Adaptive Mechanisms of *Lesquerella ludoviciana* to Survive Marginal Conditions of Illinois Sand Prairies

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INTRODUCTION

Lesquerella ludoviciana (Nutt.) Wats. (renamed *Physaria ludoviciana*) is an endangered plant in Illinois occurring only at Henry Allan Gleason Nature Preserve (HAGNP) in Mason County, although it is more common in western states (Herkert and Ebinger, 2002; Rollins and Shaw, 1973). Even in the west, populations are disjunct with plants occurring in harsh conditions. In Illinois, its presence in only one location is interesting as other apparently similar habitats exist. Reasons for this isolated distribution are unclear. Throughout its range, *L. ludoviciana* is located in poor soils with low water holding capacity, frequent disturbances, full sunlight often on southwest facing slopes, and limited competition from other species (Claerbout, 2003). Studies in Illinois demonstrate limited seed dispersal and longevity in the seed bank. Thus, seeds may need to establish themselves quickly in these disturbed areas where competition from other plants is minimal in order to thrive. *L. ludoviciana* has features that allow it to thrive in these harsh, dry conditions such as a dense trichomes, short stature, and seed development early in the season when temperatures are lower and water is more plentiful (Coons et al., 2000). However, little is known about its other plant adaptations to dry conditions such as adjustment of its water potential, root:shoot ratios, or evergreen traits to allow continued growth when demands for limited water are less. The goal of this study is to understand adaptations of *L. ludoviciana* to its environmental conditions to provide insight for understanding why its distribution is disjunct. This information will be applied to management for its preservation in Illinois sand prairies, and may provide insight for management of other sand prairie species.

The goal is to understand how *Lesquerella ludoviciana* has adapted to marginal habitat conditions, and to apply information to management of it and other species native to sand prairies. The specific objectives are:

a) to characterize the habitat of *L. ludoviciana* by comparing meteorological parameters in sand prairie locations with and without *L. ludoviciana* plants, including:
   - continuous monitoring of soil moisture, matric potential, and temperature (2 depths)
   - continuous monitoring of light (2 locations)
   - intermittent monitoring of light at various locations in and around colonies
   - monitoring movement and deposition of sand
   - comparing the above parameters to data collected from a reference weather station measuring wind speed, wind direction, air temperature, relative humidity, rainfall, and light

b) to characterize adaptations that *L. ludoviciana* uses for sand prairie conditions, including:
   - root characteristics (length, surface area, volume, branching, fresh weight, ratios to shoots)
   - water potential (different times of season when wet vs. dry conditions)
   - stomatal density (if possible with trichomes)
   - evergreen characteristics

MATERIALS AND METHODS

Meteorological Parameters.

Climatological Measurements. A datalogger (HOBO Weather Station by Onset Computer, Bourne, Massachusetts) was installed in the center of the largest *P. ludoviciana* colony (lower North Bowl) in May 2003 and has been operating with soil temperature and moisture sensors (ECH2O by Decagon Devices, Pullman, Washington) at two depths (17 and 45 cm) since May, 2003. An air temperature / relative humidity sensor at 1.5 m height was added March 31, 2006. A six-sensor line quantum sensor (LQS), manufactured by Apogee Instruments (Logan, Utah), was added June 21, 2006. A second LQS was installed along with another datalogger in the midst of the adjacent *P. ludoviciana* colony in a more vegetated area (upper North Bowl). A portable LQS of the same design was used to make measurements of light intensity at ground level at 10 locations in each of these colonies between 12:30 and 13:00 CST on June 21, 2006 when it was sunny with a few puffy clouds passing occasionally. Light measurements were made near *P. ludoviciana* plants in the North Colony—Lower Bowl (largest colony which has less plant cover from other species) and in the North Colony—Upper Bowl (colony which has more plant cover from other species). For each measurement, light readings were watched for one minute with the lowest and highest values recorded. A one minute reading was taken in each of ten areas that were selected randomly. Means and standard errors were calculated for the lowest, the highest, and the average values. Statistical analysis was a one way ANOVA at $p=0.05$ level.

Measurements regularly made and provided by the Illinois State Water Survey at nearby sites as part of the Illinois Climate Network are also included for the sake of comparison and to aid in interpretation. These measurements include soil moisture at Topeka (3 miles south of HAGNP) and a full weather station including air and soil temperature and precipitation at Kilbourne (15 miles SW of HAGNP).

