GENETIC CONTROL OF RHIZOME FORMATION AND RAPID TILLERING RATE

IN TALL FESCUE

by

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ABSTRACT OF THE DISSERTATION

Genetic Control of Rhizome Formation and Tillering Rate in Tall Fescue

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Tall fescue [*Lolium arundinaceum*, (Schreb.) Darbysh.] is commonly known as a bunch type cool season turfgrass that spreads primarily by erect tillers. Some genotypes in tall fescue were found to have rhizomes or rapidly spreading tillers. The objectives of this dissertation were to: (i) study the effects of photoperiod and temperature on the rhizome formation and tillering rate, (ii) estimate the general and specific combining abilities of tall fescue parents for rhizome formation, rapid tillering rate and ground coverage (iii) to estimate the narrow sense heritability using progeny regression analysis for rhizome formation, rapid tillering rate and ground coverage, (iv) to calculate Pearson correlation coefficient between rhizome formation, rapid tillering and ground coverage, and between NDVI and rapid tillering in tall fescue, (v) Comparison between commercial cultivars and experimental breeding populations of tall fescue for rhizome formation, rapid tillering and ground coverage.

A diallel and polycross mating design were employed to estimate the role of additive and non-additive gene effects on the rhizome formation, rapid tillering and ground coverage in tall fescue. The progenies from the rhizome parents were highest for rhizome formation whereas progenies from rapid tillering types x bunch type parents showed significant rapid tillering rate and ground coverage. Narrow sense heritability estimates for rhizome formation were low, moderately high for rapid tillering and very high for ground coverage. The combining ability analysis showed that rhizome formation was influenced by both additive and non-additive gene effects whereas tillering rate and ground coverage were controlled mainly by additive gene effects. Significant negative correlation was found between rapid tillering and rhizome formation whereas a positive correlation was found between rapid tillering and ground coverage. The results showed genotypic and phenotypic differences in tall fescue growth habits. Based on the presence of the additive genetic variance in the population, phenotypic recurrent selection should improve the rapid tillering and rhizome formation in tall fescue.

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Literature Review

Tall fescue

Tall fescue [*Lolium arundenaceum*, (Schreb.) Darbysh.] is one of the most widespread, self-incompatible, allopolyploid, perennial, cool season turfgrasses, best adapted in transition zone, parts of California and northern half of United States (Meyer, 1982; Bonos et al., 2006). It was introduced to U.S. from Europe in mid 1800s as a forage grass (Hoveland, 2009; and Buckner and Cowan, 1973). Tall fescue has gained importance as a high seed producing forage grass after the release of the cultivars 'Alta' and 'Kentucky 31', in early 1940's. (Buckner and Bush, 1979). Utilization of tall fescue as a turfgrass increased after the release of the first turf type cultivar, 'Rebel', in 1980 (Funk et al., 1982) at Rutgers University. Since then consistent efforts were continued to improve tall fescue for disease and insect resistance, drought tolerance, turf quality, turf density and growth habit. (Morris, 2006; Saxena et al., 2011). Recently released cultivars have exhibited superior performance and outperformed the older cultivars (Watkins and Meyer, 2004). Currently, available tall fescue cultivars are utilized as forage and turfgrass. Variation in tall fescue genotypes exist which allows its utility in various areas such as golf course roughs, sports fields, recreation areas and sod production (Hoveland et al., 2009; Watkins and Meyer, 2004).

Tall fescue is native to most of Europe, the Mediterranean region (North Africa, parts of Middle East, central Asia), and Siberia (Hopkins et al., 2009). Two major gene pools (the Continental and Mediterranean types) were reported by Hopkins et al. (2009) to characterize tall fescue genotypes. A third gene pool was also reported and named as

"Rhizomatous" type which originated from northwest Spain and Portugal (Borrill et al., 2002) and produce rhizomes. de Bruijn (2004) reported that germplasm originating from the Iberian Peninsula produced prevalent and longer rhizomes. Continental germplasm originated from central and northern Europe and from a portion of Asia whereas the Mediterranean type originated from southern Europe, Middle East and North Africa (Hopkins et al., 2009). The Continental type is characterized as winter hardy and summer active and often has coarser leaf texture; such as Kentucky-31; and some plants were reported to produce rhizomes (Jernstedt and Bouton, 1985; Bouton et al., 1989; and Bouton et al., 1992). Rhizomatous types are not as winter hardy as Continental types (Diesburg and Carlson, 1983). Mediterranean types are less winter hardy (Burner et al., 1988) and more winter active and often bear narrower leaves than Continental types. Mediterranean type accessions from North Africa were found to be very stiff and have wiry leaves during spring and summer (Hopkins et al., 2009). Turf type tall fescue were defined as plants with finer leaves, upright, short stature, dense tillering and dark green color and are developed mostly from Continental germplasm (Hopkins et al., 2009). The genomic constitution of northern European (Continental) tall fescue consists of six groups of chromosomes in which two groups (PP) originated from meadow fescue (*Lolium pratensis* [Huds.] Darbysh.), and four groups of chromosomes ($G_1G_1G_2G_2$) are from the tetraploid species *Festuca arundinacea* var. *glaucescens* Boiss (Humphreys et al., 1995 and Sleper and West, 1996). The genomic constitution of Mediterranean types is still to be determined, however it is considered to be different from the continental tall fescue (Hopkins et al., 2009).

With advancement in breeding programs, a large number of improved and high performing tall fescue cultivars continue to be released. These cultivars provide a wide range of morphological differences and utility purposes which can be utilized in different regions. A large amount of genetic variation exists within tall fescue turf-type cultivars. New tall fescue cultivars are expected to have desirable characteristics such as disease resistance, drought tolerance, and turf quality that would be popular with growers in seed and sod production (Brilman, 1998). Bowman and Macaulay (1991) reported that increased popularity of tall fescue is due to the improvement in turf quality, disease resistance, turf density, and mowing qualities. Watkins and Meyer (2004) reported that commercial cultivars have exhibited morphological differences when planted in the breeding nursery and characterized turf type tall fescues into dwarf, semi-dwarf, standard and forage groups. The semi-dwarf group consists of most cultivars such as Rembrandt and Millennium which have medium height, medium maturity and finer leaves than forage types. The standard group is characterized by medium maturity. Dwarf types cultivars have finer leaf texture and higher turf density than other groups. Kentucky -31 was categorized into the forage/standard group which has the lowest turf quality of the commercial cultivars (Watkins et al., 2003).

Most of the tall fescue cultivars developed after the 1980s was from the recurrent selection breeding program performed at Rutgers Plant Science Research and Extension Farm, NJ (Bouton et al., 1992).The Rutgers turf breeding program has developed germplasm collected from the old turf areas in the eastern, southern and central United States. They have also collected in Africa and Asia (Hopkins et al., 2009).

Rhizomes and Tillers

Tall fescue is commonly known as a bunch type which primarily spreads by tillers and has limited spreading ability (Buckman and Cowan, 1973; Beard, 1973). However, the rapid tillering type growth habit and rhizome formation in tall fescue have also been found. The bunch type growth habit of tall fescue has limited its adaptation to different environments and soil conditions.

Rhizomes originate from the crown as a rhizome bud and develop into lateral stems beneath the soil surface, bearing roots and shoots at the nodes. The rhizome formed in tall fescue is anatomically similar to rhizomes produced in Kentucky bluegrass (De Battista and Bouton, 1990). Tillers in contrast to rhizomes are the above ground shoots that develop within the leaf sheath of adjacent tillers and/or arise below ground from the node (Rebetzke et al., 2008); The role of rhizomes in turfgrasses is found to enhance competition in turf stands and persistence under high temperature and drought stress conditions by serving as a storage organ for carbohydrates (Evans and Ely, 1935; Weaver, 1963; De Battista and Bouton, 1990). Rhizomes fill in bare spots, provide strength to sod, and improve traffic tolerance (Bouton, 1992; Brilman, 1998).The development and growth of rhizomes in bare areas eliminates the need for interseeding (Samples et al. 2009). Porter (1958) first reported the presence of short rhizomes in tall fescue. Other subsequent studies showed that rhizome production exhibits both genetic variability and genotype × environment interactions in tall fescue (D'Uva et al., 1983). Several studies have reported the advantages of rhizome in turfgrasses. Bouton et al. (1989) reported a decrease in rhizome formation in tall fescue under the competition with bermudagrass. Dunn et al., 2002 reported that rhizome formation in Kentucky bluegrass is important for sod production and harvesting. Mueller (1941) reported the advantages of shorter rhizomes in prairie grasses that they covered more ground surface adjacent to the mother plant and provided consistent turf. Evans and Ely (1995) suggested that high frequency of new rhizomes compensated for the length of shorter rhizomes.

On the other hand, lateral tillers in tall fescue increase ground coverage and turf compactness with continuous replacement (Friend, 1965). Robson (1968) illustrated that a perennial turfgrass is defined as a dynamic population of tillers which comprises of two weeks to more than a year old tillers (Robson, 1968). Friend (1965) suggested that tillering rate was influenced by environment and genetic factors in wheat (*Triticum aestivum* L.). Tiller number has been found to be controlled by quantitative trait loci which are mainly additive as compare to dominant and epistatic effects in rice (*Oryza sativa L.*) (Tang et al., 2001). Whitehead et al. (1986) showed that rhizome formation was moderately heritable and that additive genetic variance was significant and suggested that recurrent selection could be effective for improving the trait. Nguyen et al. (1980) reported significant entry (synthetics and cultivars) x environment interactions occurred for the vegetative and reproductive growth in tall fescue. Sleper et al. (1977) found that additive gene action was important in controlling the number of tillers per plant. Recurrent selection is useful in improving the traits with low to moderate heritability and also to aggregate the favorable alleles in a population (Bouton et al., 1992). Benbelkacem et al., (1984) also reported that backcrossing can improve tillering in oats (*Avena sativa*).

Traditional tall fescue (non-rhizomatous type) has been reported to have slow recovery from wear damage and a bunchy or clumpy growth when not over-seeded (Brilman, 1998). Rodney et al. (2009) reported that blends of rhizomatous and non-rhizomatous tall fescue cultivars are available in the market. Rodney et al. (2009)

reported that after comparing the pure stands and blends of rhizomatous/ non-rhizomatous turf type tall fescue cultivars, it was found that the establishment rate and lateral spread of rhizomatous type cultivars were slower in both pure stands and blends than non-rhizomatous tall fescue cultivars. Turf breeders are continuing to improve tall fescue for rhizome formation and other agronomically important traits in tall fescue. Tall fescue cultivars recently developed have more and longer rhizomes than traditional cultivars (which have shown some short rhizome formation) in tall fescue (Brilman, 1998).

Photoperiod

Friend (1965) suggested that tillering rate was influenced by environment and genetic factors. An increase in temperature over the range of 10–25 ^{o}C increased the total number of leaves and tillers, but influenced the rate of leaf emergence more than tillering rate in wheat. Templeton et al. (1961) reported the development of new tillers was most rapid in tall fescue when the mean weekly temperature ranged between 6 to16 ^{o}C (March 12 until April 19, Lexington, KY). The rate of tillering decreased and remained low until the end of the experiment in June. The increase in tiller number was due to low temperature and short photoperiod (9 H). Less tillering occurred when tall fescue plants were subjected to an extended long photoperiod treatment (16 to17 H) than a short period (9H) in the green house (Templeton et al. 1961). They also observed an increase in number of tillers when tall fescue plants were exposed to 7 ^{o}C temperatures as compared to 22 ^{o}C. Moser et al. (1968) evaluated the influence of temperature and photoperiod on the growth and development of Kentucky bluegrass. The development of rhizomes was significantly higher under long photoperiod (18 H) and tiller production was lower under long photoperiod (18 H) than under short photoperiod (12 H). Cold treatment (0 to 2 ^{o}C) increased the tiller development but reduced rhizome formation as more crown buds differentiated into tillers and lesser into rhizomes. Evans (1949) reported that the development of rhizomes occurs during the longest photoperiod of the year under field conditions in Kentucky bluegrass. Younger (1961) reported that the roots and rhizome growth in *Zoysia spp*. increased with an increase in day-length and temperature and reached the peak at 14 H day length. There was no root growth or rhizome production at 15 ^{o}C even with the longest day length. Evans and Watkins (1939) reported that under short photoperiod conditions, tillering rate is favored in Kentucky bluegrass.

Bouton et al. (1992) have screened for the number of rhizomes in tall fescue and showed high genotypic correlation and rank correlation which indicates that field counting of rhizomes in freshly dug plants would accurately assess the genotypic differences. The rhizomes counted which were >2.5 cm in length. The inheritance studies conducted in tall fescue by Whitehead et al. (1986) showed that rhizome formation was moderately heritable, additive genetic variance was significant and suggested that recurrent selection would be effective for improving the trait. D’Uva, 1983 showed that genotype × environment interaction was significant for rhizome formation in tall fescue more than genotype × location interaction. Sleper et al. (1977) found that additive gene action was important in controlling number of tillers/plant and suggested this trait can be improved with mass selection.

