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Elizabeth M. Obee

Rutgers University, New Brunswick, New Jersey

James A. Quinn

Rutgers University, New Brunswick, New Jersey

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PHENOTYPIC PLASTICITY OF REPRODUCTION IN *SCHIZACHYRIUM SCOPARIUM* (POACEAE) POPULATIONS IN RELATION TO ECOLOGICAL HISTORY

ELIZABETH M. OBEE AND JAMES A. QUINN¹

Department of Ecology, Evolution, and Natural Resources, Rutgers University, 1 College Farm Road, New Brunswick, New Jersey 08901-1582, USA

¹Corresponding author (quinn@aesop.rutgers.edu)

ABSTRACT

Genetic differentiation in reproduction in the wide-ranging *Schizachyrium scoparium* (Poaceae) has been demonstrated in uniform gardens. However, the fine-tuning of flowering phenology and biomass allocation in relation to spatial and temporal fluctuations in the local environment is best accomplished by plastic responses to local variability. An earlier central New Jersey study suggested that *S. scoparium* populations in old fields of 2 to 40 years differed in plasticity. To test this apparent effect of ecological history on the development of different levels of plasticity, genotypes were collected from high- and low-fertility sites in New Jersey (forest biome) and in Oklahoma (grassland biome). Three greenhouse experiments manipulating light and nutrients were used to partition variation into genetic and environmental components. High light or high nutrients resulted in plasticity for increased biomass, greater reproductive allocation, and more tillers. Earlier flowering was induced by high light, but nutrient treatments had no effect. Populations were more likely to differ in plasticity across regions than within regions, and Oklahoma populations were consistently more plastic than New Jersey populations. In response to nutrients, populations from high-nutrient sites were often more plastic than those from low-nutrient sites. There were fewer differences in plasticity in response to light between high- and low-nutrient populations. The greater plasticity in Oklahoma populations is suggested to be the result of historically greater environmental unpredictability and K-selection factors such as density-dependent selection and greater competition for resources. A native grass population is more than just a Latin binomial. Evolutionary forces create an ecological unit unique and irreplaceable at the local level.

Key words: allocation, phenology, plasticity, populations, reproduction, *Schizachyrium*.

INTRODUCTION

Genetic differentiation in reproduction has been frequently demonstrated among populations of a wide-ranging grass species (Hodgkinson and Quinn 1978; Quinn 1998). Early studies utilized the differential responses of genotypes to a common environment. Equally important in reproduction, however, is the role of genetically determined plasticity in the fine-tuning of phenology and biomass allocation in response to spatial and temporal fluctuations in the local environment (Quinn 1987, 1998; Quinn and Wetherington 2002). “Phenotypic plasticity” in this paper will refer to “the amount by which the expressions of individual characteristics of a genotype are changed by different environments” (Bradshaw 1965). Plasticity is therefore the ability of an individual to respond to changes, and some individuals are clearly more responsive than others. Bradshaw (1965, 1974) emphasized, and subsequent studies have documented, that the phenotypic plasticity of a trait is genetically determined and can be affected by selection (see reviews by Schlichting 1986; Quinn 1987; Cheplick 1991; Scheiner 1993; Sultan 1995; Pigliucci 2001). The plasticity of a population is a function of the plasticity of its component genotypes.

Populations of a species may vary in plasticity in relation to local environmental variability and predictability (e.g., Bell and Quinn 1987; Quinn 1987; Bradshaw and Hardwick 1989; Kudoh et al. 1995; Balaguer et al. 2001; Quinn and Wetherington 2002). Surprisingly, only a few studies of in-

traspecific population variability in reproduction have focused on genetic differentiation in phenotypic plasticity (e.g., Roos and Quinn 1977; Neuffer and Hurka 1986; Scheiner and Teeri 1986; Counts 1993; Donohue et al. 2000; Quinn 2000; Quinn and Wetherington 2002). Additionally, the recent innovative and “cutting-edge” research on plasticity has concentrated almost totally on annual species (e.g., Pigliucci and Byrd 1998; Donohue et al. 2000; Weinig 2000; Sultan 2001). More research on populations with different ecological histories within wide-ranging perennial species is desperately needed.

Little bluestem, *Schizachyrium scoparium* (Michx.) Nash var. *scoparium*, is a warm-season, perennial bunchgrass native throughout the United States, with the exception of Nevada and the Pacific coastal states (Hitchcock 1951; Archer and Bunch 1953; Wipff 1996). It is considered a climax species in the grassland biome of the central plains and southern prairies (Hartley 1964; Gould 1968), but in the eastern temperate forest biome it is a successional species on disturbed sites and along roadsides (Bard 1952; Roos and Quinn 1977). Prior studies have documented genetically based phenological and morphological variation throughout its range (McMillan 1964, 1965a, b; Miller 1967). Although these studies did not consider plasticity, a New Jersey study (Roos and Quinn 1977) suggested that little bluestem populations in old fields of 2 to 40 years in age differed in plasticity. As a native species, little bluestem is increasingly being used for restoration projects, and it is important to

Table 1. Soil texture, pH, and concentration (parts per million) of major soil nutrients at the four population sites of *Schizachyrium scoparium*. Values are the means of two determinations on a pooled soil sample.