A soil matric potential system manufactured by Delmhorst Instrument Co. (Towaco, New Jersey) consisting of four gypsum blocks cast around two concentric electrodes and a meter for reading the resistance in the blocks was also purchased. This system was selected because other relatively cheap soil matric potential sensors such as tensiometers have a limited range that makes them inapplicable to the sandy soil found at HAGNP. However, so far, we have not been able to get the Delmhorst system to operate properly, so it has not been installed in the field. As a general rule, field measurement of soil matric potential over a wide range of values is a difficult problem, especially with a limited budget.

Erosion Measurements. Thin plastic-covered metal gardening stakes about 80 cm long equipped with washers lying at the ground surface were first used as erosion pins by pounding them into the ground and then making measurements of the distance from the top of the stake to ground surface to diagnose any cumulative erosion or deposition of soil. A set of 17 such pins laid out in a cross-shaped pattern were installed in the lower North Bowl in May 2003 but were removed by persons unknown sometime after a set of measurements were made in September 2004. They were not replaced because little to no elevation change was observed during that period.

At the same time, a set of 13 pins made of the same material were also placed in an active blowout near the middle of HAGNP between the south and north bowls where the *P. ludoviciana* colonies are found, with nine more added one month later in June 2003. Since November 2004, these have been supplemented with a more sturdy set of 26 1.2 m solid steel rods, and the old pins will be removed once their locations have been surveyed.

Two sets of sand traps (two traps each on two poles) of the "Big Spring No. 8" (BSNE) design (Custom Products, Big Spring, Texas) were installed on two sides of the active blowout in May 2004.

Plant Adaptations.

Plant Morphology. Plants were removed from three locations near the periphery of the lower bowl of the North Colony. Each larger plant had one separate, smaller plant in close association with it; therefore, all six plants were measured. Fresh weights of roots and lengths of main roots were measured. Root volumes were determined by water displacement. Root areas were determined using a Li-Cor leaf area meter. Leaf areas were estimated using a 0.5 cm^2 transparent grid, in order to keep the rosette structures intact. Shoot fresh weights and leaf numbers were measured. Root:shoot ratios were calculated for area and for fresh weight. Shoot volumes were not measured due to their dense covering of hairy trichomes and dry weights were not determined, since specimens were prepared for deposit in the EIU Stover-Ebinger Herbarium. Duplicate herbarium specimens were sent to the Illinois Natural History Survey, Champaign and the Missouri Botanical Gardens, St. Louis.

Leaf Water Potential. Leaf water potential was measured using six leaves from plants located in the largest colony at the Henry Allan Gleason Nature Preserve (North Colony—Lower Bowl) using a pressure bomb (Soil Moisture Equipment Corporation, Santa Barbara, CA). Leaves selected were intermediate in age, i.e. not the youngest or the oldest. These measurements were taken between 11:30 am-1:30 pm during March (3-31-06), June (6-21-06), and September (9-2-04). Statistical analysis was a one way ANOVA using Excel at $P=0.05$ level. Means and standard errors also were calculated.

Stomatal Densities. Leaves used for water potential measurements were taken to the laboratory to attempt to measure stomatal densities. However, due to shriveling of leaves from water loss and due to the presence of numerous trichomes on leaves, it was not possible to count stomates.

Evergreen Characteristics. Evergreen characteristics were documented with digital images taken during winter months.

RESULTS

Table 1. Light intensity (μmol/m²/sec) in two colonies of *Physaria ludoviciana* at the Henry Allan Gleason Nature Preserve (June 21, 2006—midday).

Colony	Lowest	Highest	Average
North Colony Lower Bowl	1082 ± 173[z] a	1805 ± 32 a	1443 ± 88 a
North Colony Upper Bowl	801 ± 162 a	1753 ± 57 a	1277 ± 99 a

[z] Means ± standard errors. n = 10 (1 minute each) for each colony. Mean separations within a column. p = 0.05 level.

Table 2. Morphological characteristics of *Physaria ludoviciana*.