Diallel Mating Design

A diallel cross involves intercrossing the chosen parental individuals in all possible combinations, including reciprocals, and will yield estimates of genetic variances

(Poehlman and Sleper, 1995). Given n selected parental genotypes, there are n (n – 1)/2 different combinations, but with reciprocals, that will represent a total of n (n – 1) crosses.

The parents used in this mating design ranged from inbred lines to broad genetic base varieties (Hallauer and Miranda, 1981). Primary objectives of the diallel experiment are to evaluate general combining ability and specific combining ability effects of the parents with further interpretations as to the nature of gene action, i.e. additive, dominance, or epistasis (Gardner and Eberhart, 1966; Hayman 1954a, b, 1957, 1958). The progeny test is used to estimate general combining abilities of an array of parents, as well as to determine the specific combining abilities of all possible pair crosses. Twice the GCA variance contains additive genetic variance and a portion of epistatic variance whereas SCA variance includes all the dominant genetic variance and the remaining epistatic variance (Griffing, 1956).

Polycross Mating Design

Polycross is a modification of top crossing commonly used in forage crops (Hittle, 1954; Simmonds, 1979). In polycross mating design, selected plants are placed in such a way that they pollinate each other uniformly and the parent combined with all or most of the plants expected to have same proportion in the progenies (Wit, 1952). Polycross mating design is useful in determining the genetic factors of the parents for trait(s) after inter-pollination in isolation (Wellensiek, 1952). The combination of each plant will then be evaluated for quantitative genetic information about the agronomic important traits such as yield (Wit, 1952; (Fehr, 1987). It is relatively simple than diallel mating design or factorial mating design because a large set of parents could be used and an adequate amount of seeds can easily be produced (Nguyen and Sleper, 1983). Polycross progeny test is useful in determining inheritance of disease resistance, adaptation, and general combining ability of the selected genotypes and to select the superior ones to develop synthetic varieties (Hittle, 1954).

The progeny testing was performed on the half –sibs to evaluate the general combining ability of parental lines (Simmonds, 1979). The deviations of each half-sib progeny from population mean estimates GCA (De Araujo and Coulman, 2002; Wrick and Weber, 1986) and GCA is a measurement of the additive genetic action, based on which parents are selected for a recurrent selection breeding program and synthetic cultivar development (Nguyen and Sleper, 1995). The selection should be made based on the highly combining abilities and should continue as long as considerable genetic variation exists which were utilized in the development of synthetic cultivars or hybrid production (Tysdal and Crandall, 1948).

Combing abilities

In diallel and polycross mating designs, genotypes are inter-crossed and evaluated based on progeny testing (Poehlman and Sleper, 1995). The progeny test is used to estimate general and specific combining abilities of the parents involved in all possible pair crosses (Griffing, 1956). A diallel cross analysis following the statistical methods presented by Griffing (1956) allows for the estimation of both the general and specific combining ability. These combining ability estimates can be used to determine the relative importance of the additive vs. non-additive gene effects influencing the trait of interest as well as identify potential parents that can incorporated into a breeding program (De Araujo and Coulman, 2002; Becelaere and Miller, 2004; Cisar et al., 1981). In an open-pollinated species, polycross mating produce half-sib progenies that are evaluated to determine GCA of the parent (Nguyen and Sleper, 1983a; Simmonds and Smartt, 1999). Sprague and Tatum (1914) introduced the concept of general combining ability, to distinguish between the performance of the parents in the cross from the average over all the crosses; and the specific combining ability to evaluate deviation of the individual cross from the average over all crosses (Hallauer and Miranda, 1981). SCA and GCA estimates determine non-additive and additive components of the parent's genotypic variance, respectively (Griffing, 1956; Falconer and Mackay, 1996). SCA is a measure of dominance within loci and epistasis and to obtain SCA the paired crossing is necessary, whereas GCA could be obtained from mass breeding and polycross (Sprague and Tatum, 1942). . The higher performance of hybrids depends upon the extent of complementation between the favorable genes from both the parents (Poehlman and Sleper, 1995).

A low SCA estimate indicates the average performance of the combinations lower than would be expected based on their general combining ability. Higher values of SCA indicate better performance of the combination than expected (Sprague and Tatum, 1942). The low GCA estimates indicated that particular line is average in its performance and higher GCA estimates determine that a particular line is much better than the remaining lines with which it is compared.

Akram et al. (2007) estimated the general and specific combining abilities for the number of tillers per plant, panicle length, panicle sterility and yield per plant and reported that additive gene effect was higher for the tillering rate in rice (*Oryza sativa L.*).

Kashif and Khaliq (2003) reported that mean square of GCA was highly significant and were greater than SCA and reciprocal effect for number of tiller per plant in wheat. On the other hand, Muehlbauer et al. (1971) reported that non-additive genetic variance was more important than additive genetic variance for plant height and tiller number in a three parent diallel cross in oats *(Avena sativa*), and found significant specific combining ability effects and reciprocal effects but non significance general combining ability.

Frakes and Matheson (1973) reported that general combining ability was higher than specific combining ability for forage yield in tall fescue based on the ratio of the mean squares of GCA to SCA which varied from 25.6:1 to 2.9:1; and suggested that higher the ratio, the greater the contribution of additive gene action for forage yield in tall fescue. To understand the role of gene effects on the tillering rate in wheat, Katata et al. (1976) crossed a number of cultivars to several testers and observed significant additive genetic variation in one of the two experiments he conducted. Similarly, Edwards et al. (1976) used generation means analysis to demonstrate significant additive effects for final tiller number in one of two crosses. Sleper et al. (1977) found that additive gene action was important in controlling number of tillers/plant and suggested this trait can be improved with mass selection. Sacks et al. (2006) reported that rhizome presence and expression were positively associated with percent survival and vigor and specific combining ability was significant for rhizomes, percent survival and yield in *Oryza sativa*/*O. longistaminata* population.

Breeding of cross-pollinating, perennial forage grasses is generally focused on the development of superior synthetic cultivars and improved heterogeneous populations. In order to select clones for a synthetic variety, information on the individual general combining ability (GCAi) and the value of the selfed progeny (Vi) are desirable (De Araujo and Coulman, 2002).

Heritability

The heritability is associated with the relative importance of heredity and of environment on the variations in a character (Kempthorne and Tandon, 1953).). Heritability is the proportion of genetic variation inherited from the parents to the progenies for a quantitative trait (Poehlman and Sleper, 1995The environmental influence would be more in case of parents-offspring resemblance method (Kempthorne and Tandon, 1953). The variance calculated from the variation in quantitative trait constitutes the phenotypic variance Vp. The phenotypic variance is divided into three components: genetic variance Vg, environmental variance Ve, and variance due to interaction between genotype and environment Vge. The genetic variance is comprised of additive, dominance and epistatic variance.

The partition of the phenotypic variance was reported by Fisher (1918) by subdividing the hereditary variance into additive effects, dominant effects (allelic interactions) and epistatic effects (non-allelic interactions) respectively. Cockerham (1954) illustrated that the hereditary values are actually the phenotypic values which are averaged over all the loci in the entire environment.

Narrow sense heritability

Narrow sense heritability is estimated as the measure of the ratio of additive genetic variation to total phenotypic variation and it estimates only additive genetic variance (Poehlman and Sleper, 1995; Ngyuen and Sleper, 1982; Falconer, 1981). The higher performance of hybrids depends upon the extent of complementation between the favorable genes from both the parents and the resemblance between parents and offspring is largely determined by the additive gene effect. (Poehlman and Sleper, 1995).

The narrow sense heritability provides the measure of additive gene effects, responsible for the inheritance of the traits from the parents to the offspring (Poelhman and Sleper, 1995). The parent-progeny regression analysis is used to estimate narrow sense heritability where the means of half-sib progeny would be regressed against the mean of parents, and the regression coefficient is one-half of the narrow sense heritability (Fehr, 1987, Falconer, 1981, Poehlman and Sleper, 1995). Lush (1940) and Kneebone (1958) indicated that heritability estimates aid the breeder in planning efficient breeding programs. In cross pollinated crops, narrow sense heritability estimates h^2 = 2b, if offspring are regressed on the maternal parent.

In perennial forage grasses, additive genetic action has been reported to be the major force behind genetic variation in the agronomic traits (Breese and Hayward 1972, Burton 1989, Meyer and Funk 1989) and additive genetic variance is transmitted to the next generation more predictably than non-additive genetic variance (Hill, 1977).

Maternal effect and Reciprocal effect

A maternal effect is defined as the genotype of the mother contributing more to the phenotype of the progeny than expected for equal chromosomal contribution from both the parents (Roach and Wulff, 1988). A maternal effect is important in determining the genetic correlation and predicts the response to selection of the mean phenotype in the selection (Van Vleck, 1968; Robertson, 1977; Ponzoni and James, 1978; Kirkpatrick and Lande, 1989). Mitochondria, chloroplast, and other cytoplasmic factors which have physiological effects on the progeny growth and development are transmitted directly from the mother parent to the offspring (Whitehouse, 1973 and Grun, 1976). Janssen et al. (1988) described the maternal effect often as the "troublesome part" of the environmental variance and reduce the precision of the genetic estimates and response to selection.

In reciprocal crosses, same parents are used but their roles as maternal and paternal parents are reversed. The differences in the reciprocal crosses may be caused by the differences in the effect of the pollen parent, and/or interaction between the seed/pollen parent's genetic effects with the nuclear component of the progeny (Gonzalo et al., 2007). The cause of reciprocal effects can be estimated with advancement in understanding epigenetic effects in plants. The imprinting of reciprocal effects could be an environmental influence as described by Mann et al. (1981), and Melchinger et al. (1985) that reciprocal effects were not consistent across the environments.

Normalized Difference Vegetation Index (NDVI)

Multispectral radiometer (MSR) has been used as an alternative to evaluate the turfgrass quality by measuring the reflectance of turfgrasses in the visible and near infrared part of the spectrum (Bremer et al., 2011). MSR recorded values at different wavelengths were used to calculate different vegetative indices. The NDVI ratio is calculated with measurements of reflected light from red and NIR band (Raun et al., 2001; Flowers et al., 2001). Healthy green vegetation reflects about 60% in NIR region (0.7-1.3 μm) and reflects 20% or less in green-red (0.5 to 0.7 μm) region of the spectrum. (http://www47.homepage.villanova.edu/guillaume.turcotte/studentprojects/arboretum/NDVI.htm)

The reflectance spectrum of the green canopy ranges from 0.4 to 0.7 µm in visible wavelength region and 0.7 to 1.3 µm in near infra-red region (Meyers, 1983). The reflectance in the region of visible and infra-red region is related to a variety of parameters of plant canopy determining the growth and development of plants such as biomass, leaf water content and chlorophyll content (Tucker, 1979), plant growth stage and leaf area (Wiegand et al., 1979; Leamer et al., 1980), and moisture stress (Dale et al., 1982), leaf structure and internal constituents (Gausman et al., 1970) and intercepted photosynthetically active radiation (Hartfield et al. 1984; Wiegand and Richardson, 1987). Chlorophyll absorbs the red light (0.66 µm) of radiation and reflects the near infrared light (0.85 µm) because of the cellular structure particularly spongy mesophyll of the leaves and leaf water content (Woods et al., 1999). Plant reflectance is determined by the leaf surface characteristics, biochemical content and internal structures of the plant. Therefore the reflectance techniques can be utilized to assess the biomass and physiological conditions of the plants (Penuelas and Filella, 1998).

Lukina et al. (2000) reported high correlation between NDVI and vegetative ground cover in winter wheat. Phillip et al. (2004) found a consistent correlation between tiller density and NIR digital analysis over different fields and years and reported that NIR digital counts were highly correlated ($r = 0.88$) with tiller densities (low and high) over different environments. The use of spectral reflectance techniques may provide an alternative method to evaluate the tiller density as counting tillers by hand is tedious and time consuming. This technique could be an easier way to determine the growth, reduce the labor intensity and evaluate the tiller density accurately than manual tiller counts (Phillip et al., 2004; Flower et al., 2001).

Endophyte

High numbers of tillers per plant were reported in endophyte-infected plants of tall fescue (*Lolium arundinacea*) under optimal conditions (Clay, 1987, and De Battista et al., 1990) and perennial ryegrass (*Lolium perenne*) (Latch et al. 1985; Clay 1987; Eerens et al. 1998; Cheplick 2008) as compared to the ones without endophytes. Clay (1987) reported that limited numbers of tillers were produced when the endophyte-infected plants were cultivated under low light.

A negative effect of endophyte infection in tall fescue was reported by Assuero et al. (2000) that tiller number was reduced in two different types of tall fescue cultivars (Mediterranean type and Continental type cultivars) which were artificially infected with two fungal strains of *Neotymphodium coenophialum*. The tillering of E+ Mediterranean cultivar was less than E+ Continental type cultivar. Hill et al. (1990) reported that the differences in tiller production were found with respect to the presence and absence of endophyte infection among tall fescue accessions.

I hypothesize that increased rhizome formation and tillering rate in tall fescue may allow tall fescue to spread faster and cover more ground area, which may improve its traffic tolerance and utility in sod strength. Using efficient breeding methods based on the progeny testing will aid in the development of synthetic cultivars with significant rhizome formation and rapid tillering rate in tall fescue.

