Inheritance of summer stress tolerance in tall fescue

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Abstract

High summer temperatures coupled with a lack of precipitation can lead to a drastic deterioration in overall turf quality. Limited water supply and heavy restrictions on its use in the turfgrass industry significantly limit the ability of turfgrass managers to maintain cool-season turfgrasses during summer months. The objective of this study was to evaluate the heritability of summer stress tolerance in tall fescue (*Festuca arundinacea* Schreb.). Six distinct tall fescue genotypes, three summer stress tolerant (TF-5, TF-6, and TF-10) and three summer stress sensitive (TF-2, TF-15, and TF-21), were used as parents in a full diallel cross and a polycross block. Individual progeny plants from these two populations, along with parental clones, were evaluated in the field in a space-plant nursery located at the Rutgers Adelphia Plant Science Research and Extension Farm in Freehold, New Jersey, USA. The field was unirrigated during the summers and visually rated for overall performance under summer stress. Narrow-sense heritability was estimated to be 0.637 using two-year combined data from the diallel population, and a gain from selection of 59% can be expected using a 5% selection intensity. General combining ability (GCA) effect was statistically significant in both years and accounted for more variance than specific combining ability (SCA). The results of this study suggest that additive gene action is a major component in the inheritance of summer stress tolerance in tall fescue and that recurrent selection should be an effective breeding strategy for improving summer stress tolerance in tall fescue.

Introduction

Water conservation has been one of the major challenges in turfgrass management. During summer months, it is not uncommon for an average 18-hole golf course to use as much as 1,000,000 gallons of water in a single day[1]. More than 48 gallons of water were estimated for irrigating lawns and gardens per household per day in the USA, totaling nearly 9 billion gallons per day for residential landscapes[2]. Population growth and climate change have resulted in increasing water demand and consequently intensifying freshwater scarcity[3]. Although turfgrass occupies more than three times the land of any other crop, it is not a food-crop, thus will be the first to feel the impacts of steadily increasing global water usage rates and restrictions during drought periods[4,5]. Under field conditions, drought stress is often coupled with heat stress, which makes managing cool-season turfgrasses during summer months increasingly more difficult. Beard explained that aside from supplying water and providing adequate airflow to allow for transpirational cooling, cultural practices for controlling high temperature stress are limited to syringing[6].

The development and utilization of improved, drought and heat tolerant turfgrass cultivars through breeding provide one of the best and most sustainable options for maintaining turf quality during summer months. Tall fescue (*Festuca arundinacea* Schreb.), traditionally one of the most summer stress tolerant cool-season turfgrasses[6], has shown great potential for use in a wide range of turfgrass applications in numerous environments[7]. Studies of the inheritance of increased heat and drought tolerance in agriculturally important crops, including monocots, have found it is a complex quantitatively inherited trait[8,9]. Rebetzke et al. found carbon isotope discrimination in bread wheat (*Triticum aestivum* L.), a trait previously shown to be negatively correlated to transpirational efficiency, to be controlled primarily by multiple additive genes[10]. A high degree of additive gene action was also shown in variations of excised leaf water loss rate and relative water content in wheat[11]. Research on other monocots such as sorghum (*Sorghum bicolor* [L.] Moench) has shown that various factors contributing to drought tolerance are each controlled by multiple genes[12].

Knowledge of the heritability characteristics of a trait of interest is important when beginning a breeding program. Estimates of heritability can be used to select the best breeding protocol, as well as anticipate gains that can be made[13]. Heritability is commonly expressed as broad-sense and narrow-sense heritability. Broad-sense heritability is an estimate of the variance within a population caused by all genetic factors, namely additive, dominance, and epistatic interactions[14]. Narrow-sense heritability is an estimate of the additive component of the total genetic variance[15]. While Burton & DeVane described the use of broad-sense heritability to measure the potential efficiency of selection[16], estimates of narrow-sense have been shown to be far more useful in breeding of outcrossing species[13].