	Larger Plants (Mean + s.d.)	Smaller plants (Mean + s.d.)
Length of main root (cm)	45.9 ± 12.7	30.4 ± 8.6
Total root area (cm^2)	12.8 ± 6.2	3.3 ± 2.2
Total root volume (cm^3)	4.3 ± 1.5	1.0 ± 0.9
Root fresh weight (g)	3.6 ± 2.1	0.8 ± 0.5
Leaf number	72.7 ± 47.1	23.2 ± 7.8
Leaf area (cm^2)	61.8 ± 44.7	19.1 ± 4.5
Shoot fresh weight (g)	19.1 ± 4.5	1.5 ± 1.0
Root/Leaf area (cm^2)	0.25 ± 0.14	0.17 ± 0.10
Root/Shoot fresh weight (g)	0.30 ± 0.18	0.52 ± 0.24

Table 3. Water potential of *Physaria ludoviciana* plants from Henry Allan Gleason Nature Preserve taken at midday in March, June and September.

Date	Water Potential (-MPa)	Soil Water Content (m^3/m^3)		Soil Temp. (°C)		Air Temp. (°C)
		17 cm	45 cm	17 cm	45 cm	
March 2006	1.19 $\pm$ 0.03^{z}a	0.0995	0.0776	12.8	9.9	15.1
June 2006	1.69 $\pm$ 0.08 a	0.0464	0.0510	29.1	26.9	28.2
Sept 2004	1.58 $\pm$ 0.22 a	0.0616	0.0582	26.7	25.3	21.9

^{z}Means $\pm$ standard errors. n=6. p=0.05 level.

Figure 1

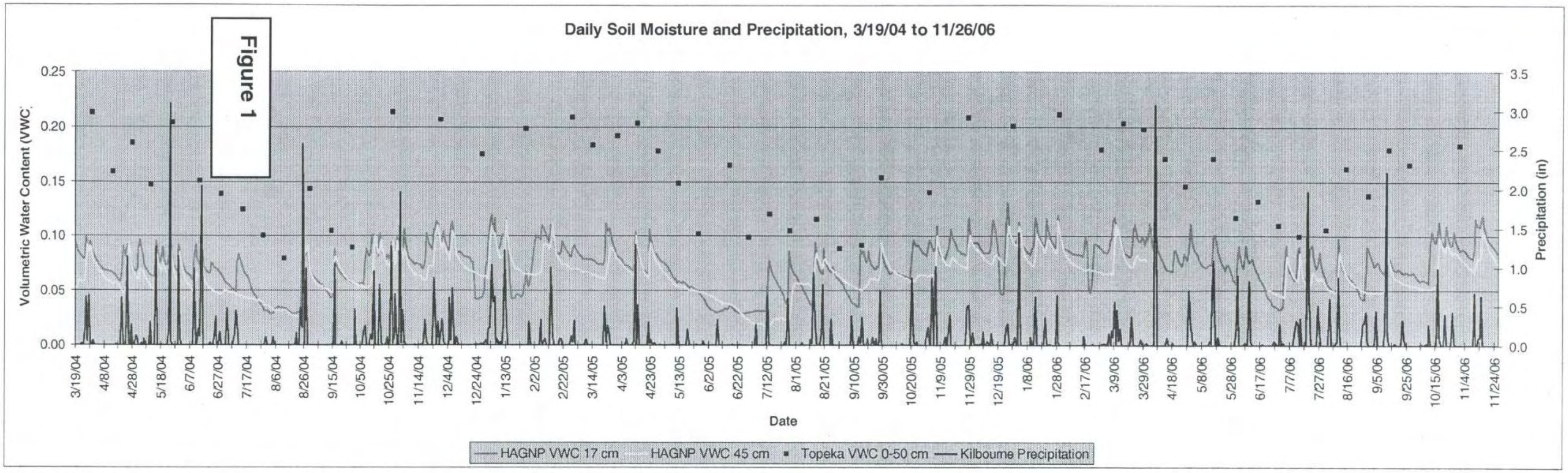
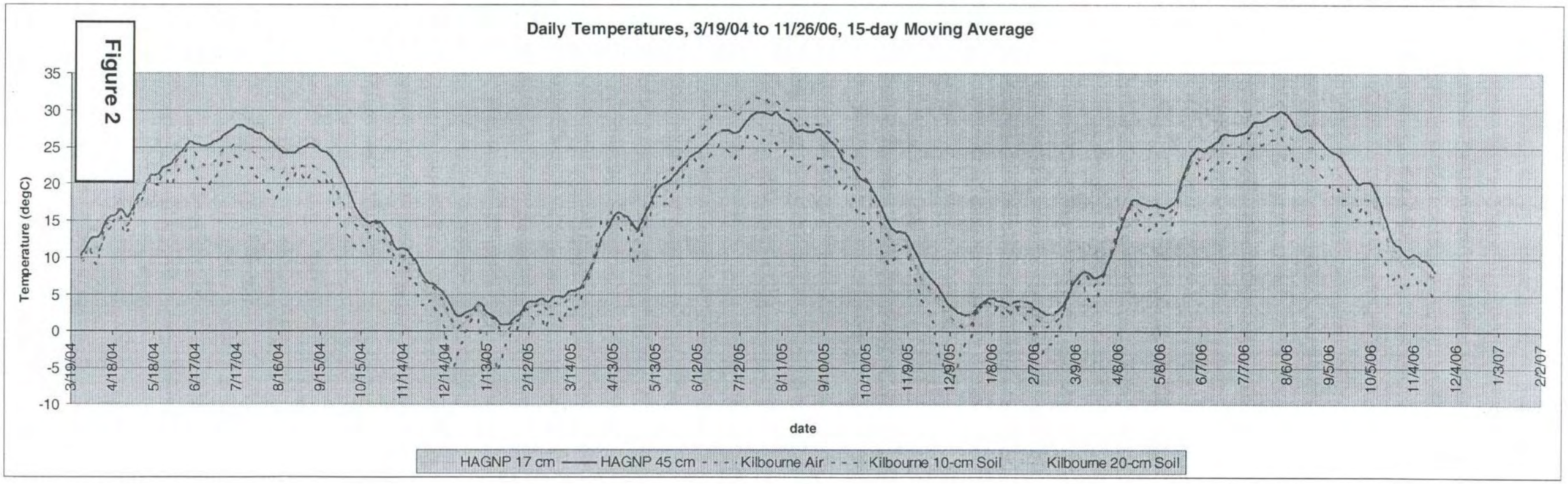