Goal of This Dissertation

This dissertation's objectives are the followings:

a) Determine the photoperiod and temperature effects on the rhizome formation and rapid tillering in tall fescue.

b) Identify the inheritance characteristics of rhizome formation, rapid tillering and ground coverage in tall fescue: narrow-sense heritability, and general and specific combing ability

c) Compare commercial cultivars and experimental breeding material for rhizome formation, rapid tillering and ground coverage in tall fescue

d) Correlate rhizome formation, rapid tillering and ground coverage characteristics and rapid tillering and NDVI in tall fescue.

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CHAPTER 1

Photoperiod and Temperature Effects on Rhizome Production and Tillering Rate in Tall Fescue

INTRODUCTION

Tall fescue (*Lolium arundinaceum* (Schreb.) Darby.), introduced into the United States in the 1800s as a forage grass (Hoveland, 2009), is now utilized as a turfgrass on home lawns, golf course roughs, sod farms and sports fields. Tall fescue is known for its wide adaptation to different environmental conditions in the transition zone and in the Pacific Northwest (Buckner and Bush, 1979; Templeton et al., 1961). Tall fescue is known as a bunch type grass (Buckman and Cowan, 1973) but the presence of rhizomes (Cowan, 1956; Porter, 1958) was also observed. Cowan (1956) and Porter (1958) reported the presence of short rhizomes in tall fescue and genetic variability for the trait in the 1950s. D'Uva et al. (1983) reported the rhizome formation in tall fescue may be the result of both genetic variability and genotype × environment interactions. Presence of rhizomes is beneficial as it has the potential to aid survival in temperature extremes and drought stress conditions, by serving as a storage organ for carbohydrates (Weaver, 1963; De Battista and Bouton, 1990). Rhizomes also assist in filling bare spots, allow close knitting of turfgrass plants in sods, fill the gaps, initiate new tillers between plants, and improve traffic tolerance (Bouton et al., 1992; Weaver, 1963). The knowledge about effects of temperature and photoperiod on rhizome formation and tillering rate may extend the utility of tall fescue to environments with more extreme temperatures or drought periods;

and in understanding the basic information required for tall fescue improvement and management.

The dynamics of tiller production contribute to the perennial life cycle of turfgrasses, though tillers are short lived and may survive from two or three weeks to sometimes up to a year (Robson, 1968). The ability to develop tillers rapidly allows turfgrass to spread laterally with continuous replacement, and cover more ground with uniform density and vigor. Friend (1965) suggested that tillering rate was influenced by environment and genetic factors in wheat (*Triticum aestivum* L.). An increase in temperature over the range of 10–25 ^{o}C increased the total number of leaves and tillers, but influenced the rate of leaf emergence more than tillering rate. Templeton et al. (1961) reported that the development of new tillers was most rapid in tall fescue when the mean weekly temperature ranged between 6 to 16 ^{o}C (March 12 until April 19, Lexington, KY). The rate of tillering decreased and remained low until the end of the experiment in June. Tiller number increased under low temperature and short photoperiod (9 h). Less tillering occurred when tall fescue plants were subjected to extended long photoperiod treatment (16 to17 h) than the short period (9 h) in the greenhouse (Templeton et al., 1961). They also observed more tillers when tall fescue plants were exposed to 7.2 ^{o}C compared to 22.2 ^{o}C.

Rhizome formation may require different temperature and photoperiod conditions than tiller production. For example, Moser et al. (1968) observed that the development of rhizomes was significantly higher under the long photoperiod (18 h) and tiller production was lower under long photoperiod (18 h) than under short photoperiod (12 h). Cold treatment (0 to 2 ^{o}C) increased tiller development but reduced rhizome formation as more crown buds differentiated into tillers and lesser into rhizomes. Evans (1949) reported that rhizome development occurred during the longest photoperiod of the year under field conditions in Kentucky bluegrass (*Poa pratensis*). Evans and Watkins (1939) reported that under short photoperiod conditions, tillering rate is favored over the rhizome formation in Kentucky bluegrass. In tall fescue, De Battista and Bouton (1990) reported rhizome formation increased with the age of the plant and development of rhizomes enhanced after one year or more under field conditions. This was supported by another experiment conducted in the greenhouse where plants produced a significant number of rhizomes at seven to 11 months of age or more. Cowan (1956) reported the aggressive rhizome formation in some tall fescue plants spread up to 0.3 m per year. The timing of rhizome formation may vary by grass species and occurs at different times of year. Evans and Ely (1935) reported the highest rhizome formation in Kentucky bluegrass and Canada bluegrass *(Poa compressa*) during June to August and August to early September, respectively.

The commercially available tall fescue cultivars vary in tillering rate and/or rhizome formation. Rhizomatous tall fescue cultivars are available in the market such as Turbo Rz (http://www.burlinghamseeds.com/grass-seeds/tall-fescues), Cezanne Rz (http://www.lebanonturf.com/products/items/5866903/index.aspx), Rhambler SRP (http://www.turfmerchants.com/turf_type_tall_fescue/rhambler-srp.php), Grande II (http://www.sroseed.com/Products/PDF/grande_II_ts.pdf) and Regiment II (http://www.sroseed.com/Products/PDF/regiment_II_ts.pdf). The rhizomatous cultivars are marketed as exhibiting high rhizome formation, increased ground coverage, dark green color, fine texture, drought tolerance and self-repair (Rodney et al., 2009, http://www.rtfsod.com). Understanding the interactive effects of temperature and photoperiod on the initiation and development of rhizomes and tillering rate in tall fescue would enhance tall fescue improvement and help in the development of new cultivars for different regions. The objectives of the present study were to assess the influence of photoperiod and temperature on rhizome formation and tillering rate in tall fescue.

MATERIALS AND METHODS

Five genotypes of tall fescue: 1109 and 9291 (rapid tillering types), 1367 (rhizome type) 1579 and 5070 (intermediate type: both rapid tillering and rhizome type) were selected based on the presence and absence of rhizomes and/or rapid tillering rate. The genotypes were selected from the germplasm collection, maintained by the Rutgers turfgrass breeding program at the New Jersey Agriculture Experiment Station (NJAES). Four vegetative replicates of each genotype were grown for three months from single tillers in a greenhouse at which time they were planted into 7.7 cm^2 pots (Kord Production, Toronto, Canada) containing Promix soil-less media (Premier Pro-mix BX, Premium Tech Horticulture, Quakertown, PA, USA). The pots were kept in a greenhouse (average day time temperature: 20 ^oC and night temperature: 15.5 ^oC; light duration 10 hours and light intensity ranges from 377 to 550 µmol m^{-2} s^{-1}) for four weeks prior to initiating the experiment in the growth chambers.

The experimental design was a randomized complete block design. Four growth chambers at the NJAES (New Jersey Agricultural Experiment Station, New Brunswick, NJ), were used for the experiment. The trial was conducted for three months and repeated twice; the growth chambers were randomized in the second trial. Each growth chamber had different combinations of photoperiod and temperature: i) long day photoperiod (18 h) and low temperature (day/night 15/10 ^{o}C) (LL), ii) long day photoperiod (18 h) and high temperature (day/night 25/15 ^{o}C) (LH), iii) short day photoperiod (9 h) and low temperature (day/night 15/10 ^{o}C) (SL), and iv) short day photoperiod (9 h) and high temperature (day/night 25/15 ^{o}C) (SH). The photosynthetic-active radiation level in all chambers was maintained at 450 µmol m^{-2} s^{-1}. The four treatments were assigned in four different growth chambers each containing four replicates (four pots) of each genotype. The pots were fertilized with 20:20:20 (N: P: K) fertilizer after every two weeks at 0.448 gm^{-2} and watered every day or when required. The cutting height was maintained at 6 cm.

The number of rhizomes per plant, number of tillers per plant and number of aerial tillers per rhizome were counted at the end of the experiment after keeping the pots in the growth chambers for three months, to evaluate the effect of treatments, genotypes and interaction between genotypes and treatments on rhizome formation and tillering rate. The rhizomes counted were >1 cm in length away from the mother plant. The number of aerial tillers from the rhizomes was also counted at the end of the experiment.

All data were analyzed using analysis of variance by the PROC GLM procedure of SAS (SAS Institute, 2012) (Table 2 and 3) and means separation was calculated based on Fisher's LSD.

RESULTS

Significant differences in the tillering rate and rhizome formation were observed between the genotypes (Table 1 and 2). Results from the analysis of variance indicated significant treatment effect for both tillering rate and rhizome formation, but significant genotype x treatment interaction for tillering rate only. The data is presented combined over both the trials since there were no significant differences between trials.

Effects of temperature and photoperiod on rhizome and tiller formation

Low temperature treatments significantly increased the number of tillers per plant over all the genotypes. The most tillers per plant were observed in the short photoperiod with low temperature (SL) treatment, followed by long photoperiod with low temperature (LL) treatment (Fig. 1). The greatest increase in the rhizome formation was observed under the long photoperiod treatments (18 h) regardless of temperatures (LL and LH) overall the genotypes (Fig. 3).

Genotypic variations in rhizome and tiller formation

The highest number of tillers per plant was observed in the genotype 1109 (Fig. 1 and 2). This genotype was significantly higher than all other genotypes. There were no significant differences in tiller number between the other genotypes (Fig. 1). Genotype 1367 produced the least number of tillers per plant but had the highest number of rhizomes per plant (Fig. 3 and 4). Genotype 1579 had the next highest number of rhizomes per plant followed by 5070 (Fig. 3 and 5) which was not different from the other two genotypes (9291 and 1109).

Effects of interaction between genotypes x treatments on the number of tillers

The short photoperiod and low temperature (SL) treatment exhibited a higher tillering than other treatments, and all genotypes produced maximum number of tillers per plant in SL treatment considering their genotypic differences. Genotype 1109 produced highest number of tillers per plant among all the genotypes over all the treatments. Genotype

1367 and 5070 produced least number of tillers under SH treatment and genotypes 9291 and 1579 produced least number of rhizomes under LH treatment.

Genotypic variations in the number of aerial tillers produced from rhizome

The maximum number of aerial tillers per rhizomes was found in the genotypes 5070 and 1579 over all the treatments (Fig. 5 and 6). Genotype 1367 produced the greatest number of rhizomes but didn't produce the highest number of aerial tillers per rhizome. Similarly, genotype 1109 produced maximum number of tillers per plant but the least number of aerial tillers per rhizome.

DISCUSSION

The results from this growth chamber experiment indicate that long photoperiod and low temperature influenced rhizome formation and tiller production in tall fescue, respectively. The low temperature (15/10 ^{o}C) in combination with short photoperiod (9 h) greatly increased the tillering rate in tall fescue. Similar results were obtained by Templeton et al. (1961) in tall fescue who found the highest number of tillers when tall fescue plants were exposed to weekly mean low temperature (6-16 ^{o}C) during short photoperiod (9 h). In the current experiment, low temperature with long photoperiod also showed significant increase in the number of tiller per plants. Genotype 1109 exhibited the greatest number of tillers per plant over all the treatments. The pots were completely filled with the tillers by the end of the experiment as compared to the other genotypes, suggesting that genotype 1109 has a rapid tillering rate (Fig. 1 and 2). Assuero and Tognetti (2010) suggested that tiller production is almost always associated with environmental conditions favoring carbon assimilation such as low temperature, high

Red: Far Red light ratio, high nitrogen availability and high light intensity. Pinthus and Meiri (1979) also reported an increase in tillering rate and tiller development in wheat (*Triticum aestivum*) when plants were grown under 12 h photoperiod and 10/18 ^{o}C (day/night) temperature regime.

Genotype 1367 exhibited the greatest number of rhizomes per plant (Fig. 3 and 4) followed by genotype 1579 (Fig. 6). Numbers of rhizomes per plant were highest under the treatments of long photoperiod regardless of temperature indicating that photoperiod has a greater influence on rhizome formation than temperature. These results agreed with the results obtained by Moser et al. (1968) that rhizome initiation and formation were favored by 18 h photoperiod in Kentucky bluegrass.

Based on these results of tall fescue genotypes we can suggest that there are significant genetic differences among genotypes of tall fescue and that they may be used to categorize tall fescue into rapid tillering types (genotypes 1109 and 9291); rhizomatous types (genotype 1367) and intermediate types (genotypes 1579 and 5070), respectively. We can also conclude that low temperature (day/night - 15/10 ^{o}C) favored tiller production and long photoperiod (18 h) favored rhizome production in tall fescue. Maximum rhizome formation and highest tillering rate were not observed in the same genotypes, which could partly be due to the differential carbohydrate allocation between tillers and rhizomes. The synthesized carbohydrates could be utilized either in tiller production or in rhizome formation and/or stored in rhizomes depending upon the environmental conditions and genotype. Pollock (1990) suggested that low temperature favored carbon assimilate availability to the tillers in wheat and genotypic variation caused the variation in the availability of carbon assimilation among the plants. Brown

(1943) reported that autumn favors the carbohydrate accumulation in rhizomes and roots and the rapid storage occurs after mid-October when topical growth ceased in Kentucky bluegrass. The determination of carbohydrate allocation and dry weight analysis in these genotypes would help in understanding more about the initiation and development of rhizomes and rapid tiller production in tall fescue.

