Ecophysiological Response of Native and Invasive Grasses with Warming

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An Undergraduate Thesis
Submitted in Partial Fulfillment for the Requirements of

Bachelor of Arts
in
Environmental Science: Conservation and Ecology
Geography and Earth Science

Carthage College
Kenosha, WI

May, 2011
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Abstract

Climate change, anthropogenic disturbances and lack of proper management practices have rendered many arid regions susceptible to invasions by exotic grasses with consequent ecohydrological, biogeochemical and socio economic implications. Thus, understanding the ecophysiological processes driving these large-scale vegetation shifts in drylands, in the context of rising temperatures and recurrent droughts is fundamental to global change research. Using the Biosphere 2 facility to maintain distinct temperature treatments of ambient and predicted warmer conditions (+ 4°C) inside, we compared the physiological responses (e.g. photosynthesis, stomatal conductance, biomass) of a native grass - *Heteropogon contortus* (tanglehead) and an invasive grass - *Pennisetum ciliare* (buffelgrass) growing in single and mixed communities. The results indicate that buffelgrass can assimilate more CO₂ per unit leaf area under current conditions, though warming seems to inhibit the performance when looking at biomass, photosynthesis and stomatal conductance. Under similar moisture regimes buffelgrass performed better than tanglehead in mixed communities regardless of the temperature. Both grasses had decreased stomatal conductance with warmer conditions when they were grown singly; however, the buffelgrass did not have the same decrease of conductance when planted in a mixed communities.

Introduction

Global change is a phenomenon that is affecting the world. There are several components to global change, including temperature changes, altered precipitation, increased CO₂ levels, altered land use, and increased nitrogen deposition. All of these contributing factors will alter natural ecosystem processes and have effects beyond environmental but also extending to social and economic implications by affecting plants, animals, and people. Global change research extends beyond the typical meaning of a changing climate because of altered greenhouse gases to also include the human spreading of invasive species and altered land use leading to change in disturbance regimes (Dukes 1999).

Global change is having effects on vegetation mostly as result of climate extremes that are placing new stresses on plants. Of these extremes are hurricanes, freezes, fires, and droughts all of which play a role in the disturbance cycles of different ecosystems (Adams 2009). Experiments that look at the effects of altered climate situations and disturbance regimes are
becoming of increasing interest for researchers. Depending on the region that is being studied the plants, temperatures, and the specific disturbance will vary in terms of what impact and severity of global change. For example, the research conducted here looks at the effects of plant community and temperature on invasive and native grasses found in the Sonoran Desert.

Atmospheric Changes

There are several components that contribute to the changing of the composition of the Earth’s atmosphere, including increases in the levels of CO$_2$ and other greenhouse gases. Also changing is the temperature of the planet with additional increases predicted in the future. These factors play a role in the physiology of plants because the changing conditions likely will cause plants to change their processes.

One component of global change is the increase in the greenhouse gas carbon dioxide, which is important for plants because carbon is absorbed by plants for photosynthesis via carbon dioxide gas. There are several ways that plants do this, including C3, C4, and CAM photosynthesis. C3 photosynthesis involves plants absorbing a 3-carbon compound and is typical of plants growing in cooler regions with plenty of water. C4 photosynthesis is more common in warmer drier regions because these plants absorb a 4-carbon compound and are able to conserve water by not having their stomata open as frequently yet they are still able to uptake enough CO$_2$ for photosynthesis. The ability of C3 plants to take advantage of increased CO$_2$ levels can be seen in an environment with enough available resources by measuring stomata and photosynthesis of the plants (Owensby 1998). However, there is no change in photosynthetic rates of the C4 plants in these conditions (Owensby 1998). Under current CO$_2$ levels a C4 plant will have decreased stomatal openings to conserve water in the case of a shortage (Owensby 1998). Increased carbon dioxide gas is believed to help plants in assimilation of CO$_2$ gas, increasing their water use efficiency, especially with C3 and C4 plants, by making carbon more accessible. Because carbon is in higher concentrations, plants would be able to keep their stomata open for less time to obtain the same amount of carbon, thus decreasing transpiration loss (Owensby 1998). Elevated levels of CO$_2$ result in a decrease in the stomatal conductance of both C3 and C4 plants of between 30 and 40%, resulting in reduced water loss through transpiration (Owensby 1998). Warmer temperatures associated with increased CO$_2$ could begin
to favor C4 plants over C3 plants because of their ability to control their water loss under hot and dry conditions resulting in an increase to their range (Dukes 1999).

Associated with the increase in CO$_2$ concentrations of the atmosphere is an expected rise in global temperatures anywhere between 1.5° and 4° C (Loik 2000). Other sources predict temperature increases between one and 3.5° C are to be expected over the next century which will favor certain species and alter the range of them (Dukes 1999). In either case, other environmental changes include higher soil temperatures and changes in soil water content.