Figure 2



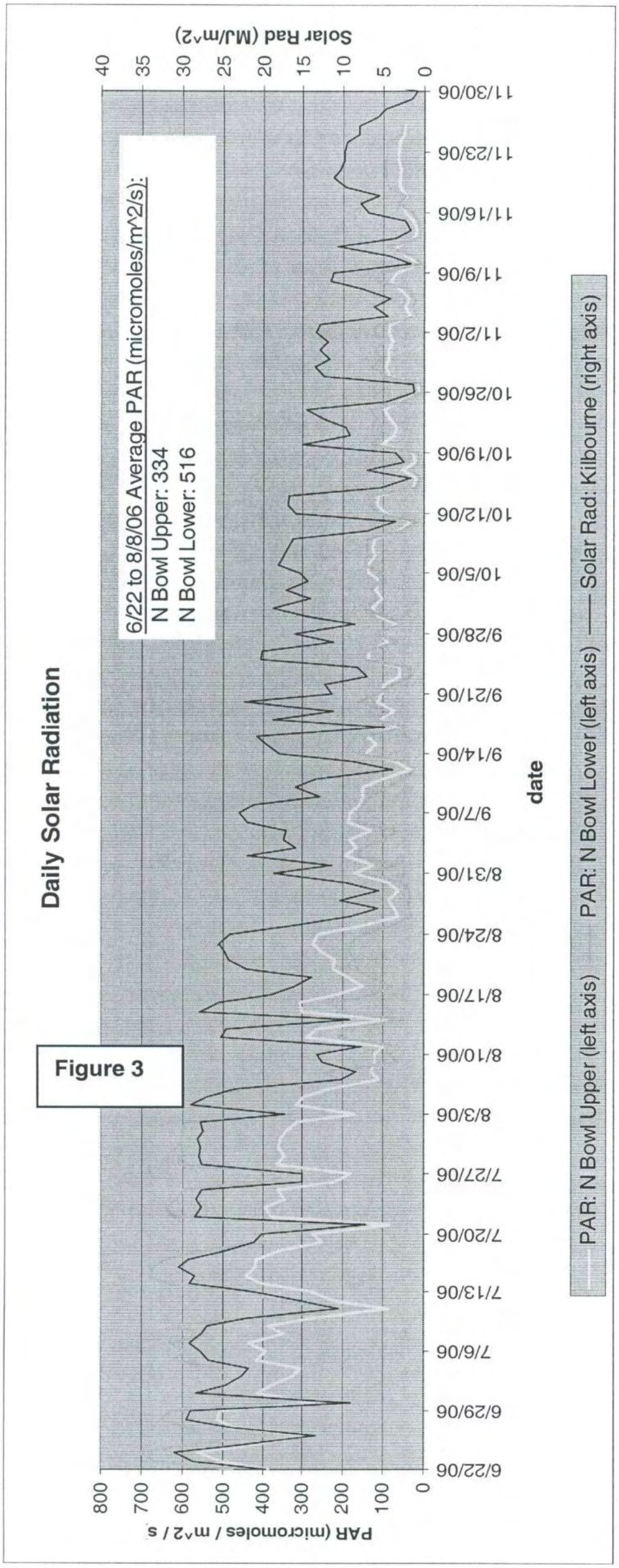
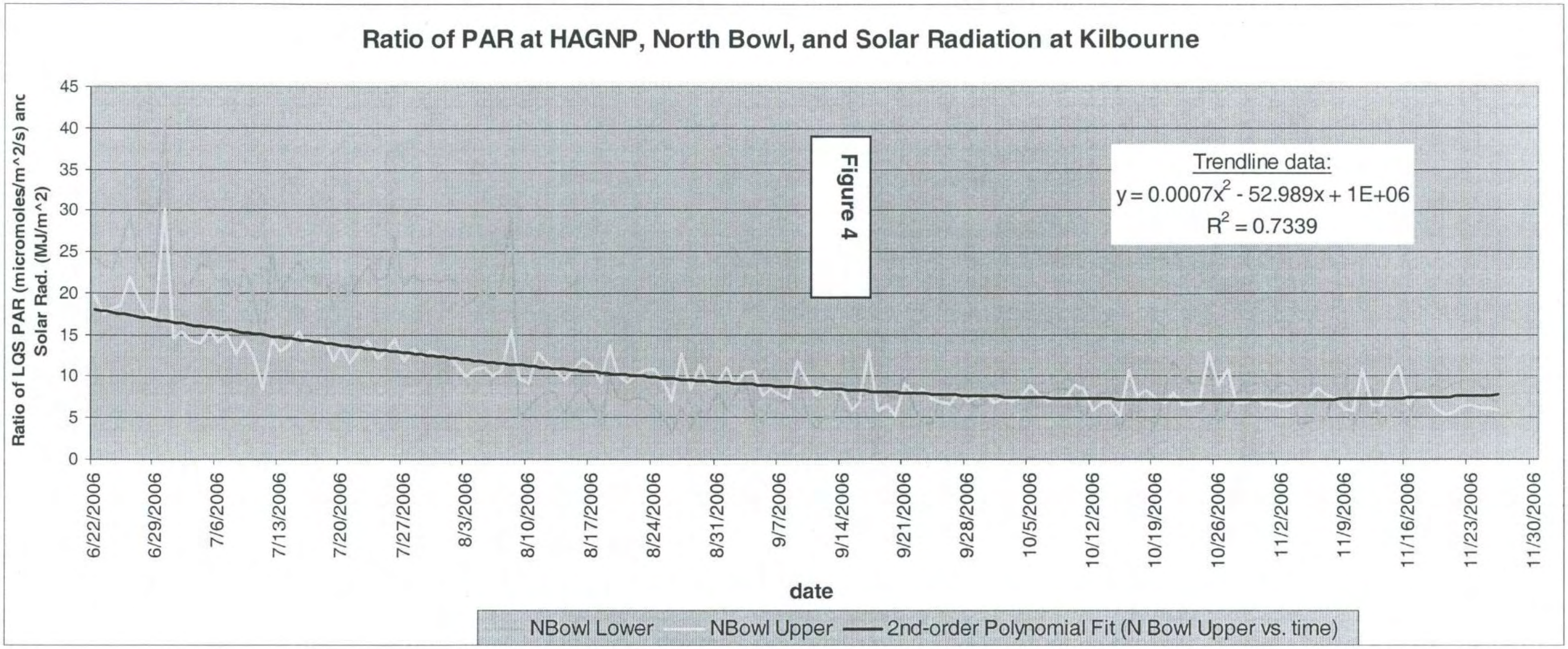