In summary, genotypes of tall fescue with different growth habits may extend the utility of species in different regions, depending upon the local environmental conditions. Genotypes with rapid tillering rate such as 1109 and 9291 can perform better in the cool temperature regions, and genotype 1367 may produce higher number of rhizomes and help the turf in extreme temperature conditions in the warm and long daylength regions of United States. The genotypes with intermediate growth habit such as 1579 and 5070 may be types to be grown in wide range of temperature and photoperiod regions. Based on the understanding of the different tall fescue growth habits, it might be helpful in determining types of tall fescue to be grown in different environmental conditions.

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Table 1.1: Analysis of variance of tillering in genotypes of tall fescue as affected by photoperiod and temperature evaluated in a growth chamber for three months.

Source of Variation	df	Mean Square	F Value	Pr > F
Genotype	4	5532.31	21.93	<0.0001
Treatment	3	12442.23	49.32	<0.0001
Replication	3	874.39	3.36	0.0229
Trial	1	180.76	0.72	0.3998
Genotype x Treatment	12	663.04	2.63	0.0053
Replication x Treatment	9	140.37	0.56	0.8283
Genotype x Replication	12	252.41	1.00	0.4565
Genotype x Treatment x Replication	36	141.03	0.56	0.9723
Error	78	252.25		

Table 1.2: Analysis of variance of rhizome formation in genotypes of tall fescue as affected by photoperiod and temperature evaluated in a growth chamber for three months.

Source of Variation	df	Mean Square	F Value	Pr > F
Genotype	4	60.51	14.84	<0.0001
Treatment	3	24.81	6.09	0.0009
Replication	3	1.60	0.39	0.7588
Trial	1	4.90	1.20	0.2763
Genotype x Treatment	12	4.70	1.15	0.3312
Replication x Treatment	9	0.75	0.18	0.9953
Genotype x Replication	12	2.15	0.53	0.9819
Genotype x Treatment x Replication	36	1.61	0.39	0.9616
Error	78	4.07		

Figure 1.1: Fig1: The effect of photoperiod and temperature on tillering rate of five genotypes of tall fescue grown for three months in a growth chamber. Means followed by the same letter are not significantly different at 0.05 probability level using Fisher's protected Least Significant Difference means separation test.

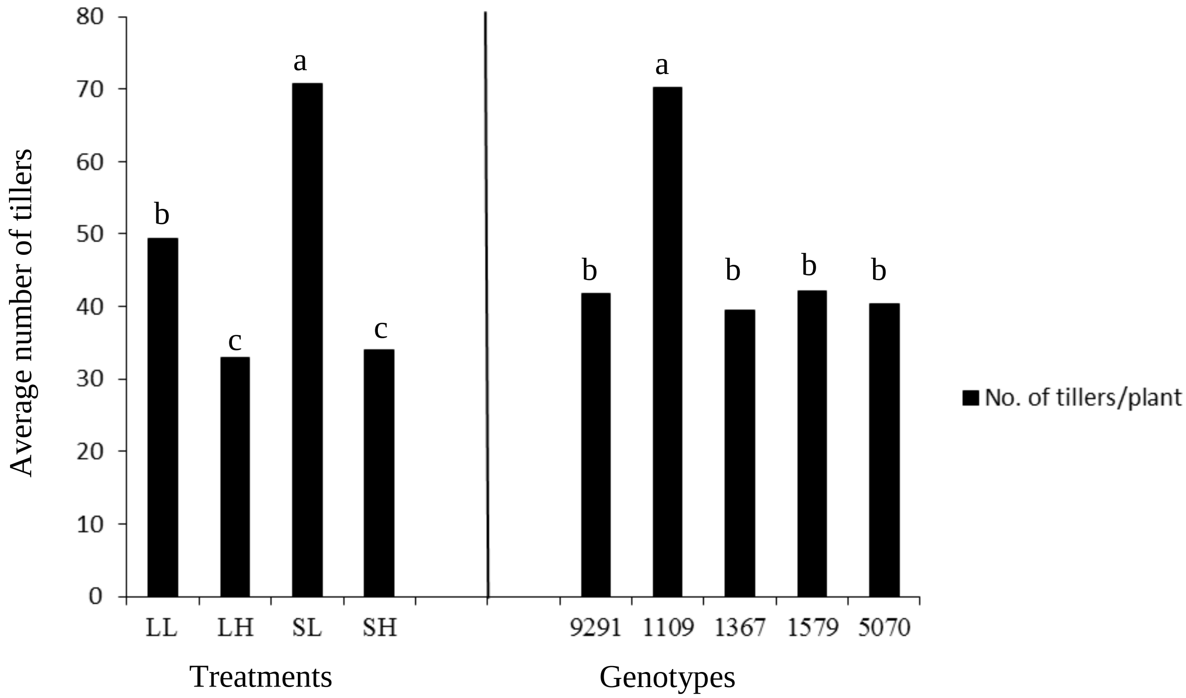

Figure 1.2: Genotype 1109 with high tillering rate under the treatment of low temperature and short photoperiod (SL).

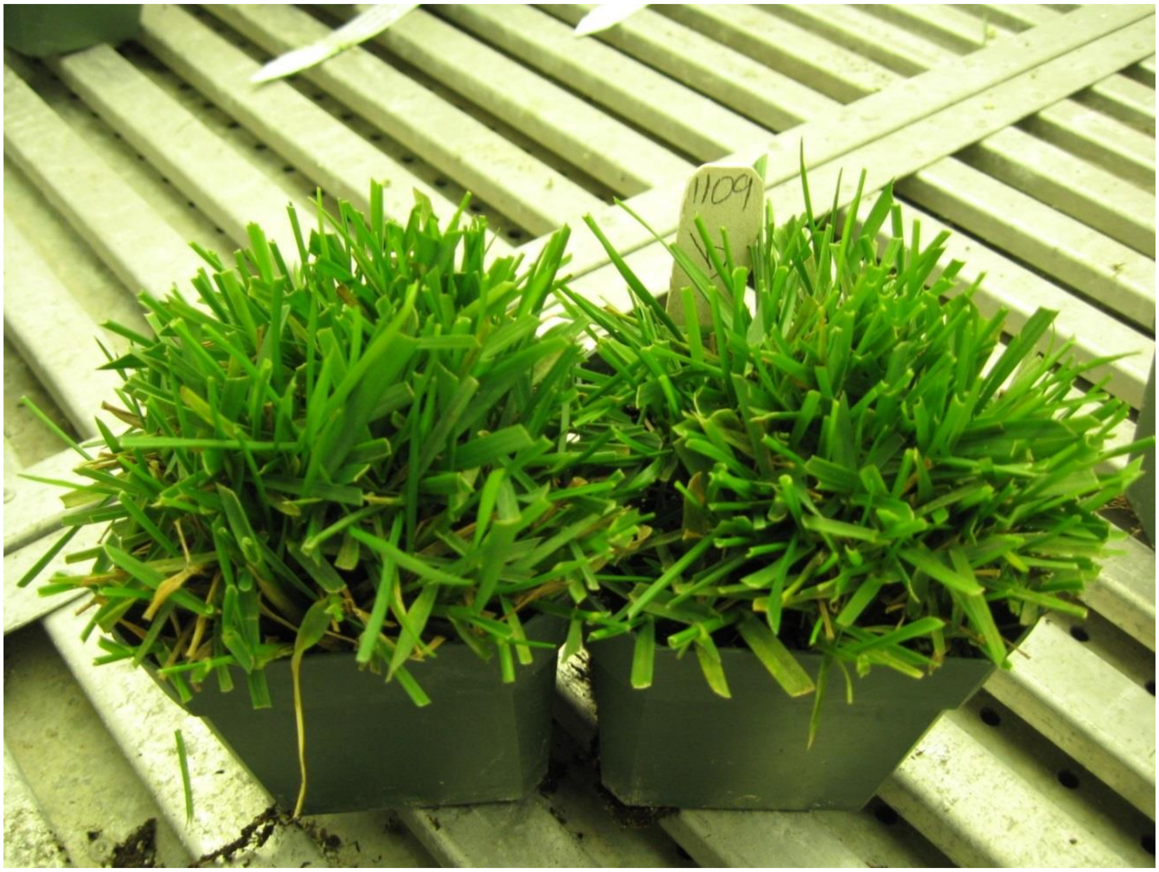

Figure 1.3: The effect of photoperiod and temperature on rhizome formation of five genotypes of tall fescue grown for three months in a growth chamber. Means followed by the same letter are not significantly different at 0.05 probability level using Fisher's protected Least Significant Difference means separation test.

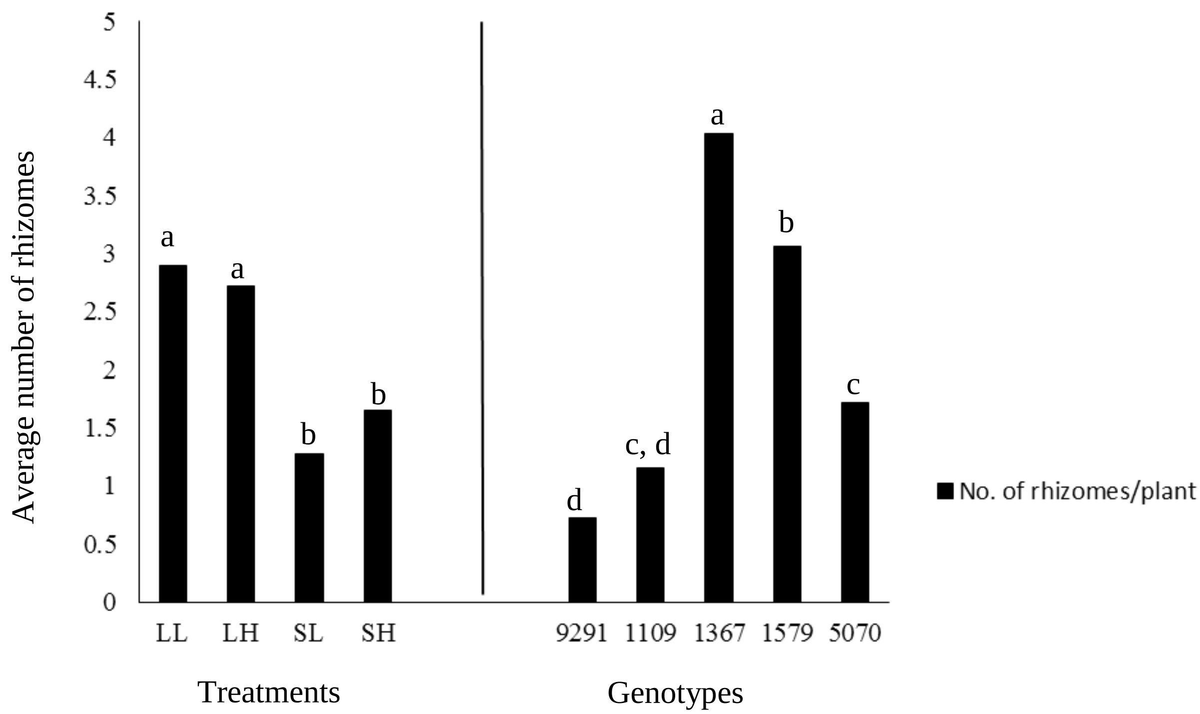

Figure 1.4: Genotype 1367 with rhizome under the treatment of long photoperiod and high temperature (LH).

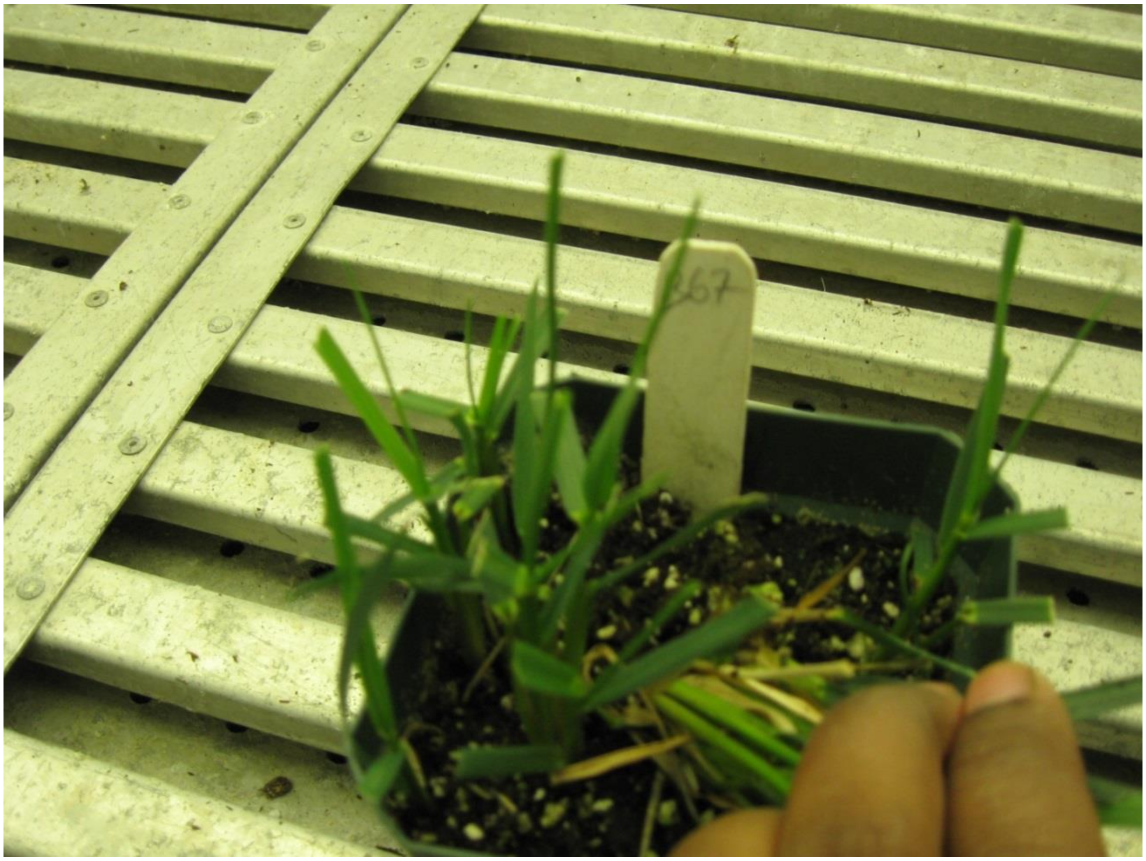

Figure 1.5: The number of aerial tillers per rhizome averaged over photoperiod and temperature treatments in four genotypes of tall fescue growth for three months in a growth chamber. Means followed by the same letter are not significantly different at 0.05 probability level using Fisher's protected Least Significant Difference means separation test.