In one experiment (Loik 2000), infra red heating was used in field plots in Colorado to measure the effects that rising temperatures would have on two cool desert shrubs *Artemisia tridentata* and *Erigeron speciosus*. For the plants being sampled there was not a significant difference in the stomatal conductance rates between the heated and controlled plots and it is instead presumed that the differences occurred with a decrease in water potential from the lower soil moisture content (Loik 2000). Changes in heating due to infra-red warming could cause some plants to have increases in fitness and a decrease for other species, resulting in a change in the species composition of a community (Loik 2000). Data were collected for leaf temperature, leaf water potential, photosynthetic gas exchange, and chlorophyll fluorescence (Loik 2000). Changes in air temperature between the heated and non heated plots ranged from 2.5° to 5.5° C and soil temperature was 2° C for the heated plots (Loik 2000). The afternoon clouds were prevalent because of the monsoon season and were evident when looking at the decrease in the photosynthetic flux density after solar noon (Loik 2000). There were not changes in leaf temperature throughout the test between the heated and control plots and maximum CO$_2$ assimilation for both species occurred between 8 and 10 in the morning (Loik 2000). The study shows that the effects warmer temperatures can have an effect on species fitness resulting in a changed landscape of vegetation with the possibility of invasive species introduction.

**Invasive Species**

Most elements of global change promote the success of biological invaders: including increased CO$_2$ levels, altered climates, increased nitrogen deposition, changes in disturbances regimes, and increased habitat fragmentation (Dukes 1999). The effects that invasive species
contribute to global changes in ecosystems include: altering the rates and flow of resources, changes to the trophic structure of the community, and changes to the disturbance regime by affecting frequency or intensity (D’Antonio 1992).

Biological invasions are a key component to global change that is a direct effect of human actions. This is true whether a species is introduced across its natural barriers intentionally or on accident, because once an invasive species is introduced, it takes hold quickly. In some situations it is difficult to identify the difference between the spread of the invasive grasses versus the actual clearing of the land. Even with current warnings about the use of non-native grasses for rangeland and their effects on the nearby habitats they border, their use is continued and their distribution is expanding (Williams 2000). There are several reasons why biological invasions are such a large problem, starting with the fact that they have caused more species extinctions than other human factors such as climate change or atmospheric composition, both of which gain much more attention when looking at global change (D’Antonio 1992). Also the breaking of barriers and spreading of invasive species are problems that are in most situations irreversible, including the chance that the ecosystem may undergo changes that will alter its original functions (D’Antonio 1992). Humans have converted large amounts of land from native ecosystems, forest, woodlands, savannas, and grasslands to areas for livestock. Often this involves the addition of non native African C4 grasses which have effects on biogeochemical cycling and climate on both global and regional scales (Williams 2000).

Invasive grasses have several key traits including the ability to out compete native grasses in many different ecosystems, to influence the nutrient cycling and microclimate of a habitat, and to change the fire cycle (D’Antonio 1992). One trait that is helpful to a plant’s success under changing conditions include its ability for quick dispersal, allowing them to take advantage of recently disturbed environments. In addition plants with a large latitudinal range may be able to gain a competitive edge on neighboring plants that are becoming stressed because of temperature shifts (Dukes 1999). Invasive grasses have the ability to quickly spread out of their introduced areas into edges of neighboring habitats (Williams 2000).

Grass invasion of the Americas began in the 17th century mostly affecting the regions in middle and southern America as vast amounts of native tropical forest, dry forest, and savannah
ecosystems were being cleared for pasture (Williams 2000). Grasses have been introduced to several regions of the United States often with the intention to be used for grazing purposes. *Taeniatherum caput-medusae* (Medusahead), *Bromus tectorum* (cheatgrass), and *Bromus rubens* (red brome) all appear to have been brought over from Europe without purpose, but instead just came over with the introduction of sheep and cattle to the Great Basin region (D’Antonio 1992). *Agropyron cristatum* (Crested wheat grass), *Pennisetum ciliare* (buffelgrass), and *Eragrostis lehmanniana* (Lehmann lovegrass) are all grasses that were brought over with intent to not only feed cattle but also to help control erosion and even with the removal of cattle the grasses now persist in many desert regions (D’Antonio 1992). Lehmann lovegrass, which was first used to revegetate areas that were being invaded by woody plants and cacti in the south western desert regions of North America, but has since expanded beyond the regions of intentional use and had double its coverage in the state of Arizona between 1950 and 1984 (Williams 2000). *Cortaderia selloana* (Pampas grass) and *Ehrharta calycina* (Veldt grass) are species that thrive on the west coast in areas that have recently been logged and since invading these areas also quickly spread to land that has recently been disturbed by fire (D’Antonio 1992).

