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Serpentine ecosystem responses to varying water availability and prescribed fire in the U.S. Mid-Atlantic region

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Abstract. Grasslands growing atop serpentine bedrock are subject to edaphic stresses and, as a result, are low productivity ecosystems. Nutrient limitations are so severe in some serpentine grasslands that plant growth is unaffected by increased water availability. However, little is known of how serpentine grasslands in eastern North America function and respond to environmental changes, including variation in water availability. Serpentine barrens of the U.S. Mid-Atlantic region are globally rare ecosystems currently threatened by forest encroachment. Prescribed fire has been applied to maintain these ecosystems, although ecosystem responses to prescribed fire remain unquantified. Monthly measurements of CO₂ exchange and leaf area index (LAI) were made at managed and unmanaged sites over two years. Environmental factors influencing CO₂ exchange rates were monitored, and soil composition was also assessed. Unusually dry conditions in 2012 led to suppressed CO₂ exchange rates and LAI across sites, while wet conditions in 2013 resulted in higher CO₂ exchange rates and LAI. Seasonal maxima for net ecosystem production (NEP), ecosystem respiration (ER), and gross ecosystem production occurred in the late summer in 2012 and mid-summer in 2013. Over the study period, maximum NEP and ER were 13.68 and -9.40 μmol CO₂ m⁻² s⁻¹, respectively, while LAI reached 2.18 m² m⁻². Across sites, carbon storage in the top 10 cm of soil was 33.1–41.3 Mg C ha⁻¹. Prescribed fire did not affect CO₂ exchange, LAI, or soil carbon storage in the four to six years following a fire. In contrast to prior studies, Mid-Atlantic serpentine barrens responded positively to increased soil water availability and were more productive than expected. These ecosystems were functionally similar to tallgrass prairie, suggesting that fire management practices from prairies may be applicable in Mid-Atlantic serpentine barrens. Increased frequency of prescribed fire would likely reduce litter inputs to the soil and maintain the ecosystem's natural edaphic stressors, thereby combating forest encroachment.

Key words: carbon dioxide exchange; ecosystem respiration; Mid-Atlantic U.S.; net ecosystem production; prescribed fire; serpentine barren; serpentine syndrome; soil carbon.

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INTRODUCTION

Serpentine syndrome has been widely described and documented in the literature (Whittaker 1954, Brady et al. 2005); plant communities that develop atop ultramafic, serpentine bedrock are often regionally unique, with high endemism

and low productivity due to the unusual stresses posed by edaphic factors. Serpentine soils are typically shallow and macronutrient poor with low calcium to magnesium ratios, high heavy metal content (i.e., chromium, cobalt, and nickel), and low soil water holding capacity (Walker 1954, Proctor and Woodell 1975, Brady et al.

2005, Rajakaruna et al. 2009). Prior research indicates that nutrient limitations impose significant restrictions on serpentine plant productivity, such that addition of another limiting resource, specifically water, does not lead to increased growth (Going et al. 2009, Fernandez-Going and Harrison 2013). However, to date these findings are confined to serpentine grasslands in California with a Mediterranean climate.

Ecological studies of serpentine ecosystems in eastern North America are limited and provide a poor understanding of how the serpentine syndrome is manifest in the region's serpentine barrens (Rajakaruna et al. 2009). In particular, little is known of ecosystem productivity and its response to environmental drivers in the serpentine barrens of the U.S. Mid-Atlantic region (i.e., northern Maryland and southeastern Pennsylvania). Mid-Atlantic serpentine barrens are perennial, grass-dominated ecosystems embedded within the eastern deciduous forest biome, and they share many dominant plant species with grasslands of the Great Plains, including *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, and *Andropogon gerardi* Vitman (Epstein et al. 1998, Tyndall and Hull 1999, Orndorff and Coleman 2008). As such, there may be functional similarities between Mid-Atlantic serpentine barrens and Great Plains grasslands, though the extent to which any similarities are attenuated by serpentine soil properties is unknown.

In contrast to findings from nutrient-limited serpentine grasslands, grasslands of the Great Plains exhibit large variation in aboveground net primary production (ANPP), as well as annual CO₂ exchange rates, with variation in precipitation (Flanagan et al. 2002, Suyker et al. 2003, McCulley et al. 2005, Nippert et al. 2006, Bremer and Ham 2010). North American datasets indicate substantial increases in grassland ANPP in years with high precipitation, while declines in productivity during dry years are of much smaller magnitude (Knapp and Smith 2001). In addition to precipitation, other micrometeorological factors, as well as fire frequency and nitrogen availability often interact to influence grassland ANPP and CO₂ exchange rates (Seastedt and Knapp 1993, Knapp et al. 1998a, b, Heisler and Knapp 2008, Risch and Frank 2010).

Substantial effort has been made by conserva-

tion organizations to acquire and manage Mid-Atlantic serpentine barrens (e.g., Orndorff and Coleman 2008, Latham and McGeehin 2012). These ecosystems are classified as globally rare (global conservation status G1G2, NatureServe 2013) and are host to a number of threatened and endangered plants (e.g., *Phemeranthus teretifolius* Pursh (Raf.), *Sporobolus heterolepis* A. Gray (A. Gray), *Symphyotrichum depauperatum* Fernald (G.L. Nesom)), as well as rare plants and animals (Latham 1993, NRCS 2013a, Rajakaruna et al. 2009). Management is necessary in these barrens, as the lack of historical disturbance agents (i.e., human-ignited fires and grazing) has led to forest encroachment and substantial land area losses (Tyndall 1992, Tyndall and Hull 1999, Latham 2008, Latham and McGeehin 2012). The process of encroachment is thought to be partly mediated by soil organic matter accumulation (Latham 1993, Arabas 2000, Orndorff and Coleman 2008), which may attenuate the edaphic stresses in these ecosystems. Recently, many Mid-Atlantic serpentine barrens have been managed with prescribed fire to combat the buildup of organic matter, though the ecosystem-level effects of this practice have not been assessed. The application of prescribed fire in non-serpentine grasslands consumes litter and supports short-term increases in plant productivity (Seastedt et al. 1991, Knapp et al. 1998a).

