle | 0.12 | 0.002 | 0.02 | 15.4 |
| | | | $\rho_R$ | 0.08 | 0.01 | 4.0 | 10.0 |
| **Ungrazed (U)** | 0.23 | 66 | Root Mass | 0.06 | 0.03 | 0.001 | 10.7 |
| | | | Leaf Thickness | 0.06 | 0.03 | -5.0 | 10.5 |
| | | | Shoot Mass | 0.06 | 0.03 | -0.001 | 10.3 |
| | | | $\rho_R$ | 0.05 | 0.05 | 4.2 | 8.2 |
| **G 1 f** | 0.37 | 53 | $\rho_R$ | 0.23 | <0.0001 | 6.9 | 19.2 |
| | | | Leaf Angle | 0.14 | 0.002 | 0.02 | 11.7 |
| **G 1 t** | 0.11 | 62 | $\rho_R$ | - | 0.01 | 4.4 | 9.9 |
| **G 20 f** | 0.30 | 52 | Leaf Angle | 0.19 | 0.000 | 0.02 | 16.7 |
| | | | $\rho_R$ | 0.11 | 0.005 | 5.0 | 10.3 |
| **G 20 t** | 0.11 | 58 | Conductance | | 0.01 | -6.7 | 9.5 |
| **U 1 f** | 0.22 | 56 | $\rho_R$ | - | 0.0003 | 7.3 | 23.8 |
| **U 1 t** | 0.22 | 49 | Conductance | 0.10 | 0.01 | -9.6 | 14.2 |
| | | | Root Mass | 0.06 | 0.04 | 0.001 | 8.2 |
| | | | Shoot Mass | 0.06 | 0.05 | -0.001 | 7.8 |
| **U 20 f** | 0.22 | 45 | Root Mass | - | 0.001 | 0.002 | 14.9 |
| **U 20 t** | 0.23 | 47 | Root Mass | 0.09 | 0.02 | 0.002 | 9.5 |
| | | | Leaf Angle | 0.07 | 0.03 | -0.02 | 7.5 |
| | | | $\Psi_{crit}$ | 0.06 | 0.04 | -0.02 | 6.5 |

**Table 3.3 Stepwise multiple linear regression containing Mycorrhizal data. Partial $R^2$ is the proportion of the model $R^2$ contributed by each trait. Sum of Squares represented by SS. ($\alpha = 0.05$)**

| Treatment | $R^2$ | n | Trait | Partial $R^2$ | P value | Estimate | SS |
|---|---|---|---|---|---|---|---|
| **Abundance** | 0.64 | 19 | $\rho_L$ | 0.36 | 0.001 | 5.7 | 10.5 |
| | | | Shoot Mass | 0.18 | 0.01 | -0.002 | 5.1 |
| | | | Myc Root Colonization | 0.11 | 0.04 | 0.03 | 3.1 |
| **Upland (f)** | 0.61 | 18 | $\rho_L$ | 0.37 | 0.004 | 3.7 | 4.4 |
| | | | Myc Root Colonization | 0.24 | 0.014 | 0.0 | 2.9 |
| **Lowland (t)** | 0.11 | 73 | $\rho_R$ | - | 0.004 | 5.3 | 17.7 |
| **Frequent (1)** | 0.40 | 62 | $\rho_R$ | 0.20 | <.0001 | 7.7 | 29.0 |
| | | | Date first Bloom | 0.11 | 0.001 | 0.01 | 16.6 |
| | | | Leaf Angle | 0.05 | 0.02 | 0.01 | 7.4 |
| | | | Shoot Mass | 0.04 | 0.04 | -0.001 | 5.8 |
| **Infrequent (20)** | 0.09 | 72 | $\Psi$crit | - | 0.01 | -0.02 | 11.4 |
| **Grazed (G)** | 0.06 | 75 | $\rho_L$ | - | 0.04 | 2.2 | 7.7 |
| **Ungrazed (U)** | 0.67 | 19 | Myc Root Colonization | 0.28 | 0.002 | 0.1 | 11.5 |
| | | | $\rho_L$ | 0.21 | 0.01 | 5.2 | 8.8 |
| | | | Shoot Mass | 0.19 | 0.01 | -0.002 | 7.8 |
| **G 1 f** | 0.63 | 18 | $\rho_L$ | 0.43 | 0.002 | 3.63 | 4.3 |
| | | | Myc Root Colonization | 0.20 | 0.020 | 0.0 | 2.0 |
| **G 1 t** | 0.63 | 19 | $\rho_L$ | 0.33 | 0.002 | 4.4 | 6.7 |
| | | | Myc Responsiveness | 0.31 | 0.003 | 0.01 | 6.3 |
| **G 20 f** | 0.18 | 52 | Leaf Angle | - | 0.002 | 0.0 | 14.4 |
| **G 20 t** | 0.11 | 58 | Conductance | - | 0.01 | -6.7 | 9.5 |
| **U 1 f** | 0.70 | 17 | Myc Root Colonization | - | <.0001 | 0.069 | 19.9 |
| **U 1 t** | 0.68 | 16 | Myc Root Colonization | 0.26 | 0.02 | 0.05 | 6.2 |
| | | | $\rho_L$ | 0.25 | 0.02 | 5.7 | 6.0 |
| | | | $\Psi_{crit}$ | 0.18 | 0.04 | 0.03 | 4.3 |
| **U 20 f** | 0.22 | 45 | Root Mass | - | 0.001 | 0.002 | 14.9 |
| **U 20 t** | 0.27 | 41 | Date first Bloom | - | 0.001 | 0.02 | 21.4 |

# CHAPTER 4 - CONCLUSIONS

## The Utility of Plant Functional Traits in Tallgrass Prairie

The utility of plant functional traits is found in their predictive capacity. To understand why a plant lives where it does, we must understand the adaptations that permit local survival. Plants are equipped with traits that allow continued existence in a particular environment (Diaz et al., 1998; Reich et al., 2003). Plants experience a number of stresses including heat, chilling, freezing, water limitation, anoxia, pathogens, excessive irradiation, light limitation, nutrient limitation, salt stress, competition, and herbivory. Without the option to leave, plants must tolerate the stresses in order to survive and reproduce. In the tallgrass prairie, water stress is ubiquitous. Natural climatic stochasticity leads to the possibility of drought throughout the growing season and as mentioned in Chapter 2, can impose a range of severities. As a result, prairie plants must harbor adaptations to survive periodic drought.

Although some short-term physiological responses to drought are understood, the mechanisms of drought tolerance are still largely unknown. Plant functional traits related to drought tolerance have not been given as much attention as those related to other environmental stresses, especially nutrient limitation. While the strategies employed by plants to overcome high and low light conditions, high and low nutrients conditions, and disturbances are easily outlined, drought tolerance is much more of a mystery (Craine, 2009). Work in this area has been undertaken much more fervently by agricultural scientists and geneticists. However, we still have a difficult time describing what enables a plant to tolerate drought events. In order to close the gap between nutrients and water, I used a familiar experimental protocol to address the question of drought tolerance in the tallgrass prairie (Grime et al., 1997; Craine et al., 2001).

Using 121 replicated species native to Konza Prairie, a temperate mesic grassland in northeastern Kansas, I addressed the following hypotheses. 1) Tallgrass prairie species will exhibit a broad range of abilities to tolerate drought due to intrinsic diversity in the plant community. 2) Plant functional traits are related to drought tolerance and can be used to predict drought tolerance in prairie species. 3) Plants will exhibit tradeoffs between stress tolerance and physiological activity including photosynthetic rate as more energy will need to be devoted to tolerance than carbon assimilation.

Using plants drawn from 22 families, I was able to investigate not only the most common Konza species, but the subdominant community members as well. In some cases I gathered unique data on previously unmeasured species. Plants exhibited great diversity in total size, biomass allocation, photosynthetic rate, physiological drought tolerance (Ψcrit), root characteristics, and leaf characteristics.  This diversity illustrates the importance of expanding studies to include more representative samples of the communities being described. The range is best illustrated in Table A.11.

These traits were integrated using principal component analysis to understand which traits were related to drought tolerance. Physiological drought tolerance ($\Psi_{crit}$) was the central index used to quantify each species' ability to tolerate drought conditions. Using both physiological and morphological plant characteristics I was able to assemble a suite of traits that was closely correlated to $\Psi_{crit}$ and that described the natural contrasts found in the data. Traits were well segregated into three axes that described drought tolerance, photosynthetic rate, and plant size. The drought tolerance axis explained 28 % of the total variation and contained six plant traits. Plants with the tolerance strategy should have a low $\Psi_{crit}$, low average root diameter, thick leaves, high leaf tissue density, high root tissue density, and high leaf angle. Interestingly, this profile mirrors many of the most common plants present in the ecosystem: grasses. Furthermore, the strategy seems to be more reliant on a consistent physical structure rather than physiological characteristics, suggesting that some plants, especially grasses are built to be drought tolerant.

My study supports physiological drought tolerance ($\Psi_{crit}$) as a reasonable metric of a plant's ability to tolerate water limitation and continue to photosynthesize. Plants with a high $\Psi_{crit}$ [close to zero] have low tolerance and stop conducting soon after stress occurs. *Asclepias incarnata* and *Tradescantia ohiensis* are good examples of species that can tolerate very little water stress. Plants with a very low $\Psi_{crit}$ [$^{-}5$-$^{-}9$ MPa] are able to continue gas exchange for a longer period of time even as water becomes more limiting. The most tolerant species measured in my study was *Bouteloua curtipendula* which was able to maintain conductance down to critical water potentials of -8.9 MPa.

The physiological traits fell out on Axis 2. Still describing a significant portion of the variation ( 17 %, n = 121, Table 2.5), this axis is orthogonal to the drought tolerance axis, making the two independent of each other. Reduced physiological rates including photosynthesis, respiration, and relative growth rates are an integral part of the accepted stress tolerance strategy (Grime, 1977; Chapin, 1980; Craine, 2009). Removing them from my drought tolerance strategy suggests that surviving drought stress has more to do with morphology than physiological adaptations.

The work presented here provides clues to the traits that are responsible for plant survival in the drought-prone tallgrass prairie ecosystem. In order to predict drought tolerance in a species that has not been previously measured or tested, one or more of the traits in the tolerance strategy can be used as a screening tool. Pairwise correlations of these traits suggest that average root diameter would be the best predictor, followed by leaf angle (Table 2.4). However, many species from this ecosystem may prove not to possess traits that promote drought tolerance. The tallgrass prairie also supports many species that are categorized as drought intolerant. Relying on a number of adaptations that allow them to escape or avoid drought, these species will complete their life cycles when water is less limiting. The key to diversity in tallgrass prairie is an assemblage of species that effectively exploits the available resources and harbors other adaptations that allow survival despite the somewhat unpredictable climate.

Once I had a better understanding of the traits leading to drought tolerance across a broad set of prairie species, I used the same plant traits measured in Chapter 2 to test against long term relative abundance from Konza Prairie. I first wanted to see if plant traits could predict relative abundance across a landscape. I hypothesized that traits would 1) predict relative abundance across all of Konza as well as 2) differentiate between treatments and 3) topographic positions.

I used the long term data collected across a matrix of fire and grazing treatments. Seventeen years of data were averaged to yield a single relative abundance value for each plant species found in each land management treatment. I generated statistical models using the plant traits to describe each individual treatment and their combinations. These predictions were successful in the majority of treatments with only 10 % of the models describing less than 10 % of the total variation. For Konza average relative abundance, the best predictors were root tissue density and leaf angle ($R^2 = 0.19$). Root tissue density was important in 10 out of 15 models generated from the primary 10 traits. Among the treatments that were not well-described by the models [$R^2 \leq 0.11$ in both analyses] were infrequently burned, lowlands, and G20t (Table 3.2, Table 3.3).

When I assess similarities and difference in strategy among the fire and grazing treatments, there are complications. First, many of the treatments have traits in common, and few split easily into discrete groups. For example, root tissue density is shared by all but one of the contrasts (Infrequent). Root mass is easier to explain as it appears in 3 out of 4 ungrazed treatments and the ungrazed contrast. While I showed that root tissue density, leaf tissue density, leaf angle, leaf thickness, and average root diameter were all related to drought tolerance, I also know that they are all associated with the low nutrient strategy. This fact makes it impossible to differentiate between drought tolerance and low nutrient tolerance strategies in these treatments.

Incorporating mycorrhizal data from Wilson and Hartnett (1998) and phenology improved the fit of 9 models, suggesting a large contribution to abundance by mycorrhizal root colonization. However, this data was only available for 19 species, dropping the total number of species tested in the second analysis. Furthermore, many of the species included in the mycorrhizal data are dominant or common species, thereby eliminating many of the rare species included in the first analysis. While the inclusion of the mycorrhizal data illustrated the link between relative abundance and mycorrhizal symbiosis, it merely confirms previous research illustrating that many dominant species are obligate mycotrophs (Wilson and Hartnett, 1998). Collecting mycorrhizal data for more of these species would be a good way to test the validity of my results and could confirm a broader importance for mycorrhizal colonization as a functional trait.

Presenting a complete set of drought tolerance traits to the plant functional trait community will likely spur a number of experiments to either rebut or confirm my results. Regardless of the outcomes, renewed interest in pursuing these questions using plant functional traits is critical to the field. How can we hope to understand plant community composition or dynamics by leaning on our knowledge of nutrients, light, and disturbance alone? The utility of plant characteristics as functional traits is in the development of rules and the ability to understand a plant's role in its environment and predict its response (Diaz et al., 1998; Craine, 2009). While extensive work has been done on plant functional traits over the years, much more consensus has been garnered around traits relating to nutrient availability than water availability. Many of the traits measured in this study are the same ones used and often cited as adaptations to high or low nutrient environments. While the function of traits such as leaf and root tissue density or average root diameter may serve to either conserve or utilize available resources, the physical shape of the plant impacts the movement of water and may in fact serve to promote or slow water, improve surface area for absorption or influence water relations in another way. As guidance in this area is limited, further work on the flow of water through these structures will likely be the most instructive study moving toward a mechanistic understanding of drought tolerance.

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# Appendix A - Additional Traits Data

**Table A.1 Plant species taxonomy. KUT code is a species-specific unique identifier for Konza Prairie. Life history abbreviations; A = annual, B = biennial, P = perennial. Type refers to photosynthetic type. Biochemical subtype only applies to $C_4$ species.**

| KUT Code | Genus | Species | Family | Growth Form | Life History | Type | Biochemical Subtype (C4) |
|---|---|---|---|---|---|---|---|
| **106** | Achillea | millefolium | Asteraceae | Forb | P | C3 | |
| **112** | Ageratina | altissima | Asteraceae | Forb | P | C3 | |
| **121** | Amaranthus | blitoides | Amaranthaceae | Forb | A | C4 | NAD-ME |
| **123** | Amaranthus | retroflexus | Amaranthaceae | Forb | A | C4 | NAD-ME |
| **126** | ambrosia | psilostachya | Asteraceae | Forb | P | C3 | |
| **129** | Amorpha | canescens | Fabaceae | Forb | P | C3 | |
| **133** | Andropogon | gerardii | Poaceae | Grass | P | C4 | NADP-ME |
| **137** | Antennaria | neglecta | Asteraceae | Forb | P | C3 | |
| **138** | Apocynum | cannabinum | Apocynaceae | Forb | P | C3 | |
| **145** | Aristida | oligantha | Poaceae | Grass | A | C4 | NADP-ME |
| **146** | Aristida | purpurea | Poaceae | Grass | P | C4 | NADP-ME |
| **148** | Artemisia | ludoviciana | Asteraceae | Forb | P | C3 | |
| **150** | Asclepias | speciosa | Asclepiadaceae | Forb | P | C3 | |
| **152** | Asclepias | sullivantii | Asclepiadaceae | Forb | P | C3 | |
| **155** | Asclepias | verticillata | Asclepiadaceae | Forb | P | C3 | |
| **157** | Asclepias | viridis | Asclepiadaceae | Forb | P | C3 | |
| **160** | Astragalus | canadensis | Fabaceae | Forb | P | C3 | |
| **166** | Baptisia | australis | Fabaceae | Forb | P | C3 | |
| **179** | Bouteloua | curtipendula | Poaceae | Grass | P | C4 | NAD-ME or PCK |
| **181** | Bouteloua | gracilis | Poaceae | Grass | P | C4 | NAD-ME or PCK |
| **185** | Bromus | inermis | Poaceae | Grass | P | C3 | |
| **202** | Carex | annectens | Cyperaceae | Grass | P | C3 | |
| **227** | Chamaecrista | fasciculata | Fabaceae | Forb | A | C3 | |
| **231** | Chamaesyce | nutans | Euphorbiaceae | Forb | A | C4 | NADP-ME |
| **240** | Chloris | verticillata | Poaceae | Grass | P | C4 | PCK |
| **243** | Cirsium | altissimum | Asteraceae | Forb | B | C3 | |
| **260** | Cucurbita | foetidissima | Cucurbitaceae | Forb | P | C3 | |
| **285** | Desmanthus | illinoensis | Fabaceae | Forb | P | C3 | |
| **288** | Desmodium | illinoense | Fabaceae | Forb | P | C3 | |
| **294** | Dichanthelium | acuminatum | Poaceae | Grass | P | C3 | |
| **304** | Echinacea | angustifolia | Asteraceae | Forb | P | C3 | |
| **305** | Echinacea | pallida | Asteraceae | Forb | P | C3 | |