### Ecosystem Competition

Changes in the flow and competition for resources result from the introduction of an invasive grass to an ecosystem. One resource that they successfully compete for is light and they do this by producing a thick cover through which light cannot pass, which prevents seedlings from sprouting underneath (D’Antonio 1992). Water is another resource for which invasive grasses are able to outcompete native grasses. For example some species have been shown to remove water more quickly and to lower water levels from the soil, which places stress on other plants in the community (D’Antonio 1992). Nutrients and water are taken up more rapidly by invasive grasses, leading to a water shortage and requiring plants to compete with each other (D’Antonio 1992). This rapid uptake of water and nitrogen likely occurs because of the developed shallow and expansive root system in addition to the ability to block out sunlight. The result leads to the reduction in the number of native species because they are being replaced by the invasive species (D’Antonio 1992). The effects of this, decreasing biodiversity is not limited
to the grasses in competition but has been shown to also work its way up the trophic scale affecting the birds and insects that live and feed in the grass community along with prolonging the succession timeline of many grassland areas in to wooded communities (D’Antonio 1992).

Geomorphological processes are also changed with invasions and can range from the creation of dunes to altered flood patterns, to turning dry lands into wet lands and also open water into swamp land (D’Antonio 1992). Microclimate effects that grasses pose on ecosystems include changing soil moisture and temperature, which effects seed germination, seedling growth, and nutrient flows; they also provide a relatively smooth surface to wind to blow over when compared to a woodland area (D’Antonio 1992).

Fire Cycle

One of the most significant impacts that invasive grasses pose on an ecosystem is the altering of the fire regime. This is the case when looking at the impacts of invasive grasses in the Sonoran Desert. As an ecosystem, the desert is naturally protected from fire by having bare soil between plants, which results in only small fires which burn out quickly because of a lack of continuous fuel. Invasive grasses will alter this normal regime by adding to the connectivity of the desert and contributing to an altered fire regime by also changing several other components regarding to the grass invasion and altered disturbances of fire regimes as part of global change. First, it is typical of grasses to supply a standing dead material that easily ignites. Second, grass species provide a material with a high surface to volume ratio which when measured with the moisture content can be used to calculate the materials flammability. Third, grasses are capable of quick regeneration that assimilates carbon with the growing of the completely new above ground component of the plant. Also, a grass dominated landscape, when compared to a woodland forest, will have a micro climate above it that is warmer and drier, making it more susceptible to fires (D’Antonio 1992). The invasion by grasses provides a positive feedback loop by altering the ecosystem because the grasses make the habitat fire frequency and intensity rise which leads to more disturbances and more invasive species because of their quick regeneration. Another fact of the altered fire regime is changes that occur to the cycling of nutrients by changing rates of uptakes and budgets that are available to plants species, invasive
or native. Losses can become a problem with increased run-off and loss to the atmosphere with the addition of more fires (D’Antonio 1992).

Field studies that have examined grass invasion impacts on fire regimes include examples from Hawaii and Western North America (D’Antonio 1992). In Hawaii, there are two species of grasses that invade the local ecosystems, Schizachyrium condensatum and Melinis minutiflora. Beginning in the 1960’s the invasion of S condensatum spread and now there are areas that were never burned that are now composed of 80% invasive grass and the addition of this fuel source for fires have increased an average fire size from 4 ha to 205 ha (D’Antonio 1992). The number of fires has also risen increasing from 27 fires in the 48 years before the invasion to 58 fires in the 20 years post invasion (D’Antonio 1992). The increased fire resulting from the S condensatum invasion not only leads to the success of it over wooded and shrub species but also makes the environment susceptible to invasion by M minutiflora which makes the ecosystem even more at risk for fire. M minutiflora is even more flammable that S condensatum and its green leaves are capable of burning in 95% humidity making fires even more likely (D’Antonio 1992). In western North America, Bromus tectorum was brought over by Europeans and altered the landscape which was dominated by perennial grasses. B tectorum expanded quickly because of degradation of land by overgrazing and increased the fire frequency by drying out in the spring and lead to summer fires that created a post fire habitat that favors the continuous spreading of B tectorum. In Idaho, for example, the fire interval changed from a pre invasion 60-110 year cycle to 3-5 year cycle after the invasion (D’Antonio 1992). Areas in Oregon were reported to be 500 times more likely to experience a fire after experiencing invasion by B tectorum (D’Antonio 1992). The fires that spark due to the effects of B tectorum have been said to have affects on 40 million hectares and lead to increased floods and erosion, this has caused an increase of human management including the planting of fire resistant plants to disrupt the new fire cycle (D’Antonio 1992).

Also important is to view grass invasion on a larger scale and look at the global consequences of invasion, land use, and fire regimes. Most notably is the change of land use by humans. In most situations, grass is introduced or the habitat is altered to favor grasses with intent by people. This includes the clearing of land which makes the invasion from grass species
possible and the intentional introduction, like in the Sonoran Desert with the placement of Asian and African grasses to help control erosion and feed cattle. Once the positive feedback loop is formed, by increasing invasive grasses and fire frequency, it is hard to break. In some regions, invasion by C4 grasses is a growing concern because of alterations to temperature, humidity, and precipitation; this is different in the Sonoran Desert because it is an ecosystem that already contains many C4 plants and is not dominated by wooded vegetation.