Population	Texture	pH	Nitrate-N	Ammonia-N	Magnesium	Phosphorus	Potassium	Calcium
NJ High	sandy loam	5.3	4.2	3.4	161.2	21.3	327.2	489.0
NJ Low	loamy sand	5.5	3.6	3.4	71.1	0.0	26.4	480.6
OK High	silt loam	6.3	20.2	4.8	325.0	16.9	405.3	1947.5
OK Low	sandy loam	6.5	6.5	9.0	159.8	0.3	108.7	630.9

know if a seed source demonstrates those plastic responses conducive to its survival and reproduction. The objectives of our study were to (1) determine if populations from high- and low-fertility sites in New Jersey (forest biome) and in Oklahoma (grassland biome) differ in plasticity in response to light and nutrients, and (2) determine if life history traits and plasticity correlate with expectations based upon the population's ecological history (habitat, community type, and local environmental predictability).

MATERIALS AND METHODS

Population Sites and Plant Materials

Four populations of the widely distributed and common *S. scoparium* var. *scoparium* were selected, consisting of two closely adjacent populations on soils of contrasting fertility and texture in New Jersey (NJ, forest biome) and in Oklahoma (OK, grassland biome). The high- and low-nutrient sites in each state were located from county soil surveys and verified by soil analyses (Table 1), and were within 21 km of each other, experiencing a similar macroclimate. All soil analyses were performed by the Rutgers Soil Testing Laboratory, New Brunswick, New Jersey, USA, and methodologies are available upon request. The "high" and "low" designations applied to fertility levels refer only to the relative levels of fertility observed within a biome and, because of inherent fertility level differences between biomes, were not considered replicates of any specific fertility level (Table 1). In each biome, the low-nutrient site possessed sandy, well-drained soils, and a history of disturbance. In NJ, the high-nutrient site was located 2 km north of the junction of State Highways 537 and 539 on sandy loam soils on fertile Cretaceous sediments in the Cream Ridge agricultural area (Jablonski and Baumley 1989), while the low-nutrient site was located 4.8 km west of Lakehurst on loamy sands in the Pinelands (Hole and Smith 1989). In OK, the high-nutrient site was a loamy bottomland range site with a silt loam soil at the USDA-ARS Grazinglands Research Laboratory near El Reno, while the low-nutrient site was a sandy prairie with a fine sandy loam soil 12.3 km northwest of Cogar on State Highway 37 (Fisher and Swafford 1976).

Twenty genotypes were randomly selected from an area of ca. 350 m² at each site, divided into ramets, and transplanted into a standardized soil mixture in clay pots (15 cm diameter, 16.5 cm depth) in the Nelson Biological Laboratory greenhouse at Rutgers University. The standardized soil mixture was a sandy loam consisting of 12 parts soil (a NJ Piedmont loam), 8 parts coarse builder's sand, 6 parts Canadian sphagnum peat, and 0.125 parts lime.

Voucher specimens from each population have been deposited in the Chrysler Herbarium at Rutgers University

(CHRB). However, due to the lack of a curator, the specimens are in special folders identified by our numbers: NJ High (NJ1-1, NJ1-10, and NJ1-19), NJ Low (NJ2-5, NJ2-10, and NJ2-20), OK High (OK1-7, OK1-18, and OK1-20), and OK Low (OK2-12, OK2-13, and OK2-18).

Experimental Design

Genotypes from each population were subjected to high or low light levels, high or low nutrients, or combined light and nutrient levels in three separate but concurrent greenhouse experiments. A total of 13 genotypes was used from each population, with 5 genotypes in the light experiment, 5 in the nutrient experiment, and 3 in the light-nutrient experiment. In each experiment, there were three replicates (or ramets) of each genotype in each treatment or treatment combination, producing 120 15-cm pots in the light experiment (4 populations $\times$ 5 genotypes $\times$ 2 light levels $\times$ 3 replicates), 120 pots in the nutrient experiment (4 populations $\times$ 5 genotypes $\times$ 2 nutrient levels $\times$ 3 replicates), and 144 pots in the light-nutrient experiment (4 populations $\times$ 3 genotypes $\times$ 2 light levels $\times$ 2 nutrient levels $\times$ 3 replicates) (Fig. 1).

High-nutrient treatments received additional NPK fertilizer. This consisted of 350 ml per pot of NPK 25-10-10 solution, mixed as 6 g/liter of water, applied at 2 wk intervals during the first 2 mo. Due to PK accumulation, 2 g of blood meal (12-0-0) was applied to each pot once a month for the remainder of the experiment. Low-nutrient treatments received no fertilizer over the course of the experiment. High-light treatments received 100% of full greenhouse sun, which is 73–82% of full sunlight (Quinn 1991), and low-light treatment plants were blocked and enclosed within 50% shade cloth. The light experiment received fertilizer at a frequency half as often as the high-nutrient treatment. All plants were watered every 1–2 day to saturation, as needed.