In addition to estimations of heritability, other characteristics including general combining ability (GCA), specific combining ability (SCA), reciprocal effects (maternal and non-maternal

effects) are also important. Understanding whether maternal effects are involved can also help breeders understand whether progenies receive their genetic traits equally from both parents[15]. Diallel crosses are useful for plant breeders as they allow for calculations of many heritability characteristics such as narrow-sense heritability, and maternal effects[15,17,18]. These estimates can be used to quantify how useful a specific parent can be in conferring traits to its progeny as well as be used to compare the importance of additive vs. non-additive genes[15,19].

A previous study has evaluated 24 tall fescue genotypes for heat and drought stress separately and in combination under controlled environment in a growth chamber study[20]. Controlled environment conditions have some limitations including root growth in a finite space, and under field conditions, drought stress commonly occurs in combination with heat stress on cool-season turfgrasses. Therefore, this study was conducted to evaluate summer stress, a combination of heat and drought stresses, on tall fescue under field conditions. The objective of this study was to estimate narrow-sense heritability and evaluate other characteristics of inheritance (combining ability, reciprocal effects, expected gains from selection) of summer stress tolerance in tall fescue using a full diallel cross and a polycross block between summer stress tolerant and summer stress sensitive clones.

Materials and methods

Plant material

Three summer stress tolerant (TF-5, TF-6, and TF-10) and three summer stress sensitive (TF-2, TF-15, and TF-21) tall fescue clones were selected from the previously described growth chamber study[20]. Clone TF-6 and TF-10 performed well in the combined heat and drought treatment, whereas TF-5 was only moderately tolerant to the combined stress treatment but had the highest quality under heat treatment; all of which are candidates for breeding for enhanced summer stress tolerance[20]. Clone TF-2, TF-15, and TF-21 had relatively low turf quality rating under the combined heat and drought treatment but were not the worst performers[20], those were excluded to avoid low survival rates resulting in a large number of missing data under field condition. All six clones used in this study were previously determined to be endophyte positive[20], allowing us to prevent differences in turf performance due to the presence or absence of endophytic fungi as described by previous research[21,22]. The six clones used in this study have significantly different pedigrees and are considered unrelated.

Crossing scheme

Diallel cross

Crosses were made between clones in all possible combinations (tolerant × tolerant, tolerant × sensitive, and sensitive × sensitive). Seed yield of all crosses was not equal. A full description of crosses, including number of progeny plants grown from each cross, is shown in Table 1. Full-sib progenies were produced from each cross by using both clones as the female and male parents. These full-sib F_1 progenies were considered pseudo F_2's because the parents, having never been inbred or test-crossed, were likely heterozygous at most loci[23]. Flower induction was encouraged by increasing day length to 14 h using 400-W high pressure sodium lights (PL. Light Systems, Beamsville, Ontario, Canada) placed 1.5 m above the plants in

Table 1. Description of diallel crosses between three summer stress tolerant and three summer stress sensitive tall fescue genotypes and summer stress tolerance means across four replications and two years.

Cross/ parent	Female × male[a]	Number of progeny	Progeny/ parent mean[b]	SD
1	TF-2 × TF-5 (S × T)	96	5.5	0.8
2	TF-2 × TF-6 (S × T)	95	4.1	0.9
3	TF-2 × TF-10 (S × T)	96	4.3	1.0
4	TF-2 × TF-15 (S × S)	96	4.7	0.6
5	TF-2 × TF-21 (S × S)	96	3.4	0.3
6	TF-5 × TF-2 (T × S)	96	6.0	1.0
7	TF-5 × TF-6 (T × T)	96	5.3	1.5
8	TF-5 × TF-10 (T × T)	96	5.5	1.1
9	TF-5 × TF-15 (T × S)	96	6.0	0.7
10	TF-5 × TF-21 (T × S)	96	6.1	0.9
11	TF-6 × TF-2 (T × S)	95	4.1	0.5
12	TF-6 × TF-5 (T × T)	95	5.1	1.6
13	TF-6 × TF-10 (T × T)	96	4.6	0.9
14	TF-6 × TF-15 (T × S)	96	5.1	0.5
15	TF-6 × TF-21 (T × S)	96	3.3	0.5
16	TF-10 × TF-2 (T × S)	90	4.5	2.1
17	TF-10 × TF-5 (T × T)	96	5.3	0.7
18	TF-10 × TF-6 (T × T)	96	4.4	0.6
19	TF-10 × TF-15 (T × S)	91	4.2	0.8
20	TF-10 × TF-21 (T × S)	76	3.7	0.9
21	TF-15 × TF-2 (S × S)	91	5.0	1.1
22	TF-15 × TF-5 (S × T)	95	6.3	1.5
23	TF-15 × TF-6 (S × T)	96	5.2	0.8
24	TF-15 × TF-10 (S × T)	63	4.5	1.0
25	TF-15 × TF-21 (S × S)	96	4.9	0.7
26	TF-21 × TF-2 (S × S)	96	3.0	0.6
27	TF-21 × TF-5 (S × T)	96	5.3	0.6
28	TF-21 × TF-6 (S × T)	92	3.2	0.4
29	TF-21 × TF-10 (S × T)	63	3.2	0.5
30	TF-21 × TF-15 (S × S)	96	4.6	1.3
TF-5	(T)	–	6.9	1.0
TF-6	(T)	–	4.0	1.3
TF-10	(T)	–	4.6	1.2
TF-2	(S)	–	4.1	0.7
TF-15	(S)	–	5.7	0.8
TF-21	(S)	–	3.1	1.3
	$LSD_{0.05}$		0.87	