**Desert Invasions**

Degradation of desert ecosystems is often attributed to the encroachment of woody plant species which out compete with native grasses resulting in higher rates of erosion. This is a global phenomenon that is not limited to specific desert landscapes. Desertification can also occur via an alternative invasion of desert ecosystems (Figure 1) one by exotic grasses (Ravi 2009). Global change includes the spreading of invasive species, but also the changes in climate contribute to the changes in the desert ecosystems.

Figure 1. A diagram of desertification by grass invasion. (Ravi 2009)
The introduction of African grasses to the arid and semi-arid regions of North America occurred between the 19th and 20th centuries, and was done to supply more vegetation to the rangelands (Williams 2000). The African grasses were selected for their tolerance to drought, quick establishment, and high productivity; all of these are the same characteristics that make the grasses excellent invaders as well (Williams 2000).

Buffelgrass is one of the most popular African grasses that is used and also one of the most successful invaders. The grass is successful at converting the ecosystems dominated by shrubs and other vegetation into grassland, but now covers around 10x10^6 ha (Williams 2000). As of 1988, 1.2x10^6 ha of the Sonoran state of Mexico have been converted to pastures with buffelgrass with an estimated 6x10^6 ha as additional targets for buffelgrass conversion (Williams 2000).

Both types of invasion, by shrub and exotic grass, affect the distribution of soil resources despite working by two different mechanisms. Invasion by woody species is a result of years of overgrazing of the native grassland and fire suppression, which allows them to encroach on the ecosystem. Woody species will result in increased erosion and redistribution of soil which increases the heterogeneity (Ravi 2009). Exotic grasses achieve the same result but accomplish it by reducing the number of shrubs and increasing the fire frequency and soil loss, destroying the natural heterogeneity, and promoting further growth and spread of exotic grasses (Ravi 2009). Increased drought frequency and intensity, both associated with global and climate change, aid in the process of degradation by increasing wind erosion rates and rates of nutrient loss. The variability in precipitation that exists in arid regions is beneficial to the invading exotic grasses because of their ability to take advantage of the nutrient islands that exist in the vicinity of shrubs more successfully than the native grasses (Ravi 2009). The invasive grasses attribute their success in the nutrient scattered and variable precipitation environment over native grasses because of their higher phenotypic plasticity (Ravi 2009). Like the positive feedback loop of the fire regime the invasive grasses will continue to grow in numbers when the population of native grasses starts to decrease thus making more room for the invaders. If years of higher precipitation rates occur on the landscape the invasive grasses will start to spread out from their
nutrient islands and begin connecting with other pockets of grasses, this process increases the fire frequency (Ravi 2009).

In the desert southwestern United States, the native desert landscape is not adapted to fire because it has low connectivity (the plants are typically isolated with bare soil between them) which does not promote the spreading of fires and results in many of them burning themselves out. The increase in connectivity results in more fires that are larger and more intense with greater rates of erosion when the shrubs are burned (Ravi 2009). Once the fire has passed, the nutrients are shifted around from the shrub islands out in to the bare soil allowing the invasive grasses to expand in to the new areas and continue to spread their coverage. One of the mechanisms behind the increased erosion is the organic compounds which are released by some vegetation when burned. The organic compounds change the moisture absorption and retention in the soil and results in the possible weakening of the soil to resist erosion via wind and water (Ravi 2009). Second, the invasive grasses are typically not as adapted to low volume and frequency of precipitation. The invaders are capable of expanding during a series of wet years and fires pushing out the native grasses, but when not enough water is supplied the invasive grasses perish from the landscape and leave an uncovered ecosystem that is even more likely to experience erosion of soil (Ravi 2009).

The alterations to the landscape by non native grasses destroy the nutrient islands that are created by shrubs as result of the fire that they increase and do not leave a place where for the plants can retreat when there is a drought. The degradation of the world’s arid ecosystems poses a problem globally since they cover 40% of the land surface the loss of vegetation in these landscapes would result in a reduction of CO2 absorbing potential of the planet.

**Buffelgrass (Pennisetum ciliare)**

One species of invasive grass that is affecting deserts in the southwest region of the United States is *Pennisetum ciliare* (Figure 2). Its common name is buffelgrass and can also be referred to as African foxtail grass, pastor buffel, and zacate buffel. Buffelgrass, a C4 grass, has been expanding in the Sonoran desert because of warmer temperatures and higher levels of precipitation after its human introduction to the region. Most notable is the change buffelgrass
that has on the disturbances in the Sonoran ecosystem, in particular its changes to the fire regime. The change in the fire cycle has a positive feedback on the grass and helps it even more in competition with other plants like desert shrubs which are not fire resistant or quick to regenerate after a fire (Dukes 1999).

Figure 2. Picture of a buffelgrass plant.