Daily Solar Radiation
6/22 to 8/8/06 Average PAR (micromoles/m^2/s):
N Bowl Upper: 334
N Bowl Lower: 516
PAR (micromoles / m^2 / s)
Solar Rad (MJ/m^2)
date
PAR: N Bowl Upper (left axis)
PAR: N Bowl Lower (left axis)
Solar Rad: Kilbourne (right axis)
6/22/06
6/29/06
7/6/06
7/13/06
7/20/06
7/27/06
8/3/06
8/10/06
8/17/06
8/24/06
8/31/06
9/7/06
9/14/06
9/21/06
9/28/06
10/5/06
10/12/06
10/19/06
10/26/06
11/2/06
11/9/06
11/16/06
11/23/06
11/30/06

Figure 3


Ratio of PAR at HAGNP, North Bowl, and Solar Radiation at Kilbourne
Figure 4
Trendline data:
y = 0.0007x2 - 52.989x + 1E+06
R2 = 0.7339
Ratio of LQS PAR (micromoles/m^2/s) anc
Solar Rad. (MJ/m^2)
45
40
35
30
25
20
15
10
5
0
6/22/2006
6/29/2006
7/6/2006
7/13/2006
7/20/2006
7/27/2006
8/3/2006
8/10/2006
8/17/2006
8/24/2006
8/31/2006
9/7/2006
9/14/2006
9/21/2006
9/28/2006
10/5/2006
10/12/2006
10/19/2006
10/26/2006
11/2/2006
11/9/2006
11/16/2006
11/23/2006
11/30/2006
date
NBowl Lower
NBowl Upper
2nd-order Polynomial Fit (N Bowl Upper vs. time)