The present study sought to characterize ecosystem productivity in Mid-Atlantic serpentine barrens in response to natural environmental variation. As the study spanned a dry year and a wet year, it was possible to examine the influence of water availability on ecosystem productivity. Additionally, this study examined the effect of prescribed fire on productivity and edaphic factors, as maintenance of these unique ecosystems is dependent upon appropriate management. Toward these ends, the following research questions were addressed: (1) How do contrasting growing season conditions (i.e., dry vs. wet years) and management (i.e., management with fire vs. no management) affect ecosystem CO₂ exchange rates? (2) What are the principal environmental drivers of CO₂ exchange? (3) Are soil properties, including soil carbon storage, affected by management with prescribed fire? (4) How do Mid-Atlantic serpentine barrens compare to other North American grassland ecosys-

Table 1. Location, size, and management history of all study sites.

Site	Latitude	Longitude	Area (ha)	Management
Goat Hill	39°43'38.70" N	76°04'44.71" W	0.9	none
New Texas	39°44'38.54" N	76°10'51.00" W	2.7	none
Nottingham	39°43'54.55" N	76°01'59.89" W	6.1	fire, May 2008
Pink Hill	39°55'47.39" N	75°25'51.16" W	3.6	fire, April 2008
Sugartown	40°00'36.52" N	75°31'29.26" W	7.5	fire, April 2007
Unionville	39°54'43.17" N	75°42'52.29" W	1.9	none

Note: Area reported indicates the size of the particular serpentine barren patch in which chamber measurements were made.

tems (both serpentine and non-serpentine), in terms of responses to water availability and prescribed fire?

METHODS

Study sites

Serpentine barrens throughout southeastern Pennsylvania were selected for use in this study. Study sites included three sites previously managed with prescribed fire, Nottingham, Pink Hill, and Sugartown barrens, and three unmanaged sites, Goat Hill, New Texas, and Unionville barrens (Table 1). All sites are located within 70 km of one another and ranged in size from 0.9 to 7.5 ha (Table 1). In some cases, study sites are embedded within a larger matrix of serpentine barrens interspersed with encroaching forest. Serpentine bedrock underlies soils of the Chrome series (Typic Hapludalf) at all sites, and soil texture is typically described as silt loam or gravelly silty clay loam (Barton and Wallenstein 1997, NRCS 2013b).

Perennial grasses dominate vegetation at each site, and predominant species include *A. gerardii*, *S. scoparium*, *S. nutans*, and *S. heterolepis*. Tree species including *Juniperus virginiana* L., *Pinus rigida* Mill., *Pinus virginiana* Mill., *Quercus marilandica* Munchh., *Quercus stellata* Wangenh., and the exotic invasive *Elaeagnus umbellata* Thunb. are found at low density within study sites. Typically, *Quercus* sp. are found more commonly at the three northern study sites (Pink Hill, Sugartown, and Unionville barrens), while *Pinus* sp. are more common at the three southern sites (Goat Hill, New Texas, and Nottingham barrens). Nomenclature follows the PLANTS Database (NRCS 2013a).

Annual temperature averages 11.5°C in southeastern Pennsylvania, while precipitation averages 1267 mm yr⁻¹ and is distributed approximately

evenly throughout the year (ACIS 2012). Meteorological towers were installed at the Unionville and Nottingham barrens in June 2012 to serve as climate analogs for the clusters of northern and southern study sites, respectively. Each tower recorded air temperature and relative humidity (CS215, Campbell Scientific, Logan, UT), terms that were used to calculate vapor pressure deficit (D, the difference in water vapor pressure between saturated and ambient air). Photosynthetically active radiation (PAR, PQS1, Kipp and Zonen, Deft, Netherlands), precipitation (TE525, Texas Electronics, Dallas, TX), soil volumetric water content at 10 cm depth (θ , $n = 3$ sensors per site, EC-5, Decagon Devices, Pullman, WA), and soil temperature at 5 and 10 cm depth ($n = 2$ sets of sensors per site, shielded Type-T thermocouples, Omega Engineering, Stamford, CT) were also measured. All meteorological measurements were recorded every 15 s and averaged or summed over 30 min intervals by a datalogger (CR 1000, Campbell Scientific).

Field measurements

At each study site, a set of five polyethylene bases (50.8 cm × 50.8 cm × 15.2 cm) were randomly inserted into the soil ~2 weeks prior to the initiation of field measurements. Care was taken to ensure minimal soil disturbance during installation. Bases were leveled during installation and were situated approximately 2–4 cm beneath the soil surface. Base height relative to the soil surface was measured annually on all sides of each base to determine total air volume within the base. At monthly intervals, measurements of net ecosystem production (NEP, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and ecosystem respiration (ER, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were made at each base location using a custom built chamber interfaced with a LI-6400XT infrared gas analyzer (IRGA, LI-COR, Lincoln, NE).

A 0.234 m³ (50.8 cm × 50.8 cm × 90.8 cm) chamber was constructed of colorless polycarbonate and contained a 4+ m vent tube for pressure equilibration. The chamber bottom was fitted with aluminum angle bar, to which closed-cell foam was attached. This provided an airtight seal between the chamber and a base. Three 58-cm² box fans were installed within the chamber, two at the top of the chamber and one 24 cm above the chamber bottom, to provide adequate internal mixing of air. A soil chamber mounting plate and air inlet manifold (parts 9864–174 and 9864–032, respectively; LI-COR) were used to connect the IRGA sensor head to the chamber.

During measurements at base locations, the chamber was gently placed on the base to reduce the likelihood of large pressure changes within the chamber. Once the base was sealed by the chamber, a 60-s measurement period was initiated using the LI-6400XT “Custom Chamber-Closed” configuration. Data were logged at 10-s intervals and, due to the large chamber volume, no attempt was made to control chamber temperature, humidity, or CO₂ concentration.

Monthly measurements of NEP and ER were made during the growing season from June to October 2012 and from May to September 2013. Additionally, ER measurements were made at all sites in November 2012, after the end of the growing season. All measurements of NEP were made under conditions of full sun between approximately 10 AM and 1 PM, thus measurements represent maximum rates of NEP. Measurements of ER were made by covering the chamber with a ripstop nylon shade cloth that blocked 97% of incident radiation (data not shown). Weather permitting, three independent NEP measurements were made at each base location, followed by three ER measurements. The chamber was vented between each measurement to ensure that conditions inside the chamber remained as close to ambient as possible. All CO₂ flux measurements were adjusted to account for variation in measurement volume due to different base insertion depths.