## Table A.1 continued (2 of 4)

| KUT Code | Genus | Species | Family | Growth Form | Life History | Type | Biochemical Subtype (C4) |
|---|---|---|---|---|---|---|---|
| **307** | Echinodorus | berteroi | Alismataceae | Forb | P | C3 | |
| **313** | Eleusine | indica | Poaceae | Grass | A | C4 | NAD-ME |
| **315** | Elymus | canadensis | Poaceae | Grass | P | C3 | |
| **316** | Elymus | villosus | Poaceae | Grass | P | C3 | |
| **317** | Elymus | virginicus | Poaceae | Grass | P | C3 | |
| **323** | Eragrostis | pectinacea | Poaceae | Grass | A | C4 | NAD-ME |
| **326** | Erigeron | annuus | Asteraceae | Forb | A | C3 | |
| **334** | Eupatorium | altissimum | Asteraceae | Forb | P | C3 | |
| **335** | Euphorbia | corollata | Euphorbiaceae | Forb | P | C3 | |
| **338** | Euphorbia | dentata | Euphorbiaceae | Forb | A | C3 | |
| **340** | Euphorbia | marginata | Euphorbiaceae | Forb | A | C3 | |
| **344** | Festuca | subverticillata | Poaceae | Grass | P | C3 | |
| **365** | Helianthus | annuus | Asteraceae | Forb | A | C3 | |
| **369** | Helianthus | petiolaris | Asteraceae | Forb | A | C3 | |
| **370** | Helianthus | tuberosus | Asteraceae | Forb | P | C3 | |
| **371** | Heliopsis | helianthoides | Asteraceae | Forb | P | C3 | |
| **373** | Hesperostipa | spartea | Poaceae | Grass | P | C3 | |
| **379** | Hordeum | jubatum | Poaceae | Grass | P | C3 | |
| **380** | Hordeum | pusillum | Poaceae | Grass | A | C3 | |
| **396** | Koeleria | macrantha | Poaceae | Grass | P | C3 | |
| **399** | Lactuca | canadensis | Asteraceae | Forb | B | C3 | |
| **400** | Lactuca | ludoviciana | Asteraceae | Forb | B | C3 | |
| **408** | Lepidium | densiflorum | Brassicaceae | Forb | A | C3 | |
| **410** | Lepidium | virginicum | Brassicaceae | Forb | A | C3 | |
| **413** | Lespedeza | capitata | Fabaceae | Forb | P | C3 | |
| **416** | Lespedeza | violacea | Fabaceae | Forb | P | C3 | |
| **419** | Liatris | aspera | Asteraceae | Forb | P | C3 | |
| **420** | Liatris | mucronata | Asteraceae | Forb | P | C3 | |
| **421** | Liatris | punctata | Asteraceae | Forb | P | C3 | |
| **447** | Mirabilis | linearis | Nyctaginaceae | Forb | P | C3 | |
| **450** | Monarda | fistulosa | Lamiaceae | Forb | P | C3 | |
| **466** | Oenothera | biennis | Onagraceae | Forb | B | C3 | |
| **468** | Oenothera | macrocarpa | Onagraceae | Forb | P | C3 | |
| **481** | Packera | plattensis | Asteraceae | Forb | B | C3 | |
| **482** | Panicum | capillare | Poaceae | Grass | A | C4 | |
| **485** | Panicum | virgatum | Poaceae | Grass | P | C4 | |
| **488** | Pascopyrum | smithii | Poaceae | Grass | P | C3 | |

**Table A.1 continued (3 of 4)**

| KUT Code | Genus | Species | Family | Growth Form | Life History | Type | Biochemical Subtype (C4) |
|---|---|---|---|---|---|---|---|
| **494** | Penstemon | cobaea | Scrophulariaceae | Forb | P | C3 | |
| **495** | Penstemon | grandiflorus | Scrophulariaceae | Forb | P | C3 | |
| **496** | Penstemon | tubiflorus | Scrophulariaceae | Forb | P | C3 | |
| **504** | Physalis | pubescens | Solanaceae | Forb | A | C3 | |
| **513** | Plantago | rugelii | Plantaginaceae | Forb | P | C3 | |
| **516** | Poa | arida | Poaceae | Grass | P | C3 | |
| **519** | Poa | pratensis | Poaceae | Grass | P | C3 | |
| **534** | Polygonum | virginianum | Polygonaceae | Forb | P | C3 | |
| **542** | Prunella | vulgaris | Lamiaceae | Forb | P | C3 | |
| **547** | Psoralidium | tenuiflorum | Fabaceae | Forb | P | C3 | |
| **553** | Ratibida | pinnata | Asteraceae | Forb | P | C3 | |
| **565** | Rudbeckia | hirta | Asteraceae | Forb | A | C3 | |
| **566** | Ruellia | humilis | Acanthaceae | Forb | P | C3 | |
| **575** | Salvia | azurea | Lamiaceae | Forb | P | C3 | |
| **576** | Salvia | reflexa | Lamiaceae | Forb | A | C3 | |
| **592** | Setaria | pumila | Poaceae | Grass | A | C4 | NADP-ME |
| **598** | Silphium | integrifolium | Asteraceae | Forb | P | C3 | |
| **599** | Silphium | laciniatum | Asteraceae | Forb | P | C3 | |
| **603** | Solanum | carolinense | Solanaceae | Forb | P | C3 | |
| **605** | Solanum | rostratum | Solanaceae | Forb | A | C3 | |
| **606** | Solidago | canadensis | Asteraceae | Forb | P | C3 | |
| **608** | Solidago | missouriensis | Asteraceae | Forb | P | C3 | |
| **609** | Solidago | mollis | Asteraceae | Forb | P | C3 | |
| **610** | Solidago | petiolaris | Asteraceae | Forb | P | C3 | |
| **613** | Sorghastrum | nutans | Poaceae | Grass | P | C4 | NADP-ME |
| **622** | Sporobolus | heterolepis | Poaceae | Grass | P | C4 | NAD-ME |
| **625** | Stellaria | media | Caryophyllaceae | Forb | A | C3 | |
| **627** | Stenosiphon | linifolius | Onagraceae | Forb | B | C3 | |
| **633** | Symphyotrichum | laeve | Asteraceae | Forb | P | C3 | |
| **635** | Symphyotrichum | oblongifolium | Asteraceae | Forb | P | C3 | |
| **647** | Tradescantia | bracteata | Commelinaceae | Forb | P | C3 | |
| **648** | Tradescantia | ohiensis | Commelinaceae | Forb | P | C3 | |
| **651** | Tragopogon | dubius | Asteraceae | Forb | B | C3 | |
| **674** | Verbesina | alternifolia | Asteraceae | Forb | P | C3 | |
| **675** | Vernonia | baldwinii | Asteraceae | Forb | P | C3 | |
| **687** | Vulpia | octoflora | Poaceae | Grass | A | C3 | |
| **689** | Xanthium | strumarium | Asteraceae | Forb | A | C3 | |
| **693** | Zizia | aurea | Apiaceae | Forb | P | C3 | |

**Table A.1 continued (4 of 4)**

| KUT Code | Genus | Species | Family | Growth Form | Life History | Type | Biochemical Subtype (C4) |
|---|---|---|---|---|---|---|---|
| **999.001** | Baptisia | alba | Fabaceae | Forb | P | C3 | |
| **999.002** | Echinacea | atrorubens | Asteraceae | Forb | P | C3 | |
| **999.003** | Eryngium | yuccifolium | Apiaceae | Forb | P | C3 | |
| **999.004** | Eupatorium | purpureum | Asteraceae | Forb | P | C3 | |
| **999.005** | Helianthus | salicifolius | Asteraceae | Forb | P | C3 | |
| **999.006** | Liatris | pycnostachya | Asteraceae | Forb | P | C3 | |
| **999.007** | Penstemon | digitalis | Scrophulariaceae | Forb | P | C3 | |
| **999.008** | Prenanthes | aspera | Asteraceae | Forb | P | C3 | |
| **999.009** | Rudbeckia | lacinata | Asteraceae | Forb | P | C3 | |
| **999.010** | Solidago | nemoralis | Asteraceae | Forb | P | C3 | |
| **999.011** | Solidago | ulmifolia | Asteraceae | Forb | P | C3 | |
| **999.012** | Asclepias | incarnata | Asclepiadaceae | Forb | P | C3 | |

**Table A.2  Plant biomass by species.**

| KUT Code | Coarse Root (mg) | Fine Not Scan Root (mg) | Fine Scan Root (mg) | Non-SLA Leaf (mg) | SLA Leaf Mass (mg) | Stem Mass (mg) | Shoot Mass (mg) | Root Mass (mg) | Total Mass (mg) |
|---|---|---|---|---|---|---|---|---|---|
| **106** | 116.61 | 289.07 | 73.79 | 846.19 | 35.20 | 0.00 | 881.4 | 479.5 | 1360.9 |
| **112** | 20.05 | 51.54 | 31.72 | 153.04 | 90.10 | 65.96 | 309.1 | 107.4 | 393.8 |
| **121** | 13.11 | 0.00 | 33.18 | 260.87 | 16.44 | 133.80 | 411.1 | 59.0 | 659.8 |
| **123** | 126.49 | 67.04 | 55.44 | 361.80 | 149.63 | 392.21 | 903.6 | 249.0 | 1152.6 |
| **126** | 437.00 | 550.00 | 89.17 | 1180.33 | 23.30 | 817.00 | 2020.6 | 1076.2 | 3096.8 |
| **129** | 83.58 | 10.40 | 76.65 | 256.07 | 6.00 | 42.97 | 305.0 | 159.0 | 485.3 |
| **133** | 221.58 | 631.19 | 77.13 | 934.00 | 28.73 | 55.75 | 1018.5 | 929.9 | 1948.4 |
| **137** | 62.16 | 101.61 | 47.76 | 783.26 | 25.37 | 0.00 | 808.6 | 221.8 | 1108.8 |
| **138** | 131.70 | 28.88 | 49.07 | 252.45 | 81.38 | 162.57 | 496.4 | 215.2 | 783.2 |
| **145** | 162.91 | 545.36 | 49.46 | 2109.86 | 51.26 | 283.97 | 2445.1 | 757.7 | 3202.8 |
| **146** | 51.86 | 125.00 | 58.72 | 372.78 | 24.54 | 0.00 | 397.3 | 235.6 | 632.9 |
| **148** | 108.75 | 154.25 | 69.87 | 581.05 | 99.43 | 327.62 | 1008.1 | 332.9 | 1341.0 |
| **150** | 200.92 | 60.70 | 78.44 | 158.16 | 83.52 | 169.74 | 411.4 | 340.1 | 751.5 |
| **152** | 808.15 | 53.33 | 50.88 | 178.70 | 20.78 | 196.24 | 395.7 | 912.4 | 1422.8 |
| **155** | 158.70 | 63.73 | 92.35 | 160.63 | 18.25 | 82.85 | 261.7 | 380.0 | 699.9 |
| **157** | 242.64 | 5.62 | 20.02 | 84.90 | 66.64 | 43.46 | 195.0 | 268.3 | 463.3 |
| **160** | 151.46 | 31.00 | 58.00 | 400.34 | 147.58 | 171.30 | 719.2 | 240.5 | 959.7 |
| **166** | 203.10 | 42.44 | 68.06 | 403.30 | 146.29 | 157.45 | 707.0 | 313.6 | 1020.6 |
| **179** | 212.41 | 408.76 | 67.01 | 1005.99 | 52.39 | 41.11 | 1099.5 | 688.2 | 1787.7 |
| **181** | 256.26 | 444.40 | 61.80 | 747.60 | 20.16 | 334.77 | 1072.4 | 762.5 | 1692.7 |
| **185** | 178.98 | 578.26 | 57.61 | 810.29 | 27.27 | 0.00 | 837.6 | 814.9 | 1652.4 |
| **202** | 208.15 | 565.50 | 61.42 | 760.40 | 13.55 | 0.00 | 774.0 | 835.1 | 1609.0 |
| **227** | 43.19 | 121.13 | 27.26 | 854.98 | 50.88 | 438.39 | 1344.2 | 187.0 | 1646.9 |
| **231** | 173.82 | 320.91 | 73.17 | 1025.36 | 29.98 | 1003.05 | 2048.1 | 568.8 | 2829.7 |
| **240** | 137.77 | 335.22 | 59.98 | 1040.62 | 27.87 | 0.00 | 1068.5 | 533.0 | 1601.5 |
| **243** | 1035.71 | 212.91 | 56.80 | 1065.84 | 322.79 | 0.00 | 1388.6 | 1305.4 | 2694.1 |
| **260** | 2210.50 | 10.23 | 76.40 | 822.86 | 178.47 | 242.13 | 1243.5 | 2297.1 | 3540.6 |
| **285** | 178.57 | 147.52 | 68.35 | 451.72 | 43.30 | 404.50 | 876.3 | 394.4 | 1270.7 |
| **288** | 551.13 | 194.86 | 71.50 | 494.25 | 36.35 | 225.00 | 755.6 | 883.3 | 1545.4 |
| **294** | 61.80 | 79.48 | 26.10 | 391.93 | 13.90 | 0.00 | 405.8 | 167.4 | 573.2 |
| **304** | 407.85 | 0.00 | 38.92 | 214.27 | 164.10 | 0.00 | 378.4 | 446.8 | 825.1 |
| **305** | 58.10 | 0.00 | 44.90 | 16.50 | 150.90 | 29.40 | 196.8 | 103.0 | 299.8 |
| **307** | 72.10 | 0.00 | 136.20 | 122.20 | 98.50 | 0.00 | 220.7 | 208.3 | 429.0 |
| **313** | 186.82 | 238.34 | 46.86 | 1442.27 | 11.13 | 173.44 | 1626.8 | 490.7 | 2197.6 |
| **315** | 117.05 | 330.80 | 44.90 | 780.35 | 66.55 | 157.98 | 1004.9 | 492.8 | 1497.6 |
| **316** | 47.83 | 124.35 | 47.73 | 547.10 | 49.20 | 0.00 | 678.1 | 219.9 | 898.0 |

**Table A.2 continued (2 of 4)**

| KUT Code | Coarse Root (mg) | Fine Not Scan Root (mg) | Fine Scan Root (mg) | Non-SLA Leaf (mg) | SLA Leaf Mass (mg) | Stem Mass (mg) | Shoot Mass (mg) | Root Mass (mg) | Total Mass (mg) |
|---|---|---|---|---|---|---|---|---|---|
| **317** | 83.57 | 232.99 | 49.54 | 624.87 | 40.58 | 105.44 | 856.4 | 367.4 | 1249.5 |
| **323** | 247.23 | 574.17 | 67.85 | 2828.86 | 0.00 | 1361.48 | 2479.7 | 889.3 | 2967.1 |
| **326** | 332.10 | 517.80 | 50.30 | 1398.00 | 51.20 | 0.00 | 1449.2 | 900.2 | 2349.4 |
| **334** | 138.54 | 647.06 | 81.84 | 1078.48 | 274.89 | 282.44 | 1635.8 | 867.4 | 2503.2 |
| **335** | 37.90 | 123.20 | 121.80 | - | - | - | - | 282.9 | - |
| **338** | 57.05 | 110.38 | 43.56 | 445.32 | 37.61 | 722.17 | 1205.1 | 232.6 | 1556.3 |
| **340** | 60.05 | 110.10 | 19.50 | 265.25 | 114.15 | 275.55 | 655.0 | 189.7 | 844.6 |
| **344** | 123.76 | 309.08 | 40.04 | 1042.76 | 82.58 | 0.00 | 1125.3 | 472.9 | 1598.2 |
| **365** | 149.71 | 184.84 | 46.61 | 617.83 | 254.33 | 745.51 | 1617.7 | 402.9 | 2134.9 |
| **369** | 153.50 | 132.83 | 46.00 | 931.33 | 185.14 | 718.65 | 1835.1 | 332.3 | 2167.4 |
| **370** | 358.63 | 513.79 | 85.83 | 898.71 | 312.74 | 793.80 | 2005.3 | 958.2 | 2963.5 |
| **371** | 73.43 | 122.08 | 44.96 | 262.94 | 136.35 | 150.44 | 549.7 | 240.5 | 790.2 |
| **373** | 183.59 | 259.21 | 54.09 | 578.85 | 44.78 | 0.00 | 623.6 | 496.9 | 1120.5 |
| **379** | 81.51 | 248.61 | 48.98 | 867.45 | 19.12 | 67.63 | 954.2 | 379.1 | 1333.3 |
| **380** | 172.41 | 556.84 | 54.34 | 1115.65 | 33.86 | 0.00 | 1149.5 | 783.6 | 1933.1 |
| **396** | 105.66 | 161.57 | 35.14 | 311.99 | 18.72 | 0.00 | 330.7 | 302.4 | 632.0 |
| **399** | 286.25 | 458.58 | 58.53 | 543.43 | 165.58 | 129.73 | 838.7 | 803.4 | 1642.1 |
| **400** | 139.20 | 21.30 | 34.35 | 221.00 | 105.80 | 0.00 | 326.8 | 194.9 | 521.7 |
| **408** | 58.85 | 52.42 | 46.40 | 441.29 | 21.11 | 282.66 | 743.7 | 158.1 | 919.4 |
| **410** | 231.11 | 102.61 | 53.39 | 875.58 | 74.95 | 384.43 | 1335.0 | 387.1 | 1722.1 |
| **413** | 77.63 | 50.03 | 76.85 | 296.70 | 97.33 | 130.15 | 524.2 | 220.6 | 824.3 |
| **416** | 22.90 | 117.03 | 48.50 | 363.29 | 78.63 | 96.08 | 538.0 | 176.1 | 670.7 |
| **419** | 377.57 | 21.27 | 28.55 | 189.33 | 118.52 | 0.00 | 307.9 | 427.4 | 735.2 |
| **420** | 92.49 | 0.00 | 19.72 | 19.19 | 13.91 | 0.00 | 33.1 | 107.1 | 142.0 |
| **421** | 95.23 | 0.00 | 16.90 | 15.55 | 33.55 | 0.00 | 49.1 | 112.1 | 201.7 |
| **447** | 726.94 | 4.90 | 48.44 | 267.12 | 60.90 | 206.12 | 534.1 | 780.3 | 1314.4 |
| **450** | 146.32 | 522.21 | 72.58 | 1195.38 | 53.69 | 276.91 | 1336.2 | 741.1 | 2079.1 |
| **466** | 197.41 | 317.19 | 58.28 | 1438.20 | 127.01 | 30.21 | 1561.2 | 590.7 | 2217.4 |
| **468** | 131.81 | 53.91 | 59.56 | 1007.44 | 221.12 | 30.53 | 1259.1 | 245.3 | 1504.4 |
| **481** | 12.27 | 28.80 | 55.43 | 72.68 | 61.05 | 3.55 | 137.3 | 117.0 | 265.9 |
| **482** | - | 109.30 | 29.90 | 108.10 | 56.10 | 0.00 | 164.2 | - | - |
| **485** | 263.49 | 690.00 | 91.39 | 797.34 | 31.83 | 273.57 | 1102.7 | 1044.9 | 2147.6 |
| **488** | 101.20 | 162.10 | 47.80 | 569.00 | 64.60 | 313.30 | 946.9 | 311.1 | 1258.0 |
| **494** | 53.15 | 268.08 | 67.09 | 322.02 | 235.46 | 26.46 | 583.9 | 410.4 | 1440.9 |
| **495** | 32.60 | 49.15 | 51.05 | 98.88 | 189.20 | 2.55 | 290.6 | 132.8 | 423.4 |
| **496** | 172.49 | 325.18 | 74.11 | 1160.97 | 150.10 | 42.98 | 522.6 | 571.8 | 649.0 |