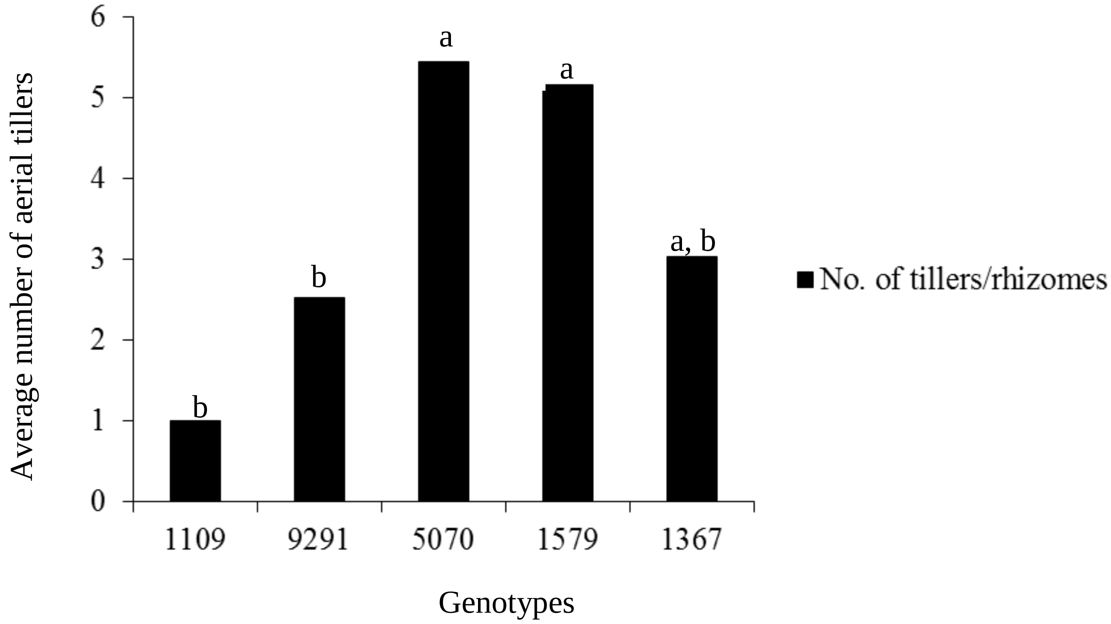

Figure 1.6: The rhizome formation and aerial tillers shown by the genotype 1579 under the treatment of long photoperiod and low temperature (LL).

CHAPTER 2

Genetic Control of Rhizome Formation and Rapid Tillering Rate in Tall Fescue

INTRODUCTION

Diallel mating system allows crossing of genotypes in all possible combinations including reciprocals and provides an advantage to evaluate parents based on the progeny testing (Poehlman and Sleper, 1995). Hopkins et al. (2009) reported that use of progeny testing would increase the probability of identifying the superior parents for desirable traits. The progeny test is use to estimate general combining abilities and specific combining abilities of the parents (Griffing, 1956). A diallel cross analysis following the statistical methods presented by Griffing (19956) allows for the estimation of both the GCA and SCA. These combining ability estimates can be used to determine the relative importance of the additive vs. non-additive gene effects influencing brown patch resistance in tall fescue as well as identifying potential parents that can contribute in resistance, if incorporated in tall fescue and found that additive gene effects directly influenced the number of tillers per plant, total yield per plant and yield per tiller.

Tall fescue has gained increased attention as a turf type after the release of first commercial turf type tall fescue cultivar “Rebel” in 1980 (Funk et al., 1982). Since then consistent efforts are continued to improve tall fescue for disease and insect resistance, drought tolerance, turf quality, turf density, growth habit, through cycles of selection and hybridization (Morris, 2006; Saxena et al., 2011). Tall fescue is categorized into two major gene pools: Continental type and Mediterranean type (Hopkins et al., 2009). The third “Rhizomatous” type, originated from northwest Spain and Portugal (Borrill et al.,

1971) and produce rhizomes. de Brujin (2004) reported that rhizomatous tall fescue originated from Iberian Peninsula have more prevalent and extensive rhizomes.

Although tall fescue is commonly known as a bunch type which grows primarily with vertical tillers and has limited spreading ability (Buckman and Cowan, 1973), rhizomes have been reported to produce short rhizomes in tall fescue (Cowan, 1956; Porter, 1958) which grow underground horizontally, and bear nodes and internodes (De Battista and Bouton, 1990). Rhizomes functions to store carbohydrates, enhance competitiveness and persistence under temperature extremes and drought conditions (Evans and Ely, 1935; Weaver, 1963 and De Battista and Bouton, 1990), re-establish damage areas (Brilman, 1998), and survived better under the competition with Bermudagrass as compared to non or weakly rhizomatous genotypes (Bouton et al. 1989).

Whitehead et al. (1986) showed that rhizome formation was moderately heritable and additive genetic variance was significant and suggested that recurrent selection could be effective for improving the trait. Nguyen et al. (1980) reported significant entry (synthetics/cultivars) x environment interactions occurred for the vegetative and reproductive growth in tall fescue. Sleper et al. (1977) found that additive gene action was important in controlling the number of tillers per plant and suggested this trait can be improved with mass selection. The recurrent selection method is useful in improving the traits with low to moderate heritability and also to aggregate the favorable alleles in a population (Bouton et al., 1992). Most of the tall fescue cultivars developed after 1980s were from the recurrent selection method (Bouton, 1992) based on the proportion of the additive gene effects.

The rapid tillering trait could enhance the lateral spread in tall fescue while maintaining the uniform density. Tillers in contrast to rhizomes are the above ground stems that develop within the leaf sheath of adjacent tillers and/or arise below ground from the coleoptilar node (Rebetzke et al., 2008); they have shorter internodes than rhizomes (De Battista and Bouton, 1990). The formation of rhizomes and tillers in tall fescue are anatomically and morphologically similar to rhizomes and tillers in Kentucky bluegrass (De Battista and Bouton, 1990). High tiller density is one of the important characteristics of turfgrasses necessary for smooth ball roll and to resist weed infestation (Cattani and Struik, 2001). Friend (1965) suggested that tillering rate was influenced by environment and genetic factors in wheat (*Triticum aestivum* L.). To understand the role of gene effects on the tillering rate in wheat, Katata et al. (1976) reported significant additive genetic variation for tillering rate in wheat, when a number of cultivars were crossed with several testers. Similarly, Edwards et al. (1976) used generation means analysis in winter wheat to demonstrate significant additive effects for final tiller number in one of two crosses. G × E interaction was not addressed in any of the studies for the tillering rate. Benbelkacem et al. (1984) studied tillering rate in oats (*Avena sativa*) and stated that backcrossing and selection would be useful to develop promising high tillering lines. Tiller number was found to be controlled by quantitative traits which were mainly additive as compare to dominant and epistatic effects (Tang et al., 2001). Kashif and Khaliq (2003) reported that the mean square of GCA (general combining ability) was highly significant and was greater than SCA (specific combining ability) for number of tiller per plant in wheat.

Heritability is the proportion of genetic variation inherited from the parents to the progenies for a quantitative trait (Poehlman and Sleper, 1995). The resemblance between parents and offspring is largely determined by the additive gene effect (Poehlman and Sleper, 1995). Narrow sense heritability is estimated as the ratio of additive genetic variation to total phenotypic variation and it estimates only additive genetic variance (Poehlman and Sleper, 1995; Ngyuen and Sleper, 1982; Falconer, 1981). Additive gene effects are of major importance in selection of the superior genotypes because it contributes a greater extent to the genetic variation useful for breeding than other gene effects (Hopkins et al., 2009). The higher performance of hybrids depends upon the extent of complementation between the favorable genes from both the parents (Poehlman and Sleper, 1995).

Narrow sense heritability estimates for rhizome formation in tall fescue were low (0.38) on an individual plant basis and were high (0.88) using parent-progeny regression analysis (Bouton et al., 1992). Whitehead (1986) reported that narrow sense heritability estimates for the number of rhizomes per plant were very low on the individual plant basis (h^2 = 0.12) and on an entry-mean basis (h^2 = 0.31) in tall fescue. Sleper et al. (1977) reported low narrow sense heritability for number of tillers per plant in tall fescue and suggest that the number of tillers per plant in tall fescue can be improved by mass selection method.

Sprague and Tatum (1914) introduced the concept of general combining ability (GCA) and specific combining ability (SCA). GCA was defined as the average performance of a line in a hybrid combination and SCA was defined as the deviation of the individual cross from the average over all crosses (Hallauer and Miranda, 1981). SCA and GCA estimates the non-additive and additive components of the parent's genotypic variance, respectively (Griffing, 1956). Sprague and Tatum (1942) refer to specific combining ability (SCA) as the certain combinations perform better or worse than would be expected as compare to their average performances. Low SCA estimate indicates the average performance of the combinations is lower than would be expected based on their general combining ability. Higher value of SCA estimates indicates the better performance of the specific combination than expected based on GCA (Sprague and Tatum, 1942). The low GCA estimates indicates that a particular line is average in its performance compared to other lines and a higher value of GCA indicates that a particular line is much better than the other parental lines with which it is compared.

Akram et al. (2007) estimated the general and specific combining abilities for the number of tillers per plant, panicle length, panicle sterility and yield per plant in rice *(Oryza sativa)* and reported that additive gene effects were highest for tillering rate. Contrarily, Muehlbauer et al. (1971) reported that non-additive genetic variance was more significant than additive genetic variance for plant height and tiller number in a three parent diallel cross in oats and found significant specific combining ability effects were significant whereas general combining ability was not.

Frakes and Matheson (1973) reported that general combining ability was significantly higher than specific combining ability for forage yield in tall fescue based on the ratio of the mean squares of GCA to SCA which varied from 25.6:1 to 2.9:1; and suggested that the higher the ratio, the greater the contribution of additive gene action for forage yield in tall fescue.

Maternal effects, defined as the contribution of the mother genotype to the phenotype of the progeny is more than expected from equal chromosomal contribution from both the parents (Roach and Wulff, 1988). Mitochondria, chloroplast, and other cytoplasmic factors are maternal effects which have physiological effects on progeny growth and development and are transmitted directly from the mother parent to the offspring (Whitehouse, 1973; Grun, 1976). Janssen et al. (1988) described maternal effects as the "troublesome part" of the environmental variance and reduce the precision of the genetic estimates and response to selection.

In reciprocal crosses, the same parents are used but their roles as maternal and paternal parents are reversed. The differences in the reciprocal crosses may be caused by the differences in the effect of the pollen parent, and/or interaction between the seed/pollen parent's genetic effects with the nuclear component of the progeny (Gonzalo et al., 2007). The imprinting of reciprocal effects could be environmental influence, however Mann et al. (1981), and Melchinger et al. (1985) reported that reciprocal effects were not consistent across the environments. Maternal effects have not been reported to influence the tillering rate and rhizome formation in tall fescue; therefore, it is important to understand the contribution of maternal effect in the inheritance of these traits.

Multispectral radiometer (MSR) has been used as an alternative to evaluate the turfgrass quality by measuring the reflectance of turfgrasses in the visible and near infrared part of the spectrum (Bremer et al., 2011). MSR recorded values at different wavelength were used to calculate different vegetative indices. The NDVI ratio is calculated with measurements of reflected light from red and NIR band (Raun et al., 2001; Flowers et al., 2001). Phillip et al. (2004) illustrated consistent correlation between tiller density and NIR digital counts over different fields and years in wheat. The research was conducted over different fields and tillering densities: low tiller density and high tiller density and found that NIR digital counts were highly correlated (r = 0.88) over different environments. Phillip et al. (2004) and Flower et al. (2001) mentioned that the use of spectral reflectance techniques may provide an alternative method to evaluate the tiller density as counting tillers by hands is tedious and time consuming. This technique could be an easier way to determine the growth, reduce the labor intensity and evaluate the tiller density accurately.