Environmental measurements were made to accompany CO₂ flux measurements at each base location. Soil temperatures at 5 and 10 cm depth were measured with a thermocouple and thermistor, respectively (Type-E, MHP-CXSS-316U-6-SMP-M-NP, Omega Engineering; Temp 5, Oak-

ton Instruments, Vernon Hills, IL). Measurements of chamber air temperature (T_{chamber}) and relative humidity were recorded by the LI-6400XT, and these values were used to compute D. A quantum sensor (LI-190, LI-COR) affixed to the top of the chamber measured PAR. Soil cores from 0–5 cm depth were taken at distances of 30–50 cm from each base location on every measurement date to determine gravel-free soil gravimetric water content (GWC).

Monthly measurements of leaf area index (LAI, LAI-2200, LI-COR) were made at the center of each base, approximately 7–10 cm above the soil surface. To ensure that LAI measurements did not include the sides of the base as leaf area, the instrument’s fifth ring was masked during field measurements. Two sets of LAI measurements, comprised of one above canopy measurement and four below canopy measurements, were logged at each base, and values were averaged to determine LAI at each base location. Measurements of LAI were not made in the months of May because vegetation was too short or November because the majority of vegetation had senesced. Measurements of LAI made in October 2012 were halved because approximately half the vegetation at each base location had senesced (*personal observation*).

Early in the 2013 growing season, soil samples from 0 to 5 and 5 to 10 cm depth were collected from five random sample points in each study site. At each sample point, three soil cores per depth interval were collected from a 1 m diameter area and composited. A fourth core was collected for soil bulk density determination. Composited samples were air dried and passed through a 2-mm mesh sieve. All soil samples tested negative for the presence of carbonates using 1.0 M HCl. Subsamples of the sieved soil were crushed and packed into tin capsules for determination of percent carbon by elemental analysis (Costech ECS4010, Costech Analytical, Valencia, CA). Ten duplicate soil samples were analyzed and showed a mean difference of 0.20%. Sieved soils were also analyzed via X-ray fluorescence spectrometry (Omega Handheld XRF Analyzer, Model XPD 4000, InnoveX Systems, Woburn, MA) to determine the concentration of chromium, cobalt, and nickel in the soils.

Data processing and statistical analyses

Gross ecosystem production (GEP) was computed separately for each base on each measurement date by using the average NEP and ER measurements for each base in the equation:

$$\text{GEP} = \text{NEP} - \text{ER}$$

where positive values indicate CO₂ uptake by the ecosystem and negative values indicate CO₂ release from the ecosystem.

All statistical analyses described below were performed with R (version 3.0.1, R Core Team 2013). Repeated measures ANOVAs were used to examine whether LAI, NEP, ER, and GEP varied with treatment (i.e., management with fire vs. no management), growing season (i.e., 2012 vs. 2013), or the treatment by growing season interaction. Repeated measures were coded as random effects in a mixed-effects model (Schaubberger and Pierce 2002) as base nested within site.

To examine the effect of environmental variation on CO₂ exchange rates, stepwise multiple regressions with backward and forward selection were used. Parameters to be included in the final model were selected through minimization of the Akaike Information Criterion (AIC, R Package MASS, stepAIC function). Full models for NEP and GEP included the variables temperature, GWC, LAI, D, and PAR, while full models for ER included the variables temperature, GWC, and LAI. Three separate versions of the full model were run to accommodate three highly correlated temperature variables (data not shown): T_{chamber} , soil temperature at 5 cm depth ($T_{\text{soil}, 5 \text{ cm}}$), and soil temperature at 10 cm depth ($T_{\text{soil}, 10 \text{ cm}}$). Final model selection was made based on the AIC statistic. Because significant differences in CO₂ exchange rates were observed between years (see below), multiple regression analyses were performed separately for data collected in 2012 and 2013. Note that environmental data used for the multiple regression analyses were not those collected by the meteorological towers, rather those collected in conjunction with chamber measurements.

Individual two-way ANOVAs were used to determine whether soil bulk density, percent soil carbon, or soil carbon storage varied with treatment, soil depth (i.e., 0–5 cm vs. 5–10 cm), or the treatment by soil depth interaction.

Identical analyses were used to examine variation in the chromium, cobalt, and nickel content of the soil. Note that the unburned Goat Hill site was excluded from all soil composition statistical analyses because surface soils were mechanically removed (i.e., scraped) from the site in 1998.

RESULTS

Meteorological data

Air and soil temperature at 5 cm depth were similar throughout the study, with growing season temperatures increasing toward a maximum in July and declining afterward (Fig. 1A). This pattern was observed in both the 2012 and 2013 growing seasons. Variation in D was less consistent across growing seasons, increasing toward a high >2 kPa in early July 2012 and then varying below 1.5 kPa for the remainder of the growing season (Fig. 1B). In contrast, D did not spike during the 2013 growing season, but consistently varied below 1.5 kPa (Fig. 1B). Light levels, as PAR_{max}, followed expected seasonal patterns in both 2012 and 2013 (Fig. 1C).

Patterns of precipitation and θ showed substantial variation between 2012 and 2013 (Fig. 1D, Table 2). The 2012 growing season was characterized by lower than average rainfall from May through September (Table 2). The lack of precipitation, particularly in June and early July led to extremely low θ in mid-July, with minimum values reaching 0.12 m³ m⁻³ (Fig. 1D). Following this dry period, θ slowly increased over the remainder of the growing season, with values typically greater than 0.3 m³ m⁻³ (Fig. 1D). In contrast to 2012, the 2013 growing season was substantially wetter than average, with 134%, 72%, and 32% more precipitation in June, July, and August, respectively, relative to the long-term mean (Table 2). As a result, θ remained relatively high throughout the growing season, with values rarely falling below 0.25 m³ m⁻³ (Fig. 1D).