Randomization of each experiment was designed to minimize position effects; however, randomization of high- and low-light treatments was not possible due to the use of shade cloth frames (Fig. 1). For the light experiment, the five genotypes per population were placed into each of the three blocks for each light level. Each row of plants on a bench contained one plant from each population. For the nutrient experiment, the five genotypes per population were subjected to the two nutrient levels, with three replicate blocks (Fig. 1). Each row of four pots on a greenhouse bench contained two high- and two low-nutrient treatments, and one plant from each population. Each half of a block contained either a high- or low-nutrient treatment for each genotype. For the combined light-nutrient experiment, the three genotypes per population were placed into the two light and two nutrient

Light Experiment

Nutrient Experiment

Light-Nutrient Experiment

Fig. 1.—Schematic of greenhouse design for light, nutrient, and light-nutrient experiments. Each small rectangle denotes a pot, and each more inclusive rectangular array denotes a block. High-nutrient treatment designated by an H.

Table 2. Light experiment variance components (vc) and percentage of variance explained. Significance of corresponding F -tests from individual ANOVAs is indicated by ** ($P < 0.01$), *** ($P < 0.001$), and **** ($P < 0.0001$).

Source of variation	% Reproductive biomass		Reproductive biomass		Total biomass		Date of flowering		Tiller number	
	vc	%	vc	%	vc	%	vc	%	vc	%
Population	0.0142**	14.2	0.075	2.9	0.043	1.5	0.709**	27.3	0.023	6.2
Genotype	0.0119****	12.0	0.182****	6.9	0.143***	5.0	0.826****	31.8	0.035****	9.7
Light	0.0548****	54.9	2.089****	79.4	2.227****	78.2	0.239***	9.2	0.173****	47.2
Population $\times$ Light	0.0010	1.1	−0.012	−0.5	0.091**	3.2	−0.030	−1.2	0.032*	8.7
Genotype $\times$ Light	0.0030	2.5	0.023	0.9	−0.042	−1.5	0.204	7.9	0.016	4.4
Error	0.0150	15.3	0.274	10.0	0.385	13.5	0.652	25.1	0.087	23.8

Fig. 2.—Percentage reproductive biomass (reproductive/total aboveground biomass) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the light experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

Fig. 3.—Date of flowering (days after first flowering in the experiments) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the light experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

levels with three replicate blocks of high- and low-nutrient treatments within each of two light blocks (Fig. 1). Randomization of nutrient treatments within blocks was the same as for the nutrient study.

Data Collection and Analyses

Duration of the concurrent experiments was 16 wk, with the following data collected on each plant (ramet): date of first anthesis, reproductive and vegetative aboveground biomass (dry weight), and initial and final tiller number. Reproductive biomass was measured for each tiller as all biomass above the lowest node with reproductive branches. Data were square root transformed (Zar 1984) and analyzed by analysis of variance, using PROC GLM of SAS and Type

III sums of squares (SAS Institute 1989). Variance was partitioned into components for populations, genotypes nested within populations, treatments (light and/or nutrients), and interaction terms. Genotype was considered a random effect, and all other terms were considered fixed (Bennington and Thayne 1994). *F*-tests were performed, based upon the expected mean square calculations of the Scheffe model, which excludes mixed interactions from the expected mean squares of random effects (Ayres and Thomas 1990). This method allows for the estimation of genetic and phenotypic variance under defined environmental conditions (Fry 1992). To determine the amount of variation each factor contributes to the total phenotypic variance in a population, variance components for genotype, treatment (light and/or nutrients), and genotype $\times$ treatment were calculated for each population

Table 3. Significance of differences in means between pairs of populations as determined by univariate *F*-tests for each experiment and trait. Traits with no significant differences for a given experiment are not listed. Significance indicated as * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$).

Experiment and trait	NJ high vs. NJ low	NJ high vs. OK high	NJ high vs. OK low	NJ low vs. OK high	NJ low vs. OK low	OK high vs. OK low
Light						
% Reproductive biomass				*	**	
Reproductive biomass					*	*
Total biomass				*		
Date of flowering			*		***	
Number of tillers		***	*			
Nutrient						
% Reproductive biomass				**	***	
Reproductive biomass			**			*
Total biomass	**	**	**	*		
Date of flowering	*	*		***	***	*
Light–Nutrient						
% Reproductive biomass			**			
Reproductive biomass			**			
Date of flowering		*	**	**	***	

Table 4. Significance of differences in plasticity between pairs of populations as indicated by univariate *F*-tests for each experiment and trait. Significant differences which resulted in changes in the rank order of populations across environments are indicated with an R. Significance indicated as * ($P < 0.05$) and ** ($P < 0.01$).