Buffelgrass is a perennial grass that is native to Africa, Arabia, Canary Islands, Indonesia, northern India, Madagascar, and Pakistan. The grass grows in bunches with a knotty base typically with heights up to 3.5 feet tall and when mature can grow to 3-4 feet in diameter. Root growth can reach depths of 6 to 8 feet in the soil and in some cases even depths of 10 feet. The leaves are flat and between 3 and 11 inches long. Buffelgrass disperses via seeds and rhizomes; the seeds are spread in wind, water, the fur of animals, and human clothing. The preferred growing habitats have frost free winters and a summer rainy season with 6 to 24 inches of rainfall. Buffelgrass can grow in a variety of habitats including roadsides, farm fields, recently disturbed sites, vacant lots, rangeland, mountain slopes, and riparian zones.

Buffelgrass first came to be in the United States when it was introduced to improve rangeland in the 1930’s. Benefits to rangeland from the grass that led to the introduction were its abilities to aid in erosion control and provide food to cattle. Problems with the non native grass were not known until the 1980’s when the expansion of the grass was first noticed by scientists. The states that buffelgrass is distributed in are: Alabama, Arizona, California, Florida, Hawaii,
Louisiana, Mississippi, Missouri, New Mexico, New York, Oklahoma, Puerto Rico, Texas, and the Virgin Islands.

Buffelgrass stands to be a problem economically because of its environmental hazards and the effects it has on the desert ecosystem. The desert landscape draws in millions of tourists which in turn brings in billions of dollars to local economies and also accounts for almost 40,000 jobs. Another effect that the grass has in the area deals with real estate values by putting many scenic homes at risks because of increased fires putting the homes at risk.

**Biosphere 2**

In the Sonoran desert, research is being conducted at Biosphere 2 (Figure 3), which is located an hour northwest of Tucson, Arizona. The Biosphere 2 department at the University of Arizona runs and operates the facility where experiments focusing on studies that looking at global change are constantly being run inside.

Figure 3. Picture from the outside of the biosphere.
For example, in an experiment inside of Biosphere 2 by Adams (2009), pinon pine trees were grown over a temperature variation of ambient and ambient plus 4.3 degrees Celsius (Adams 2009). Selected trees were given a drought treatment and the experiment continued until all of the drought selected trees had died (Adams 2009). In the southwest United States, one disturbance that draws the attention of many researchers is drought because of its ability to change the already limited wet seasons of the region. Droughts have many implications for South West ecosystems, including an increase in change for invasive species takeover, changes in the regional hydrologic cycle, new communities of species to the region, and changes to the function of the ecosystem (Adams 2009). In turn, carbon sequestering abilities of the ecosystem and therefore carbon cycle are also affected (Adams 2009). It is hypothesized that warmer temperature could be responsible for the tree mortality. The increase in temperature causes the closing of stomata to maintain enough water to keep xylem pressure up and rely on stored carbohydrates or stomata are kept open and xylem pressure will eventually drop making it possible to be blocked with air bubbles (Adams 2009). The results show that all of the drought treated trees died in the warmer conditions before the ambient ones. Yet, hydraulic failure was not the cause of die off amongst the trees. Instead, based on predawn samples comparing the different temperature treatments, carbon starvation was the cause of death, meaning the there was a change in the stomatal openings of trees (Adams 2009). The results show vegetation with higher rates of mortality and resulting widespread vegetation die-off at increased frequencies (Adams 2009).

Biosphere 2 was originally a part of Space Biospheres Ventures which started in 1984 by millionaire Ed Bass. The project’s aim was to look at the development and research of self sustaining space colonization technology to be used as for profit science. The Biosphere 2 facility was constructed to research the possibilities of space colonization beginning in 1986 near the town of Oracle, Arizona, about an hour northwest of Tucson. The facility is 3.14 acres in size under the glass complete with 5 biomes, ocean, mangrove, tropical rainforest, savannah, and coastal fog desert. Temperature and precipitation in the biomes is controlled on site and can vary between biomes as well as within them. The Biosphere was sealed from the outside with 6500 windows and a 500 ton steel liner underneath to ensure complete enclosure. Missions began in 1991 with up to eight Biospherians being sealed in for 2 years with the aim of 50 missions being
launched in the next 100 years. The missions ended in 1994 because it was decided that the project was diverging from its original intent and the Columbia University took over management starting in 1996 with the goal of scientific research. Columbia pulled out in 2003 and the facility sat unmanaged until 2007 when the University of Arizona received a $30 million gift to take over the facility for 10 years. Additional funding is obtained through research grants and profits from daily tours. The aim of the facility now is to combine scientific research with public interactions focusing on global climate change projects. Currently the facility consists of a 40 acre campus with visitor center, café, housing for researchers, conference rooms, and an energy center.

**Experiment and Hypothesis**

The aim of this experiment is to use the facilities at Biosphere 2 to study invasive and native grasses under controlled conditions. The grasses will be grown across a temperature gradient in different types of communities in order to look at changes to their physiology. Measurements will be made looking at their photosynthetic performance and stomatal conductance. Two hypotheses are being tested in the experiment: (1) when comparing grasses grown at different temperatures the higher temperature will cause the grasses to have lower photosynthesis and stomata measurements and (2) native grass will be out performed by invasive grasses in the mixed communities by having lower photosynthesis and stomata measurements.