[a] S in the parentheses denotes summer stress sensitive, and T denotes summer stress tolerant. [b] Summer stress tolerance ratings were taken on a 1 to 9 scale with 1 being a completely wilted or dormant plant, and 9 being a green, fully turgid, actively growing plant. Turfgrass color, texture, and disease were not considered when evaluating summer stress responses.

the greenhouse. Clones were either placed under, or removed from the long day treatment depending on their particular maturity in order to synchronize anthesis. Prior to anthesis, clones were matched with the desired cross, and crosses were isolated using plastic chambers. A waxed paper envelope was placed over one seed head on each plant in order to measure the degree of selfing. No viable seed was present in any of the seed heads that were placed in envelopes to test for selfing. Plant inflorescences were manually tapped during anthesis to promote pollen movement between clones.

Polycross block

Two clones of each of the six genotypes described above were used to create a polycross block. Parental genotype TF-10 produced only 95 viable seeds while all other genotypes produced more than the 96 used for evaluation in this experiment. A full description of the polycross block is presented in Table 2. Flowering was induced as described above. Clones

used in the polycross block were arranged in a randomized complete block design (RCBD), isolated in a separate room from the diallel crosses, and re-randomized every second day in an attempt to limit assortative mating. Oscillating fans were also used in addition to manual tapping to assist in pollen movement. Progeny plants from the polycross block were half-sibs because the pollen source is considered the same for the entire block[24]. Polycross blocks are the most common method of synthetic cultivar production in turfgrass breeding[25]. Polycross isolation nurseries allow for random intermating between selected plants, fixing gene frequency in the population, and beginning the process of seed increase[26].

For both the diallel crosses and polycross block, seeds from each clone were harvested separately, bagged, and dried in a commercial seed dryer at 37 °C for four weeks. Once dry, the seeds were manually cleaned and treated with 0.2% KNO_3 in order to break dormancy and induce germination. After the three-day treatment in 0.2% KNO_3, the seeds from each cross were sown into a 20-cm diameter bulb pan (The HC Companies, Twinsburg, OH, USA) and watered two times per day through germination. Following germination, 96 seedlings (when available) from both parents in each diallel cross were randomly selected and planted in individual cells where they were allowed to grow for three months. Ninety-six (when available) seedlings from each maternal genotype in the polycross block were randomly selected and planted in the same manner.