The variation in growth habits of tall fescue has been widely known since the rhizome formation was first reported in the 1950s'. To evaluate the inheritance and differences in growth habits of tall fescue, the present investigation was conducted. The objective of this study were (i) to estimate the narrow sense heritability of six tall fescue parents for rapid tillering rate, rhizome formation and ground coverage, (ii) to estimate the combining ability of the six parents for rapid tillering, rhizome formation and ground coverage, (iii) correlation between rapid tillering and NDVI.

MATERIALS AND METHODS

Six tall fescue genotypes were selected in summer 2009 based on their growth habits: Bunch type: B1, B2; Rhizome type: R1, R2; and Rapid tillering type: T1, T2. Bunch type refers to the lines/genotypes producing more vertical tillers and limited lateral spread; rhizome type refers to the lines/genotypes producing rhizomes; and rapid tillering type refers to the lines which produce more lateral tillers and cover more ground surface than bunch types. All the selected genotypes were endophyte positive containing strain of

Neotymphodium. These parents were selected from the germplasm collected and maintained in the Rutgers turfgrass breeding program and have undergone numerous cycles of selection and hybridization to improve quality. Each parent plant was clonally propagated and planted in the field in September 2009. The parents received the cold temperature treatment required for flower induction during winter. In spring 2010, parent clones were brought into the greenhouse and were subjected to 18 hour daylengths to provide the long photoperiod treatment for flowering induction. The parent clones were matched together and isolated from all other controlled crosses before anthesis began. Isolation was made by using plastic partitions placed around each pair of parents. Both parents in each cross were used as male and female parents and pollen transfer was facilitated by manual tapping of the turfgrass plants. Few inflorescences from each parent were covered with white paper bags to determine if any self-pollination occurred. The seeds harvested from those inflorescences did not produce any viable seeds. The seeds were harvested from each parent from the controlled crosses and dried and sown into seed trays and placed in a cold dark room to break the seed dormancy. One hundred seedlings were randomly selected from each parent, transplanted to single cell trays filled with potting Promix soil-less media (Premier Pro-mix BX, Premium Tech Horticulture, Quakertown, PA, USA) and kept in the green house before establishing the field trial.

The field experiment was designed and established at Rutgers, Plant Biology Research and Extension Farm, Freehold, NJ. The soil type of the field was a Freehold sandy-loam (fine-loamy, mixed, active, mesic Aquic Hapludult) and progenies were planted along with vegetative replicates of each parent in a randomized complete block design on October 20th, 2010. The experimental design was composed of four replications and each replication contained 24 individual plants from each cross, planted in two rows at the spacing of 0.46 meters along with the three clones of each parent in each replication. The plants were mowed with a Toro Groundmaster (Toro Corp. Bloomington, MN) twice a week during the growing season at the height of 6 cm. In 2011 and 2012, the application of 9-0-18 (N: P: K) fertilizer was done during the months of May, October and April respectively, at the rate of 0.4 g N m^{-2}. Brown patch was controlled by spraying Heritage (Azoxystrobin), as labeled. Annual weeds were controlled with Acclaim (fenoxaprop-p-ethyl) as labeled and broad leaf weeds by spraying 2,4 D and Banvel 3,6-dichloro-o-anisic acid) @ 32 oz. acre and 8 oz/ acre, respectively.

A diallel mating design was deployed to assess the inheritance patterns for rapid tillering, rhizome formation and ground coverage in tall fescue. The diallel design involved intercrossing the selected genotypes in all possible combinations: n (n-1), where n is number of the parents. The combinations that resulted comprised of reciprocals crosses to estimate the genetic variances (Poehlman and Sleper, 1995). In the current experiment the total numbers of crosses obtained for diallel were 30 (including 15 reciprocals).

The data was collected for rapid tillering (number of tillers per 7.62 cm plug size), rhizome formation (number of rhizomes per plant) and ground coverage (average of length (cm) and breadth (cm)) on each individual plant. The tiller counting was done at the end of the trial in September 2012 because it destructed plants by cutting a 7.62 cm size plugs out from each plant. The rhizomes were counted in the field on intact plants in May, 2012 and only the ones which were ≥2 cm apart from the mother plant were counted. Ground coverage was calculated by measuring the length (cm) and breadth (cm) and averaged on each individual plant in May 2011 and May 2012. The data was analyzed for ground coverage using combined average across both years (2011-2012).

To evaluate NDVI, a TCM 500 Turf Color Meter was used in this experiment. The TCM500 meter was mounted on the wooden structure at the height of 10 cm to capture the spectral reflectance of different wavelengths in 5 cm region of the plant. This equipment works effectively under the sun light and do not require additional light source. The data was collected in full sun days in June, 2012. The data was collected on the individual plant and then transferred into the computer installed with Field Scout software to download the data. The values from Red and NIR wavelengths were used to measure the NDVI. The data collected for rapid tillering from each individual plant and averaged for each cross was used in the analysis.

All data were analyzed using analysis of variance by the PROC GLM procedure of SAS (SAS Institute, 2012) and means separation was calculated based on Fisher's LSD.

Statistical Analysis

All data analysis was conducted using combined averages across all the four replications. The combining ability analysis was done based on the method 3 (one set of parents and reciprocals) and model 1 (fixed effect) (Griffing, 1956)

$$X_{ijk} = \mathrm{u} + g_i + g_j + S_{ij} + r_{ij} + 1/bc\sum\sum e_{iikl} \qquad \text{eq. (i)}$$

Where:

$i,j = 1,\ldots\ldots,p$; $k = 1,\ldots\ldots., b$; $l = 1, \ldots.., c$.

X_{ijk} = observed rhizome formation and tillering rate of *ij*-th cross in the *k*-th block, u = population mean, g_i = GCA effect of the *i*-th parent, g_j = GCA effect of the *j*-th parent, s_{ij} = specific combining ability (SCA) effect for *ij*-th cross, r_{ij} = reciprocal genotypic effect such that $r_{ij} = -r_{ji}$ and e_{ijkl} = error effect peculiar to the $ijkl^{th}$ observation. The restrictions are $\sum g_i = 0$, $\sum_{i \neq j} sij = 0$ (for each j). Data was analyzed using DIALLEL-SAS05 (Zhang et al., 2005).

Narrow sense heritability was estimated based on data collected and averaged on each date. It was estimated by the mid parent-progeny regression analysis, where means of the F1 progeny will be regressed against the average of their two parents and slope of the regression line equals the narrow sense heritability (Poehlman and Sleper, 1995).

NDVI was calculated by measuring the reflected light from turf grass in the red (0.6 µm) and near infrared (0.85 µm) spectral bands through Field Scout TCM 500 “NDVI” Turf Color Meter (Spectrum Technologies, Inc., IL). Its value varies from -1.0 to + 1.0.

NDVI = NIR – Red / NIR + Red

(http://www47.homepage.villanova.edu/guillaume.turcotte/studentprojects/arboretum/NDVI.htm)

RESULTS

Rapid tillering (Number of tillers per 7.62 cm plug)

The mean squares of the analysis of variance are presented in Table 1 and 2. The analysis of variance showed significant genotypic and cross effects for rapid tillering in tall fescue (Table 1 and 3). The bunch type and rapid tillering type parents (B2 and T1) exhibited higher mean values for rapid tillering, respectively. The lower mean value for rapid tillering was shown by rhizome parents (R1 and R2) (Table 2). The full sibs obtained from the crosses between B2 x T1 and their reciprocal (T1 x B2) had the highest mean value for rapid tillering in tall fescue. The lowest mean value was found in the crosses between the rhizome parents (R1 x R2) and their reciprocal (R2 x R1) (Table 4).

Based on the progeny testing, both GCA and SCA effects were significant for rapid tillering in tall fescue and mean square of GCA was much higher than mean squares of SCA, maternal and reciprocal effects (Table 3). Bunch type parent (B2) and rapid tillering type parents (T1and T2) showed significant positive GCA estimates whereas significant negative GCA estimates were found in rhizome parents (R1 and R2) (Table 5). The crosses between rhizome parents (R1 and R2), rhizome x bunch type parents, and rapid tillering x bunch type parents showed significant positive SCA estimates for rapid tillering in tall fescue. Significant negative SCA estimates were found between rhizome type x rapid tillering type parents, between rapid tillering type parents, and between bunch type parents (Table 6). Significant positive reciprocal effects were obtained in the progenies from bunch types x rapid tillering type parents (Table 7). Significant negative reciprocal effects were found in the crosses between rhizome types, rhizome x bunch types, rhizome types x rapid tillering types and bunch type parents. Significant positive maternal effects were found in rapid tillering type parents and significant negative maternal effect was found in the rhizome parent (R1) and bunch type parent (B2) (Table 11). Moderately high narrow sense heritability estimates (h^2 = 0.88 ± 0.61) using parent progeny regression analysis for rapid tillering in tall fescue (Fig. 1).

Rhizome formation (number of rhizomes per plant)

Analysis of variance revealed significant genotypic and cross effects for rhizome formation in tall fescue (Table 8 and 9). Rhizome parents showed significant higher mean values for the rhizome formation whereas bunch type parents and rapid tillering type parent (B1 = B2 = T1 = 0) showed no rhizome formation (Table 2). The crosses between the rhizome parents and their reciprocals exhibited significant higher mean value followed by the cross between rhizome type and rapid tillering type. The highest rhizome formation was found in the crosses between rhizome type parents followed by the cross between R1 x T2 (Table 4). No rhizome formation was found in the crosses between bunch type, bunch type x rapid tillering type parents and between rapid tillering type parents.

Significant GCA and SCA effects, maternal and reciprocal effect were found for rhizome formation in tall fescue based on the progeny testing (Table 9). The mean values of SCA and GCA were very high for rhizome formation than mean square value of maternal and reciprocal effects (Table 9). Significant positive GCA estimates were found in the rhizome type parents whereas significant negative GCA estimates were found in the crosses between bunch types, between rapid tillering type parents (Table 5). Significant positive SCA estimates for rhizome formation in tall fescue were exhibited in the crosses between rhizome type parents, between rapid tillering type, rapid tillering type x bunch type parents and between bunch type parents. Significant negative SCA estimates were found in the crosses between rhizome parent x rapid tillering type; and bunch type parents (Table 10). Narrow sense heritability estimate was moderate (h^2 = 0.56 ± 0.03) for rhizome formation in tall fescue (Fig 2).

Ground Coverage

Genotypic and cross effects were significant for ground coverage in tall fescue using ANOVA (Table 7 and 12). The highest mean value for the ground coverage was found in rapid tillering type; and bunch type parents, and lowest mean value were found in rapid tillering type (T1) and bunch type parents (B1) (Table 2). The significantly higher mean value for ground coverage was found between bunch type x rapid tillering type and their reciprocal and between rapid tillering types. The lower mean values were found between bunch type x rhizome type parents (B1 x R1) and their reciprocal (R1 x B1), respectively (Table 4).

The GCA effect was highly significant whereas SCA effect, reciprocal effect, maternal effect and non-maternal effect were non-significant for ground coverage in tall fescue (Table 10). GCA × year interaction was significant and GCA estimates were presented for both years. The significant positive GCA estimate was found in the rapid tillering type parent (T1) and negative GCA estimate was found in the rhizome type parent (R1) for ground coverage (Table 5). Narrow sense heritability estimates were high in both years, 2011 (h^2 = 0.93 ± 0.14) and 2012 (h^2 = 0.88 ± 0.14), respectively (Fig. 3 and 4).

NDVI and Number of tillers per plant

High correlation (r = 0.74) was found between rapid tillering and NDVI (Fig. 5). The crosses between rapid tillering type parent and bunch type parent (T1 x B2) showed highest NDVI values followed by the crosses between the rapid tillering type parents (T1 x T2). The lowest correlation was obtained in the crosses between rhizome parents.

Pearson Correlation Coefficient

Significant positive correlation between rapid tillering type and ground coverage in the crosses (r = 0.577; P value = 0.024) whereas negative correlation between rapid tillering and rhizome formation was found in the crosses (r = -0.58; P value = 0.022) and in parents (r = -0.82; P value = 0.0001). No significant correlation was found between rhizome formation and ground coverage in tall fescue.

DISCUSSION

In this study, a diallel mating design was used to evaluate the genetic factors responsible for inheritance of bunch type, rhizome type and rapid tillering type in tall fescue and to estimate general and specific combining abilities of the genotypes and determine gene effects responsible for inheritance of different growth habits in tall fescue. The results from this study showed that different growth habits are genetically controlled and heritable in tall fescue.

From the analysis of variance, significant cross effect indicated that genetic factors were transmitted from parents to offspring in tall fescue for the rhizome formation and tillering traits in tall fescue. The rhizome formation was significant in the crosses between rhizome parents whereas no rhizome formation was found between bunch type x rapid tillering type parents. The similar results were shown by D'Uva et al. (1982) who reported that rhizome type genotypes produced more number of rhizomes, whereas non-rhizomatous types did not show any rhizome formation. The rapid tillering (number of tillers per 7.62 cm plug) and ground coverage were higher for bunch type parents and rapid tillering type parents. On the contrary, rhizome formation was least in the bunch and rapid tillering parents. This indicated that parent selection does influence the rapid tillering, rhizome formation and ground coverage in tall fescue. Cowan (1956) reported that some plants of tall fescue have spread up to 0.3 m per year because of rhizomes. Bouton et al. (1992) mentioned that rhizome types spread more than non-rhizomatous or weakly rhizomatous types.