**Table A.2 continued (3 of 4)**

| KUT Code | Coarse Root (mg) | Fine Not Scan Root (mg) | Fine Scan Root (mg) | Non-SLA Leaf (mg) | SLA Leaf Mass (mg) | Stem Mass (mg) | Shoot Mass (mg) | Root Mass (mg) | Total Mass (mg) |
|---|---|---|---|---|---|---|---|---|---|
| **504** | 500.25 | 120.00 | 71.38 | 363.75 | 24.87 | 44.25 | 507.2 | 805.2 | 1693.6 |
| **513** | 194.76 | 383.26 | 39.39 | 1310.75 | 242.11 | 98.15 | 1651.0 | 617.4 | 2268.4 |
| **516** | 196.88 | 370.03 | 50.95 | 1374.83 | 119.77 | 0.00 | 1494.6 | 617.9 | 2164.7 |
| **519** | 408.64 | 1065.64 | 67.37 | 1191.50 | 17.13 | 0.00 | 1227.7 | 1541.6 | 2770.6 |
| **534** | 116.66 | 134.60 | 44.25 | 604.76 | 203.25 | 428.59 | 1236.6 | 295.5 | 1534.4 |
| **542** | 103.93 | 269.20 | 37.45 | 1297.91 | 281.06 | 180.23 | 1759.2 | 445.5 | 2405.1 |
| **547** | 534.17 | 0.00 | 27.93 | 46.87 | 33.20 | 30.70 | 110.8 | 562.1 | 672.9 |
| **553** | 79.95 | 340.87 | 52.70 | 714.97 | 174.73 | 0.00 | 889.7 | 473.5 | 1363.2 |
| **565** | 89.93 | 257.00 | 38.85 | 647.50 | 188.00 | 0.00 | 835.5 | 385.8 | 1221.3 |
| **566** | 48.52 | 298.43 | 104.67 | 612.97 | 118.49 | 176.34 | 907.8 | 451.2 | 1357.3 |
| **575** | 332.01 | 357.93 | 96.54 | 697.73 | 104.45 | 223.77 | 1026.0 | 786.5 | 1873.9 |
| **576** | 33.88 | 231.75 | 52.69 | 355.13 | - | 623.63 | - | 318.3 | - |
| **583** | 358.87 | 705.81 | 79.31 | 899.66 | 39.18 | 0.00 | 938.8 | 1144.0 | 2082.8 |
| **591** | 295.74 | 105.09 | 75.76 | 900.38 | 191.00 | 160.36 | 1251.7 | 481.2 | 1855.0 |
| **592** | 241.56 | 756.02 | 75.83 | 1361.54 | 22.52 | 718.44 | 2102.6 | 1124.9 | 3223.7 |
| **598** | 271.50 | 849.65 | 71.30 | 894.88 | 132.90 | 0.00 | 1027.8 | 1192.5 | 2220.2 |
| **599** | 851.22 | 81.01 | 59.63 | 318.65 | 204.27 | 0.00 | 522.9 | 1010.4 | 1548.2 |
| **603** | 251.58 | 87.13 | 68.55 | 373.18 | 140.05 | 92.78 | 606.0 | 386.8 | 1003.1 |
| **605** | 223.72 | 68.24 | 32.83 | 461.45 | 79.68 | 359.38 | 900.5 | 333.4 | 1313.8 |
| **606** | - | 439.90 | - | 518.70 | 0.00 | 176.20 | 694.9 | - | - |
| **608** | 106.33 | 351.00 | 86.97 | 374.00 | 20.95 | 0.00 | 570.0 | 636.8 | 1206.7 |
| **609** | 25.30 | 163.00 | 36.45 | 81.87 | 89.53 | 2.13 | 173.5 | 251.3 | 584.2 |
| **610** | 66.10 | 116.56 | 51.84 | 273.10 | 127.78 | 2.91 | 403.8 | 234.5 | 638.3 |
| **613** | 158.18 | 263.53 | 56.43 | 643.93 | 57.60 | 0.00 | 701.5 | 478.1 | 1179.7 |
| **622** | - | - | - | - | - | - | - | - | - |
| **625** | - | - | - | 608.70 | 4.30 | 556.90 | 1169.9 | - | - |
| **627** | 292.03 | 46.41 | 52.36 | 532.16 | 115.59 | 39.69 | 687.4 | 390.8 | 1078.2 |
| **633** | 81.00 | 156.03 | 58.28 | 292.15 | 132.68 | 0.00 | 424.8 | 295.3 | 720.1 |
| **635** | 71.27 | 374.92 | 89.25 | 511.92 | 107.73 | 9.47 | 629.1 | 535.4 | 1164.6 |
| **647** | 230.66 | 425.81 | 60.55 | 356.88 | 77.64 | 21.65 | 456.2 | 717.0 | 1173.2 |
| **648** | 375.44 | 74.50 | 55.72 | 200.66 | 66.60 | 0.00 | 267.3 | 505.7 | 772.9 |
| **651** | 465.18 | 28.77 | 81.03 | 374.83 | 100.40 | 0.00 | 475.2 | 575.0 | 1050.2 |
| **674** | 209.62 | 624.32 | 107.62 | 625.08 | 190.97 | 430.26 | 1291.9 | 941.6 | 2283.7 |
| **675** | 287.46 | 581.26 | 82.55 | 506.66 | 146.53 | 176.88 | 830.1 | 928.7 | 1817.6 |
| **687** | 58.16 | 206.74 | 28.20 | 586.60 | 9.12 | 0.00 | 595.7 | 293.1 | 888.8 |
| **689** | 124.50 | 230.97 | 51.17 | 648.03 | 223.47 | 742.47 | 1614.0 | 406.6 | 2020.6 |

**Table A.2 continued (4 of 4)**

| KUT Code | Coarse Root (mg) | Fine Not Scan Root (mg) | Fine Scan Root (mg) | Non-SLA Leaf (mg) | SLA Leaf Mass (mg) | Stem Mass (mg) | Shoot Mass (mg) | Root Mass (mg) | Total Mass (mg) |
|---|---|---|---|---|---|---|---|---|---|
| **693** | 21.30 | 8.20 | 30.00 | 55.10 | 117.20 | 0.00 | 172.3 | 59.5 | 231.8 |
| **999.001** | 431.53 | 26.30 | 43.14 | 397.90 | 141.37 | 156.37 | 695.6 | 501.0 | 1196.6 |
| **999.002** | 429.60 | 5.65 | 93.74 | 153.28 | 148.36 | 0.00 | 301.6 | 476.2 | 750.5 |
| **999.003** | 177.13 | 249.76 | 79.31 | 476.18 | 180.55 | 43.75 | 700.5 | 506.2 | 1206.7 |
| **999.004** | 135.68 | 486.33 | 73.29 | 773.69 | 147.63 | 475.31 | 1396.6 | 756.7 | 2097.7 |
| **999.005** | 109.85 | 258.88 | 60.52 | 339.13 | 83.27 | 210.55 | 633.0 | 429.3 | 1062.2 |
| **999.006** | 210.03 | 114.75 | 33.53 | 673.33 | 135.85 | 0.00 | 809.2 | 358.3 | 1167.5 |
| **999.007** | 194.15 | 518.10 | 110.05 | 1078.49 | 61.27 | 0.47 | 1140.2 | 832.3 | 2056.1 |
| **999.008** | 189.93 | 164.50 | 32.00 | 133.27 | 33.50 | 0.00 | 166.8 | 284.4 | 727.9 |
| **999.009** | 168.72 | 497.12 | 59.66 | 717.93 | 51.95 | 0.00 | 769.9 | 748.3 | 1644.8 |
| **999.010** | 112.13 | 253.82 | 43.33 | 426.81 | 134.89 | 29.79 | 591.5 | 409.3 | 1016.0 |
| **999.011** | 104.04 | 367.86 | 82.51 | 890.01 | 178.51 | 29.81 | 1098.3 | 554.4 | 1652.8 |
| **999.012** | 147.02 | 666.60 | 109.43 | 240.59 | 40.52 | 486.03 | 755.1 | 923.1 | 1678.1 |

**Table A.3 Leaf-level physiology by species. See table Table A.11 for units.**

| KUT Code | Genus species | Photo synthetic Rate | Cond to $H_2O$ | Trans-piration Rate | Inter-cellular $CO_2$ Conc. | Crit Water Potential (bars) |
|---|---|---|---|---|---|---|
| **106** | Achillea millefolium | 5.689 | 0.082 | 1.784 | 258.0 | -58.83 |
| **112** | Ageratina altissima | 8.100 | 0.148 | 3.007 | 283.3 | -29.00 |
| **121** | Amaranthus blitoides | 7.089 | 0.053 | 1.363 | 161.2 | -29.50 |
| **123** | Amaranthus retroflexus | 12.641 | 0.108 | 2.213 | 175.3 | -42.50 |
| **126** | Ambrosia psilostachya | 4.521 | 0.061 | 1.705 | 255.7 | -75.67 |
| **129** | Amorpha canescens | 2.179 | 0.031 | 0.820 | 270.8 | -54.50 |
| **133** | Andropogon gerardii | 13.312 | 0.122 | 2.999 | 190.9 | -73.90 |
| **137** | Antennaria neglecta | 7.144 | 0.221 | 4.708 | 306.9 | -40.75 |
| **138** | Apocynum cannabinum | 10.793 | 0.110 | 2.353 | 214.7 | -37.20 |
| **145** | Aristida oligantha | 16.201 | 0.118 | 2.593 | 161.6 | -72.20 |
| **146** | Aristida purpurea | 14.464 | 0.098 | 2.156 | 154.3 | -84.25 |
| **148** | Artemisia ludoviciana | 8.435 | 0.102 | 1.943 | 223.5 | -39.80 |
| **150** | Asclepias speciosa | 15.200 | 0.190 | 3.710 | 239.2 | -20.00 |
| **152** | Asclepias sullivantii | 9.861 | 0.127 | 3.298 | 239.8 | -66.00 |
| **155** | Asclepias verticillata | 13.523 | 0.160 | 3.638 | 231.3 | -22.00 |
| **157** | Asclepias viridis | 11.696 | 0.119 | 2.401 | 207.2 | -17.00 |
| **160** | Astragalus canadensis | 13.360 | 0.162 | 3.178 | 230.4 | -29.33 |
| **166** | Baptisia australis | 6.177 | 0.055 | 1.290 | 184.8 | -28.50 |
| **179** | Bouteloua curtipendula | 19.014 | 0.166 | 3.401 | 180.1 | -89.00 |
| **181** | Bouteloua gracilis | 11.040 | 0.063 | 1.674 | 108.7 | -82.00 |
| **185** | Bromus inermis | 9.537 | 0.123 | 2.938 | 249.1 | -62.00 |
| **202** | Carex annectens | 11.434 | 0.240 | 5.564 | 292.7 | -58.40 |
| **227** | Chamaecrista fasciculata | 10.803 | 0.116 | 2.444 | 214.7 | -32.83 |
| **231** | Chamaesyce nutans | 5.789 | 0.043 | 1.326 | 182.0 | -18.33 |
| **240** | Chloris verticillata | 17.472 | 0.128 | 2.678 | 159.5 | -84.80 |
| **243** | Cirsium altissimum | 11.136 | 0.134 | 2.747 | 222.9 | -42.80 |
| **260** | Cucurbita foetidissima | 13.293 | 0.153 | 3.160 | 222.7 | -25.17 |
| **285** | Desmanthus illinoensis | 8.658 | 0.086 | 1.978 | 209.9 | -62.42 |
| **288** | Desmodium illinoense | 5.107 | 0.043 | 1.337 | 187.3 | -53.00 |
| **294** | Dichanthelium acuminatum | 6.653 | 0.121 | 2.595 | 285.5 | -85.00 |
| **304** | Echinacea angustifolia | 16.200 | 0.297 | 4.694 | 269.4 | -52.75 |
| **305** | Echinacea pallida | 13.700 | 0.155 | 3.390 | 233.0 | -33.00 |

**Table A.3 continued (2 of 4)**

| KUT Code | Genus species | Max Photo Rate | Cond to $H_2O$ | Trans-piration Rate | Inter-cellular $CO_2$ Conc. | Crit Water Potential (bars) |
|---|---|---|---|---|---|---|
| **307** | Echinodorus berteroi | 13.725 | 0.185 | 3.796 | 253.8 | -22.00 |
| **313** | Eleusine indica | 11.320 | 0.083 | 2.554 | 158.2 | -30.50 |
| **315** | Elymus canadensis | 9.810 | 0.134 | 3.025 | 252.5 | -70.00 |
| **316** | Elymus villosus | 4.280 | 0.085 | 1.821 | 304.8 | -72.33 |
| **317** | Elymus virginicus | 12.165 | 0.156 | 3.224 | 246.1 | -66.63 |
| **323** | Eragrostis pectinacea | 10.271 | 0.074 | 2.165 | 172.4 | -62.13 |
| **326** | Erigeron annuus | 24.500 | 0.195 | 5.130 | 173.0 | - |
| **334** | Eupatorium altissimum | 7.714 | 0.102 | 2.085 | 216.9 | -36.17 |
| **335** | Euphorbia corollata | - | - | - | - | - |
| **338** | Euphorbia dentata | 2.677 | 0.028 | 0.853 | 296.0 | -18.29 |
| **340** | Euphorbia marginata | 9.755 | 0.135 | 2.645 | 254.0 | - |
| **344** | Festuca subverticillata | 5.390 | 0.068 | 1.758 | 258.2 | -69.80 |
| **365** | Helianthus annuus | 16.944 | 0.198 | 3.446 | 211.5 | -31.17 |
| **369** | Helianthus petiolaris | 20.963 | 0.282 | 4.719 | 223.4 | -36.00 |
| **370** | Helianthus tuberosus | 7.321 | 0.058 | 1.405 | 171.8 | -27.67 |
| **371** | Heliopsis helianthoides | 10.720 | 0.170 | 3.131 | 255.0 | -48.50 |
| **373** | Hesperostipa spartea | 8.163 | 0.151 | 3.128 | 287.0 | -80.14 |
| **379** | Hordeum jubatum | 12.846 | 0.163 | 3.621 | 246.3 | -69.71 |
| **380** | Hordeum pusillum | 13.313 | 0.222 | 4.393 | 275.0 | -88.43 |
| **396** | Koeleria macrantha | 13.182 | 0.202 | 4.431 | 266.8 | -81.94 |
| **399** | Lactuca canadensis | 14.350 | 0.160 | 3.430 | 223.3 | -28.50 |
| **400** | Lactuca ludoviciana | 13.100 | 0.234 | 4.065 | 270.0 | -25.00 |
| **408** | Lepidium densiflorum | 6.845 | 0.093 | 2.409 | 248.7 | -69.00 |
| **410** | Lepidium virginicum | 6.615 | 0.081 | 1.698 | 259.4 | -51.57 |
| **413** | Lespedeza capitata | 11.455 | 0.233 | 4.383 | 266.8 | -26.00 |
| **416** | Lespedeza violacea | 7.345 | 0.082 | 1.850 | 230.8 | -42.83 |
| **419** | Liatris aspera | 11.375 | 0.180 | 3.820 | 267.3 | -60.25 |
| **420** | Liatris mucronata | 12.129 | 0.230 | 4.820 | 294.0 | -51.00 |
| **421** | Liatris punctata | 11.900 | 0.252 | 5.365 | 304.5 | -77.50 |
| **447** | Mirabilis linearis | 12.996 | 0.126 | 2.516 | 192.4 | -58.00 |
| **450** | Monarda fistulosa | 5.819 | 0.058 | 1.490 | 203.5 | -38.65 |
| **466** | Oenothera biennis | 6.620 | 0.079 | 2.109 | 229.2 | -34.71 |
| **468** | Oenothera macrocarpa | 9.135 | 0.136 | 2.659 | 261.9 | -35.79 |
| **481** | Packera plattensis | 11.085 | 0.154 | 3.165 | 250.5 | -29.00 |
| **482** | Panicum capillare | 19.000 | 0.157 | 3.620 | 180.0 | - |
| **485** | Panicum virgatum | 12.174 | 0.082 | 2.078 | 142.6 | -32.67 |
| **488** | Pascopyrum smithii | 20.250 | 0.220 | 3.320 | 230.5 | -30.00 |