Experiment and trait	NJ high vs. NJ low	NJ high vs. OK high	NJ high vs. OK low	NJ low vs. OK high	NJ low vs. OK low	OK high vs. OK low
Light						
Total biomass		*R	*	*	**R	
Number of tillers				*	*R	
Nutrient						
% Reproductive biomass			*	*	**	*
Reproductive biomass		*R	*	**R	**R	
Total biomass		**R	**	**R	**R	
Number of tillers				*R		
Light–Nutrient						
for light:						
% Reproductive biomass		*				
for nutrients:						
Number of tillers			*		*	
for light × nutrients:						
Number of tillers			**R		*R	

by equating mean squares and expected mean squares. Block effects due to greenhouse bench position were not significant in initial analyses and were excluded from further calculations.

Significance of the population term indicated that significant genetic differences existed between populations. Significance of the environment (light and/or nutrients) term for a trait indicated that *S. scoparium* exhibited plasticity for that trait. Significance of the population by environment interaction term indicated that at least two populations differed in plasticity, and pairwise ANOVAs (analysis of variance) were used to indicate which populations accounted for these significant differences. Differences in plasticity between populations were also indicated by differences in the slopes of reaction norms, where a reaction norm for a population is a graph of the mean values of a trait expressed over a range of environments (Quinn and Wetherington 2002). Differences in patterns of plasticity were indicated by changes in rank order of populations in different environments, i.e., a crossing of their reaction norms.

RESULTS

Light Experiment

Genetic differences between populations explained from 3 to 27% of the total phenotypic variation, depending on the trait (Table 2). Populations differed significantly in percentage of reproductive biomass and flowering date. New Jersey populations allocated significantly more resources to reproduction (Fig. 2) and flowered earlier (Fig. 3) than OK populations. There were nine cases of significant differences in means between populations (Table 3), but the only significant difference between high- and low-nutrient populations within a region was less total reproductive allocation in the OK low population than in the OK high population.

Light treatments produced significant differences between populations in plasticity (population by treatment interaction) in total biomass and tiller production (Table 2). All

significant differences in plasticity between populations occurred across regions (Table 4), with the greatest amount of plasticity in OK. Separate ANOVAs by population for the light (= plasticity) component indicate that not only the value of the variance component but also the percentage of variation explained by that component are greater in OK for total biomass and tiller production (Table 5). A change in the rank order of populations was relatively rare but did occur for total biomass and tiller number (Table 4). In the overall analysis (Table 2) and in separate analyses by population (Table 5), almost no significant differences in plasticity (genotype by light interaction) were found between genotypes within populations.

Nutrient Experiment

Genetic differences between populations explained up to 28% of the total phenotypic variation (Table 6). Populations differed in response to nutrients in percentage reproductive allocation, total reproductive biomass, total biomass, and date of flowering. New Jersey low allocated significantly more resources to reproduction (Fig. 4), and NJ populations flowered earlier than OK populations (Fig. 5). Significant differences in means between populations within a region were found in reproductive allocation, total biomass, and flowering date (Table 3), but 9 of the 13 significant differences in means between populations occurred across regions.

Nutrient treatments produced significant differences between populations in plasticity (population by nutrient interaction) in percentage reproductive allocation, total reproductive allocation, total biomass, and tiller production (Table 4). Half of the significant differences in plasticity resulted in a change in the rank order of populations, mostly in reproductive biomass or total biomass.

Separate ANOVAs by population for the nutrient (or plasticity) component indicated that the OK populations had significantly greater plasticity for percentage reproductive allocation and total reproductive biomass (Table 7), but OK

Table 5. Light experiment variance components (vc) by population and percentage of variance explained. Significance of *F*-tests of individual ANOVAs is indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), and **** ($P < 0.0001$).

Source of variance	% Reproductive biomass		Reproductive biomass		Total biomass		Date of flowering		Tiller number	
	vc	%	vc	%	vc	%	vc	%	vc	%
Genotype										
NJ High	0.0260****	21.7	0.479****	22.1	0.512****	28.1	0.938*	36.2	0.0007	0.2
NJ Low	0.0060*	8.1	0.050	2.2	-0.011	-0.6	0.338**	30.3	0.0888*	35.3
OK High	0.0060*	11.0	0.106	3.3	0.023	0.6	1.937****	70.8	-0.0044	-1.8
OK Low	0.0098	14.3	0.095*	3.9	0.055	1.6	0.054*	7.9	0.0567**	13.0
Light										
NJ High	0.0700**	59.5	1.429**	66.0	1.026**	56.4	-1.094	-42.3	0.2040*	66.5
NJ Low	0.0560****	77.5	2.026****	87.6	1.623****	85.1	0.273*	24.4	-0.0534	-21.2
OK High	0.0290*	48.9	2.612**	81.0	3.460****	85.2	0.326*	11.9	0.2182****	87.1
OK Low	0.0440**	65.0	2.172***	89.0	3.231***	92.8	0.474**	69.3	0.3193****	73.3
Genotype × Light										
NJ High	0.0103*	8.7	0.092	4.2	0.040	2.2	1.122	43.3	0.0365	11.9
NJ Low	-0.0036	-4.9	-0.053	-2.3	-0.102	-5.4	-0.023	-2.1	0.0370	14.7
OK High	0.0044	7.4	0.057	1.8	-0.064	-1.6	-0.037	-1.4	-0.0111	-4.4
OK Low	-0.0009	-1.3	0.002	0.1	-0.032	-0.9	-0.005	-0.7	0.0027	0.6
Error										
NJ High	0.0119	10.1	0.166	7.7	0.241	13.3	1.624	62.7	0.0655	21.3
NJ Low	0.0140	19.3	0.289	12.5	0.398	20.9	0.528	47.4	0.1789	71.2
OK High	0.0194	32.7	0.449	13.9	0.642	15.8	0.509	18.6	0.0479	19.1
OK Low	0.0150	21.9	0.171	7.0	0.229	6.6	0.161	23.5	0.0567	13.0