Growing season and management influences on LAI and CO₂ exchange

Leaf area index was significantly higher during the 2013 growing season, relative to the 2012 growing season ($p < 0.0001$; Fig. 2, Table 3). In comparing LAI across the two growing seasons, it was apparent that maximum average LAI, 1.67

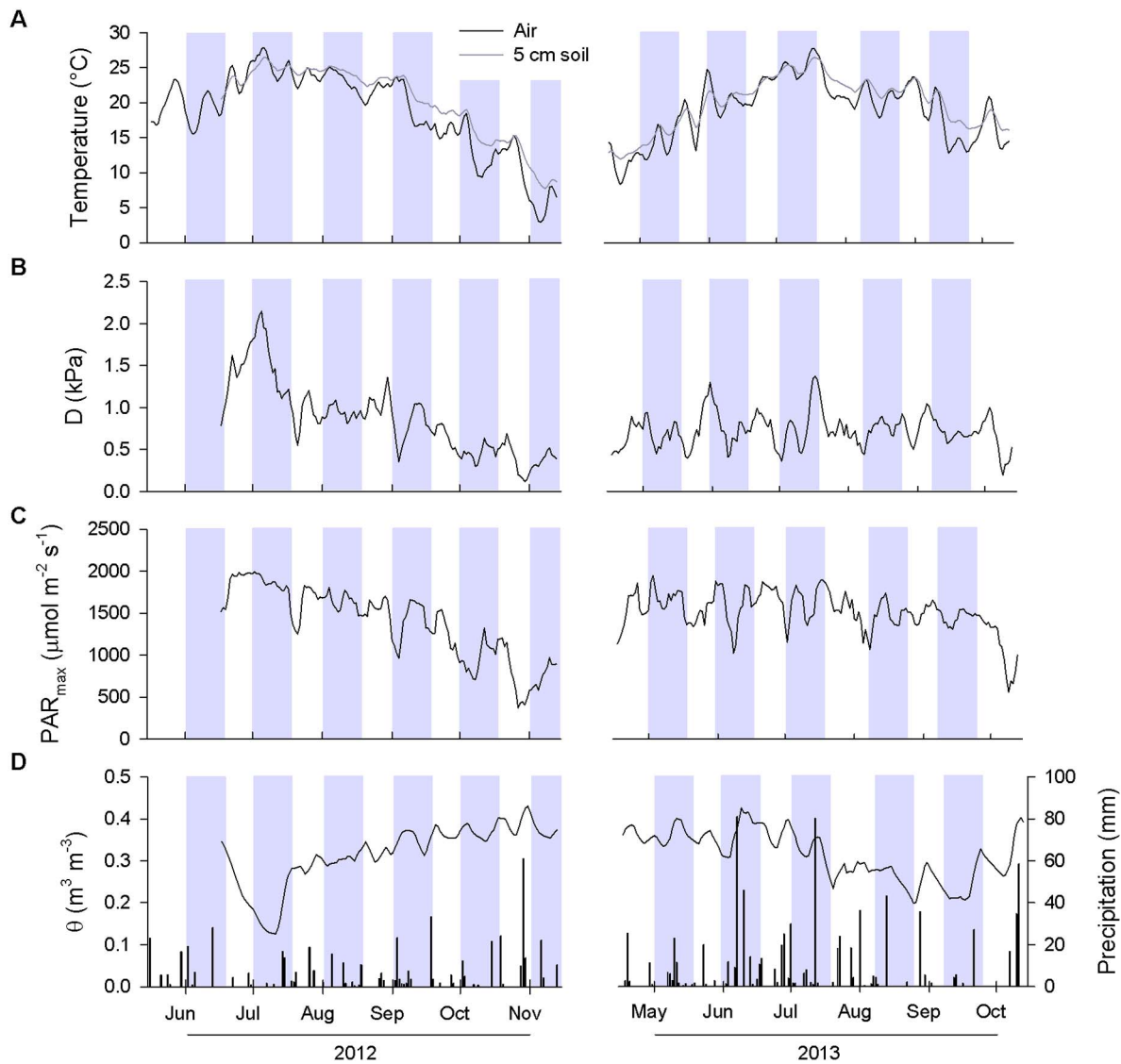


Fig. 1. Meteorological data for the 2012 and 2013 growing seasons. Reported values were averaged from data collected at the weather towers installed at the Unionville and Nottingham field sites. All graphs with continuous lines were compiled by computing five day running means. Data reported include air and soil temperature at 5 cm depth ($^{\circ}\text{C}$, A), vapor pressure deficit during daytime hours (D, kPa, B), maximum daytime photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$, C), soil volumetric water content (θ , $\text{m}^3 \text{m}^{-3}$, D), and precipitation (mm, D). Vertical grey bars indicate the two-week periods each month during which chamber measurements were made. Air temperature and precipitation data prior to weather tower installation in mid-June 2012 are from meteorological stations within the study area radius (NCDC 2013).

$\text{m}^2 \text{m}^{-2}$, was achieved in late September during the drier 2012 growing season, while maximum average LAI, $2.18 \text{m}^2 \text{m}^{-2}$, occurred in August during the wetter year, 2013 (Fig. 2). Similarly, the rate at which mean LAI increased toward its

peak was slower in 2012 and faster in 2013 (slopes = 0.21 and $0.43 \text{m}^2 \text{m}^{-2}$ per month in 2012 and 2013, respectively). Leaf area index did not vary significantly across managed vs. unmanaged study sites ($p > 0.05$; Fig. 2, Table 3).

Table 2. Monthly precipitation totals during the 2012 and 2013 growing seasons, compared to the long-term (30 year) regional mean monthly precipitation (NOAA 2012).

Month	Precipitation (mm)			Percent above or below average	
	2012	2013	30 year average	2012	2013
May	112.8	80.3	114.6	-2	-30
June	66.8	250.7	106.9	-38	+134
July	72.8	198.4	115.1	-37	+72
August	58.6	135.3	102.1	-43	+32
September	91.8	40.5	132.3	-31	-69
October	151.3	109.9	110.7	+37	-1

Note: Precipitation data for May and early June 2012, prior to weather tower installation, are from regional weather stations (NCDC 2013).