**Table A.3 continued (3 of 4)**

| KUT Code | Genus species | Max Photo Rate | Cond to $H_2O$ | Trans-piration Rate | Inter-cellular $CO_2$ Conc. | Crit Water Potential (bars) |
|---|---|---|---|---|---|---|
| **494** | Penstemon cobaea | 12.950 | 0.168 | 3.276 | 245.9 | -41.88 |
| **495** | Penstemon grandiflorus | 11.035 | 0.125 | 2.540 | 222.5 | -19.67 |
| **496** | Penstemon tubiflorus | 7.648 | 0.098 | 2.466 | 231.6 | -39.38 |
| **504** | Physalis pubescens | 1.955 | 0.033 | 1.058 | 290.0 | -35.25 |
| **513** | Plantago rugelii | 9.493 | 0.159 | 2.910 | 251.4 | -63.67 |
| **516** | Poa arida | 10.179 | 0.127 | 2.704 | 216.2 | -57.00 |
| **519** | Poa pratensis | 11.781 | 0.168 | 4.601 | 259.0 | -73.00 |
| **534** | Polygonum virginianum | 7.122 | 0.077 | 1.708 | 215.8 | -42.00 |
| **542** | Prunella vulgaris | 5.645 | 0.070 | 1.515 | 229.9 | -64.17 |
| **547** | Psoralidium tenuiflorum | 11.615 | 0.201 | 3.559 | 276.6 | -43.80 |
| **553** | Ratibida pinnata | 11.443 | 0.125 | 3.065 | 216.2 | -40.00 |
| **565** | Rudbeckia hirta | 11.068 | 0.139 | 3.085 | 221.8 | -37.00 |
| **566** | Ruellia humilis | 7.929 | 0.133 | 2.448 | 254.1 | -33.66 |
| **575** | Salvia azurea | 6.818 | 0.087 | 1.920 | 242.9 | -48.21 |
| **576** | Salvia reflexa | 7.017 | 0.105 | 3.206 | 270.3 | -85.63 |
| **583** | Schizachyrium scoparium | 11.879 | 0.097 | 2.507 | 179.2 | -69.80 |
| **591** | Senna marilandica | 8.628 | 0.080 | 2.011 | 183.2 | -28.50 |
| **592** | Setaria pumila | 8.019 | 0.054 | 1.682 | 140.6 | -38.89 |
| **598** | Silphium integrifolium | 9.353 | 0.095 | 2.103 | 211.5 | -25.00 |
| **599** | Silphium laciniatum | 8.212 | 0.122 | 2.467 | 235.6 | -30.33 |
| **603** | Solanum carolinense | 6.467 | 0.067 | 1.548 | 222.0 | -48.75 |
| **605** | Solanum rostratum | 4.936 | 0.087 | 1.741 | 307.1 | -83.80 |
| **606** | Solidago canadensis | - | - | - | - | - |
| **608** | Solidago missouriensis | 2.313 | 0.028 | 0.705 | 253.0 | -29.50 |
| **609** | Solidago mollis | 8.020 | 0.167 | 2.860 | 303.0 | -45.50 |
| **610** | Solidago petiolaris | 15.800 | 0.200 | 4.236 | 240.7 | -26.50 |
| **613** | Sorghastrum nutans | 18.442 | 0.121 | 2.590 | 119.1 | -78.73 |
| **622** | Sporobolus heterolepis | 5.630 | 0.064 | 1.460 | 241.0 | - |
| **625** | Stellaria media | - | - | - | - | - |
| **627** | Stenosiphon linifolius | 12.683 | 0.165 | 3.373 | 224.3 | -27.20 |
| **633** | Symphyotrichum laeve | 12.200 | 0.192 | 3.477 | 250.7 | -28.50 |
| **635** | Symphyotrichum oblongifolium | 13.618 | 0.178 | 3.218 | 226.2 | -45.75 |
| **647** | Tradescantia bracteata | 10.084 | 0.110 | 2.669 | 200.5 | -11.17 |
| **648** | Tradescantia ohiensis | 12.712 | 0.154 | 2.996 | 237.8 | - |
| **651** | Tragopogon dubius | 13.860 | 0.156 | 3.366 | 221.2 | -15.50 |
| **674** | Verbesina alternifolia | 4.353 | 0.050 | 1.388 | 250.1 | -87.67 |
| **675** | Vernonia baldwinii | 6.573 | 0.069 | 1.633 | 202.9 | -35.83 |

**Table A.3 continued (4 of 4)**

| KUT Code | Genus species | Max Photo Rate | Cond to $H_2O$ | Trans-piration Rate | Inter-cellular $CO_2$ Conc. | Crit Water Potential (bars) |
|---|---|---|---|---|---|---|
| **687** | Vulpia octoflora | 6.068 | 0.107 | 2.236 | 270.0 | -72.67 |
| **689** | Xanthium strumarium | 21.800 | 0.216 | 3.623 | 192.3 | - |
| **693** | Zizia aurea | 11.700 | 0.260 | 4.500 | 297.0 | - |
| **999.001** | Baptisia alba | 6.944 | 0.064 | 1.515 | 194.7 | -32.60 |
| **999.002** | Echinacea atrorubens | 11.940 | 0.189 | 3.526 | 248.6 | -55.67 |
| **999.003** | Eryngium yuccifolium | 12.494 | 0.265 | 4.091 | 258.9 | -36.29 |
| **999.004** | Eupatorium purpureum | 5.131 | 0.054 | 1.257 | 199.3 | -38.80 |
| **999.005** | Helianthus salicifolius | 6.423 | 0.070 | 1.580 | 203.6 | -34.50 |
| **999.006** | Liatris pycnostachya | 8.155 | 0.083 | 2.153 | 222.5 | -23.00 |
| **999.007** | Penstemon digitalis | 8.069 | 0.133 | 2.920 | 263.6 | -35.90 |
| **999.008** | Prenanthes aspera | 13.997 | 0.303 | 5.450 | 294.0 | -33.00 |
| **999.009** | Rudbeckia lacinata | 6.785 | 0.095 | 2.023 | 252.9 | -48.00 |
| **999.010** | Solidago nemoralis | 9.830 | 0.148 | 2.809 | 247.3 | -36.80 |
| **999.011** | Solidago ulmifolia | 7.214 | 0.076 | 1.720 | 204.3 | -30.83 |
| **999.012** | Asclepias incarnata | 5.726 | 0.092 | 2.310 | 257.2 | -25.50 |

## Table A.4 Field Comparison Data

| KUT Code | Genus species | Field thickness (mm) | Field leaf angle (degrees) | Field leaf tissue density (g cm$^{-3}$) | Field SLA (cm$^{2}$ g$^{-1}$) | Leaf thickness (mm) | Leaf Angle (degrees) | Leaf tissue density(g cm$^{-3}$) | SLA (cm$^{2}$ g$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| **126** | Ambrosia psilostachya | 0.22 | 30 | 0.405 | 112.2 | 0.242 | 40.00 | 0.451 | 97.9 |
| **129** | Amorpha canescens | 0.13 | 45 | 0.598 | 128.6 | 0.124 | 3.83 | 0.314 | 261.3 |
| **133** | Andropogon gerardii | 0.1 | 75 | 0.777 | 128.7 | 0.136 | 68.75 | 0.862 | 135.1 |
| **137** | Antennaria neglecta | 0.18 | 60 | 0.327 | 170.0 | 0.206 | 52.40 | 0.324 | 151.5 |
| **148** | Artemisia ludoviciana | 0.12 | 45 | 0.690 | 120.7 | 0.186 | 45.00 | 0.419 | 146.8 |
| **166** | Baptisia australis | 0.3 | 90 | 0.276 | 120.9 | 0.253 | 70.00 | 0.317 | 143.4 |
| **179** | Bouteloua curtipendula | 0.12 | 65 | 0.691 | 120.5 | 0.117 | 35.00 | 0.548 | 162.5 |
| **181** | Bouteloua gracilis | 0.13 | 50 | 0.585 | 131.4 | 0.142 | 71.67 | 0.472 | 157.1 |
| **185** | Bromus inermis | 0.15 | 65 | 0.409 | 163.1 | 0.180 | 65.00 | 0.474 | 149.6 |
| **240** | Chloris verticillata | 0.12 | 50 | 0.428 | 194.7 | 0.081 | 55.00 | 0.519 | 273.3 |
| **260** | Cucurbita foetidissima | 0.95 | 50 | 0.066 | 160.1 | 0.290 | 20.00 | 0.304 | 122.9 |
| **288** | Desmodium illinoense | 0.25 | 45 | 0.335 | 119.6 | 0.182 | 75.00 | 0.357 | 157.9 |
| **304** | Echinacea angustifolia | 0.35 | 60 | 0.297 | 96.2 | 0.376 | 35.00 | 0.292 | 100.5 |
| **313** | Eleusine indica | 0.16 | 75 | 0.522 | 119.8 | 0.083 | 56.67 | 0.723 | 239.8 |
| **315** | Elymus canadensis | 0.13 | 10 | 0.464 | 166.0 | 0.143 | 35.00 | 0.466 | 159.3 |
| **334** | Eupatorium altissimum | 0.28 | 50 | 0.469 | 76.2 | 0.244 | 25.00 | 0.588 | 85.9 |
| **340** | Euphorbia marginata | 0.28 | 45 | 0.236 | 151.6 | 0.250 | - | 0.226 | 187.4 |
| **365** | Helianthus annuus | 0.37 | 20 | 0.246 | 109.8 | 0.286 | 15.00 | 0.410 | 95.0 |
| **380** | Hordeum pusillum | 0.1 | 60 | 0.547 | 182.9 | 0.099 | 70.00 | 0.558 | 192.5 |
| **396** | Koeleria macrantha | 0.15 | 75 | 0.475 | 140.2 | 0.144 | 73.38 | 0.487 | 160.7 |
| **408** | Lepidium densiflorum | 0.13 | 75 | 0.275 | 280.0 | 0.126 | 57.50 | 0.568 | 163.4 |
| **413** | Lespedeza capitata | 0.22 | 10 | 0.525 | 86.6 | 0.163 | 0.00 | 0.409 | 156.2 |
| **416** | Lespedeza violacea | 0.16 | 45 | 0.640 | 97.6 | 0.103 | 15.00 | 0.585 | 191.2 |
| **419** | Liatris aspera | 0.25 | 75 | 0.545 | 73.4 | 0.353 | 75.00 | 0.352 | 90.8 |
| **421** | Liatris punctata | 0.23 | 70 | 0.824 | 52.8 | 0.410 | 75.00 | 0.389 | 54.9 |
| **450** | Monarda fistulosa | 0.2 | 0 | 0.347 | 144.2 | 0.205 | 2.42 | 0.336 | 163.7 |
| **468** | Oenothera macrocarpa | 0.33 | 45 | 0.245 | 123.7 | 0.320 | 7.50 | 0.319 | 109.8 |
| **481** | Packera plattensis | 0.37 | 60 | 0.265 | 102.0 | 0.220 | 20.00 | 0.422 | 130.3 |
| **485** | Panicum virgatum | 0.15 | 60 | 0.570 | 116.9 | 0.151 | 58.00 | 0.435 | 164.1 |
| **488** | Pascopyrum smithii | 0.22 | 70 | 0.355 | 128.1 | 0.230 | 50.00 | 0.517 | 63.2 |
| **494** | Penstemon cobaea | 0.32 | 55 | 0.347 | 90.0 | 0.319 | 10.00 | 0.409 | 78.3 |
| **495** | Penstemon grandiflorus | 0.28 | 25 | 0.275 | 129.8 | 0.313 | 50.00 | 0.296 | 96.5 |
| **519** | Poa pratensis | 0.08 | 60 | 0.564 | 221.5 | 0.148 | 80.75 | 0.459 | 140.8 |
| **547** | Psoralidium tenuiflorum | 0.22 | 0 | 0.429 | 106.0 | 0.288 | 0.00 | 0.371 | 100.8 |
| **565** | Rudbeckia hirta | 0.24 | 55 | 0.171 | 244.3 | 0.393 | 50.00 | 0.226 | 119.1 |
| **566** | Ruellia humilis | 0.17 | 45 | 0.446 | 131.8 | 0.165 | 15.00 | 0.365 | 181.2 |

## Table A.4 continued (2 of 2)

| KUT Code | Genus species | Field thick ness (mm) | Field leaf angle (deg) | Field leaf density (g cm$^{-3}$) | Field SLA (cm$^2$ g$^{-1}$) | Leaf thick ness (mm) | Leaf Angle (deg) | Leaf tissue density (g cm$^{-3}$) | SLA (cm$^2$ g$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| **575** | Salvia azurea | 0.24 | 10 | 0.426 | 97.7 | 0.202 | 27.00 | 0.443 | 118.9 |
| **576** | Salvia reflexa | 0.17 | 15 | 0.325 | 197.9 | 0.204 | 1.00 | - | - |
| **583** | Schizachyrium scoparium | 0.1 | 70 | 0.770 | 129.8 | 0.103 | 78.86 | 0.677 | 176.3 |
| **591** | Senna marilandica | 0.15 | 90 | 0.519 | 128.4 | 0.138 | 0.00 | 0.646 | 129.5 |
| **592** | Setaria pumila | 0.09 | 60 | 0.346 | 320.8 | 0.107 | 72.17 | 0.443 | 259.2 |
| **598** | Silphium integrifolium | 0.41 | 55 | 0.239 | 101.9 | 0.340 | 30.00 | 0.398 | 98.6 |
| **599** | Silphium laciniatum | 0.45 | 90 | 0.312 | 71.2 | 0.568 | 75.39 | 0.494 | 60.2 |
| **603** | Solanum carolinense | 0.2 | 35 | 0.359 | 139.3 | 0.164 | 0.00 | 0.393 | 164.1 |
| **605** | Solanum rostratum | 0.18 | 60 | 0.241 | 230.2 | 0.163 | 10.00 | 0.640 | 115.1 |
| **606** | Solidago canadensis | 0.24 | 60 | 0.526 | 79.2 | - | - | - | - |
| **608** | Solidago missouriensis | 0.26 | 40 | 0.507 | 75.9 | 0.290 | 40.00 | 0.260 | 133.3 |
| **613** | Sorghastrum nutans | 0.15 | 75 | 0.628 | 106.2 | 0.142 | 61.67 | 0.485 | 165.9 |
| **622** | Sporobolus heterolepis | 0.12 | 70 | 0.957 | 87.1 | 0.220 | - | - | - |
| **627** | Stenosiphon linifolius | 0.15 | 60 | 0.527 | 126.4 | 0.333 | 15.00 | 0.289 | 106.6 |
| **635** | Symphyotrichum oblongifolium | 0.22 | 30 | 0.434 | 104.8 | 0.203 | 25.00 | 0.462 | 136.6 |
| **651** | Tragopogon dubius | 0.15 | 70 | 0.561 | 118.9 | 0.262 | 70.00 | 0.377 | 110.2 |
| **675** | Vernonia baldwinii | 0.3 | 70 | 0.266 | 125.4 | 0.180 | 50.00 | 0.369 | 162.1 |
| **693** | Zizia aurea | 0.13 | 20 | 0.221 | 347.7 | 0.190 | - | 0.359 | 146.8 |

## Table A.5  Principal Components

| KUT Code | Genus species | PCA Axis 1 | PCA Axis 2 | PCA Axis 3 |
|---|---|---|---|---|
| **106** | Achillea millefolium | -0.021 | -0.507 | 0.133 |
| **112** | Ageratina altissima | 0.665 | -0.718 | -1.566 |
| **121** | Amaranthus blitoides | 0.052 | -1.752 | -1.356 |
| **123** | Amaranthus retroflexus | -0.632 | -0.598 | -0.567 |
| **126** | Ambrosia psilostachya | -0.689 | -0.692 | 2.240 |
| **129** | Amorpha canescens | -0.857 | -2.278 | -1.433 |
| **133** | Andropogon gerardii | -1.807 | 0.727 | 0.913 |
| **137** | Antennaria neglecta | 0.092 | 0.401 | -0.804 |
| **138** | Apocynum cannabinum | -0.353 | -0.435 | -1.006 |
| **145** | Aristida oligantha | -1.155 | 0.799 | 1.896 |
| **146** | Aristida purpurea | -1.350 | 0.776 | -0.912 |
| **148** | Artemisia ludoviciana | -0.065 | -0.524 | -0.237 |
| **150** | Asclepias speciosa | 1.438 | 0.140 | -1.002 |
| **152** | Asclepias sullivantii | 0.773 | 0.535 | 0.488 |
| **155** | Asclepias verticillata | 1.270 | -0.235 | -1.067 |
| **157** | Asclepias viridis | 0.963 | -0.473 | -1.160 |
| **160** | Astragalus canadensis | 0.232 | 0.224 | -0.763 |
| **166** | Baptisia australis | 0.491 | -0.854 | -0.291 |
| **179** | Bouteloua curtipendula | -1.837 | 1.304 | 0.408 |
| **181** | Bouteloua gracilis | -1.589 | 0.296 | 0.746 |
| **185** | Bromus inermis | -0.667 | 0.428 | 0.526 |
| **202** | Carex annectens | -1.295 | 1.448 | 0.287 |
| **227** | Chamaecrista fasciculata | -0.233 | -0.864 | -0.491 |
| **231** | Chamaesyce nutans | -0.727 | -1.984 | 0.949 |
| **240** | Chloris verticillata | -1.695 | 1.076 | 0.118 |
| **243** | Cirsium altissimum | 0.957 | 0.467 | 2.172 |
| **260** | Cucurbita foetidissima | 1.275 | 0.525 | 3.648 |
| **285** | Desmanthus illinoensis | -0.642 | -0.982 | -0.485 |
| **288** | Desmodium illinoense | -0.415 | -0.558 | 0.672 |
| **294** | Dichanthelium acuminatum | -1.377 | 0.009 | -1.315 |
| **304** | Echinacea angustifolia | 0.647 | 2.087 | -0.465 |
| **305** | Echinacea pallida | 0.098 | 0.281 | -1.402 |
| **307** | Echinodorus berteroi | 0.968 | 0.237 | -1.297 |
| **313** | Eleusine indica | -1.475 | -0.444 | 0.512 |
| **315** | Elymus canadensis | -0.869 | 0.093 | -0.082 |
| **316** | Elymus villosus | -1.638 | -0.564 | -0.843 |
| **317** | Elymus virginicus | -1.381 | 0.816 | -0.389 |

## Table A.5 continued (2 of 4)

| KUT Code | Genus species | PCA Axis 1 | PCA Axis 2 | PCA Axis 3 |
|---|---|---|---|---|
| **323** | Eragrostis pectinacea | -0.941 | -0.054 | 2.253 |
| **326** | Erigeron annuus | 0.023 | 2.033 | 1.325 |
| **334** | Eupatorium altissimum | 0.476 | -0.697 | 1.392 |
| **335** | Euphorbia corollata | 0.239 | -0.179 | -0.432 |
| **338** | Euphorbia dentata | -0.255 | -2.419 | -0.467 |
| **340** | Euphorbia marginata | 0.938 | 0.105 | -0.747 |
| **344** | Festuca subverticillata | -1.899 | -0.419 | 0.074 |
| **365** | Helianthus annuus | 0.891 | 0.846 | 0.539 |
| **369** | Helianthus petiolaris | 0.982 | 1.844 | 0.667 |
| **370** | Helianthus tuberosus | 1.361 | -1.315 | 2.035 |
| **371** | Heliopsis helianthoides | 0.700 | -0.013 | -0.967 |
| **373** | Hesperostipa spartea | -2.114 | 0.436 | -0.425 |
| **379** | Hordeum jubatum | -1.087 | 1.089 | -0.260 |
| **380** | Hordeum pusillum | -1.678 | 1.729 | 0.502 |
| **396** | Koeleria macrantha | -1.757 | 1.536 | -1.006 |
| **399** | Lactuca canadensis | 1.344 | 0.194 | 0.306 |
| **400** | Lactuca ludoviciana | 1.377 | 0.727 | -1.268 |
| **408** | Lepidium densiflorum | -2.045 | -0.443 | -0.868 |
| **410** | Lepidium virginicum | -1.352 | -1.168 | 0.134 |
| **413** | Lespedeza capitata | 0.378 | -0.037 | -1.304 |
| **416** | Lespedeza violacea | -0.413 | -1.285 | -1.211 |
| **419** | Liatris aspera | 0.048 | 1.414 | -0.339 |
| **420** | Liatris mucronata | -0.075 | 1.776 | -1.172 |
| **421** | Liatris punctata | 0.170 | 2.154 | -1.125 |
| **447** | Mirabilis linearis | -0.396 | 0.462 | 0.441 |
| **450** | Monarda fistulosa | 0.407 | -1.434 | 0.759 |
| **466** | Oenothera biennis | 0.183 | -0.750 | 0.896 |
| **468** | Oenothera macrocarpa | 1.066 | -0.557 | -0.028 |
| **481** | Packera plattensis | 0.858 | -0.295 | -1.517 |
| **482** | Panicum capillare | 0.023 | 1.247 | -0.746 |
| **485** | Panicum virgatum | -0.163 | -0.107 | 1.183 |
| **488** | Pascopyrum smithii | -0.256 | 1.651 | -0.275 |
| **494** | Penstemon cobaea | 1.040 | 0.177 | -0.354 |
| **495** | Penstemon grandiflorus | 1.090 | -0.079 | -1.007 |
| **496** | Penstemon tubiflorus | 0.278 | -0.309 | -0.056 |
| **504** | Physalis pubescens | 0.487 | -1.620 | 0.420 |
| **513** | Plantago rugelii | 0.363 | 0.016 | 0.836 |
| **516** | Poa arida | -0.977 | 0.361 | 0.809 |
| **519** | Poa pratensis | -1.249 | 1.404 | 2.142 |