Table 6. Nutrient experiment variance components (vc) and percentage of variance explained. Significance of corresponding *F*-tests from individual ANOVAs is indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), and **** ($P < 0.0001$).

Source of variation	% Reproductive biomass		Reproductive biomass		Total biomass		Date of flowering		Tiller number	
	vc	%	vc	%	vc	%	vc	%	vc	%
Population	0.0127**	27.7	0.091*	9.7	0.266***	21.8	0.189*	8.6	-0.008	-2.0
Genotype	0.0110****	24.6	0.085*	9.0	0.063*	5.2	1.205***	55.0	0.042***	10.5
Nutrient	0.0020****	4.5	0.025****	2.7	0.090****	7.4	-0.007	-0.3	0.068****	16.9
Population × Nutrient	0.0040**	8.6	0.255***	27.0	0.326***	26.8	-0.047	-0.2	0.070*	17.3
Genotype × Nutrient	0.0002	0.4	0.034	3.6	0.033	2.7	0.065	3.0	0.115****	28.7
Error	0.0160	34.3	0.456	4.8	0.441	36.1	0.786	35.9	0.115	28.7

Fig. 4.—Percentage reproductive biomass (reproductive/total aboveground biomass) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the nutrient experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

low displayed less plasticity for tiller number than the other populations. Oklahoma high showed the greater plasticity in total biomass, while NJ low had the least plasticity in total biomass (Fig. 6).

Light-Nutrient Experiment

Genetic differences between populations accounted for considerably less of the total phenotypic variation than in the separate light or nutrient experiments (Table 8). Differences in means within populations (between genotypes) were significant for all traits, explaining up to 20% of the phenotypic variation (Table 8). The variation within populations was greater than the variation between populations for all traits.

Traits with significant differences in means between pop-

Fig. 5.—Date of flowering (days after first flowering in the experiments) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the nutrient experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

Table 7. Nutrient experiment variance components (vc) by population and percentage of variance explained. Significance of F -tests of individual ANOVAs is indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), and **** ($P < 0.0001$).

Source of variance	% Reproductive biomass		Reproductive biomass		Total biomass		Date of flowering		Tiller number	
	vc	%	vc	%	vc	%	vc	%	vc	%
Genotype										
NJ High	0.0297****	52.4	0.129	12.3	-0.034	-4.6	0.519*****	42.2	0.037*	13.5
NJ Low	0.0064*	23.0	0.015*	3.8	0.059*	11.7	0.649*****	25.2	0.087***	30.0
OK High	0.0017	4.4	-0.021	-4.5	-0.010	-1.1	0.029	6.8	-0.014	-2.1
OK Low	0.0073*	10.2	0.049	9.8	0.070	9.5	0.132*****	45.8	0.060*	21.5
Nutrient										
NJ High	0.0064	11.3	0.264*	25.2	0.442*****	60.1	-0.043	-3.5	0.043*	15.9
NJ Low	0.0038	13.6	0.010	2.7	0.039	7.8	-0.135	-5.2	0.038	13.3
OK High	0.0251*****	63.9	0.135*****	29.1	0.381***	42.9	-0.011	-2.5	0.327*	49.0
OK Low	0.0514*****	72.0	0.190*****	38.0	0.345*****	47.3	0.017	6.0	0.005*	1.7
Genotype × Nutrient										
NJ High	0.0078	13.7	0.055	5.3	-0.140	-19.1	0.420**	34.2	0.075*	27.8
NJ Low	-0.0001	-0.4	-0.122	-31.4	-0.069	-13.8	-0.009	-0.4	0.089**	30.9
OK High	-0.0042	-10.7	-0.094	-20.3	0.006	0.6	-0.097	-22.9	0.217**	32.5
OK Low	-0.0028	-3.9	-0.035	-6.9	0.003	0.5	-0.032	-11.1	0.080	28.7
Error										
NJ High	0.0128	22.6	0.597	57.1	0.467	63.5	0.334	27.1	0.116	42.8
NJ Low	0.0179	63.8	0.486	124.9	0.473	94.3	2.074	80.4	0.075	25.8
OK High	0.0167	42.4	0.444	95.6	0.511	57.6	0.504	118.6	0.138	20.6
OK Low	0.0155	21.7	0.295	59.1	0.312	42.7	0.171	59.4	0.134	48.1

Fig. 6.—Total aboveground biomass (g dry weight) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the nutrient experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

ulations were percentage reproductive allocation and flowering date (Table 8). New Jersey populations allocated more to percentage reproductive biomass (Fig. 7) and flowered earlier (Fig. 8), as in the separate light and nutrient experiments. All significant differences in means between pairs of populations occurred across regions (Table 3).