Carbon dioxide exchange rates were significantly higher in 2013 relative to 2012 ($p \leq 0.0001$; Fig. 3, Table 3). The 2012 growing season was characterized by low CO_2 exchange rates in July when θ was at its minimum and D was at its maximum. With the exception of July, maximum rates of CO_2 exchange were fairly similar from June to September in 2012 (Fig. 3). This consistency in CO_2 exchange rates was not observed in 2013. Instead, there was a clear seasonal pattern with all exchange rates increasing toward a seasonal maximum in July and then declining (Fig. 3). In keeping with the LAI data, none of the measured CO_2 exchange parameters varied significantly with management regime ($p > 0.05$).

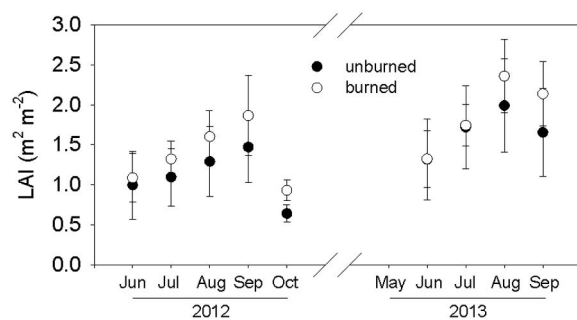


Fig. 2. Leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$; mean \pm SE) for unburned sites (black circles) and sites managed with prescribed fire (open circles). Data are reported for each month in which chamber measurements were made. Note that October 2012 measurements were halved to account for leaf senescence. No data are reported for November 2012 due to leaf senescence, or for May 2013 because new growth was too short to be measured.

Environmental drivers of CO_2 exchange

During the 2012 growing season, variation in NEP and GEP was best explained by the parameters temperature (as T_{chamber}), GWC, LAI, D, and PAR, while in 2013, GWC was not an important predictor variable (Table 4). Similarly, ER was best predicted by temperature (as T_{chamber}), GWC, and LAI in 2012, but only by temperature (as $T_{\text{soil}, 5\text{cm}}$) and LAI in 2013 (Table 4). Both NEP and GEP were positively affected by temperature, GWC, LAI, and PAR when those parameters appeared in the final model examining environmental drivers of CO_2 exchange (Table 4). Ecosystem respiration rates also increased with temperature, GWC, and LAI (Table 4).

While all models exploring the role of environmental variation on rates of CO_2 exchange

Table 3. Results of mixed-effects model analyses to examine whether treatment (i.e., management with fire vs. no management) and year (i.e., 2012 vs. 2013) affect leaf area index (LAI) or CO_2 exchange rates.

Statistic	Treatment	Year	Treatment \times year
LAI			
F	0.1116	42.5127	0.0064
p	0.7551	<0.0001	0.9363
NEP			
F	0.0160	15.0909	0.5272
p	0.9053	0.0001	0.4684
ER			
F	0.2178	31.2372	0.5531
p	0.6650	<0.0001	0.4577
GEP			
F	0.0496	15.8141	0.5324
p	0.8347	0.0001	0.4663

Note: Separate analyses were performed for LAI, net ecosystem production (NEP), ecosystem respiration (ER), and gross ecosystem production (GEP). Random effects (i.e., repeated measures) for all models were base nested within site.