**Methods**

*Study Site*

The study was conducted inside the University of Arizona’s Biosphere 2. The Biosphere’s original intent was to explore the possibilities of sustainable space colonization throughout its five different biomes, rain forest, savannah, desert, ocean, and mangroves, all contained and controlled under glass. Now that the Biosphere is managed by the University of Arizona, it is used to educate the public and conduct research focusing on global change. The site was selected because of the controls over temperature and precipitation. The lower savannah portion of the Biosphere was used and kept and temperatures at ambient conditions to the
Sonoran Desert along with the desert biome where temperatures were kept 4 degrees Celsius warmer.

Experimental Design

Two grasses were chosen for the experiment, a native tanglehead and an invasive buffelgrass. The grasses were transplanted in pots, 8 plants per pot, in single and mixed communities and allowed to grow in the conditions prior to measurements. Mixed communities had four of each species in them. Pots were fitted with soil moisture sensors, a transparent tube with numbered windows in the middle for looking at roots, and tubes in the bottom for leaching (Figure 4). Three plants from every single community and four plants from each mixed community, two of each species, were selected to be measured throughout the summer. Pots were in 12 groups of three, each group having a single community of tanglehead and buffelgrass and a mixed community with four of each species for a total of 36 pots. Groups 1 through 6 were placed in the lower savannah at a temperature that was ambient to the Sonoran desert. Groups 7 through 12 were placed in the desert biome and kept at a temperature four degrees warmer. Three pots of bare soil were also placed in each biome. All plants received equal amounts of water. Pots were watered at the same time when the soil was dry, this was based on the savannah pots which took longer to dry out, and each given one pitcher (32 oz) of water. Every other Monday there was a leaching test that was done in which the pots were flushed out with enough pitchers of water until samples could be collected from the bottom which usually was done with five to seven pitchers depending on the week.
**Stomatal conductance**

The stomata of all the plants were sampled in order to compare the two species and temperatures. The stomata indicates how the plants are partitioning their water and uptake of CO2. High stomatal conductance shows high uptakes of CO2 and high loss of water while low stomatal conductance shows low uptakes of CO2 and low water loss. Samples were taken using a porometer two to three times per week (Figure 5). A porometer measures the humidity on each side of the leaf and uses formulas to calculated the conductance of the stomata in mmol/m²'s. The same plants were sampled from each pot everytime, three plants from each single community and four individuals (2 of each species) from the mixed pots. Samples were completed first in the desert and then in the savannah before noon each day to make sure the measurements were accurate and comparable. Taking measurements at different times in the day would not be accurate because the grasses shut down photosynthesis in the afternoon when temperatures are too high. All results were recorded by hand then entered in to Excel.

![Figure 5. Taking field samples using a porometer.](image)

**Photosynthesis**

The photosynthesis rates by the grasses were collected to compare the species and biome temperatures. These measurements indicate how productive the plants are and how well they are using their resources. One round of photosynthetic rates measurements was done using a Licor
Sampling was done in the morning and only the selected plants in pot groups 1-3 and 10-12 was completed because of time constraints. One leaf was selected from each plant to measure. Data were stored in the licor and downloaded later.

**Biomass**

Sampling for biomass was taken by measuring plants height from the soil to the tallest point and the number of tillers each plants had. This was done for the selected plants.

**Statistics**

Recorded measurements for stomatal conductance, photosynthesis, and biomass were averaged to compare differences in species, community, and biome. ANOVA were also run on the average stomatal conductances by pot to look at the different environmental factors. Additionally, ANOVA were run for photosynthesis and conductance as recorded by the LICOR 6400 looking to see which factors were contributing to differences. P values of less that 0.05 were considered significant.

**Results**

**Stomatal Conductance**

Stomatal conductance measurements (Figures 6 a-d) show that the plants in the desert, for both tanglehead and buffelgrass, had lower stomatal conductance that the grasses that were grown in the savannah. The tanglehead in the savannah had daily averages for the grasses ranging from 101.0 to 148.7 mmol/m²/s and varied between 61.4 and 140.0 mmol/m²/s in the desert. The buffelgrass plants daily averages for all the plants in the savannah between 73.1 and 199.6 mmol/m²/s and averages that varied between 59.0 and 144.0 mmol/m²/s. Through the summer the grasses of both species had trends of declining stomatal conductance.

The plant community in which the grasses were grown had an effect on the tanglehead plants more that the buffel grass plants. In single communities the tanglehead plants would average between 91.8 and 150.3 mmol/m²/s daily for all both biomes compared to daily averages between in mixed communities 62.2 to 126.3 mmol/m²/s. The change in community did not have as much effect on the buffel grass plants. In single communities daily averages were between
74.3 and 145.0 mmol/m²/s with the mixed communities averages ranging from 70.5 to 168.4 mmol/m²/s.