Field planting and evaluation

Progeny plants from both parents of each diallel cross, along with clonally propagated parents, were planted in the field in a RCBD with four replicates at the Rutgers Adelphia Plant Science Research and Extension Farm, in Freehold, NJ, USA in October of 2011. This location has a humid subtropical (Cfa) climate type according to Köppen–Geiger climate classification and an average July daily high temperature of 29 °C. Soil type was a Freehold sandy loam, made up of 69% sand, 21% silt, and 10% clay. Each of the four replicates contained 24 progenies from each parent (when possible) in the diallel cross as well as four clonal plants of each parent. Some crosses did not produce enough viable seed to provide enough progeny to have 24

individuals in each replication. In instances where there were not 96 progenies, the available progenies were divided equally among the four replicates. In the diallel study, 2,877 plants were planted and evaluated. Plants were placed 31 cm apart. A border row was planted around the perimeter of the field in order to provide more uniform root competition throughout the experiment and alleviate edge effects. Empty plots where there were not enough progenies from a particular cross were also planted with border plants for the same reason. Progenies from each maternal genotype of the polycross block, along with clonally propagated parents (totaling 624 plants), were planted in an adjacent field using an identical method. Immediately following planting, 10.0–4.4–8.3 (N–P–K) fertilizer was applied at a rate of 3.66 g·N·m⁻². Plants were maintained at a 6.4-cm height during the growing season with a rotary mower. Rainfall was supplemented with irrigation as needed following planting as well as during the following spring to assure proper establishment.

Two fertilizer applications on March 15 and April 12 2012 and one application on April 11 2013 were made at the rate of 3.66 g·N·m⁻² each using a 19.0–0–5.0 (N–P–K) fertilizer. Rainfall was supplemented with irrigation until the month of June, at which point supplemental irrigation was ceased. Summer stress tolerance ratings of each plant were taken on a 1 to 9 scale with 1 being a completely wilted or dormant plant, and 9 being a green, fully turgid, actively growing plant. Turfgrass color, texture, and disease were not considered when evaluating summer stress responses. From 26 June through 25 July 2012, rainfall was not more than 0.8 cm on any one day and totaled only 3.3 cm. During this period, the average daily high temperature was 32 °C and nine of the 30 d had high temperatures reaching or exceeding 35 °C. The most severe summer stress was observed on 25 July 2012, significant stress was not observed on the plants due to regular heavy rains after July 26 in that year. During the same period in 2013, the average daily high temperature was 32 °C and seven days had high temperatures reaching or exceeding 35 °C. However, the weather in that period in 2013 was not conducive for drought. Therefore, summer stress tolerance ratings were taken when the highest

Table 2. Description and analysis of variance (ANOVA) table of the polycross block using three summer stress tolerant and three summer stress sensitive tall fescue genotypes. Summer stress tolerance means were averaged across four replications and two years.

Maternal parent	Number of progeny	Maternal mean[a][b]	SD	Paternal mean[a][c]	Mid-parent mean[a]	Pseudo F_2 mean[a][b]	SD
TF-5	96	6.1a	1.0	3.2	4.7	6.0a	0.8
TF-6	96	2.9cd	1.5	3.8	3.4	4.5bc	0.9
TF-10	95	3.4c	1.2	3.7	3.6	4.2bc	0.9
TF-2	96	2.9cd	1.2	3.8	3.4	4.6b	1.0
TF-15	96	4.5b	1.7	3.5	4.0	5.9a	1.0
TF-21	96	2.3d	1.2	4.0	3.1	4.0c	0.7
LSD$_{0.05}$		0.95				0.54	

ANOVA of the Pseudo F_2			
Source of variation	df	Pr > F	
Year	1	0.0970	NS
Replication (year)	6	<0.0001	***
Polycross	5	<0.0001	***
Polycross × year	5	0.0703	NS
Residuals	30		

[a] Summer stress tolerance ratings were taken on a 1 to 9 scale with 1 being a completely wilted or dormant plant, and 9 being a green, fully turgid, actively growing plant. Turfgrass color, texture, and disease were not considered when evaluating summer stress responses. [b] Means followed by different lowercase letters indicated significant differences ($p < 0.05$) within the column. [c] Pollen source was considered one homogeneous entity for all crosses. Paternal means were calculated based on all clones involved in the polycross block excluding the maternal parent because of self-incompatibility.

visible drought stress was observed on 31 August 2013, however, at that time, heat stress was less severe with the average daily high temperature of 28 °C and no days in August reaching or exceeding 35 °C.