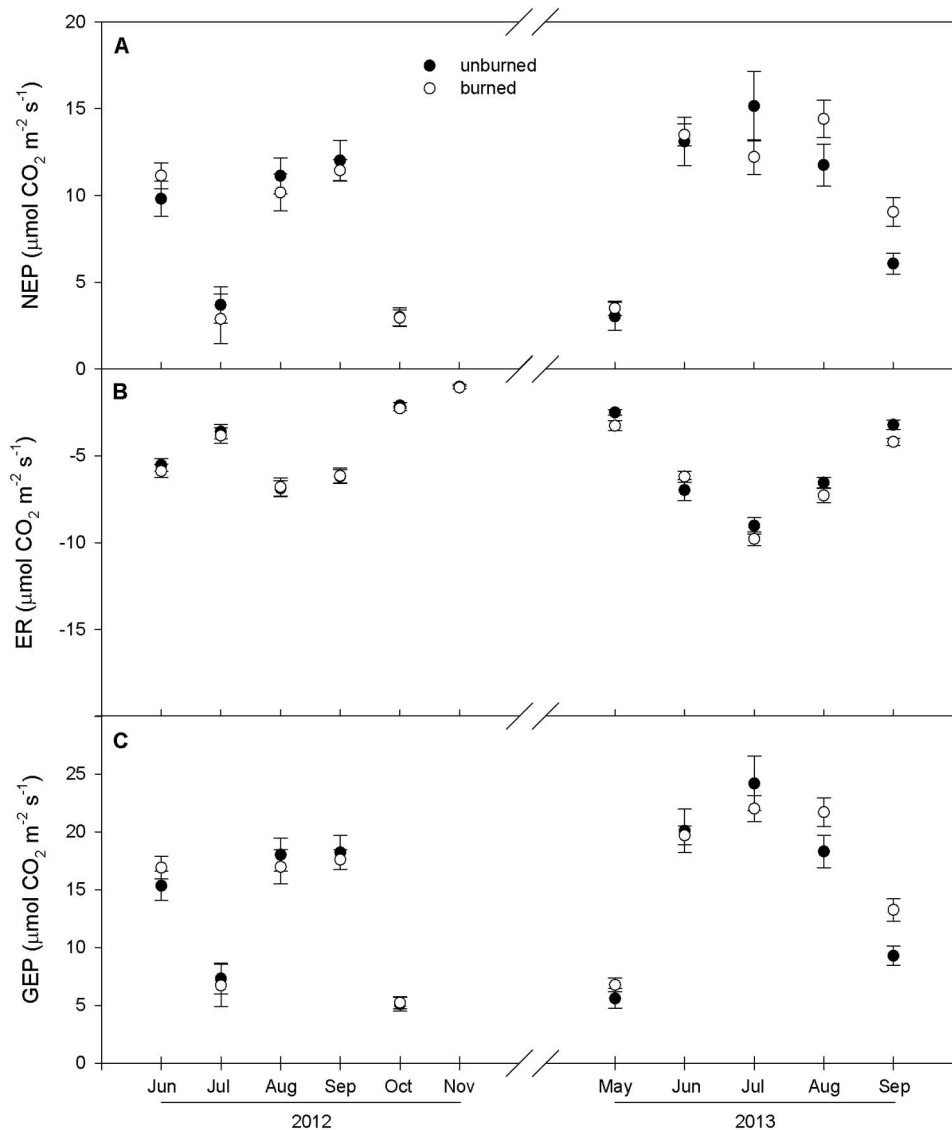


Fig. 3. CO₂ exchange rates ($\mu\text{mol m}^{-2} \text{ s}^{-1}$; mean \pm SE) for unburned sites (black circles) and sites managed with prescribed fire (open circles). Net ecosystem production (NEP, A), ecosystem respiration (ER, B), and gross ecosystem production (GEP, C) rates are reported monthly for the 2012 and 2013 growing seasons. Note that the scale for GEP measurements differs from that for NEP and ER. Positive values indicate CO₂ uptake by the ecosystem, while negative values indicate CO₂ release from the ecosystem.

were significant ($p < 0.0001$), there were differences in the amount of variation explained by these models. Notably, the models constructed for the 2012 growing season explained less variation in the data (R^2_{adj} from 0.59 to 0.63) than did the models for 2013 (R^2_{adj} from 0.62 to 0.79) (Table 4).

Soil composition

Management strategy did not affect percent soil carbon or soil bulk density ($p > 0.05$; Tables 5 and 6). Therefore, soil carbon storage values computed from percent soil carbon and bulk density did not vary significantly across treatments ($p > 0.05$; Tables 5 and 6). However, the percentage of soil carbon stored in the top 0–5 cm

Table 4. Parameter estimates and statistics for environmental variables that best predicted variation in CO₂ exchange rates in 2012 and 2013.

Parameter	NEP		ER		GEP	
	2012	2013	2012	2013	2012	2013
Intercept	-25.3	-12.6	5.29	5.26	-34.7	-17.1
T _{chamber}	1.12	0.747	-0.212	NA	1.39	NA
T _{soil} 5 cm	NA	NA	NA	-0.500	NA	NA
T _{soil} 10 cm	NA	NA	NA	NA	NA	1.29
GWC	5.17	...	-3.10	...	8.68	...
LAI	1.73	2.24	-0.992	-0.453	2.77	2.61
D	-4.77	-4.25	NA	NA	-5.27	-1.16
PAR	0.00189	0.00311	NA	NA	0.00391	0.00460
F	43.07	62.53	103.6	286.3	45.62	98.57
R ² _{adj}	0.59	0.62	0.63	0.79	0.60	0.73
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
AIC	370.9	388.1	155.6	71.66	458.5	436.4

Note: Parameters to be included in the final model were determined through backward and forward stepwise multiple regression analyses, using the AIC statistic for model selection. All parameter estimates were significant at $p < 0.001$, with the exception of PAR ($p = 0.098-0.0031$ for NEP and GEP models) and D ($p = 0.066$ for the GEP 2013 model). An ellipsis indicates parameters that were excluded from the final model, while NAs indicate parameters that were not included in the full model.

of soil was significantly greater than that found at 5–10 cm depth ($p < 0.0001$; Tables 5 and 6). Soil samples from 5 to 10 cm depth had a significantly greater bulk density than those at 0–5 cm depth ($p < 0.0001$; Tables 5 and 6). Soil carbon storage was significantly greater in soils from 0–5 cm depth than 5–10 cm depth ($p = 0.0207$). Across sites (excluding the scraped Goat Hill site), soil carbon storage averaged 19.71 ± 1.13 Mg C ha⁻¹ from 0–5 cm depth and 15.96 ± 1.02 Mg C ha⁻¹ from 5 to 10 cm depth.

Soil chromium, cobalt, and nickel content did not vary significantly with site management or soil depth ($p > 0.05$; Table 5). The content of chromium, cobalt, and nickel in the upper 10 cm of soils at all serpentine barren sites was relatively high (Table 7). Levels of chromium were between 2098 and 7379 mg kg⁻¹, while cobalt levels were from 721 to 1969 mg kg⁻¹ and nickel levels were from 1415 to 4727 mg kg⁻¹ (Table 7).

DISCUSSION

Growing season and management influences on LAI and CO₂ exchange

Significant differences in CO₂ exchange rates and LAI were observed across contrasting growing seasons. Specifically, there was a clear suppression of CO₂ exchange and LAI development in the drier than average 2012 growing season, relative to the wetter than average 2013 growing season. Temporal patterns of CO₂

exchange also varied across years, with seasonal maxima in August to September in 2012 and in July during 2013. Variation in environmental conditions during the study period, particularly water availability, clearly exerted strong control over CO₂ exchange and plant development in Mid-Atlantic serpentine barren ecosystems.

Table 5. Results of two-way ANOVAs to examine the role of treatment (i.e., management with fire or no management) and soil depth (i.e., 0–5 cm or 5–10 cm) on the soil parameters bulk density, % soil carbon (C), total C storage, soil chromium (Cr), soil cobalt (Co), and soil nickel (Ni).

Statistic	Treatment	Soil depth	Treatment × Soil depth
Bulk density			
F	0.1150	35.1984	0.0133
p	0.7362	<0.0001	0.9086
% soil C			
F	1.7812	51.0545	0.8119
p	0.1886	<0.0001	0.3723
C storage			
F	1.4262	5.7581	0.3759
p	0.2388	0.0207	0.5430
Cr			
F	0.3068	1.1832	1.8479
p	0.5824	0.2824	0.1807
Co			
F	3.1476	0.4861	0.0804
p	0.0827	0.4892	0.7780
Ni			
F	0.0805	1.8453	0.4652
p	0.7780	0.1810	0.4986

Note: The Goat Hill (unburned) site was excluded from these analyses because surface soils were mechanically removed from the site in 1998.

Table 6. Soil bulk density (g cm^{-3}), % soil carbon (C), and total soil C storage (Mg C ha^{-1}) from 0–5 and 5–10 cm soil depth at each study site. Values are means \pm SE.