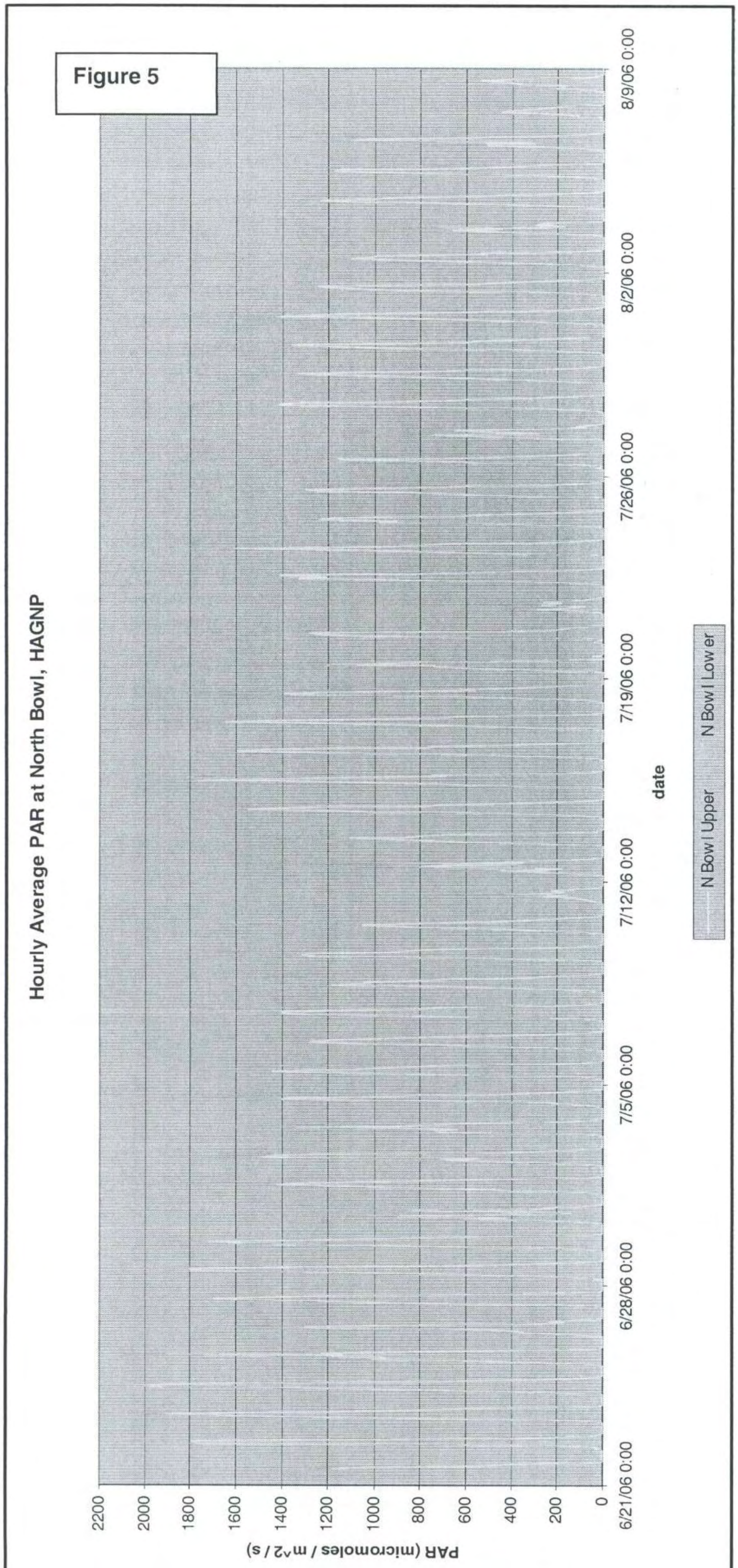


Figure 5
Hourly Average PAR at North Bowl, HAGNP
PAR (micromoles / m^2 / s)
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
6/21/06 0:00
6/28/06 0:00
7/5/06 0:00
7/12/06 0:00
7/19/06 0:00
7/26/06 0:00
8/2/06 0:00
8/9/06 0:00
date
N Bowl Upper
N Bowl Lower

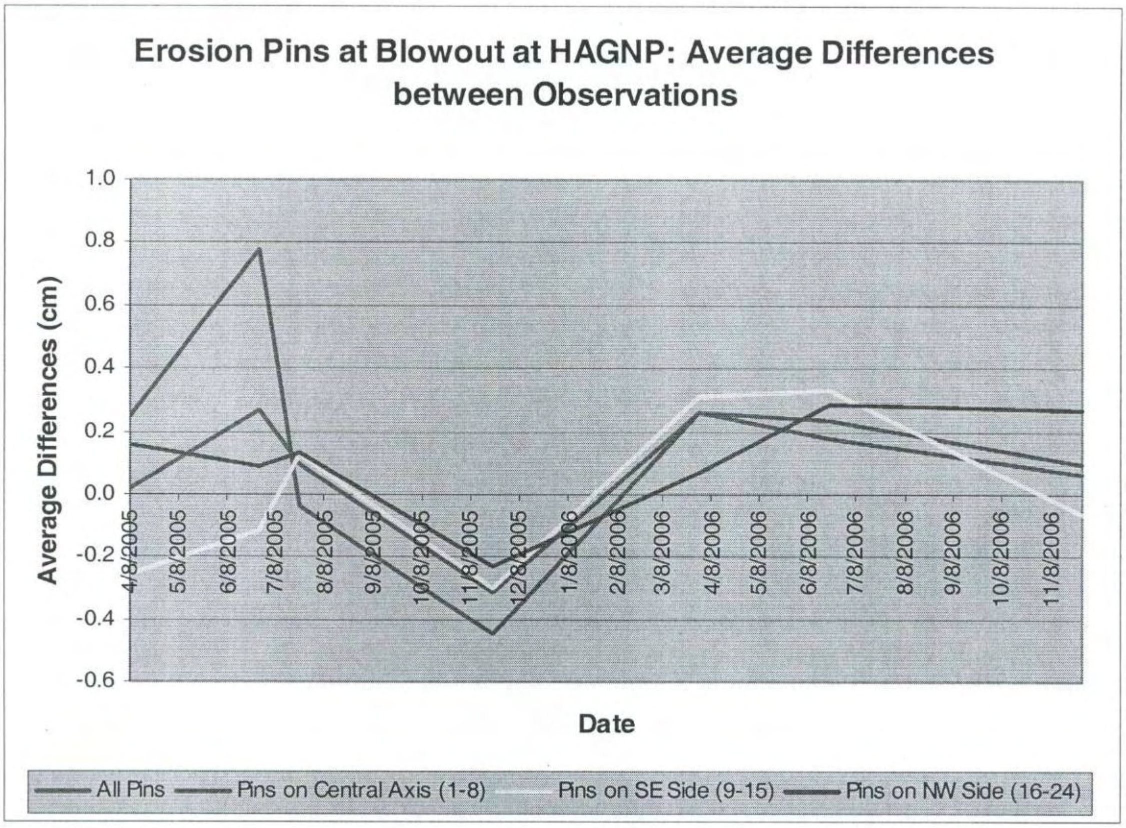

Erosion Pins at Blowout at HAGNP: Average Differences between Observations
Average Differences (cm)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
4/8/2005
5/8/2005
6/8/2005
7/8/2005
8/8/2005
9/8/2005
10/8/2005
11/8/2005
12/8/2005
1/8/2006
2/8/2006
3/8/2006
4/8/2006
5/8/2006
6/8/2006
7/8/2006
8/8/2006
9/8/2006
10/8/2006
11/8/2006
Date
All Pins
Pins on Central Axis (1-8)
Pins on SE Side (9-15)
Pins on NW Side (16-24)