Phenotypic plasticity in response to light was significant in univariate analyses for all traits, as in the separate light experiment (Table 8). Although the amounts of plasticity in response to nutrients were less in some cases than in the separate nutrient experiment, the results followed the same trends, e.g., flowering date was not significantly affected by nutrients (Table 8).

Separate ANOVAs by population for combined light-nutrients (Table 9) indicated that plasticity for light often explained a large portion of the total phenotypic variation, and was significant for all populations for percentage reproductive allocation, total reproductive allocation, and total biomass (Table 9).

Also, as in the separate light or nutrient experiments, the region with the greatest amount of plasticity is OK (Table 4). All significant differences in plasticity occurred across regions, and some of these resulted in a change in the rank order of populations.

DISCUSSION

Differences in Plasticity and Relationships to Ecological History

The first objective of this study was to determine if populations from high- and low-fertility sites in New Jersey (forest biome) and in Oklahoma (grassland biome) differ in plasticity in response to light and nutrients. Both genetic differences in responses to treatments and differences in amounts of phenotypic plasticity were found to contribute to trait differences between populations (Tables 2–9). Both separate light and nutrient treatments produced significant amounts of phenotypic plasticity in every measured trait, with the exception of flowering date which responded only to light

Table 8. Combined light-nutrient experiment variance components (vc) and percentage of variance explained. Significance of corresponding *F*-tests from individual ANOVAs is indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), and **** ($P < 0.0001$).

Source of variation	% Reproductive biomass		Reproductive biomass		Total biomass		Date of flowering		Tiller number	
	vc	%	vc	%	vc	%	vc	%	vc	%
Population	0.0012**	1.7	0.019	0.7	0.074	2.8	0.1274****	6.7	0.005	0.6
Genotype	0.0037****	5.0	0.057**	2.2	0.223****	8.3	0.3822****	20.2	0.014*	1.7
Light	0.0313****	42.0	1.187****	46.7	1.170****	43.7	0.5276****	27.8	0.071**	8.5
Nutrient	0.0110**	14.8	0.504****	19.8	0.415****	15.5	-0.0080	-0.4	0.130*	15.5
Light $\times$ Nutrient	0.0011	1.5	0.388****	15.3	0.393****	14.7	0.0285*	1.5	0.151****	18.1
Population $\times$ Light	0.0019	2.5	-0.003	-0.1	0.005	0.2	0.0327	1.7	-0.012	-1.4
Population $\times$ Nutrient	0.0016	2.1	0.012	0.5	0.024	0.9	-0.0030	-0.2	0.036	4.4
Population $\times$ Light $\times$ Nutrient	-0.0004	-0.5	0.034	1.3	0.043	1.6	-0.0229	-1.2	0.035	4.2
Genotype $\times$ Light	-0.0003	-0.4	-0.039	-1.6	-0.034	-1.3	0.0761	4.0	0.045*	5.5
Genotype $\times$ Nutrient	0.0072****	9.6	0.075*	3.0	0.016	0.6	-0.0128	-0.7	0.172****	20.6
Genotype $\times$ Light $\times$ Nutrient	0.0003	0.5	-0.038	-1.5	-0.086	-3.2	0.0001	0.0	0.021	2.5
Error	0.0160	21.4	0.346	13.6	0.432	16.2	0.7679	40.5	0.166	19.9

Fig. 7.—Percentage reproductive biomass (reproductive/total aboveground biomass) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the combined light-nutrient experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

Fig. 8.—Date of flowering (days after first flowering in the experiments) in New Jersey (NJ) and Oklahoma (OK) high- and low-nutrient populations in the combined light-nutrient experiment. Symbols denote means. Bars indicate mean $\pm$ 1 SE.

treatments (Tables 2, 6). These separate light and nutrient experiments were more sensitive in producing differences between treatments than were combination treatments in a factorial design (Table 8). This result is probably due to the greater overall variation in the combined light-nutrient experiment, interactive effects between light and nutrients, and the use of only three genotypes per population.

Oklahoma populations were consistently more plastic than NJ populations, and differences were also found between high- and low-nutrient populations in each region (Tables 4, 5, 7, 9). In all cases where significant differences between populations in plasticity were found, the region with the greatest amount of plasticity was OK (Tables 5, 7, 9). Populations were more likely to differ in plasticity across regions (by 23 to 1) (Table 4). Half of the significant differences in plasticity resulted in a change in the rank order of the populations, i.e., a crossing of their reaction norms.