Site	Soil depth (cm)	Bulk density (g cm^{-3})	% soil C	C storage (Mg ha^{-1})
Unburned sites:				
Goat Hill	0–5	0.71 ± 0.09	2.46 ± 0.34	8.99 ± 1.82
	5–10	0.80 ± 0.09	1.45 ± 0.21	5.86 ± 1.16
New Texas	0–5	0.66 ± 0.03	5.37 ± 0.54	17.84 ± 2.04
	5–10	0.99 ± 0.04	3.07 ± 0.12	15.25 ± 0.99
Unionville	0–5	0.57 ± 0.05	6.57 ± 0.37	18.27 ± 1.15
	5–10	0.78 ± 0.03	4.03 ± 0.28	15.78 ± 1.24
Burned sites:				
Nottingham	0–5	0.54 ± 0.04	6.10 ± 0.43	16.09 ± 1.03
	5–10	0.81 ± 0.07	4.37 ± 0.25	17.51 ± 1.41
Pink Hill	0–5	0.53 ± 0.04	8.93 ± 0.89	24.15 ± 3.79
	5–10	0.80 ± 0.11	4.03 ± 0.57	17.14 ± 4.14
Sugartown	0–5	0.78 ± 0.02	5.64 ± 0.50	21.92 ± 2.03
	5–10	1.10 ± 0.02	2.79 ± 0.49	13.68 ± 2.92

These findings contrast with those from the more intensively studied serpentine grasslands of California.

Three years of experimental water additions at an annual-dominated California serpentine grassland did not significantly alter aboveground plant biomass, and it was found that nutrient limitations precluded vegetation growth responses to increased water availability (Going et al. 2009, Fernandez-Going and Harrison 2013). However, variation in plant species richness and community composition in response to precipitation was reported over a 20-year study period in a similar California serpentine grassland (Hobbs et al. 2007). While these grasslands are not unresponsive to variation in precipitation, these findings indicate that nutrient limitations attenuate ecosystem responses to increased water availability. The relative responsiveness of Mid-

Atlantic serpentine barrens to variation in precipitation may indicate that these ecosystems are less constrained by low nutrient availability than similar systems in California; however, additional research is required to clarify these relationships.

In addition to responding differently to water availability, CO_2 exchange rates and seasonal patterns reported in the present study also contrast with findings from other serpentine ecosystems. To my knowledge, the only other serpentine grassland in which CO_2 exchange has been studied is at central California's Jasper Ridge Biological Preserve, a site with a Mediterranean climate that is dominated by annual C_3 grasses. At this site, maximum rates of net CO_2 uptake ranged from $\sim 2\text{--}8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and were observed in spring months (i.e., February to May) before the onset of seasonal water stress

Table 7. Content of chromium (Cr), cobalt (Co), and nickel (Ni) (mg kg^{-1}) in the top 0–5 and 5–10 cm of soil at all field sites. Values are means \pm SE.

Site	Soil depth (cm)	Cr (mg kg^{-1})	Co (mg kg^{-1})	Ni (mg kg^{-1})
Unburned sites				
Goat Hill	0–5	2112 ± 268	1042 ± 71	3779 ± 520
	5–10	2110 ± 336	1171 ± 118	4682 ± 943
New Texas	0–5	3704 ± 450	824 ± 62	2793 ± 97
	5–10	3145 ± 244	922 ± 95	2848 ± 121
Unionville	0–5	3836 ± 606	1238 ± 53	3020 ± 221
	5–10	3776 ± 817	1230 ± 50	3280 ± 274
Burned sites				
Nottingham	0–5	2504 ± 224	1119 ± 47	2861 ± 94
	5–10	3867 ± 440	1172 ± 102	3238 ± 135
Pink Hill	0–5	5385 ± 925	1845 ± 223	3551 ± 447
	5–10	7379 ± 830	1969 ± 225	4727 ± 587
Sugartown	0–5	2098 ± 213	721 ± 57	1415 ± 127
	5–10	2278 ± 280	907 ± 59	1594 ± 161

(Fredeen et al. 1995, Valentini et al. 1995). Further, maximum LAI was typically 1.0–1.5 $\text{m}^2 \text{m}^{-2}$ (Valentini et al. 1995). In the present study, maximum rates of CO_2 exchange were observed in mid to late summer months, NEP was frequently $>10 \mu\text{mol CO}_2 \text{m}^2 \text{s}^{-1}$, and LAI peaked between 1.7 and 2.2 $\text{m}^2 \text{m}^{-2}$. Variation in climatic conditions and vegetation composition likely played a role in the observed differences in CO_2 uptake and LAI between serpentine ecosystems.

The present study makes it clear that Mid-Atlantic serpentine barrens share functional similarities with Great Plains grasslands, particularly in terms of seasonal responses to water availability. Tallgrass prairie is among the most mesic of the Great Plains grasslands, and these ecosystems share a number of dominant C_4 species in common with Mid-Atlantic serpentine barrens. Across ecosystems in average to wet years, seasonal peaks in tallgrass prairie CO_2 exchange were observed in July (Suyker et al. 2003, Bremer and Ham 2010), while in years with mid-growing season soil moisture stress coupled with high D, there were declines in CO_2 uptake and negative consequences for the seasonal rate of LAI increase (Suyker et al. 2003, Fischer et al. 2012). These patterns mirror those observed in the present study.

Despite these similarities, reported CO_2 exchange rates and LAI values were much higher in tallgrass prairie than in Mid-Atlantic serpentine barrens. Maximum net CO_2 uptake rates in tallgrass prairies ranged from 31.8 to 47.7 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, maximum ER was -9.1 to $-15.9 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, and LAI reached maxima of 1.3 to 3.5 $\text{m}^2 \text{m}^{-2}$ (Ham et al. 1995, Suyker and Verma 2001, Bremer and Ham 2002, Suyker et al. 2003, Owensby et al. 2006, Bremer and Ham 2010). All of the tallgrass prairie ecosystems from which these data are drawn were subject to regular (i.e., annual or bi-annual) burning, a management practice with consequences for plant growth and productivity (see below). In general, findings from tallgrass prairies point toward the likelihood of much higher above-ground biomass gain than in serpentine barrens. Productivity limitations in serpentine barrens may be due in part to variation in management strategy, but are also likely related to the unusual edaphic conditions presented by serpentine

barrens.