**Table A.5 continued (3 of 4)**

| KUT Code | Genus species | PCA Axis 1 | PCA Axis 2 | PCA Axis 3 |
|---|---|---|---|---|
| **534** | Polygonum virginianum | -0.573 | -1.096 | -0.181 |
| **542** | Prunella vulgaris | -0.738 | -1.226 | 0.675 |
| **547** | Psoralidium tenuiflorum | 0.602 | 0.208 | -0.711 |
| **553** | Ratibida pinnata | 1.003 | 0.307 | 0.214 |
| **565** | Rudbeckia hirta | 1.201 | 0.582 | 0.137 |
| **566** | Ruellia humilis | 0.648 | -0.962 | -0.328 |
| **575** | Salvia azurea | -0.050 | -0.880 | 0.598 |
| **576** | Salvia reflexa | -0.715 | -0.492 | -0.471 |
| **583** | Schizachyrium scoparium | -1.746 | 0.530 | 1.187 |
| **591** | Senna marilandica | -0.034 | -1.459 | 0.057 |
| **592** | Setaria pumila | -0.864 | -0.600 | 2.215 |
| **598** | Silphium integrifolium | 1.454 | -0.369 | 1.649 |
| **599** | Silphium laciniatum | 1.338 | 0.687 | 1.444 |
| **603** | Solanum carolinense | -0.143 | -1.363 | -0.664 |
| **605** | Solanum rostratum | -1.219 | -0.864 | -0.455 |
| **606** | Solidago canadensis | -0.002 | 0.012 | -0.157 |
| **608** | Solidago missouriensis | 0.460 | -1.696 | 0.145 |
| **609** | Solidago mollis | 0.383 | -0.076 | -1.356 |
| **610** | Solidago petiolaris | 0.269 | 0.606 | -1.169 |
| **613** | Sorghastrum nutans | -1.185 | 1.303 | -0.151 |
| **622** | Sporobolus heterolepis | -0.022 | -0.969 | 0.063 |
| **625** | Stellaria media | 0.004 | -0.023 | 0.293 |
| **627** | Stenosiphon linifolius | 1.113 | 0.181 | -0.271 |
| **633** | Symphyotrichum laeve | 1.078 | 0.394 | -0.890 |
| **635** | Symphyotrichum oblongifolium | 0.106 | 0.463 | -0.305 |
| **647** | Tradescantia bracteata | 1.484 | -0.063 | 0.274 |
| **648** | Tradescantia ohiensis | 0.624 | 1.030 | -0.375 |
| **651** | Tragopogon dubius | 0.964 | 0.524 | -0.104 |
| **674** | Verbesina alternifolia | 0.548 | -0.362 | 1.558 |
| **675** | Vernonia baldwinii | 0.268 | -0.846 | 0.701 |
| **687** | Vulpia octoflora | -2.151 | -0.081 | -0.796 |
| **689** | Xanthium strumarium | 2.797 | 1.882 | 1.140 |
| **693** | Zizia aurea | 0.346 | 1.083 | -1.773 |
| **999.001** | Baptisia alba | 0.464 | -0.507 | -0.024 |
| **999.002** | Echinacea atrorubens | 0.628 | 1.120 | -0.120 |
| **999.003** | Eryngium yuccifolium | 1.541 | 1.709 | 0.141 |
| **999.004** | Eupatorium purpureum | 0.737 | -1.634 | 0.745 |
| **999.005** | Helianthus salicifolius | 0.657 | -1.462 | -0.498 |

**Table A.5 continued (4 of 4)**

| KUT Code | Genus species | PCA Axis 1 | PCA Axis 2 | PCA Axis 3 |
|---|---|---|---|---|
| **999.006** | Liatris pycnostachya | 1.063 | -0.475 | -0.160 |
| **999.007** | Penstemon digitalis | 0.739 | -0.134 | 0.964 |
| **999.008** | Prenanthes aspera | 0.327 | 1.706 | -1.382 |
| **999.009** | Rudbeckia lacinata | 0.688 | -0.294 | 0.398 |
| **999.010** | Solidago nemoralis | 0.297 | -0.184 | -0.712 |
| **999.011** | Solidago ulmifolia | -0.343 | -1.133 | 0.111 |
| **999.012** | Asclepias incarnata | 0.735 | -1.303 | 0.432 |

## Table A.6 Leaf and Root Morphology

| KUT Code | Genus species | Leaf Thickness (mm) | Leaf Angle (deg) | Total Root Length (cm) | Avg Root Dia (mm) | Root Volume (cm3) |
|---|---|---|---|---|---|---|
| **106** | Achillea millefolium | 0.274 | 49.17 | 427.3 | 0.250 | 0.209 |
| **112** | Ageratina altissima | 0.183 | 0.00 | 417.2 | 0.239 | 0.182 |
| **121** | Amaranthus blitoides | 0.192 | 5.71 | 224.9 | 0.229 | 0.071 |
| **123** | Amaranthus retroflexus | 0.190 | 0.00 | 883.2 | 0.134 | 0.124 |
| **126** | Ambrosia psilostachya | 0.242 | 40.00 | 690.6 | 0.206 | 0.225 |
| **129** | Amorpha canescens | 0.124 | 3.83 | 470.0 | 0.194 | 0.127 |
| **133** | Andropogon gerardii | 0.136 | 68.75 | 346.5 | 0.270 | 0.197 |
| **137** | Antennaria neglecta | 0.206 | 52.40 | 510.0 | 0.243 | 0.207 |
| **138** | Apocynum cannabinum | 0.152 | - | 266.1 | 0.305 | 0.175 |
| **145** | Aristida oligantha | 0.126 | 50.00 | 580.0 | 0.195 | 0.166 |
| **146** | Aristida purpurea | 0.120 | 70.00 | 363.9 | 0.261 | 0.187 |
| **148** | Artemisia ludoviciana | 0.186 | 45.00 | 422.7 | 0.283 | 0.238 |
| **150** | Asclepias speciosa | 0.194 | 0.00 | 271.1 | 0.405 | 0.334 |
| **152** | Asclepias sullivantii | 0.311 | 37.60 | 385.5 | 0.309 | 0.282 |
| **155** | Asclepias verticillata | 0.173 | 5.00 | 268.0 | 0.429 | 0.340 |
| **157** | Asclepias viridis | 0.198 | 30.00 | 80.4 | 0.364 | 0.081 |
| **160** | Astragalus canadensis | 0.170 | 45.00 | 209.5 | 0.346 | 0.186 |
| **166** | Baptisia australis | 0.253 | 70.00 | 245.9 | 0.341 | 0.219 |
| **179** | Bouteloua curtipendula | 0.117 | 35.00 | 605.2 | 0.183 | 0.121 |
| **181** | Bouteloua gracilis | 0.142 | 71.67 | 841.0 | 0.167 | 0.166 |
| **185** | Bromus inermis | 0.180 | 65.00 | 561.9 | 0.229 | 0.227 |
| **202** | Carex annectens | 0.154 | 77.60 | 914.2 | 0.146 | 0.144 |
| **227** | Chamaecrista fasciculata | 0.106 | 0.00 | 357.6 | 0.256 | 0.169 |
| **231** | Chamaesyce nutans | 0.102 | 15.00 | 783.1 | 0.189 | 0.217 |
| **240** | Chloris verticillata | 0.081 | 55.00 | 448.7 | 0.209 | 0.148 |
| **243** | Cirsium altissimum | 0.344 | 30.00 | 585.5 | 0.252 | 0.273 |
| **260** | Cucurbita foetidissima | 0.290 | 20.00 | 408.5 | 0.292 | 0.195 |
| **285** | Desmanthus illinoensis | 0.108 | 6.67 | 347.9 | 0.254 | 0.163 |
| **288** | Desmodium illinoense | 0.182 | 75.00 | 780.4 | 0.225 | 0.272 |
| **294** | Dichanthelium acuminatum | 0.087 | 55.00 | 423.1 | 0.168 | 0.098 |
| **304** | Echinacea angustifolia | 0.376 | 35.00 | 190.1 | 0.276 | 0.115 |
| **305** | Echinacea pallida | - | - | 215.4 | 0.283 | 0.135 |
| **307** | Echinodorus berteroi | 0.200 | - | 232.9 | 0.431 | 0.339 |
| **313** | Eleusine indica | 0.083 | 56.67 | 1259.0 | 0.125 | 0.149 |
| **315** | Elymus canadensis | 0.143 | 35.00 | 423.8 | 0.215 | 0.154 |
| **316** | Elymus villosus | 0.110 | 70.00 | 704.3 | 0.150 | 0.131 |
| **317** | Elymus virginicus | 0.130 | 66.67 | 804.3 | 0.172 | 0.179 |

## Table A.6 continued (2 of 4)

| KUT Code | Genus species | Leaf Thickness (mm) | Leaf Angle (deg) | Total Root Length (cm) | Avg Root Dia (mm) | Root Volume (cm3) |
|---|---|---|---|---|---|---|
| **326** | Erigeron annuus | - | - | 315.6 | 0.248 | 0.153 |
| **334** | Eupatorium altissimum | 0.244 | 25.00 | 388.4 | 0.352 | 0.361 |
| **335** | Euphorbia corollata | - | - | 315.5 | 0.375 | 0.348 |
| **338** | Euphorbia dentata | 0.117 | 10.00 | 553.5 | 0.209 | 0.173 |
| **340** | Euphorbia marginata | 0.250 | - | 209.2 | 0.344 | 0.197 |
| **344** | Festuca subverticillata | 0.087 | 80.00 | 648.9 | 0.174 | 0.148 |
| **365** | Helianthus annuus | 0.286 | 15.00 | 397.7 | 0.296 | 0.257 |
| **369** | Helianthus petiolaris | 0.371 | 0.00 | 475.4 | 0.234 | 0.188 |
| **370** | Helianthus tuberosus | 0.303 | 5.00 | 270.6 | 0.396 | 0.338 |
| **371** | Heliopsis helianthoides | 0.211 | 10.00 | 249.5 | 0.382 | 0.283 |
| **373** | Hesperostipa spartea | 0.116 | 70.00 | 742.8 | 0.149 | 0.125 |
| **379** | Hordeum jubatum | 0.129 | 75.00 | 738.5 | 0.185 | 0.183 |
| **380** | Hordeum pusillum | 0.099 | 70.00 | 800.7 | 0.183 | 0.197 |
| **396** | Koeleria macrantha | 0.144 | 73.38 | 968.8 | 0.127 | 0.109 |
| **399** | Lactuca canadensis | 0.180 | 15.00 | 208.3 | 0.399 | 0.258 |
| **400** | Lactuca ludoviciana | 0.225 | - | 100.9 | 0.418 | 0.139 |
| **408** | Lepidium densiflorum | 0.126 | 57.50 | 1689.1 | 0.097 | 0.109 |
| **410** | Lepidium virginicum | 0.190 | 20.00 | 939.3 | 0.118 | 0.102 |
| **413** | Lespedeza capitata | 0.163 | 0.00 | 343.7 | 0.297 | 0.238 |
| **416** | Lespedeza violacea | 0.103 | 15.00 | 223.3 | 0.315 | 0.171 |
| **419** | Liatris aspera | 0.353 | 75.00 | 398.5 | 0.222 | 0.155 |
| **420** | Liatris mucronata | 0.375 | 90.00 | 161.9 | 0.245 | 0.055 |
| **421** | Liatris punctata | 0.410 | 75.00 | 98.2 | 0.304 | 0.075 |
| **447** | Mirabilis linearis | 0.320 | 35.00 | 331.1 | 0.203 | 0.103 |
| **450** | Monarda fistulosa | 0.205 | 2.42 | 663.2 | 0.234 | 0.266 |
| **466** | Oenothera biennis | 0.256 | 39.79 | 971.2 | 0.184 | 0.272 |
| **468** | Oenothera macrocarpa | 0.320 | 7.50 | 238.8 | 0.348 | 0.189 |
| **481** | Packera plattensis | 0.220 | 20.00 | 166.6 | 0.418 | 0.206 |
| **482** | Panicum capillare | 0.150 | - | 553.6 | 0.183 | 0.146 |
| **485** | Panicum virgatum | 0.151 | 58.00 | 506.5 | 0.266 | 0.249 |
| **488** | Pascopyrum smithii | 0.230 | 50.00 | 566.7 | 0.195 | 0.168 |
| **494** | Penstemon cobaea | 0.319 | 10.00 | 152.8 | 0.420 | 0.202 |
| **495** | Penstemon grandiflorus | 0.313 | 50.00 | 194.1 | 0.364 | 0.178 |
| **496** | Penstemon tubiflorus | 0.276 | 49.29 | 566.0 | 0.249 | 0.259 |
| **504** | Physalis pubescens | 0.335 | 20.00 | 808.0 | 0.173 | 0.189 |
| **513** | Plantago rugelii | 0.253 | 0.00 | 455.3 | 0.254 | 0.220 |
| **516** | Poa arida | 0.197 | 60.00 | 1212.9 | 0.135 | 0.170 |

Table A.6 continued (3 of 4)

| KUT Code | Genus species | Leaf Thickness (mm) | Leaf Angle (deg) | Total Root Length (cm) | Avg Root Dia (mm) | Root Volume (cm3) |
|---|---|---|---|---|---|---|
| **519** | Poa pratensis | 0.148 | 80.75 | 1534.1 | 0.143 | 0.185 |
| **534** | Polygonum virginianum | 0.165 | 22.50 | 730.9 | 0.149 | 0.125 |
| **542** | Prunella vulgaris | 0.214 | 0.00 | 400.0 | 0.256 | 0.208 |
| **547** | Psoralidium tenuiflorum | 0.288 | 0.00 | 87.6 | 0.318 | 0.062 |
| **553** | Ratibida pinnata | 0.316 | 50.00 | 239.7 | 0.369 | 0.236 |
| **565** | Rudbeckia hirta | 0.393 | 50.00 | 522.7 | 0.275 | 0.293 |
| **566** | Ruellia humilis | 0.165 | 15.00 | 194.3 | 0.425 | 0.258 |
| **575** | Salvia azurea | 0.202 | 27.00 | 355.4 | 0.305 | 0.241 |
| **576** | Salvia reflexa | 0.204 | 1.00 | 943.7 | 0.172 | 0.217 |
| **583** | Schizachyrium scoparium | 0.103 | 78.86 | 552.1 | 0.217 | 0.199 |
| **591** | Senna marilandica | 0.138 | 0.00 | 301.0 | 0.328 | 0.245 |
| **592** | Setaria pumila | 0.107 | 72.17 | 903.6 | 0.175 | 0.210 |
| **598** | Silphium integrifolium | 0.340 | 30.00 | 229.5 | 0.393 | 0.277 |
| **599** | Silphium laciniatum | 0.568 | 75.39 | 314.8 | 0.329 | 0.256 |
| **603** | Solanum carolinense | 0.164 | 0.00 | 518.0 | 0.227 | 0.208 |
| **605** | Solanum rostratum | 0.163 | 10.00 | 517.0 | 0.195 | 0.147 |
| **606** | Solidago canadensis | - | - | - | - | - |
| **608** | Solidago missouriensis | 0.290 | 40.00 | 323.3 | 0.262 | 0.150 |
| **609** | Solidago mollis | 0.165 | 40.00 | 154.8 | 0.384 | 0.178 |
| **610** | Solidago petiolaris | 0.158 | 35.00 | 191.9 | 0.331 | 0.159 |
| **613** | Sorghastrum nutans | 0.142 | 61.67 | 420.7 | 0.237 | 0.182 |
| **622** | Sporobolus heterolepis | 0.220 | - | - | - | - |
| **625** | Stellaria media | - | - | - | - | - |
| **627** | Stenosiphon linifolius | 0.333 | 15.00 | 370.8 | 0.292 | 0.177 |
| **633** | Symphyotrichum laeve | 0.258 | 25.00 | 343.5 | 0.322 | 0.269 |
| **635** | Symphyotrichum oblongifolium | 0.203 | 25.00 | 361.5 | 0.315 | 0.270 |
| **647** | Tradescantia bracteata | 0.325 | 65.00 | 220.3 | 0.371 | 0.176 |
| **648** | Tradescantia ohiensis | 0.273 | 75.00 | 256.3 | 0.329 | 0.227 |
| **651** | Tragopogon dubius | 0.262 | 70.00 | 190.9 | 0.435 | 0.233 |
| **674** | Verbesina alternifolia | 0.312 | 60.67 | 331.4 | 0.454 | 0.382 |
| **675** | Vernonia baldwinii | 0.180 | 50.00 | 292.3 | 0.332 | 0.238 |
| **687** | Vulpia octoflora | 0.106 | 70.00 | 1230.5 | 0.112 | 0.117 |
| **689** | Xanthium strumarium | 0.550 | 0.00 | 238.9 | 0.455 | 0.323 |
| **693** | Zizia aurea | 0.190 | - | 297.8 | 0.311 | 0.226 |
| **999.001** | Baptisia alba | 0.211 | 80.00 | 181.0 | 0.379 | 0.221 |
| **999.002** | Echinacea atrorubens | 0.448 | 55.00 | 319.6 | 0.300 | 0.203 |
| **999.003** | Eryngium yuccifolium | 0.434 | 60.00 | 288.8 | 0.370 | 0.325 |