The second objective of this study was to determine if life history traits and plasticity correlate with expectations based on the population's ecological history (habitat, community type, and local environmental predictability). Populations that differed in habitat and site factors did have variable life history strategies, including differences in trait means and in plasticity. New Jersey populations flowered earlier and allocated more resources to reproduction (Fig. 2–5, 7, 8). These differences can be partially explained using traditional r-K selection theory and subsequent models (Abrahamson and Gadgil 1973; Roos and Quinn 1977; Taylor et al. 1990). New Jersey successional populations could be considered to be r-selected for earlier flowering and greater reproductive allocation, while OK populations were K-selected in allocation strategies (greater vegetative allocation and delayed reproduction) for superior competitive ability. The population (NJ low) with the greatest history of disturbance (frequent fires of the Pinelands), the lowest nutrient levels (Table 1), and a loamy sand soil of low moisture-holding capacity consistently showed the greatest percentage allocation to re-

production (Fig. 2, 4, 7) and the earliest flowering (Fig. 3, 5, 8).

High-nutrient site plants were generally more responsive to nutrient treatments than low-nutrient site plants; NJ low displayed less plasticity for total biomass, and OK low displayed less plasticity for tiller number (Table 7). Soil nutrient levels are generally higher in OK than in NJ (Table 1), even at the low-nutrient location. Elevated nutrients resulted in the largest differences between the populations in total biomass (Fig. 6). The OK high- and low-nutrient populations were not significantly different, but OK populations had more total biomass than NJ populations (Table 3, Fig. 6). This was primarily due to the inability of the NJ low population to respond to elevated nutrient levels (Fig. 6). Plants from unproductive habitats have been predicted to be less plastic and show allocation to maintenance and defense rather than to growth (Grime 1977; Taylor et al. 1990).

The greater plasticity of OK populations correlates with an ecological history of greater unpredictability of environmental conditions. Temperature and precipitation are especially unpredictable factors in OK, which is subject to droughts and high temperatures. For example, in Canadian County, OK (location of OK high and low), May has an average monthly rainfall of 13 cm, but one year in every ten will have less than 4 cm and one year in every ten will have rainfall greater than 26 cm (Fisher and Swafford 1976). While temperatures and rainfall also fluctuate in NJ, the seasonal pattern is more consistent. Standard deviations for the Palmer drought severity index range monthly from 2.31 to 2.55 in central OK, but only 1.78 to 1.98 in southern NJ (Karl et al. 1983a, b). The annual rainfall total in OK is only 68% of that in NJ (1961–1990 normals, National Oceanic and Atmospheric Administration 1993a, b). Temperatures are hotter and more variable in OK, averaging 4.4°C higher than NJ on a monthly basis, with mean monthly standard deviations of 1.8°C as opposed to 1.5°C in NJ (Karl et al. 1983a, b).

This relation of greater plasticity for the OK populations

Table 9. Combined light-nutrient experiment variance components (vc) by population and percentage of variance explained. Significance of *F*-tests of individual ANOVAs is indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), and **** ($P < 0.0001$).