Figure 6 a. Single communities of tanglehead at different temperatures

Figure 6 b. Tanglehead in mixed communities at different temperatures.
Figure 6c. Single community buffelgrass at different temperatures.

Figure 6d. Bufflegrass grown in mixed communities at different temperatures.
The combination of the community and temperature groupings supported measurements with all the plants. Buffelgrass in mixed communities located in the savannah had a greater range of daily averages than the tanglehead in the same community location. The single communities of the savannah had a smaller range of conductance for the buffelgrass compared its mixed communities. The tanglehead range changed from 90.8 to 159.6 mmol/m²’s in the mixed communities to 111.1 to 200.4 mmol/m²’s in the single communities.

In the desert the single plant communities of the tanglehead and the buffelgrass had close ranges of daily average conductance with highs of 148.1 and 146.1 mmol/m²’s respectively. The mixed communities of the desert yielded daily lows for the two plants similar to each other like the highs. The difference came in the buffelgrass where in the mixed communities had the highest recorded daily average with 170.0 mmol/m²’s.

After running an ANOVA test on the stomatal conductance values it was found that temperature is significant (P<0.001). In addition to this the combination of plant type and community was also significant (P=0.002).

Photosynthesis

The photosynthesis measurements (Figure 7) that were taken show that both of the species in single and mixed communities all had lower photosynthesis in warmer temperatures. This decrease with warmer temperatures was also true for the conductance measurements taken by the LICOR 6400. The tanglehead had decreased in photosynthesis from its single community pots to the mixed community pots, whereas buffelgrass did not experience the same drop in photosynthesis.

ANOVA test of the photosynthesis data show that contributing factors to the differences included temperature (P<0.001). Community and species together had an interaction to also be a factor in the photosynthesis of the grass (0.009).

Conductance measured (Figure 8) using the LICOR 6400 also showed a decrease when temperature was increased for both of the species when in single and mixed communities. Single species buffelgrass had the highest conductance and mixed community tanglehead had the lowest in the savannah. The conductance in the desert was similar for buffelgrass and tanglehead in
both single and mixed communities. ANOVA test of the recorded conductance measurements showed that only the temperature was a factor (P<0.001).

Figure 7. Measurements of photosynthesis comparing species, community, and biome.

Figure 8. Measurements of conductances comparing species, community, and biome.
Biomass

The buffelgrass in the savannah had the greatest average height for the measured grasses along with the highest average number of tillers and the lowest average height was the desert tanglehead (Figure 9). In the savannah and the desert the buffelgrass plants had a higher number of average tillers compared the tanglehead plants in each, which only averaged 2 tillers per plant.

![Average Biomass](image)

Figure 9. Measurements of biomass comparing species and biome.

Discussion

The hypotheses were supported by the results. Buffelgrass had stomatal measurements that were higher that the tanglehead plants. Also, the higher temperature plants had lower measurements of photosynthesis and stomatal conductance than the lower temperature grasses. The results from the study confirm that the impacts of global change may have an effect on the Sonoran Desert through the altering of the native species physiology. In the Biosphere, the warmer temperature had an effect on the grasses, both the tanglehead and buffelgrass (Figures 6-8). The decrease in stomatal conductance and photosynthesis is due to the plants trying to manage their resources, in this situation mainly water loss, to ensure survival. Despite the use of C4 plants in the experiment, there is clearly a temperature threshold that the plants will begin to
close their stomata, thus inhibiting the uptake of CO$_2$ and lowering their photosynthesis potential.

Despite a decrease in the photosynthesis brought on by the warmer temperatures, the tanglehead plants did not suffer a change in average biomass between the desert and the savannah biomes (Figure 9). The average number of tillers stayed exactly the same, meaning that the tanglehead is able to somehow compensate for the higher temperatures and lower carbon uptake to produce plants that are near the same size under the ambient conditions modeled in the savannah. The buffelgrass plants were not able to do this and showed a decrease in average height and number of tillers under the warmer temperatures in the desert biome. Despite this decrease with the buffelgrass in warmer temperatures, it still was able to stay close in average height and still had more average tillers that the tanglehead in the same conditions which show that with increasing temperature buffelgrass will continue to be a problem in competition. Comparison between plants grown inside the Biosphere and naturally occurring buffelgrass and tanglehead plants would be a good measure to see if the ambient temperature grown plants in the savannah biome truly reflect the Sonoran Desert plants.

The changes that are occurring in the Sonoran Desert are not limited to just a rise in temperatures. The introduction of invasive species is also having an effect on the native vegetation. In the experiment, buffelgrass was able to keep similar levels of photosynthesis and stomatal conductance between its single and mixed communities in each of the temperature settings (Figures 6 c and d, 7). The tanglehead was not able to maintain similar levels and showed a decrease when it was grown in a mixed community with the invasive buffelgrass (Figures 6 a and b, 7). Competition in mixed communities is dominated by the buffelgrass because of its ability to continue carbon assimilation with the presence of other grasses. The inability of tanglehead to do the same helps to show why the invasive buffelgrass is able to overtake an ecosystem despite the presence of a native grass.