Statistical analyses

Data analyses were conducting using 25 July 2012 and 31 August 2013 rating dates when drought stress was most severe in each year. Analysis of variance was conducted using averages of each cross/parent in each of the four replications to avoid pseudoreplication[27]. In the diallel experiment, GCA, SCA, and reciprocal effects were analyzed with the R package (lmDiallel) developed by Onofri et al.[28] based on the Griffing's model 1[17]. Mean, standard deviation (SD), and least significant difference (LSD at $p < 0.05$) values for the diallel and polycross experiments were calculated using the General Linear Model procedure in SAS 9.4 (SAS Institute Inc., Cary, NC, USA). In the diallel experiment, data were analyzed for each year separately due to the significant year effect and interactions (Table 3). Narrow-sense heritability estimates and standard errors were calculated by performing a regression analysis of mid-parent and progeny means[15,29] using lm() function in R. In the diallel cross, progeny means in each replication were regressed against their mid-parent means for each cross in the same replication to reduce replication effect in the RCBD for each year and the two-year data combined. The slope of the regression line is equal to the narrow-sense heritability[15,30].

Expected gain from selection was calculated using the formula: $G_S = (i) (\sigma_p) (h^2)$ where G_S is the expected gain from selection, i is the selection intensity, σ_p is the phenotypic standard deviation of the entire population, and h^2 is the narrow-sense heritability[15].

Results and discussion

Severe summer stress caused a significant deterioration in the overall quality of tall fescue parental clones and progenies. Stress symptoms were present in all plants evaluated. Some only suffered minor reductions in overall turf quality, while the growth of others was completely ceased, indicated by a wide range of tolerance ratings under summer stress.

Significant differences in summer stress responses were observed between the two years, likely due to the environmental conditions in which the most severe stress was observed in the different time of the year in 25 July 2012 and 31 August

2013. Analysis of variance was performed for each year, GCA effect was highly significant for both years in the diallel study (Table 3). The SCA was statistically significant in 2012 and had a probability of 0.08 (only marginally significant at the probability of 0.1) in 2013 (Table 3). Because tall fescue is an outcrossing allohexaploid with genomic constitution of $PPG_1G_1G_2G_2$[31], the inheritance of tolerance to combined abiotic stresses, heat and drought, in tall fescue is expected to be complex. Nevertheless, the GCA explained the most of the variance in the model in both years suggesting the strongest effect on the summer stress tolerance trait (Table 3). Narrow-sense heritability were analyzed separately for each year and two years combined (Table 4) due to the significant year effect. Casler reported potential bias caused by genotype × environment interactions when performing the parent/offspring regression analysis[32]. Taking year (environment) and replication effects from the RCBD into account, we used progeny means for each replication to regress against their mid-parent means for each cross in the same replication for each year and the two-year data combined where data were not averaged across two years creating more data points for regression analysis.

Narrow-sense heritability was estimated using mid-parent/progeny regression analysis, with the slope of the regression line being the narrow-sense heritability. Narrow-sense heritability values of 0.578, 0.825, and 0.637 were estimated for the diallel study in 2012, 2013, and two years combined, respectively (Table 4). Narrow-sense heritability estimates the effect of additive genes only, which removes the effects of dominant genes and epistasis that are not as useful to plant breeders and more difficult to select for[33]. Other studies in outcrossing grass species also show that narrow-sense heritability can vary in different years[34−36]. Heritability estimates for the polycross are not reported in this study because the six-clone polycross had only six different combinations due to the assumption of a uniform pollen source, therefore the regression analysis is far less powerful and less accurate in the polycross than for the 30 diallel crosses. With a larger number of polycross families, a study evaluating 25 half sib-families of forage-type tall fescue reported narrow-sense heritability estimate ranging from 0.44 to 0.49 in various traits, plant height, panicle length, number of fertile tillers, and seed weight[37].

Lehman & Engelke estimated the narrow-sense heritability of root growth, a trait associated with summer stress tolerance, in creeping bentgrass (*Agrostis stolonifera* L.) to be between 0.62

Table 3. Analysis of variance table for the full diallel cross study.