Interesting results were found in this study that rapid tillering parent (T2) have shown significantly higher rhizome formation in the mowed spaced planting as compare to other rapid tillering and bunch type parents. The other rapid tillering type and bunch type showed either little or no rhizome formation in the field. The crosses between rhizome type and rapid tillering parent (T2) yielded significant number of rhizomes as compared to crosses between rhizome parents and other tillering parent and bunch types. The presence of rhizomes in T2 parent could be environmental effect or phenotypic plasticity of parent. The phenotypic plasticity referred to capacity of genotype to produce different phenotype under the influence of different environments (Sultan, 2000). The expression of phenotype depends upon the given genotype's "external and internal environment". The recent studies are focusing on the role of phenotypic plasticity on the functional and reproductive ability of the plants in the given environments (Sultan, 2000).

A high heritability indicated that most of the variation observed in the population is caused by variation in genotypes and the phenotype of an individual is a good predictor of the genotype. However, phenotypic expression cannot be certain even if the genotype is known because the environment can change or it can be manipulated to alter the phenotype. On the other hand, a low heritability refers that of all observed variation, a small proportion is caused by genetic variation in genotypes. However, it does not mean that the additive genetic variance is small. This difference matters because the response to natural or artificial selection depends on the amount of genetic variation in the population (Visscher et al., 2008). The moderate narrow (h^2 = 0.56 ± 0.03) sense heritability was found for rhizome formation in 2012, suggesting additive gene effects contributed relatively higher proportion of genetic variance as compare to non-additive and/or environment effects. Bouton et al. (1992) estimated narrow sense heritability for rhizome formation in tall fescue which was higher ((h^2 = 0.88) than estimated in the current study (h^2 = 0.56). The different results obtained in two studies might be due the different types of the genotypes used in the researches. Bouton et al. (1992) used six genotypes which were all rhizomatous whereas in the current study out of six genotypes: only two were rhizomatous and four non-rhizomatous types (two rapid tillering types and two bunch types).

The additive gene effect is important in a breeding program and because additive gene effect is the one which fixed the trait and transferred from generation to next (Sprague and Tatum, 1942). Sanford and Ytoma (1995) suggested that trait with moderate heritability should be amenable to selection. Sleper et al. (1977) reported low narrow sense heritability estimates in tall fescue for number of tiller per plant and suggested mass selection could improve rhizome formation. Higher narrow sense heritability for rapid tillering indicated that additive gene effects have more influence than non-additive gene effects. Narrow sense heritability measures the additive gene effect contributes mostly in the trait (Nyquist, 1991, Poehlman and Sleper, 1995). Sanford and Ytoma (1995) described tillering rate as an elastic trait which could be influenced by the environment such as planting density. Narrow sense estimates for the ground coverage were very high in both years (2011 and 2012) indicating more proportion of additive gene effect than non-additive gene effects contributing in genetic variance. Narrow sense heritability estimate for ground coverage was higher in 2011 than in 2012, indicating environment influence had increased in 2012 on the ground coverage.

The significant GCA and SCA effects were found in tall fescue for rhizome formation indicated that both additive and non-additive gene effects were involved. Bouton et al. (1992) reported to improve the trait by selection; sufficient additive genetic variance is required. The mean square value of GCA was much higher for rapid tillering than SCA, reciprocal and maternal effects indicating additive gene effects were more important that non-additive gene effects as observed by narrow sense heritability for rapid tillering in tall fescue. Additive gene effects are the one which effectively selected in a breeding program and can be used to predict the gain from selection (Sprague and Tatum, 1942). Frakes and Matheson (1973) also reported that GCA effect was more significant for the tiller number in forage type tall fescue. Similar results were also obtained by Akram et al. (2007) that additive gene effect was higher for the tillering rate than non-additive gene effects in rice. However, Muehlbauer et al. (1971) reported that SCA effect was significant for tiller number in a three parent diallel cross in oats and non-additive gene effects governs the trait than additive gene effect. The mean square of general combining ability was much higher than the mean square of specific combining ability, reciprocal and maternal effects for rapid tillering, indicating that additive gene effects governs the major portion of genetic variance for rapid tillering in tall fescue. However, to fully understand the role of maternal and reciprocal effect on rapid tillering in tall fescue, the experiment should be conducted for more than one year at multiple locations. GCA was significantly higher than SCA estimates for ground cover averaged over two years (2011-2012), indicating presence of additive gene effect. Significant GCA estimates and high narrow sense heritability indicate that additive gene effect contributed more to inheritance of ground coverage than non-additive gene effect in tall fescue. However, Thiravira (1974) reported that both GCA and SCA effects were significant for the plant spread in tall fescue and both additive and non-additive gene actions influenced the trait. For rapid tillering T1, T2 and B2; for rhizomes, R1 and R2 types; and for ground coverage T1 type parents were identified as having good general combining ability and could be incorporated into a breeding program for tall fescue improvement. The detection of significant SCA effects for some of the parents indicated that progeny performed better or worse than what was predicted by the average performance of their parents. To successfully breed for growth habits, progeny testing is needed to avoid the unfavorable combinations which yield significant positive SCA effects. Likewise, progeny testing will also allow for the selection of beneficial combinations between parents resulting in negative SCA effects.

The greater ground coverage was exhibited by rapid tillering types due to development of lateral tillers and this was confirmed by the Pearson correlation coefficient. Significant positive correlation was found between rapid tillering and ground coverage suggesting with increase in rapid tillering with increase in ground coverage. However, there was no correlation between rhizome formation and ground coverage. Significant negative correlation was found between rapid tillering and rhizome formation indicating that increase in rhizome formation will reduce the rapid tillering. Positive correlation between rapid tillering and ground coverage would enhance the selection and breeding process for rapid tillering and lateral spread in tall fescue. To improve rhizome formation in tall fescue without compromising rapid tillering and uniform ground coverage in tall fescue, strategic breeding methods and selection of superior genotypes would be required.

High correlation between tiller count and the NDVI suggested that the reflectance from the plant were proportionate to rapid tillering and spectral reflectance technique is efficient in understanding the growth of plants. This correlation provided useful information about rapid tillering in tall fescue and as an alternative way to evaluate turfgrass characteristics.

CONCLUSION

Based on ANOVA genetic differences were present between the parents for rhizome and tillering traits in tall fescue and genetic factors were transmitted from the parents to the progenies.

General combining ability of the parents was significantly higher for rapid tillering, rhizome formation and ground coverage, whereas specific combining ability was significantly higher for rhizome formation only. Additive gene effects governed major portion of genetic variance in rapid tillering rate and ground coverage but for rhizome formation, both additive gene effect and non-additive gene effect contributed in the genetic variance.

Narrow sense heritability estimates were high for rapid tillering and ground coverage in tall fescue and moderate for rhizome formation, indicating major additive gene effects on the inheritance of rhizome and tillering traits in tall fescue. High correlation was found between NDVI and rapid tillering in tall fescue.

The limitation to this study is that the genotypes for this analysis were considered fixed effects; therefore these findings apply only to these populations studied. The data from this study suggests that growth habits can be improved by progeny testing and by selecting parents with significant GCA values to be used in tall fescue improvement breeding program.

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Table 2.1: Analysis of variance of rapid tillering (No. of tillers per 7.62 cm plug) of six tall fescue parents used in diallel crosses evaluated in a mowed spaced planting in Freehold, NJ in 2012.

Source of Variation	df	Mean Square
Genotype	5	11571.8***
Replication	3	105.44
Genotype x Replication	15	283.73
Error	48	230.93

***Significant at the 0.05 probability level

Table 2.2: Mean value of six parents used in diallel crosses to evaluate rapid tillering (no. of tillers per 7.62 cm plug), rhizome formation (no. of rhizomes per plant) and ground coverage (cm) in a mowed spaced planting in Freehold, NJ in 2011 - 2012.

Parents	Rapid tillering	Rhizome formation	Ground coverage
R1	36.75	3.83	27.92
R2	47	5.42	28.83
T1	92.92	0	32.56
T2	72.25	0.42	25.75
B1	83.42	0	27.68
B2	121.67	0	30.58
LSD (5%)	12.47	1.13	1.37

Table 2.3: Analysis of variance for rapid tillering (no. of tillers per 7.62 cm plug) of a diallel cross of six tall fescues evaluated in a mowed spaced planting in Freehold, NJ in 2012.

Source of Variation	df	Mean Square
Cross	29	56.68***
Replication	3	15.0
Cross* Replication	87	3.35
GCA	5	235.94***
SCA	9	8.86***
Reciprocal	15	6.40***
Maternal	5	9.99***
Error	2700	537.94

***Significant at the 0.05 probability level

Table 2.4: Effect of crosses on the rapid tillering (No. of tillers per 7.62 cm plug), rhizome formation (no. rhizomes per plant), and ground coverage (cm) of thirty tall fescues crosses evaluated in a mowed spaced planting in Adelphia, NJ in 2011-2012.

Crosses	Rapid tillering	Rhizome formation	Ground coverage
B1 X B2	91.92	0	28.57
B1 X R1	78.53	0.125	23.7
B1 X R2	74.64	0.104	27.08
B1 X T1	106.89	0	29.77
B1 X T2	83.41	0.086	28.43
B2 X R1	70.91	0.152	24.56
B2 X R2	79.8	0.29	28.33
B2 X T1	112.81	0	32.11
B2 X T2	97.71	0.01	28.75
B2 XB1	102.7	0	27.7
R1 X B1	68.99	0.19	24.1
R1 X R2	43.33	5.56	24.77
R1 X T1	69.27	0.125	29.29
R1 X T2	62.9	1.44	25.14
R1 XB2	63.62	0.202	25.63
R2 X B1	78.55	0.104	28.27
R2 X R1	56.87	4.36	26.09
R2 X T1	71.05	0.367	30.81
R2 XB2	77.41	0.096	29.11
R2 XT2	64.4	0.463	28.4
T1 X B1	103.35	0	29.83
T1 X B2	111.04	0.02	31.27
T1 X R1	70.01	0.125	29.36
T1 X R2	80.32	0.125	29.79
T1 X T2	104.71	0	30.52
T2 X B1	84.55	0.052	28.74
T2 X B2	105.28	0.0833	27.84
T2 X R1	59.85	0.686	24.53
T2 X R2	69.01	0.307	28.63
T2 XT1	97.87	0	31.46
LSD (5%)	6.64	0.81	1.96

Table 2.5: Estimation of general combining ability (GCA) effects in diallel crosses of six tall fescue parents using combined data for the rapid tillering (no. of tillers per 7.62 cm plug), rhizome formation (no. of rhizomes per plant) and ground coverage (cm) evaluated in a mowed spaced planting in Freehold, NJ in 2011-2012.

GCA estimates	Rhizome Formation	Rapid Tillering	Ground Coverage
G1	0.87***	-21.63***	-3.74***
G2	0.72***	-16.36***	0.03
G3	-0.65***	13.79***	3.9***
G4	-0.35***	9.56***	-0.89
G5	-0.29***	-1.39	0.34
G6	-0.31***	16.04***	0.43

***Significant at the 0.05 probability level

Table 2.6: Estimation of specific combining ability (SCA) effects in diallel crosses of six tall fescue parents using combined data for the rapid tillering (no. of tillers per 7.62 cm plug), evaluated in a mowed spaced planting in Adelphia, NJ in 2012.

Parents	R1	R2	T1	T2	B1
R2	5.41**				
T1	-0.71	-4.36**			
T2	-9.16***	-9.23***	-4.64**		
B1	14.17***	11.77***	10.16***	13.55***	
B2	16.05***	-3.68	-0.45	36.44***	-22.54***

***Significant at the 0.05 probability level

Table 2.7: Analysis of variance for ground coverage (cm) of diallel crosses evaluated in a mowed spaced planting in Adelphia, NJ in 2011 and 2012.

Source of Variation	df	Mean square
Crosses	29	1022.3***
Rep (Env)	6	21.7
Env	1	1475.6***
Cross*Env	29	20.03
GCA	5	879.6***
SCA	9	14.86
Reciprocal	15	13.9
Maternal	5	13.31
GCA*Env	5	54.98***
SCA*Env	9	8.78
Rec*Env	15	15.73
Mat*Env	5	12.31
Error	5426	15.66

***Significant at the 0.05 probability level

Table 2.8: Analysis of Variance of rhizome formation (no. of rhizomes per plant) of diallel crosses evaluated in a mowed spaced planting in Adelphia, NJ in 2012.

Source of Variation	df	Mean square
Crosses	29	147.56***
Rep	3	2.39
Rep*Crosses	87	0.49
GCA	5	272.01***
SCA	9	247.96***
Reciprocal	15	6.91***
Maternal	5	10.79***
Error	2723	0.98

***Significant at the 0.05 probability level

Table 2.9: Estimation of specific combining ability (SCA) effects in diallel cross of six tall fescue parents using combined data for the rhizome formation (no. of rhizomes per plant), evaluated in a mowed spaced planting in Adelphia, NJ in 2012.