The results generated from the experiment were unfortunately not normally distributed making the statistical test on them potentially less accurate; however, the very low P-values (P<0.002) suggest that these patterns are robust in spite of this issue. Leaf porometer data varies greatly between plants and in future studies more sampling would be useful to obtain data that is
more normally distributed. Also, testing was done at the same time of day for the plants during the summer. Collecting data at different times and comparing them might have given a better idea as to which leaf porometer recordings were outliers. For example, any predawn reading would show stomatal conductance levels that reflect the plant during a period of non photosynthetic activities and a minimum could be determined to see when stomatal conductance levels were high enough to reflect a photosynthetic active grass.

The Sonoran Desert landscape is likely to change because of the successful abilities of the invasive buffelgrass to alter the landscape. It has been known that invasive grasses have been changing the disturbance regimes of the desert by increasing the connectivity of the shrub islands that have been formed by their encroachment to the native grass lands. Biomass measurements show that the buffelgrass does have more tillers than tanglehead accounting for the increased connectivity because of more mass of the plant. Buffelgrass has also shown its ability to maintain its stomatal openings and photosynthesis rates in mixed communities which partially accounts for its success as an invader. The decrease in stomatal openings by the tanglehead also contributes this phenomena and the desert landscape is slowly taken over and altered by the buffelgrass. While it is clear that the plant stomata are affected in both spiecies a good test to run also would be to look at the water potential in the grasses throughout the day. Measurements of how the grasses are using their water may also help to explain any changes in the stomatal opening that are cause by the varying temperatures.

Changes to the Sonoran Desert have many consequences beyond just affecting the physiology of plants. For example buffelgrass changes the fire cycle by increasing the fuel load and is able to use its quick dispersal and regeneration to further perpetuate this cycle of increased fire. Since the ecosystem is so unique buffelgrass’s effects could alter the biodiversity. In this experiment only two species of vegetation were used. Further studies would prove beneficial to include other types of native vegetation in mixed communities as buffelgrass grown in the wild would be a part of the entire desert ecosystem and interact with more than just one species of native grass.

Globally the implications for warmer temperatures, from an increase in greenhouse gases especially CO₂, will lead to a decrease in the sequestering potential of many ecosystems. The
increase in temperatures in the desert biome led to a decrease in stomatal conductance and photosynthesis meaning less carbon uptake by the plants. This being true for both of the species, shows that increase in CO$_2$ leading to warmer temperatures will not lead to increase in absorption of carbon by desert plants because of the already warm temperatures increases with cause the plants to lower their photosynthetic rates. Additional testing of the carbon cycling through the plants would also yield useful data to see exactly where the carbon is going and where it is being held. The fragile desert that is already being altered by invaders could potentially be invaded by other species as temperatures begin to impact the plant processes of the current vegetation in place, native and invasive.

The changes buffelgrass makes to the landscape and fire cycle may lead to desertification of the land. Because of the positive feedback that it has, buffelgrass only enhances itself with time. This becomes an issue because with such a decrease in biodiversity the ecosystem would be severely damaged if disease or drought were to eliminate the buffelgrass population leaving the landscape without vegetation. A landscape with zero vegetation would have no carbon sequestering capabilities.

There are organizations working to control the buffelgrass problem in the southwest. The Southern Arizona Buffelgrass Coordination Center (SABCC) is one such organization. The SABCC mission statement is “is to provide a regional information center that emphasizes an integrated management approach to control buffelgrass (Pennisetum ciliare) in Southern Arizona.” They do this by informing the public, mapping regions that are at risk and under current invasion (Figure 10), and by organizing groups to go in to the desert and attempt to manage the buffelgrass. The mapping of the high sirk areas for the spread of buffelgrass is important to maximize any resources that are being used to combat the invasive species. Many of the red areas on the map align along roadways and streams which will help in the concentration of efforts when sending out crews to remove buffelgrass from the most important areas first. Additionally the map displaying the management difficulties in different areas can also be used to make sure that any resources being used to remove buffelgrass are not being wasted. Also important for management efforts is to use all their data and map in conjunction
with others because overlaying the information could show that areas high risk of spreading invasives and are easily managed to provide the best chance for success.

Figure 10. Maps released from the SABCC showing levels of risks for spreading of buffelgrass (top) and of management difficulty (bottom)
The further study of invasive species is important to increase our knowledge of the processes behind invasion. Many of the Earth’s ecosystems are experiencing changes because of global changes and the future of them is unknown. The more that can be learned about the potential changes the better the odds of managing threats to sensitive ecosystems.

Acknowledgments

I would like to thank Dr Travis Huxman and Dr Sujith Ravi for materials and guidance in data collection along with the staff at Biosphere 2 and other summer REU students for help in the field. Dr Tracy Gartner and Dr Joy Mast for help in writing and editing. Funding for the fieldwork was provided by an NSF summer REU grant.
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