Figure 6

DISCUSSION

Soil Moisture (Figure 1). Soil moisture fluctuated in response to precipitation. Soil moisture was consistently lower at HAGNP than at the Illinois State Water Survey site at Topeka; we expect this is because of the presence of some soil development and sod cover at Topeka. As expected, more fluctuations occurred in soil moisture at 17 cm than at 45 cm. During periods of low rainfall, soil was drier at the surface than deeper in the soil. During periods of high rainfall, soil was wetter at the surface than deeper in the soil. The soil moisture was generally low (rarely above 10%); however, this low soil moisture does not necessarily imply a large negative soil water potential in this relatively clean, sandy soil.

Soil Temperature (Figure 2). During the summer, soil temperatures generally were hotter at 17 cm than at 45 cm. Also summer soil temperatures were hotter at HAGNP than at the Illinois State Water Survey weather station near Kilbourne except during the drought of 2005. Soil temperatures in summer were typically warmer than air temperatures by as much as 5°C. In the winter, soil temperatures were more similar. Thus, soil temperatures were more extreme at HAGNP than at Kilbourne.

Light Intensity (Table 1; Figures 3-5). Light intensities (photosynthetically active radiation; PAR) at ground level were higher in lower bowl than in upper bowl (both part of the North Colony), which is as expected because of greater vegetation cover in the upper bowl as compared to the lower bowl. The lower bowl PAR intensities were observed to be 13% higher than those of the upper bowl based upon spatially random measurements taken throughout each bowl near noon on June 21 (Table 1), but 55% higher based upon readings taken over time with sensors at set locations in each bowl (Figure 3). This discrepancy may be partly the result of the choice of the fixed locations where the PAR instruments were installed, but is likely also to be the result of the greater shading effect of vegetation when the sun is lower (early or late in the day and later in the summer) and of increased vegetation cover later in the summer in the upper bowl. These effects are also seen in the decreasing ratio of upper bowl PAR to Kilbourne solar radiation shown in Figure 4, and from the lower mid-day PAR values in the upper bowl as compared to the lower bowl observed in the later part of the period shown in Figure 5. Note the low PAR values at the lower bowl beginning 8/9/06 are because of the sensor being flipped on its side, probably by a deer.

Sand Deposition (Figure 6). Sand is actively moving in the blowouts between the North and South Colonies as indicated by fluctuations in erosion pin heights shown in Figure 6, which indicates an annual cycle, with erosion in the spring and deposition in the fall. Most of the sand is moving close to the ground surface, so amount collected in traps from blowing sand was very little.

Plant Morphology (Table 2). As plants grew larger, their roots increased in length, surface area, volume and fresh weight with larger plants having roots ~45 cm long. Relative to shoot development, larger plants had an average of 73 leaves. Root:shoot ratios for fresh weights decreased as plants grew larger, suggesting that more allocations were put into roots than shoots during early growth relative to later growth. Initially, the plants develop roots which is typical of plants adapted to soils with low water and/or nutrients. Once roots are developed sufficiently to reach lower regions in the soil profile with water and nutrients, it appears that *P. ludoviciana* plants increase allocations into shoot development to maximize competition for light. Overall, the roots do not appear to be storing any water as they are rather slender, but very deep.

Leaf Water Potential (Table 3). Leaf water potentials were not significantly different when sampled in March, June and September. This lack of significance may be due to variability in samples, as the May values appear somewhat higher (less negative) than the others when comparing means using standard errors. Water potentials were highest when water content was highest and when soil/air temperatures were lowest. These values are typical values for plants exhibiting only mild water stress (-0.8 to -2.0 MPa).

Evergreen Characteristics. Plants demonstrated an evergreen appearance as shown in digital images on enclosed CD. Also, by mid-March, flower buds were observed on plants in the field, suggesting their initiation, and persistence from the previous year.

LITERATURE CITED

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