**Table A.6 continued (4 of 4)**

| KUT Code | Genus species | Leaf Thickness (mm) | Leaf Angle (deg) | Total Root Length (cm) | Avg Root Dia (mm) | Root Volume (cm3) |
|---|---|---|---|---|---|---|
| **999.004** | Eupatorium purpureum | 0.164 | 0.00 | 427.4 | 0.316 | 0.331 |
| **999.005** | Helianthus salicifolius | 0.202 | 0.00 | 335.1 | 0.324 | 0.232 |
| **999.006** | Liatris pycnostachya | 0.277 | 50.00 | 412.3 | 0.280 | 0.239 |
| **999.007** | Penstemon digitalis | 0.297 | 42.33 | 429.0 | 0.316 | 0.325 |
| **999.008** | Prenanthes aspera | 0.207 | 45.00 | 613.7 | 0.215 | 0.223 |
| **999.009** | Rudbeckia lacinata | 0.228 | 53.38 | 381.9 | 0.337 | 0.280 |
| **999.010** | Solidago nemoralis | 0.127 | - | 199.1 | 0.376 | 0.202 |
| **999.011** | Solidago ulmifolia | 0.120 | - | 371.0 | 0.309 | 0.266 |
| **999.012** | Asclepias incarnata | 0.180 | 11.43 | 516.7 | 0.320 | 0.328 |

**Table A.7 Mycorrhizal data. Wilson and Hartnett, 1998.**

| KUT Code | Genus species | Mycorrhizal Responsiveness* (%) | Mycorrhizal Root Colonization* (%) |
|---|---|---|---|
| **185** | Bromus inermis | -33.3 | 10.4 |
| **380** | Hordeum pusillum | -16.7 | 14.4 |
| **396** | Koeleria macrantha | -16.7 | 26.2 |
| **379** | Hordeum jubatum | -8.8 | 19 |
| **419** | Liatris aspera | -0.4 | 59.2 |
| **315** | Elymus canadensis | 5.3 | 15.1 |
| **106** | Achillea millefolium | 22.9 | 35.3 |
| **466** | Oenothera biennis | 29.6 | 40.8 |
| **148** | Artemisia ludoviciana | 44.3 | 30.7 |
| **181** | Bouteloua gracilis | 67.9 | 32.8 |
| **285** | Desmanthus illinoensis | 75.8 | 32 |
| **166** | Baptisia australis | 85.2 | 37.4 |
| **179** | Bouteloua curtipendula | 86.5 | 54.3 |
| **575** | Salvia azurea | 87.8 | 58.4 |
| **304** | Echinacea angustifolia | 89.3 | 24.8 |
| **999.010** | Solidago nemoralis | 93 | 57.7 |
| **553** | Ratibida pinnata | 96 | 37.8 |
| **155** | Asclepias verticillata | 97.2 | 51.7 |
| **565** | Rudbeckia hirta | 97.8 | 24.8 |
| **413** | Lespedeza capitata | 98 | 24.4 |
| **485** | Panicum virgatum | 98.2 | 61.4 |
| **133** | Andropogon gerardii | 99.1 | 50.2 |
| **583** | Schizachyrium scoparium | 99.4 | 51.2 |
| **613** | Sorghastrum nutans | 99.5 | 44.7 |

## Table A.8 Calculated traits.

| KUT Code | Genus species | SLA ($cm^2$ $g^{-1}$) | SRL (m $g^{-1}$) | Leaf Density (g $cm^{-3}$) | Root Density (g $cm^{-3}$) | Fraction Root | Root: Shoot | Water use efficiency | Date first bloom |
|---|---|---|---|---|---|---|---|---|---|
| **106** | Achillea millefolium | 146.0 | 65.51 | 0.279 | 0.351 | 0.352 | 0.552 | 3.189 | 129.6 |
| **112** | Ageratina altissima | 257.8 | 168.97 | 0.281 | 0.161 | 0.258 | 0.332 | 2.694 | 223 |
| **121** | Amaranthus blitoides | 215.7 | 64.61 | 0.244 | 0.534 | 0.126 | 0.125 | 5.202 | - |
| **123** | Amaranthus retroflexus | 155.6 | 181.45 | 0.410 | 0.492 | 0.216 | 0.313 | 5.713 | - |
| **126** | Ambrosia psilostachya | 97.9 | 109.24 | 0.451 | 0.374 | 0.348 | 0.549 | 2.652 | 208 |
| **129** | Amorpha canescens | 261.3 | 73.78 | 0.314 | 0.586 | 0.343 | 0.479 | 2.657 | 156.2 |
| **133** | Andropogon gerardii | 135.1 | 45.70 | 0.862 | 0.400 | 0.477 | 1.026 | 4.439 | 200.2 |
| **137** | Antennaria neglecta | 151.5 | 104.49 | 0.324 | 0.226 | 0.215 | 0.275 | 1.517 | 93.4 |
| **138** | Apocynum cannabinum | 146.6 | 54.04 | 0.555 | 0.327 | 0.302 | 0.361 | 4.586 | 139.6 |
| **145** | Aristida oligantha | 173.6 | 126.95 | 0.517 | 0.303 | 0.237 | 0.348 | 6.248 | - |
| **146** | Aristida purpurea | 188.9 | 68.76 | 0.461 | 0.327 | 0.372 | 0.586 | 6.709 | - |
| **148** | Artemisia ludoviciana | 146.8 | 62.04 | 0.419 | 0.295 | 0.248 | 0.323 | 4.342 | 244 |
| **150** | Asclepias speciosa | 208.0 | 35.06 | 0.272 | 0.233 | 0.453 | 0.679 | 4.097 | - |
| **152** | Asclepias sullivantii | 146.0 | 80.13 | 0.223 | 0.184 | 0.697 | 2.408 | 2.990 | 157.3 |
| **155** | Asclepias verticillata | 172.5 | 29.21 | 0.308 | 0.266 | 0.592 | 1.079 | 3.718 | 168.7 |
| **157** | Asclepias viridis | 219.7 | 41.57 | 0.265 | 0.321 | 0.579 | 1.146 | 4.872 | 131.4 |
| **160** | Astragalus canadensis | 146.3 | 59.02 | 0.432 | 0.308 | 0.251 | 0.321 | 4.204 | - |
| **166** | Baptisia australis | 143.4 | 38.02 | 0.317 | 0.313 | 0.307 | 0.425 | 4.788 | 121.7 |
| **179** | Bouteloua curtipendula | 162.5 | 100.63 | 0.548 | 0.551 | 0.385 | 0.628 | 5.590 | 183.8 |
| **181** | Bouteloua gracilis | 157.1 | 149.71 | 0.472 | 0.384 | 0.416 | 0.469 | 6.596 | 202.7 |
| **185** | Bromus inermis | 149.6 | 97.60 | 0.474 | 0.254 | 0.493 | 0.985 | 3.246 | 141 |
| **202** | Carex annectens | 182.4 | 146.37 | 0.480 | 0.418 | 0.519 | 1.041 | 2.055 | - |
| **227** | Chamaecrista fasciculata | 163.9 | 128.35 | 0.633 | 0.165 | 0.122 | 0.162 | 4.420 | 206.3 |
| **231** | Chamaesyce nutans | 124.7 | 112.10 | 0.713 | 0.336 | 0.217 | 0.284 | 4.367 | - |
| **240** | Chloris verticillata | 273.3 | 74.34 | 0.519 | 0.405 | 0.333 | 0.849 | 6.523 | 174 |
| **243** | Cirsium altissimum | 102.2 | 119.68 | 0.326 | 0.206 | 0.485 | 1.001 | 4.054 | 221 |
| **260** | Cucurbita foetidissima | 122.9 | 67.42 | 0.304 | 0.399 | 0.649 | 1.867 | 4.207 | 160.8 |
| **285** | Desmanthus illinoensis | 140.9 | 53.50 | - | 0.417 | 0.310 | 0.455 | 4.378 | 172.9 |
| **288** | Desmodium illinoense | 157.9 | 137.82 | 0.357 | 0.263 | 0.539 | 1.485 | 3.820 | 167.8 |
| **294** | Dichanthelium acuminatum | 309.4 | 180.90 | 0.337 | 0.264 | 0.292 | 0.490 | 2.564 | - |

## Table A.8 continued (2 of 4)

| KUT Code | Genus species | SLA (cm$^2$ g$^{-1}$) | SRL (m g$^{-1}$) | Leaf Density (g cm$^{-3}$) | Root Density (g cm$^{-3}$) | Fraction Root | Root: Shoot | Water use efficieny | Date first bloom |
|---|---|---|---|---|---|---|---|---|---|
| **304** | Echinacea angustifolia | 100.5 | 87.82 | 0.292 | 0.343 | 0.541 | 1.051 | 3.451 | 149 |
| **305** | Echinacea pallida | 103.4 | 47.96 | - | 0.333 | 0.344 | 0.523 | 4.041 | - |
| **307** | Echinodorus berteroi | 189.8 | 17.10 | 0.263 | 0.402 | 0.486 | 0.944 | 3.616 | - |
| **313** | Eleusine indica | 239.8 | 271.47 | 0.723 | 0.314 | 0.232 | 0.357 | 4.432 | 208 |
| **315** | Elymus canadensis | 159.3 | 100.33 | 0.466 | 0.293 | 0.329 | 0.545 | 3.243 | 165.7 |
| **316** | Elymus villosus | 180.6 | 148.17 | 0.407 | 0.404 | 0.245 | 0.333 | 2.351 | - |
| **317** | Elymus virginicus | 167.4 | 167.05 | 0.544 | 0.278 | 0.300 | 0.439 | 3.773 | - |
| **323** | Eragrostis pectinacea | - | 128.74 | - | 0.372 | 0.264 | 0.355 | 4.744 | - |
| **326** | Erigeron annuus | 242.2 | 62.75 | - | 0.329 | 0.383 | 0.621 | 4.776 | 138.7 |
| **334** | Eupatorium altissimum | 85.9 | 57.35 | 0.588 | 0.226 | 0.347 | 0.497 | 3.700 | - |
| **335** | Euphorbia corollata | - | 25.90 | - | 0.350 | - | - | - | 210.4 |
| **338** | Euphorbia dentata | 177.6 | 121.35 | 0.542 | 0.278 | 0.162 | 0.182 | 3.137 | - |
| **340** | Euphorbia marginata | 187.4 | 110.69 | 0.226 | 0.105 | 0.225 | 0.313 | 3.688 | 192.1 |
| **344** | Festuca subverticillata | 163.9 | 177.38 | 0.673 | 0.269 | 0.296 | 0.422 | 3.066 | - |
| **365** | Helianthus annuus | 95.0 | 98.98 | 0.410 | 0.185 | 0.199 | 0.249 | 4.917 | 179 |
| **369** | Helianthus petiolaris | 84.4 | 107.60 | 0.346 | 0.262 | 0.153 | 0.201 | 4.442 | - |
| **370** | Helianthus tuberosus | 79.5 | 38.30 | 0.429 | 0.254 | 0.323 | 0.446 | 5.213 | 241.2 |
| **371** | Heliopsis helianthoides | 143.2 | 58.61 | 0.407 | 0.171 | 0.304 | 0.377 | 3.423 | 200.6 |
| **373** | Hesperostipa spartea | 287.3 | 141.63 | 0.623 | 0.435 | 0.443 | 1.576 | 2.609 | 142 |
| **379** | Hordeum jubatum | 280.5 | 150.89 | 0.373 | 0.271 | 0.284 | 0.425 | 3.547 | - |
| **380** | Hordeum pusillum | 192.5 | 157.16 | 0.558 | 0.279 | 0.405 | 1.834 | 3.031 | 149 |
| **396** | Koeleria macrantha | 160.7 | 283.30 | 0.487 | 0.334 | 0.478 | 0.923 | 2.975 | 145.9 |
| **399** | Lactuca canadensis | 247.6 | 37.44 | 0.228 | 0.228 | 0.489 | 0.941 | 4.184 | - |
| **400** | Lactuca ludoviciana | 274.7 | 28.44 | 0.163 | 0.266 | 0.374 | 0.515 | 3.223 | - |
| **408** | Lepidium densiflorum | 163.4 | 361.83 | 0.568 | 0.451 | 0.175 | 0.208 | 2.841 | 134 |
| **410** | Lepidium virginicum | 129.2 | 198.05 | 0.570 | 0.554 | 0.225 | 0.369 | 3.897 | - |
| **413** | Lespedeza capitata | 156.2 | 46.38 | 0.409 | 0.358 | 0.296 | 0.428 | 2.614 | 224.6 |
| **416** | Lespedeza violacea | 191.2 | 51.67 | 0.585 | 0.288 | 0.247 | 0.500 | 3.971 | 244 |
| **419** | Liatris aspera | 90.8 | 144.06 | 0.352 | 0.191 | 0.581 | 1.300 | 2.978 | 235.8 |
| **420** | Liatris mucronata | 69.0 | 92.39 | 0.402 | 0.286 | 0.764 | 4.061 | 2.516 | 227.7 |
| **421** | Liatris punctata | 54.9 | 118.81 | 0.389 | 0.168 | 0.695 | 3.059 | 2.218 | 233.3 |
| **447** | Mirabilis linearis | 85.8 | 86.22 | 0.434 | 0.509 | 0.594 | 1.419 | 5.166 | - |
| **450** | Monarda fistulosa | 163.7 | 91.96 | 0.336 | 0.274 | 0.357 | 0.629 | 3.904 | 162.2 |
| **466** | Oenothera biennis | 121.5 | 160.43 | 0.328 | 0.267 | 0.274 | 0.390 | 3.139 | 220.1 |
| **468** | Oenothera macrocarpa | 109.8 | 44.69 | 0.319 | 0.311 | 0.163 | 0.195 | 3.435 | 128.3 |
| **481** | Packera plattensis | 130.3 | 35.29 | 0.422 | 0.270 | 0.460 | 0.785 | 3.502 | 108.8 |
| **482** | Panicum capillare | 315.5 | 185.16 | 0.211 | 0.205 | - | - | 5.249 | - |
| **485** | Panicum virgatum | 164.1 | 56.76 | 0.435 | 0.358 | 0.487 | 0.928 | 5.857 | 208.7 |

**Table A.8 continued (3 of 4)**

| KUT Code | Genus species | SLA (cm$^2$ g$^{-1}$) | SRL (m g$^{-1}$) | Leaf Density (g cm$^{-3}$) | Root Density (g cm$^{-3}$) | Fraction Root | Root: Shoot | Water use efficiency | Date first bloom |
|---|---|---|---|---|---|---|---|---|---|
| **488** | Pascopyrum smithii | 63.2 | 122.15 | 0.517 | 0.285 | 0.247 | 0.565 | 6.099 | 171.5 |
| **494** | Penstemon cobaea | 78.3 | 23.10 | 0.409 | 0.343 | 0.413 | 0.434 | 3.953 | 135.9 |
| **495** | Penstemon grandiflorus | 96.5 | 35.95 | 0.296 | 0.288 | 0.314 | 0.467 | 4.344 | 135.1 |
| **496** | Penstemon tubiflorus | 132.4 | 83.70 | 0.337 | 0.293 | 0.522 | 0.226 | 3.102 | 159.7 |
| **504** | Physalis pubescens | 119.3 | 116.22 | 0.253 | 0.386 | 0.614 | 1.459 | 1.848 | - |
| **513** | Plantago rugelii | 128.2 | 128.42 | 0.373 | 0.176 | 0.272 | 0.578 | 3.262 | - |
| **516** | Poa arida | 110.1 | 258.71 | 0.487 | 0.296 | 0.292 | 0.451 | 3.765 | - |
| **519** | Poa pratensis | 140.8 | 302.77 | 0.459 | 0.343 | 0.557 | 1.362 | 2.560 | 125.2 |
| **534** | Polygonum virginianum | 165.5 | 192.06 | 0.398 | 0.358 | 0.193 | 0.261 | 4.169 | - |
| **542** | Prunella vulgaris | 83.4 | 113.25 | 0.831 | 0.177 | 0.202 | 0.225 | 3.727 | 205.6 |
| **547** | Psoralidium tenuiflorum | 100.8 | 34.26 | 0.371 | 0.426 | 0.835 | 6.482 | 3.264 | 135.8 |
| **553** | Ratibida pinnata | 118.1 | 49.98 | 0.302 | 0.217 | 0.347 | 0.446 | 3.733 | - |
| **565** | Rudbeckia hirta | 119.1 | 138.57 | 0.226 | 0.134 | 0.316 | 0.441 | 3.588 | 166 |
| **566** | Ruellia humilis | 181.2 | 19.06 | 0.365 | 0.413 | 0.332 | 0.517 | 3.239 | 154.1 |
| **575** | Salvia azurea | 118.9 | 45.56 | 0.443 | 0.404 | 0.434 | 0.733 | 3.551 | 183 |
| **576** | Salvia reflexa | - | 187.07 | - | 0.246 | - | - | 2.189 | 174 |
| **583** | Schizachyrium scoparium | 176.3 | 75.63 | 0.677 | 0.426 | 0.549 | 6.456 | 4.739 | 232.1 |
| **591** | Senna marilandica | 129.5 | 51.81 | 0.646 | 0.330 | 0.278 | 0.342 | 4.290 | 200.3 |
| **592** | Setaria pumila | 259.2 | 122.98 | 0.443 | 0.387 | 0.349 | 0.508 | 4.766 | 182 |
| **598** | Silphium integrifolium | 98.6 | 32.96 | 0.398 | 0.257 | 0.537 | 1.146 | 4.447 | 179.6 |
| **599** | Silphium laciniatum | 60.2 | 65.88 | 0.494 | 0.225 | 0.659 | 1.977 | 3.329 | 168.1 |
| **603** | Solanum carolinense | 164.1 | 90.13 | 0.393 | 0.309 | 0.390 | 0.646 | 4.177 | 149.4 |
| **605** | Solanum rostratum | 115.1 | 170.32 | 0.640 | 0.225 | 0.270 | 0.453 | 2.835 | 159.4 |
| **606** | Solidago canadensis | .- | - | - | - | - | - | - | 219 |
| **608** | Solidago missouriensis | 133.3 | 83.99 | 0.260 | 0.455 | 0.528 | 1.178 | 3.282 | 196.1 |
| **609** | Solidago mollis | 154.3 | 43.37 | 0.386 | 0.205 | 0.592 | 0.755 | 2.804 | - |
| **610** | Solidago petiolaris | 162.4 | 36.81 | 0.413 | 0.331 | 0.367 | 0.540 | 3.730 | - |
| **613** | Sorghastrum nutans | 165.9 | 78.73 | 0.485 | 0.320 | 0.405 | 0.858 | 7.120 | 230.6 |
| **622** | Sporobolus heterolepis | - | - | - | - | - | - | 3.856 | 269 |
| **625** | Stellaria media | 169.8 | - | - | - | - | - | - | - |
| **627** | Stenosiphon linifolius | 106.6 | 71.67 | 0.289 | 0.293 | 0.362 | 0.534 | 3.760 | 174.2 |
| **633** | Symphyotrichum laeve | 163.6 | 86.72 | 0.265 | 0.200 | 0.410 | 1.429 | 3.509 | 241.2 |
| **635** | Symphyotrichum oblongifolium | 136.6 | 44.80 | 0.462 | 0.324 | 0.460 | 0.808 | 4.232 | 252.2 |
| **647** | Tradescantia bracteata | 188.3 | 92.01 | 0.176 | 0.337 | 0.611 | 1.714 | 3.778 | 136.4 |
| **648** | Tradescantia ohiensis | 194.4 | 84.37 | 0.203 | 0.239 | 0.654 | 2.327 | 4.243 | 142.7 |
| **651** | Tragopogon dubius | 110.2 | 22.84 | 0.377 | 0.371 | 0.547 | 1.105 | 4.118 | 131.3 |