Source of variationª	df	Sum square	Mean square	F value	Pr >F	
2012						
Replication	3	13.9	4.62	9.60	1.180e-05	***
GCA	5	141.9	28.38	58.94	<2.2e-16	***
SCA	15	25.4	1.69	3.51	7.064e-05	***
Reciprocal	15	5.5	0.36	0.76	0.7207	NS
Residuals	105	50.6	0.48			
2013						
Replication	3	14.8	4.94	4.66	0.00426	**
GCA	5	103.0	20.59	19.41	1.211e-13	***
SCA	15	25.9	1.73	1.63	0.07834	NS
Reciprocal	15	14.1	0.94	0.89	0.58211	NS
Residuals	105	111.4	1.06			

ª GCA, general combining ability; SCA, specific combining ability. ** Significant at the 0.01 probability level. *** Significant at the 0.001 probability level. NS not significant at the 0.05 probability level.

Table 4. Narrow-sense heritability estimates and their standard errors for summer stress tolerance ratings from the diallel study in 2012 and 2013 based on mid-parent/offspring regression.

Year	Narrow-sense heritability	Standard error	
2012	0.578	0.059	***
2013	0.825	0.144	***
Combined	0.637	0.062	***

*** Significant at the 0.001 probability level.

and 0.72[38]. Similar tall fescue narrow-sense heritability estimates of 0.67 and 0.86 have been estimated for seed yield and maturity, respectively[39]. Ekanayake et al. had similar narrow-sense heritability estimates for characteristics associated with drought resistance in rice; narrow-sense heritability was estimated to be 0.56–0.92 for dry root weight, 0.44–0.77 for root length density, and 0.61–0.80 for root thickness[40]. The moderate-high narrow-sense heritability estimated in the diallel population in this study indicates that summer stress tolerance in tall fescue is primarily controlled by multiple additive genes. The high proportion of additive genes involved with summer stress tolerance in tall fescue is similar to findings in other monocots[38,40].

Narrow-sense heritability estimates additionally can be used to estimate gain from selection. Based on equation $G_S = (i)\,(\sigma_p)\,(h^2)$, standard deviation on a phenotypic mean basis (1.75) and narrow-sense heritability of the two-year data combined (0.637) were used to estimate gain from selection in summer stress tolerance to be 2.3, which is a 49% gain from the population mean of 4.7 achieved from a selection of the top 5% (selection intensity = 2.06) of the diallel population. Bonos et al. estimated gain from a 2%–4% selection intensity for root mass of the 30 cm and longer portion in tall fescue, and found expected gains to be 41% for a genetically narrow population and 81% for a genetically diverse population[41]. Burton & DeVane also calculated expected gain from selection of the top 5% of a population of tall fescue growing as space-plants during the summer in Tifton, Georgia, USA; the expected gains in greenness ratings and yield of green tissue were estimated to be 39.4% and 60.5%, respectively[16].

The summer stress tolerant line TF-5 and its progeny plants performed well in both polycross and diallel experiments (Tables 1 & 2), making them good candidates for recurrent selection. Surprisingly, TF-15, previously identified as a summer stress sensitive line from a growth chamber study[20], also performed relatively well under summer stress in this study (Tables 1 & 2). In the growth chamber study[20], the day and nighttime temperatures were 38 °C and 33 °C , respectively, which are likely more severe conditions than our field study. Moreover, field evaluations do not always reflect greenhouse or growth chamber screenings. In both polycross and diallel experiments, TF-21 performed poorly under summer stress (Tables 1 & 2). The progenies from TF-21 maternal line in the polycross study were sensitive to summer stress (Table 2), whereas in the diallel study, progenies from crosses when TF-21 was used as the female parent performed poorly except for when TF-5 was used as male parent (Table 1). This explains that even though the GCA was a major factor explaining the phenotypic differences, SCA also played a role in affecting summer stress tolerance (Table 3). Our results indicated that TF-21, when used as the female parent, had a negative effect on

summer stress tolerance. These findings are similar to those of Bonos et al.[42] who found maternal effects pertaining to disease resistance in creeping bentgrass related to the poor performance of a particular genotype.

This study indicates that summer stress tolerance is mainly controlled by genetic factors, and more specifically, additive gene action. The relatively high narrow-sense heritability suggests that breeding programs involving recurrent selection and/or multiple cycles of progeny testing would be successful in improving the overall summer stress tolerance of tall fescue.

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Conflict of interest

The authors declare that they have no conflict of interest.

Dates

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