Source of variance	% Reproductive biomass		Reproductive biomass		Total biomass		Date of flowering		Tiller number	
	vc	%	vc	%	vc	%	vc	%	vc	%
Genotype										
NJ High	-0.018	-0.8	0.0036	5.5	0.081	4.1	0.485**	32.6	0.016*	10.1
NJ Low	0.077**	3.4	0.0069*	7.3	0.080*	4.2	0.906****	25.2	0.027**	9.1
OK High	0.172	7.1	0.0027**	5.3	0.740****	22.6	0.162	11.5	0.014	0.9
OK Low	-0.003	-0.1	0.0016	2.1	-0.013	-0.4	-0.024	-4.5	0.002	0.1
Light										
NJ High	1.285**	59.0	0.0404*	60.9	0.934*	47.5	0.205	13.8	0.011	7.1
NJ Low	1.219*	53.3	0.0474**	50.3	0.928**	49.1	1.205	33.6	0.076	25.8
OK High	1.108*	45.7	0.0128**	25.0	1.639**	49.8	0.447*	31.7	0.012	0.8
OK Low	1.126**	36.0	0.0279**	36.5	1.228**	38.6	0.300	55.9	0.144*	11.3
Nutrient										
NJ High	0.247	11.4	0.0013	1.9	0.186	9.5	-0.035	-2.3	0.009	5.6
NJ Low	0.154	6.8	-0.0072	-7.7	0.159	8.4	-0.035	-1.0	-0.020	-6.9
OK High	0.660*	27.2	0.0232**	45.5	0.482**	14.6	0.019	1.4	0.107*	6.9
OK Low	1.004	32.1	0.0325	42.5	0.912	28.6	0.011	2.0	0.547	42.9
Light × Nutrient										
NJ High	0.147	6.8	-0.0033	-5.0	0.233	11.9	0.210	14.1	0.008	5.0
NJ Low	0.397	17.4	0.0021*	2.2	0.373*	19.8	-0.267	-7.4	0.065	21.9
OK High	0.184	7.6	-0.0011	-2.2	0.150	4.5	0.111	7.9	0.163	10.6
OK Low	0.889	28.4	0.0050****	6.6	0.913**	28.7	0.003	0.6	0.472**	36.9
Genotype × Light										
NJ High	-0.056	-2.5	-0.0037	-5.6	-0.039	-2.0	-0.012	-0.8	0.005	3.3
NJ Low	-0.022	-1.0	0.0048	5.1	-0.017	-0.9	0.360	10.0	0.012	4.2
OK High	-0.058	-2.4	-0.0014	-2.8	-0.058	-1.8	-0.095	-6.7	0.173*	11.2
OK Low	-0.018	-0.6	-0.0008	-1.1	-0.016	-0.5	0.051	9.6	-0.007	-0.5
Genotype × Nutrient										
NJ High	0.038	1.8	0.0023	3.5	0.029	1.5	-0.047	-3.1	0.024	15.4
NJ Low	0.260****	11.3	0.0245**	26.0	0.127*	6.8	-0.062	-1.7	0.071**	24.0
OK High	0.010	0.4	0.0007	1.4	-0.080	-2.4	0.076	5.4	0.600****	39.0
OK Low	-0.001	0.0	0.0012	1.6	-0.009	-0.3	-0.018	-3.3	-0.007	-0.5
Genotype × Light × Nutrient										
NJ High	-0.047	-2.2	0.0020	3.1	-0.091	-4.6	-0.226	-15.0	0.006	3.8
NJ Low	-0.006	-0.3	0.0035	3.7	-0.053	-2.8	0.473	13.2	0.010	3.3
OK High	-0.027	-1.1	-0.0010	-2.0	-0.130	-4.0	-0.161	-11.0	0.115	7.5
OK Low	-0.062	-2.0	-0.0030	-3.9	-0.060	-1.9	-0.085	-16.0	-0.046	-3.6
Error										
NJ High	0.582	26.7	0.0237	35.8	0.633	32.2	0.908	61.0	0.077	49.6
NJ Low	0.207	9.1	0.0123	13.1	0.290	15.4	1.010	28.1	0.055	18.6
OK High	0.387	15.6	0.0152	29.7	0.548	16.6	0.852	60.3	0.354	23.0
OK Low	0.191	6.1	0.0120	15.7	0.228	7.2	0.298	55.5	0.171	13.4

subjected to greater unpredictability of environmental conditions corresponds to prior research on 15 populations of *Panicum virgatum* L. and 16 populations of *Sporobolus cryptandrus* (Torr.) A. Gray (Quinn and Wetherington 2002), where there was a significant correlation of plastic variation with an environmental index.

The OK high population was influenced by a history of competition with a diverse assemblage of tallgrass species not present at any of the other locations, due to its relatively high soil nutrient concentrations, loam soil, and late successional status. This population showed the greatest ability to maintain its reproductive allocation under low-light conditions (Fig. 2), and the greatest ability to respond to higher nutrients (Fig. 4, 6, 7). Plant species of high-resource, competitive habitats are often highly plastic in their foraging responses to environmental conditions, maximizing resource capture (Grime et al. 1986).

Implications and Significance

A native grass population is more than just a Latin binomial; Antonovics (2003) has even suggested that it “may be salutary for ecologists to preface (at least in their thoughts) any Latin binomial that they use by the qualifier ‘the quasi-species . . .’.” Evolutionary forces frequently create an ecological unit unique and irreplaceable at the local level. Unfortunately, ecologists (e.g., Pigliucci 2001) continue to persist in their use of an outmoded ecotype terminology developed in the 1920s that has no consistent usage and does not adequately recognize the significant genetic variability among the genotypes and populations of a species, even those populations of a locality or specific habitat-type (Quinn 1987). In our study, the two OK populations should not be considered an OK ecotype even though they are in close geographic proximity, as they differ significantly in life history traits and plasticity. Likewise, our study illustrates that a low-nutrient ecotype (or high-nutrient ecotype) may consist of populations profoundly different in life history traits, morphology, and plasticity. Each population is the unique end product of its genetic and ecological histories, and, as such, the population should be the focal unit for the ecologist and the evolutionary biologist (Quinn 1987).

It follows that seed sources for little bluestem in reclamation/restoration should not only be local but site-specific, e.g., high vs. low fertility, especially if specific goals are the maintenance of local genetic integrity and/or local adaptation (Knapp and Rice 1996). Only 21 km separated the high- and low-nutrient populations in each region in our study, but in each case there were significant differences in their growth and plastic responses. Dyer and Rice (1997) suggested care in transferring germplasm for the purposes of conservation when little is known about how local selection gradients related to topography and soil depth might affect small scale genetic differentiation.

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