**Table A.8 continued (4 of 4)**

| KUT Code | Genus species | SLA (cm$^2$ g$^{-1}$) | SRL (m g$^{-1}$) | Leaf Density (g cm$^{-3}$) | Root Density (g cm$^{-3}$) | Fraction Root | Root: Shoot | Water use efficieny | Date first bloom |
|---|---|---|---|---|---|---|---|---|---|
| **674** | Verbesina alternifolia | 135.3 | 26.56 | 0.249 | 0.312 | 0.422 | 0.826 | 3.137 | 211.6 |
| **675** | Vernonia baldwinii | 162.1 | 45.46 | 0.369 | 0.349 | 0.528 | 1.042 | 4.026 | 190.4 |
| **687** | Vulpia octoflora | 233.5 | 437.35 | 0.731 | 0.244 | 0.330 | 0.939 | 2.714 | - |
| **689** | Xanthium strumarium | 166.6 | 43.08 | 0.100 | 0.161 | 0.201 | 0.410 | 6.017 | - |
| **693** | Zizia aurea | 146.8 | 99.26 | 0.359 | 0.133 | 0.257 | 0.345 | 2.600 | 128.6 |
| **999.001** | Baptisia alba | 133.7 | 47.42 | 0.373 | 0.216 | 0.419 | 0.691 | 4.583 | - |
| **999.002** | Echinacea atrorubens | 107.9 | 35.08 | 0.225 | 0.489 | 0.612 | 1.621 | 3.386 | - |
| **999.003** | Eryngium yuccifolium | 98.6 | 57.28 | 0.242 | 0.216 | 0.419 | 0.658 | 3.054 | - |
| **999.004** | Eupatorium purpureum | 237.9 | 67.92 | 0.312 | 0.217 | 0.351 | 0.480 | 4.081 | - |
| **999.005** | Helianthus salicifolius | 148.7 | 62.00 | 0.374 | 0.266 | 0.404 | 0.642 | 4.066 | - |
| **999.006** | Liatris pycnostachya | 177.2 | 126.91 | 0.214 | 0.137 | 0.307 | 0.419 | 3.789 | - |
| **999.007** | Penstemon digitalis | 112.4 | 59.37 | 0.344 | 0.308 | 0.422 | 0.620 | 2.764 | - |
| **999.008** | Prenanthes aspera | 161.3 | 191.78 | 0.330 | 0.143 | 0.630 | 0.641 | 2.568 | - |
| **999.009** | Rudbeckia lacinata | 218.5 | 66.38 | 0.214 | 0.224 | 0.493 | 0.969 | 3.354 | - |
| **999.010** | Solidago nemoralis | 150.3 | 53.38 | 0.452 | 0.202 | 0.409 | 0.610 | 3.499 | - |
| **999.011** | Solidago ulmifolia | 157.9 | 45.69 | 0.606 | 0.315 | 0.335 | 0.473 | 4.194 | - |
| **999.012** | Asclepias incarnata | 166.2 | 50.03 | 0.342 | 0.330 | 0.550 | 1.208 | 2.479 | - |

**Table A.9 Konza species abundance, contrasts. (Log 10 transformed)**

| KUT Code | Genus species | Konza Avg Abd | Upland (f) | Lowland (t) | Grazed (G) | Ungrazed (U) | Frequent (1) | Infrequent (20) |
|---|---|---|---|---|---|---|---|---|
| **106** | Achillea millefolium | -0.374 | -0.371 | -0.414 | -0.421 | -0.990 | -0.856 | -0.548 |
| **112** | Ageratina altissima | -4.276 | - | -3.993 | -4.139 | - | - | -4.276 |
| **121** | Amaranthus blitoides | - | - | - | - | - | - | - |
| **123** | Amaranthus retroflexus | -3.975 | -3.692 | - | -3.838 | - | - | -3.975 |
| **126** | Ambrosia psilostachya | 0.981 | 0.928 | 0.996 | 0.776 | 0.621 | 0.797 | 0.521 |
| **129** | Amorpha canescens | 0.736 | 0.715 | 0.720 | 0.477 | 0.511 | 0.579 | 0.216 |
| **133** | Andropogon gerardii | 1.646 | 1.559 | 1.688 | 1.074 | 1.463 | 1.509 | 1.080 |
| **137** | Antennaria neglecta | -1.069 | -1.008 | -1.184 | -1.120 | -1.715 | -1.353 | -1.388 |
| **138** | Apocynum cannabinum | -0.508 | -1.997 | -0.233 | -0.394 | -1.961 | -1.308 | -0.583 |
| **145** | Aristida oligantha | -2.294 | -2.502 | -2.180 | -2.339 | -2.620 | -2.757 | -2.477 |
| **146** | Aristida purpurea | - | - | - | - | - | - | - |
| **148** | Artemisia ludoviciana | 0.284 | 0.275 | 0.256 | 0.112 | -0.109 | -0.130 | 0.072 |
| **150** | Asclepias speciosa | - | - | - | - | - | - | - |
| **152** | Asclepias sullivantii | -1.265 | - | -0.982 | -3.139 | -1.932 | -1.278 | -2.799 |
| **155** | Asclepias verticillata | -0.244 | -0.431 | -0.142 | -0.879 | -0.243 | -0.281 | -1.332 |
| **157** | Asclepias viridis | -0.190 | -0.298 | -0.134 | -0.524 | -0.379 | -0.284 | -0.903 |
| **160** | Astragalus canadensis | - | - | - | - | - | - | - |
| **166** | Baptisia australis | -0.916 | -0.760 | -1.228 | -1.989 | -0.956 | -0.994 | -1.696 |
| **179** | Bouteloua curtipendula | 0.306 | 0.507 | -0.176 | 0.011 | 0.088 | 0.180 | -0.295 |
| **181** | Bouteloua gracilis | -0.409 | -0.127 | -2.613 | -0.530 | -0.788 | -0.588 | -0.879 |
| **185** | Bromus inermis | -0.406 | -0.240 | -0.749 | -0.334 | -1.123 | -1.576 | -0.436 |
| **202** | Carex annectens | - | - | - | - | - | - | - |
| **227** | Chamaecrista fasciculata | - | - | - | - | - | - | - |
| **231** | Chamaesyce nutans | -1.500 | -2.671 | -1.233 | -1.499 | -1.936 | -1.568 | -2.342 |
| **240** | Chloris verticillata | -2.829 | -2.578 | -3.692 | -2.707 | -4.139 | -3.373 | -2.975 |
| **243** | Cirsium altissimum | -0.655 | -1.160 | -0.449 | -1.233 | -0.654 | -1.401 | -0.741 |
| **260** | Cucurbita foetidissima | - | - | - | - | - | - | - |
| **285** | Desmanthus illinoensis | -1.656 | -2.222 | -1.440 | -1.597 | -2.418 | -1.751 | -2.365 |
| **288** | Desmodium illinoense | -1.233 | -1.717 | -1.032 | -1.866 | -1.793 | -1.323 | -1.962 |
| **294** | Dichanthelium acuminatum | - | - | - | - | - | - | - |
| **304** | Echinacea angustifolia | -1.396 | -1.182 | -1.944 | -1.358 | -2.069 | -1.948 | -1.539 |
| **305** | Echinacea pallida | - | - | - | - | - | - | - |
| **307** | Echinodorus berteroi | - | - | - | - | - | - | - |
| **313** | Eleusine indica | - | - | - | - | - | - | - |

## Table A.9 continued (2 of 4)

| KUT Code | Genus species | Konza Average Abd | Up-land (f) | Low-land (t) | Grazed (G) | Un-grazed (U) | Fre quent (1) | Infre quent (20) |
|---|---|---|---|---|---|---|---|---|
| **315** | Elymus canadensis | -0.739 | -0.894 | -0.654 | -0.667 | -1.587 | -1.283 | -0.886 |
| **316** | Elymus villosus | - | - | - | - | - | - | - |
| **317** | Elymus virginicus | -2.072 | -2.952 | -1.820 | -1.965 | -3.139 | -2.702 | -2.188 |
| **323** | Eragrostis pectinacea | - | - | - | - | - | - | - |
| **326** | Erigeron annuus | -2.255 | -3.993 | -1.976 | -2.122 | -4.139 | -2.255 | - |
| **334** | Eupatorium altissimum | -0.667 | -1.348 | -0.434 | -0.782 | -0.928 | -1.348 | -0.768 |
| **335** | Euphorbia corollata | -1.760 | - | -1.477 | - | -1.623 | -2.155 | -1.984 |
| **338** | Euphorbia dentata | -2.509 | -2.726 | -2.391 | -2.620 | -2.732 | -2.997 | -2.679 |
| **340** | Euphorbia marginata | -1.393 | -1.842 | -1.199 | -1.688 | -1.498 | -1.827 | -1.593 |
| **344** | Festuca subverticillata | - | - | - | - | - | - | - |
| **365** | Helianthus annuus | -1.199 | -2.481 | -0.928 | -1.081 | -2.431 | -1.403 | -1.626 |
| **369** | Helianthus petiolaris | - | - | - | - | - | - | - |
| **370** | Helianthus tuberosus | - | - | - | - | - | - | - |
| **371** | Heliopsis helianthoides | - | - | - | - | - | - | - |
| **373** | Hesperostipa spartea | -2.986 | - | -2.703 | -2.849 | - | - | -2.986 |
| **379** | Hordeum jubatum | - | - | - | - | - | - | - |
| **380** | Hordeum pusillum | -0.920 | -0.680 | -1.664 | -0.784 | -3.294 | -1.268 | -1.179 |
| **396** | Koeleria macrantha | 0.055 | 0.324 | -1.157 | -0.599 | -0.632 | -0.016 | -0.768 |
| **399** | Lactuca canadensis | -4.276 | - | -3.993 | -4.139 | - | - | -4.276 |
| **400** | Lactuca ludoviciana | -2.416 | -2.437 | -2.431 | -3.139 | -2.364 | -3.235 | -2.487 |
| **408** | Lepidium densiflorum | -0.921 | -0.732 | -1.347 | -0.841 | -2.124 | -1.106 | -1.381 |
| **410** | Lepidium virginicum | - | - | - | - | - | - | - |
| **413** | Lespedeza capitata | -0.128 | -0.621 | 0.076 | -1.022 | -0.376 | -0.169 | -1.170 |
| **416** | Lespedeza violacea | 0.700 | -1.993 | 0.983 | -0.459 | 0.417 | 0.620 | -0.072 |
| **419** | Liatris aspera | - | - | - | - | - | - | - |
| **420** | Liatris mucronata | - | - | - | - | - | - | - |
| **421** | Liatris punctata | -0.533 | -0.255 | -2.257 | -0.397 | -3.537 | -1.986 | -0.549 |
| **447** | Mirabilis linearis | -2.532 | -2.380 | -2.832 | -2.977 | -2.548 | -2.643 | -3.179 |
| **450** | Monarda fistulosa | -1.124 | -1.636 | -0.917 | -1.054 | -1.859 | -1.964 | -1.192 |
| **466** | Oenothera biennis | -3.799 | - | -3.516 | -3.838 | -4.139 | -3.975 | -4.276 |
| **468** | Oenothera macrocarpa | -2.270 | -1.987 | - | -2.136 | -4.139 | -3.322 | -2.310 |
| **481** | Packera plattensis | -1.768 | -1.557 | -2.303 | -1.989 | -2.287 | -1.868 | -2.456 |
| **482** | Panicum capillare | -1.752 | -2.932 | -1.485 | -2.390 | -1.696 | -1.905 | -2.280 |
| **485** | Panicum virgatum | 0.734 | 0.349 | 0.912 | -0.157 | 0.636 | 0.675 | -0.163 |
| **488** | Pascopyrum smithii | -1.087 | -0.804 | - | -1.557 | -1.072 | -1.550 | -1.270 |
| **494** | Penstemon cobaea | -2.334 | -2.061 | -3.692 | -2.255 | -3.139 | -2.845 | -2.494 |

## Table A.9 continued (3 of 4)

| KUT Code | Genus species | Konza Avg Abd | Upland (f) | Lowland (t) | Grazed (G) | Ungrazed (U) | Frequent (1) | Infrequent (20) |
|---|---|---|---|---|---|---|---|---|
| **495** | Penstemon grandiflorus | -2.392 | -2.109 | - | -2.777 | -2.410 | -2.548 | -2.914 |
| **496** | Penstemon tubiflorus | -3.146 | -2.863 | - | -3.008 | - | - | -3.146 |
| **504** | Physalis pubescens | -3.401 | - | -3.118 | - | - | -3.401 | - |
| **513** | Plantago rugelii | - | - | - | - | - | - | - |
| **516** | Poa arida | - | - | - | - | - | - | - |
| **519** | Poa pratensis | 0.815 | 0.844 | 0.744 | 0.518 | 0.727 | -0.346 | 0.784 |
| **534** | Polygonum virginianum | - | - | - | - | - | - | - |
| **542** | Prunella vulgaris | -4.276 | . | -3.993 | -4.139 | . | -4.276 | . |
| **547** | Psoralidium tenuiflorum | -0.633 | -0.631 | -0.673 | -3.661 | -0.825 | -0.727 | -1.346 |
| **553** | Ratibida pinnata | - | - | - | - | - | - | - |
| **565** | Rudbeckia hirta | - | - | - | - | - | - | - |
| **566** | Ruellia humilis | 0.078 | -0.176 | 0.212 | -0.621 | 0.083 | -0.164 | -0.291 |
| **575** | Salvia azurea | 0.399 | 0.652 | -0.488 | -0.017 | 0.230 | 0.337 | -0.475 |
| **576** | Salvia reflexa | -4.276 | - | -3.993 | -4.139 | - | -4.276 | - |
| **583** | Schizachyrium scoparium | 1.054 | 1.129 | 0.917 | 0.264 | 0.905 | 1.009 | 0.047 |
| **591** | Senna marilandica | -2.986 | - | -2.703 | -2.849 | - | -3.401 | -3.197 |
| **592** | Setaria pumila | -2.869 | -2.803 | -2.993 | -2.749 | -4.139 | -2.905 | -3.975 |
| **598** | Silphium integrifolium | -2.329 | -3.993 | -2.051 | -2.197 | -4.139 | -2.329 | - |
| **599** | Silphium laciniatum | -1.095 | -2.789 | -0.817 | -0.962 | -2.934 | -1.136 | -2.138 |
| **603** | Solanum carolinense | -1.168 | -1.593 | -0.980 | -1.326 | -1.337 | -1.695 | -1.321 |
| **605** | Solanum rostratum | -2.975 | -2.879 | -3.148 | -2.883 | -3.838 | -3.276 | -3.276 |
| **606** | Solidago canadensis | 0.746 | -0.639 | 1.019 | -0.005 | 0.671 | 0.470 | 0.418 |
| **608** | Solidago missouriensis | 0.122 | 0.072 | 0.133 | -0.450 | -0.031 | -0.075 | -0.317 |
| **609** | Solidago mollis | - | - | - | - | - | - | - |
| **610** | Solidago petiolaris | - | - | - | - | - | - | - |
| **613** | Sorghastrum nutans | 1.152 | 1.042 | 1.209 | 0.551 | 1.046 | 1.080 | 0.335 |
| **622** | Sporobolus heterolepis | 0.120 | 0.198 | -0.022 | -0.952 | 0.088 | -0.118 | -0.256 |
| **625** | Stellaria media | - | - | - | - | - | - | - |
| **627** | Stenosiphon linifolius | -2.450 | -2.355 | -2.622 | -2.500 | - | -2.887 | -2.648 |
| **633** | Symphyotrichum laeve | -2.460 | -2.570 | -2.402 | -2.329 | - | -2.837 | -2.696 |
| **635** | Symphyotrichum oblongifolium | 0.402 | 0.674 | -0.932 | -0.398 | -0.002 | 0.250 | -0.129 |
| **647** | Tradescantia bracteata | -2.679 | - | -2.396 | -2.654 | -4.139 | -2.691 | -4.276 |
| **648** | Tradescantia ohiensis | - | - | - | - | - | - | - |
| **651** | Tragopogon dubius | -1.882 | -1.673 | -2.408 | -1.968 | -2.141 | -2.785 | -1.941 |
| **674** | Verbesina alternifolia | - | - | - | - | - | - | - |
| **675** | Vernonia baldwinii | 0.074 | 0.016 | 0.093 | -0.032 | -0.298 | -0.159 | -0.306 |