In the four to six years following the use of prescribed fire as a management tool, rates of CO_2 exchange and LAI in managed serpentine barrens were no different from those at unmanaged sites. This result is in keeping with our understanding of prescribed fire as a management practice in grassland ecosystems. Fires consume plant litter, thereby increasing light availability and soil temperature (Knapp and Seastedt 1986), while also modifying nutrient (i.e., nitrogen) availability (Seastedt et al. 1991). At fire return intervals of approximately four years, these alterations promote increased plant productivity given adequate moisture, however pulses in productivity are short-lived (Seastedt et al. 1991, Knapp et al. 1998a). Further, productivity pulses following fire appear to be confined to aboveground biomass (Blair 1997). Therefore, any increases in CO_2 exchange rates accompanying aboveground biomass increases following fire, are also likely to be short-lived. Given that there are functional and compositional similarities between tallgrass prairie and Mid-Atlantic serpentine barrens, shorter intervals between prescribed burns may promote more robust plant growth in serpentine barrens, perhaps helping to combat forest encroachment; however, further research is required to examine this possibility.

Environmental drivers of CO_2 exchange

The differences in precipitation between 2012 and 2013 led to substantial differences in soil moisture between the two growing seasons. Analyses of environmental drivers of CO_2 exchange showed that soil moisture influenced CO_2 exchange only in the dry 2012 growing season, indicating that below a threshold level ($\theta < 0.2$ to $0.25 \text{m}^3 \text{m}^{-3}$), Mid-Atlantic serpentine barrens responded strongly to variation in soil moisture. Again, these findings support the idea that these serpentine barrens are more sensitive to water availability than California's serpentine grasslands (i.e., Going et al. 2009, Fernandez-Going and Harrison 2013).

Clearly, precipitation and the availability of soil moisture play important roles in the CO_2 exchange dynamics and rate of LAI accumulation in Mid-Atlantic serpentine barrens. This sensitivity to water availability is similar to that observed in non-serpentine grasslands (Suyker et

al. 2003, Fischer et al. 2012), but it remains uncertain whether productivity responses in Mid-Atlantic serpentine barrens mirror the generally observed pattern across North American grasslands (i.e., large ANPP increases in wet years and small reductions in ANPP in dry years; Knapp and Smith 2001). While significantly greater GEP and LAI were observed in the wetter 2013 season, relative to the drier 2012, there are as yet no data for average years.

Soil composition

Soil carbon storage was an additional component of the carbon cycle that was compared between burned and unburned sites in the present study, though similar to CO₂ exchange rates, it did not vary with management strategy. These findings suggest that either prescribed fire did not affect soil carbon storage or these sites recovered soil organic matter quickly following prescribed fire. Current thinking by land management practitioners is that forest encroachment into serpentine barrens is facilitated by the buildup of soil organic matter (e.g., Orndorff and Coleman 2008). Prescribed fire is used in part to reduce litter inputs to the soils; however, the carbon content of serpentine soils in both managed and unmanaged sites was relatively high. Soil carbon storage in the upper 10 cm of serpentine soils ranged from 33.1 to 41.3 Mg C ha⁻¹ (note that data from the scraped Goat Hill site are excluded), values that overlap with the low end of the range reported for tallgrass prairie (~40–72 Mg C ha⁻¹; McCulley et al. 2005, Bremer and Ham 2010).

Globally, grasslands have a substantial soil carbon storage capacity (Jobbágy and Jackson 2000), and in keeping with this pattern, Mid-Atlantic serpentine barrens contain relatively large carbon pools in surface soils. Further, the relatively high carbon content of these soils likely played a role (Chapin et al. 2011) in the unexpectedly high soil water potentials observed at these sites during the 2012 growing season when precipitation was below average (Schedlbauer and Pistoia 2013). When considering these findings in light of the moderate rates of CO₂ uptake and LAI increase reported in the present study, there is accumulating evidence that Mid-Atlantic serpentine barrens function differently from other serpentine grasslands. The classic

description of serpentine syndrome highlights serpentine ecosystems as low productivity systems with poorly developed soils and low soil moisture availability (Whittaker 1954, Brady et al. 2005), but does not adequately describe Mid-Atlantic serpentine barrens.

However, some classic serpentine characteristics are evident in these ecosystems. In particular, soils tend to be shallow (Barton and Wallenstein 1997, Arabas 2000), and the chromium, cobalt, and nickel content of the soils at all study sites was high. Further, there is evidence from one of the sites included in the present study of very low Ca:Mg ratios and nutrient limitations (Barton and Wallenstein 1997). Therefore, plants growing in these ecosystems do experience more stressful environments than would be found on soils not derived from serpentine bedrock. While these edaphic properties may exert some limitations on plant productivity, the present study shows that Mid-Atlantic serpentine barrens are by no means a low-productivity ecosystem, and there is considerable functional similarity to non-serpentine grassland ecosystems.

CONCLUSIONS

The serpentine barrens of the U.S. Mid-Atlantic region are unique relative to other serpentine grasslands. Ecosystem CO₂ exchange and LAI responded positively to increased soil water availability, indicating that these ecosystems may be less constrained by nutrient limitations than other serpentine grasslands. Additionally, CO₂ exchange rates and LAI were relatively high, and Mid-Atlantic serpentine barrens share functional and compositional similarities with tallgrass prairie. These findings argue for a broader interpretation of the serpentine syndrome in grasslands to better encompass the serpentine barrens of eastern North America.

Limited understanding of ecosystem function in the Mid-Atlantic serpentine barrens has made it difficult to develop sound management practices for the maintenance of these areas. The present study shows that the use of prescribed fire as a management tool had no discernable effect on rates of CO₂ exchange, LAI, or soil carbon storage in four to six years following a burn. The consistent size of soil carbon pools found across study sites suggests that reductions

in litter inputs to the soil following infrequent fires are relatively insubstantial or that recovery of soil carbon pools is rapid. Forest encroachment, a process that must be prevented if Mid-Atlantic serpentine barrens are to persist on the landscape, is thought to be facilitated by soil organic matter accumulation (Latham 1993, Arabas 2000, Orndorff and Coleman 2008). Therefore, if land managers wish to reduce the buildup of soil organic matter, more frequent prescribed fires may be required.

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