## Table A.9 continued (4 of 4)

| KUT Code | Genus species | Konza Avg Abd | Up-land (f) | Low-land (t) | Grazed (G) | Un-grazed (U) | Fre quent (1) | Infre quent (20) |
|---|---|---|---|---|---|---|---|---|
| **687** | Vulpia octoflora | -1.705 | -1.477 | -2.350 | -1.589 | -2.896 | -1.855 | -2.241 |
| **689** | Xanthium strumarium | -3.975 | - | -3.692 | -3.838 | - | - | -3.975 |
| **693** | Zizia aurea | -4.276 | - | -3.993 | - | -4.139 | -4.276 | - |
| **999.001** | Baptisia alba | - | - | - | - | - | - | - |
| **999.002** | Echinacea atrorubens | - | - | - | - | - | - | - |
| **999.003** | Eryngium yuccifolium | - | - | - | - | - | - | - |
| **999.004** | Eupatorium purpureum | - | - | - | - | - | - | - |
| **999.005** | Helianthus salicifolius | - | - | - | - | - | - | - |
| **999.006** | Liatris pycnostachya | - | - | - | - | - | - | - |
| **999.007** | Penstemon digitalis | - | - | - | - | - | - | - |
| **999.008** | Prenanthes aspera | - | - | - | - | - | - | - |
| **999.009** | Rudbeckia lacinata | - | - | - | - | - | - | - |
| **999.010** | Solidago nemoralis | - | - | - | - | - | - | - |
| **999.011** | Solidago ulmifolia | - | - | - | - | - | - | - |
| **999.012** | Asclepias incarnata | - | - | - | - | - | - | - |

## Table A.10 Konza Abundance, treatment combinations. (Log 10 transformed)

| KUT Code | Genus species | G1f | G1t | G20f | G20t | U1f | U1t | U20f | U20t |
|---|---|---|---|---|---|---|---|---|---|
| **106** | Achillea millefolium | 0.633 | 0.048 | 1.333 | 1.822 | 0.082 | 0.049 | 0.397 | 0.347 |
| **112** | Ageratina altissima | - | - | - | 0.001 | - | - | - | - |
| **121** | Amaranthus blitoides | - | - | - | - | - | - | - | - |
| **123** | Amaranthus retroflexus | - | - | 0.001 | - | - | - | - | - |
| **126** | Ambrosia psilostachya | 17.08 | 15.65 | 17.15 | 10.58 | 5.450 | 6.46 | 8.47 | 8.77 |
| **129** | Amorpha canescens | 14.15 | 6.09 | 8.87 | 1.247 | 4.022 | 5.90 | 3.79 | 7.65 |
| **133** | Andropogon gerardii | 25.38 | 33.05 | 30.43 | 31.20 | 42.43 | 51.23 | 53.84 | 46.59 |
| **137** | Antennaria neglecta | 0.224 | 0.002 | 0.232 | 0.310 | 0.032 | 0.051 | 0.028 | 0.001 |
| **138** | Apocynum cannabinum | 0.072 | 0.473 | - | 3.536 | - | 0.011 | 0.001 | 0.071 |
| **145** | Aristida oligantha | - | - | - | 0.046 | 0.012 | 0.001 | - | - |
| **146** | Aristida purpurea | - | - | - | - | - | - | - | - |
| **148** | Artemisia ludoviciana | 2.450 | 0.895 | 4.186 | 5.551 | 0.372 | 0.244 | 4.080 | 2.433 |
| **150** | Asclepias speciosa | - | - | - | - | - | - | - | - |
| **152** | Asclepias sullivantii | - | 0.001 | - | 0.007 | - | 0.048 | - | 0.013 |
| **155** | Asclepias verticillata | 0.259 | 0.681 | 0.035 | 0.363 | 1.010 | 1.708 | 0.039 | 0.177 |
| **157** | Asclepias viridis | 0.916 | 0.937 | 0.784 | 0.393 | 0.471 | 1.302 | 0.300 | 0.238 |
| **160** | Astragalus canadensis | - | - | - | - | - | - | - | - |
| **166** | Baptisia australis | 0.061 | 0.043 | - | - | 0.315 | 0.119 | 0.292 | 0.012 |
| **179** | Bouteloua curtipendula | 3.594 | 2.450 | 3.499 | 0.846 | 4.706 | 0.450 | 2.673 | 0.209 |
| **181** | Bouteloua gracilis | 1.146 | 0.013 | 1.828 | - | 0.884 | 0.002 | 0.008 | - |
| **185** | Bromus inermis | 0.257 | 0.055 | 3.143 | 1.233 | 0.030 | - | 0.772 | 0.001 |
| **202** | Carex annectens | - | - | - | - | - | - | - | - |
| **227** | Chamaecrista fasciculata | - | - | - | - | - | - | - | - |
| **231** | Chamaesyce nutans | 0.007 | 0.287 | 0.002 | 0.024 | 0.002 | 0.036 | 0.002 | 0.029 |
| **240** | Chloris verticillata | 0.004 | 0.001 | 0.015 | - | 0.000 | - | - | - |
| **243** | Cirsium altissimum | 0.004 | 0.009 | 0.044 | 0.535 | 0.007 | 0.135 | 0.467 | 1.257 |
| **260** | Cucurbita foetidissima | - | - | - | - | - | - | - | - |
| **285** | Desmanthus illinoensis | 0.018 | 0.206 | 0.001 | 0.031 | - | 0.005 | 0.026 | 0.004 |
| **288** | Desmodium illinoense | - | 0.035 | 0.003 | 0.100 | 0.009 | 0.045 | 0.046 | 0.005 |
| **294** | Dichanthelium acuminatum | - | - | - | - | - | - | - | - |
| **304** | Echinacea angustifolia | 0.058 | 0.051 | 0.303 | 0.032 | 0.011 | - | 0.073 | - |
| **305** | Echinacea pallida | - | - | - | - | - | - | - | - |
| **307** | Echinodorus berteroi | - | - | - | - | - | - | - | - |
| **313** | Eleusine indica | - | - | - | - | - | - | - | - |

**Table A.10 continued (2 of 4)**

| KUT Code | Genus species | G1f | G1t | G20f | G20t | U1f | U1t | U20f | U20t |
|---|---|---|---|---|---|---|---|---|---|
| **315** | Elymus canadensis | 0.344 | 0.234 | 0.442 | 1.156 | 0.008 | 0.018 | 0.104 | 0.094 |
| **316** | Elymus villosus | - | - | - | - | - | - | - | - |
| **317** | Elymus virginicus | 0.004 | 0.019 | 0.001 | 0.086 | 0.002 | 0.000 | - | 0.003 |
| **323** | Eragrostis pectinacea | - | - | - | - | - | - | - | - |
| **326** | Erigeron annuus | 0.001 | 0.076 | - | - | - | 0.000 | - | - |
| **334** | Eupatorium altissimum | 0.007 | 0.141 | 0.064 | 1.460 | 0.024 | 0.142 | 0.219 | 0.535 |
| **335** | Euphorbia corollata | - | - | - | - | - | 0.045 | - | 0.120 |
| **338** | Euphorbia dentata | - | 0.013 | - | 0.012 | 0.001 | - | 0.013 | 0.004 |
| **340** | Euphorbia marginata | 0.013 | 0.081 | 0.037 | 0.076 | 0.004 | 0.034 | 0.040 | 0.170 |
| **344** | Festuca subverticillata | - | - | - | - | - | - | - | - |
| **365** | Helianthus annuus | 0.013 | 0.529 | 0.005 | 0.292 | 0.003 | - | - | 0.027 |
| **369** | Helianthus petiolaris | - | - | - | - | - | - | - | - |
| **370** | Helianthus tuberosus | - | - | - | - | - | - | - | - |
| **371** | Heliopsis helianthoides | - | - | - | - | - | - | - | - |
| **373** | Hesperostipa spartea | - | - | - | 0.014 | - | - | - | - |
| **379** | Hordeum jubatum | - | - | - | - | - | - | - | - |
| **380** | Hordeum pusillum | 0.595 | 0.147 | 0.914 | 0.006 | 0.001 | 0.002 | - | - |
| **396** | Koeleria macrantha | 0.590 | 0.007 | 1.905 | 0.046 | 0.992 | 0.049 | 0.391 | 0.048 |
| **399** | Lactuca canadensis | - | - | - | 0.001 | - | - | - | - |
| **400** | Lactuca ludoviciana | 0.004 | 0.001 | - | 0.002 | - | 0.000 | 0.025 | 0.017 |
| **408** | Lepidium densiflorum | 0.648 | 0.270 | 0.505 | 0.038 | 0.015 | 0.005 | 0.032 | 0.005 |
| **410** | Lepidium virginicum | - | - | - | - | - | - | - | - |
| **413** | Lespedeza capitata | 0.145 | 0.444 | 0.138 | 0.235 | 0.177 | 1.566 | 0.226 | 0.299 |
| **416** | Lespedeza violacea | 0.002 | 0.007 | - | 3.507 | 0.015 | 8.467 | 0.001 | 6.838 |
| **419** | Liatris aspera | - | - | - | - | - | - | - | - |
| **420** | Liatris mucronata | - | - | - | - | - | - | - | - |
| **421** | Liatris punctata | 0.121 | 0.018 | 3.899 | 0.022 | 0.001 | 0.000 | - | - |
| **447** | Mirabilis linearis | - | 0.002 | - | 0.008 | 0.015 | - | 0.001 | - |
| **450** | Monarda fistulosa | 0.001 | - | 0.017 | 0.875 | 0.075 | 0.000 | - | - |
| **466** | Oenothera biennis | - | 0.001 | - | - | - | - | - | 0.001 |
| **468** | Oenothera macrocarpa | 0.006 | - | 0.068 | - | 0.000 | - | - | - |
| **481** | Packera plattensis | 0.057 | 0.006 | 0.040 | 0.001 | 0.017 | 0.006 | 0.002 | 0.005 |
| **482** | Panicum capillare | - | 0.040 | 0.001 | 0.001 | 0.004 | 0.058 | . | 0.059 |
| **485** | Panicum virgatum | 1.055 | 2.311 | 1.401 | 2.281 | 4.026 | 14.19 | 1.432 | 3.767 |
| **488** | Pascopyrum smithii | - | - | 0.281 | - | 0.211 | - | 0.510 | - |
| **494** | Penstemon cobaea | 0.010 | 0.001 | 0.044 | - | 0.004 | - | - | - |
| **495** | Penstemon grandiflorus | - | - | 0.017 | - | 0.021 | - | - | - |

**Table A.10 continued (3 of 4)**

| KUT Code | Genus species | G1f | G1t | G20f | G20t | U1f | U1t | U20f | U20t |
|---|---|---|---|---|---|---|---|---|---|
| **496** | Penstemon tubiflorus | - | - | 0.010 | - | - | - | - | - |
| **504** | Physalis pubescens | - | - | - | - | - | - | - | - |
| **513** | Plantago rugelii | - | - | - | - | - | - | - | - |
| **516** | Poa arida | - | - | - | - | - | - | - | - |
| **519** | Poa pratensis | 1.293 | 0.712 | 18.77 | 12.55 | 0.184 | 0.274 | 31.87 | 19.91 |
| **534** | Polygonum virginianum | - | - | - | - | - | - | - | - |
| **542** | Prunella vulgaris | - | 0.001 | - | - | - | - | - | - |
| **547** | Psoralidium tenuiflorum | - | 0.001 | - | 0.001 | 0.238 | 0.209 | 0.330 | 0.269 |
| **553** | Ratibida pinnata | - | - | - | - | - | - | - | - |
| **565** | Rudbeckia hirta | - | - | - | - | - | - | - | - |
| **566** | Ruellia humilis | 0.772 | 0.707 | 0.322 | 0.618 | 0.892 | 2.065 | 1.380 | 4.063 |
| **575** | Salvia azurea | 6.418 | 0.913 | 1.961 | 0.428 | 7.677 | 0.331 | 2.262 | 0.164 |
| **576** | Salvia reflexa | - | 0.001 | - | - | - | - | - | - |
| **583** | Schizachyrium scoparium | 6.623 | 4.091 | 5.505 | 2.352 | 21.19 | 16.05 | 2.702 | 4.282 |
| **591** | Senna marilandica | - | 0.006 | - | 0.009 | - | - | - | - |
| **592** | Setaria pumila | 0.011 | 0.006 | - | 0.001 | 0.000 | - | - | - |
| **598** | Silphium integrifolium | - | 0.064 | - | - | 0.000 | - | - | - |
| **599** | Silphium laciniatum | - | 1.003 | - | 0.101 | 0.006 | - | - | - |
| **603** | Solanum carolinense | 0.001 | 0.231 | 0.001 | 0.245 | 0.004 | 0.019 | 0.192 | 0.200 |
| **605** | Solanum rostratum | 0.001 | 0.005 | 0.007 | - | 0.001 | - | - | - |
| **606** | Solidago canadensis | 0.043 | 4.704 | 0.060 | 5.190 | 0.224 | 7.417 | 1.240 | 24.83 |
| **608** | Solidago missouriensis | 1.396 | 0.798 | 0.288 | 1.109 | 0.762 | 1.269 | 4.013 | 1.355 |
| **609** | Solidago mollis | - | - | - | - | - | - | - | - |
| **610** | Solidago petiolaris | - | - | - | - | - | - | - | - |
| **613** | Sorghastrum nutans | 9.220 | 11.35 | 6.931 | 8.507 | 20.30 | 28.04 | 6.644 | 7.062 |
| **622** | Sporobolus heterolepis | 0.334 | 0.031 | 0.301 | 0.463 | 1.506 | 1.237 | 4.258 | 2.528 |
| **625** | Stellaria media | - | - | - | - | - | - | - | - |
| **627** | Stenosiphon linifolius | 0.001 | - | 0.031 | - | - | - | - | - |
| **633** | Symphyotrichum laeve | 0.019 | - | - | 0.028 | - | - | - | - |
| **635** | Symphyotrichum oblongifolium | 0.550 | 0.022 | 3.443 | 0.031 | 1.502 | 0.215 | 7.135 | 0.271 |
| **647** | Tradescantia bracteata | - | 0.022 | - | - | - | - | - | 0.001 |
| **648** | Tradescantia ohiensis | - | - | - | - | - | - | - | - |
| **651** | Tragopogon dubius | 0.018 | 0.001 | 0.064 | 0.026 | 0.002 | 0.000 | 0.075 | 0.001 |
| **674** | Verbesina alternifolia | - | - | - | - | - | - | - | - |
| **675** | Vernonia baldwinii | 1.402 | 2.907 | 2.767 | 2.324 | 0.941 | 0.737 | 1.041 | 0.676 |
| **687** | Vulpia octoflora | 0.177 | 0.017 | 0.051 | 0.015 | - | - | 0.014 | - |
| **689** | Xanthium strumarium | - | - | - | 0.001 | - | - | - | - |

## Table A.10 continued (4 of 4)

| KUT Code | Genus species | G1f | G1t | G20f | G20t | U1f | U1t | U20f | U20t |
|---|---|---|---|---|---|---|---|---|---|
| **693** | Zizia aurea | - | - | - | - | - | 0.0003 | - | - |
| **999.001** | Baptisia alba | - | - | - | - | - | - | - | - |
| **999.002** | Echinacea atrorubens | - | - | - | - | - | - | - | - |
| **999.003** | Eryngium yuccifolium | - | - | - | - | - | - | - | - |
| **999.004** | Eupatorium purpureum | - | - | - | - | - | - | - | - |
| **999.005** | Helianthus salicifolius | - | - | - | - | - | - | - | - |
| **999.006** | Liatris pycnostachya | - | - | - | - | - | - | - | - |
| **999.007** | Penstemon digitalis | - | - | - | - | - | - | - | - |
| **999.008** | Prenanthes aspera | - | - | - | - | - | - | - | - |
| **999.009** | Rudbeckia lacinata | - | - | - | - | - | - | - | - |
| **999.010** | Solidago nemoralis | - | - | - | - | - | - | - | - |
| **999.011** | Solidago ulmifolia | - | - | - | - | - | - | - | - |
| **999.012** | Asclepias incarnata | - | - | - | - | - | - | - | - |

**Table A.11 Univariate statistics. n = 121**

| | $A_{max}$ (μmol $CO_2$ $m^{-2}$ $s^{-1}$) | $g_s$ (mol $H_2O$ $m^{-2}s^{-1}$) | Intercellular $CO_2$ Concentration | Water Use Efficiency ($A_{max}/g_s$) | $\Psi_{crit}$ (bars) | Leaf Thickness (mm) | Leaf Angle (degrees) | Total Root Length (cm) | Avg. Root Diameter (mm) | Root Volume (cm3) |
|---|---|---|---|---|---|---|---|---|---|---|
| **Mean** | 10.3 | 0.13 | 231.2 | 3.84 | -46.7 | 0.22 | 38.6 | 469.5 | 0.27 | 0.20 |
| **Standard Deviation** | 4.3 | 0.06 | 41.8 | 1.07 | 20.6 | 0.10 | 27.2 | 294.9 | 0.09 | 0.07 |
| **Max** | 24.5 | 0.30 | 307.1 | 7.12 | -11.2 | 0.57 | 90.0 | 1689.1 | 0.45 | 0.38 |
| **Median** | 10.2 | 0.12 | 232.3 | 3.75 | -40.0 | 0.20 | 40.0 | 393.1 | 0.27 | 0.20 |
| **Min** | 2.0 | 0.03 | 108.7 | 1.52 | -89.0 | 0.08 | 0.0 | 80.4 | 0.10 | 0.05 |

| | SLA ($cm^2$ $g^{-1}$) | SRL (m $g^{-1}$) | $\rho_L$ (g $cm^{-3}$) | $\rho_R$ (g $cm^{-3}$) | Shoot Mass (g) | Root Mass (g) | Root: Shoot | Fraction Root | Date of First Bloom | Mycorrhizal Responsiveness (%) | Mycorrhizal Root Colonization (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Mean** | 156.1 | 99.1 | 0.41 | 0.30 | 860.5 | 524.0 | 0.86 | 0.39 | 178.6 | 58.2 | 37.3 |
| **Standard Deviation** | 54.1 | 70.6 | 0.14 | 0.10 | 522.3 | 343.5 | 0.96 | 0.15 | 39.6 | 46.8 | 15.6 |
| **Max** | 315.5 | 437.4 | 0.86 | 0.59 | 2479.7 | 2297.1 | 6.48 | 0.84 | 269.0 | 99.5 | 61.4 |
| **Median** | 152.9 | 81.9 | 0.39 | 0.30 | 771.9 | 446.8 | 0.55 | 0.36 | 174.0 | 85.9 | 36.4 |
| **Min** | 54.9 | 17.1 | 0.10 | 0.11 | 33.1 | 59.0 | 0.13 | 0.12 | 93.4 | -33.3 | 10.4 |