Parents	R1	R2	T1	T2	B1
R2	2.76***				
T1	-0.69***	-0.42***			
T2	-0.06	-0.59***	0.401***		
B1	-1.02***	-0.93***	0.34***	-0.12	
B2	-0.98***	-0.82***	0.37***	0.04	1.39***

***Significant at the 0.05 probability level

Table 2.10: Analysis of variance for ground coverage (cm) of six tall fescue parents used in diallel crosses evaluated in a mowed spaced planting in Adelphia, NJ in 2011 and 2012.

Source of variation	df	Mean square
genotype	5	137.33***
Year	1	706.67**
Rep (year)	3	29.02
Genotype x rep	15	94.62***
Genotype x year	5	10.23
Genotype x year x rep	15	7.3
Error	48	1.88

***Significant at the 0.05 probability level

Table 2.11: Analysis of variance of rhizome formation (no. of rhizomes per plant) of six tall fescue parents used in diallel crosses evaluated in mowed spaced planting in Freehold, NJ in 2012.

Source of variation	df	Mean square
genotype	5	68.7***
Replication	3	1.93
Genotype x Replication	15	8.47
Error	71	1.89

***Significant at the 0.05 probability level

Table 2.12: Maternal and reciprocal effects for the rapid tillering (no. of tillers per 7.62 cm size plug) in a diallel cross of six tall fescue parents evaluated in a mowed spaced planting in Adelphia, NJ in 2011-2012.

Reciprocal Effect	
(R1 x R2, R2 x R1)	-6.67***
(R1 x T1, T1 x R1)	-4.84***
(R1 x T2, T2 x R1)	1.38
(R1 x B1, B1 x R1)	-4.81***
(R1 x B2, B2 x R1)	-3.56
(R2 x T1, T1 x R2)	-4.67***
(R2 x T2, T2 x R2)	-2.30
(R2 x B1, B1 x R2)	1.97
(R2 x B2, B2 x R2)	-1.19
(T1 x T2, T2 x T1)	3.43
(T1 x B1, B1 x T1)	-1.77
(T1 x B2, B2 x T1)	-0.96
(T2 x B1, B1 x T2)	7.33***
(T2 x B2, B2 x T2)	33.33***
(B1 x B2, B2 x B1)	-5.44***
Maternal Effect	
M1	-3.06***
M2	0.08
M3	1.69***
M4	6.36***
M5	-1.36
M6	-3.71***

***Significant at the 0.05 probability level

Table 2.13: Correlation between rapid tillering, rhizome formation and ground coverage for the diallel crosses evaluated in mowed spaced planting in Adelphia, NJ in 2011-2012.

Traits	Correlation coefficient	
	Offspring	Parents
rapid tillering vs rhizome formation	-0.582***	-0.823***
rapid tillering vs ground coverage	0.577***	0.319
rhizome formation vs ground coverage	-0.315	-0.198

***Significant at the 0.05 probability level

Figure 2.1: Mid-parent-offspring regression of F1 population means regressed on the mid-parent value from 15 crosses between six tall fescue parental genotypes evaluated for rapid tillering (no. of tillers per 7.62 cm plug) in a mowed spaced planting in Adelphia, NJ in 2012.

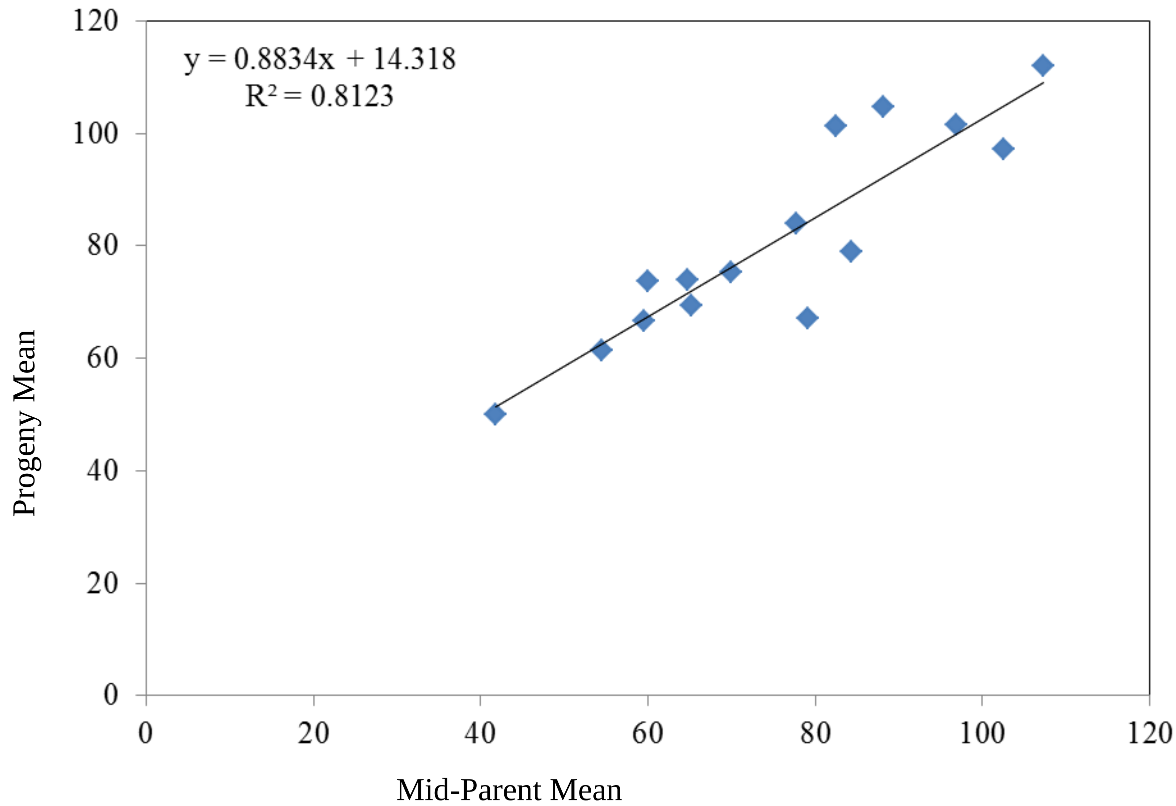


Figure 2.2: Mid-parent-offspring regression of F1 population means regressed on the mid-parent value from 15 crosses between six tall fescue parental genotypes evaluated for rhizome formation (number of rhizomes per plant) in a mowed spaced planting in Adelphia, NJ in 2012.

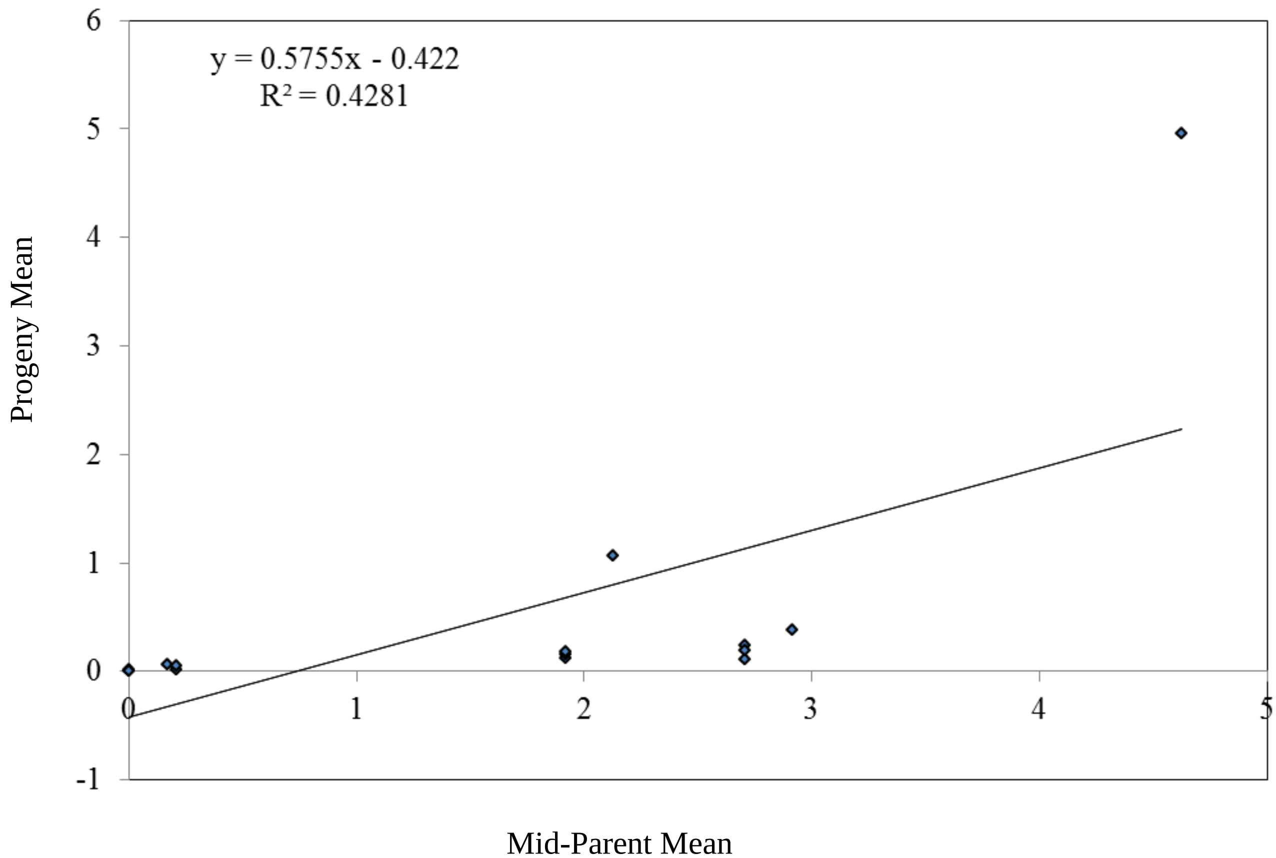


Figure 2.3: Mid-parent-offspring regression of F1 population means regressed on the mid-parent value from 15 crosses between six tall fescue parental genotypes evaluated for ground coverage (cm) in a mowed spaced planting in Adelphia, NJ in 2011.

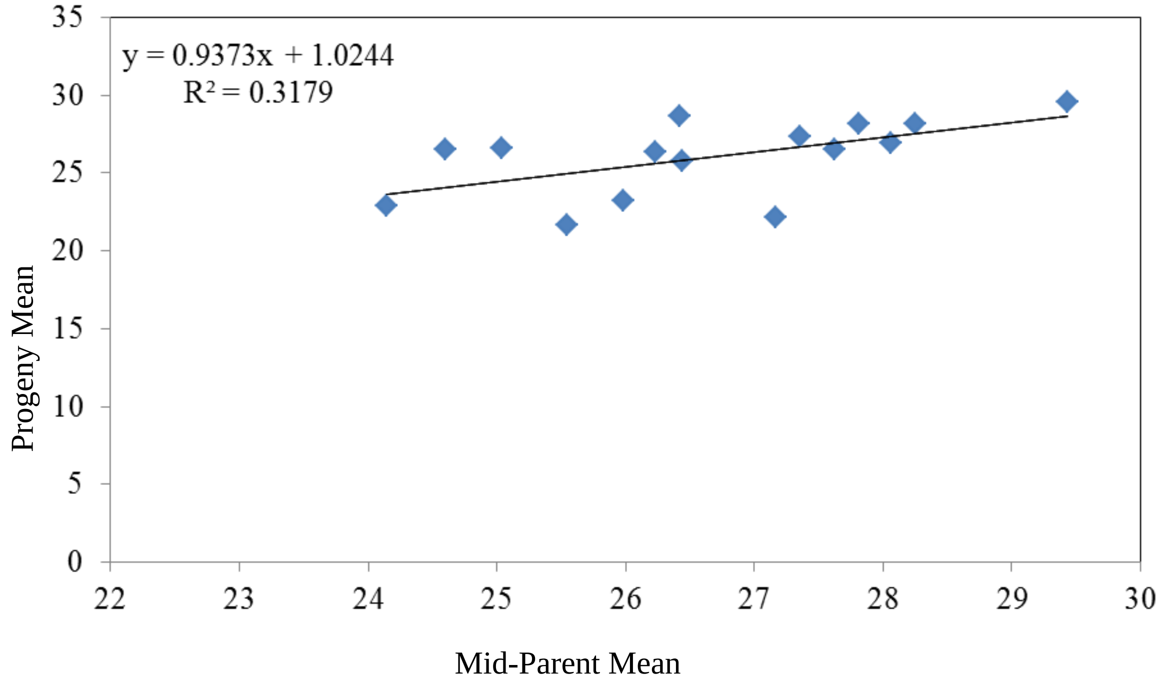


Figure 2.4: Mid-parent-offspring regression of F1 population means regressed on the mid-parent value from 15 crosses between six tall fescue parental genotypes evaluated for ground coverage (cm) in a mowed spaced planting in Adelphia, NJ in 2012.

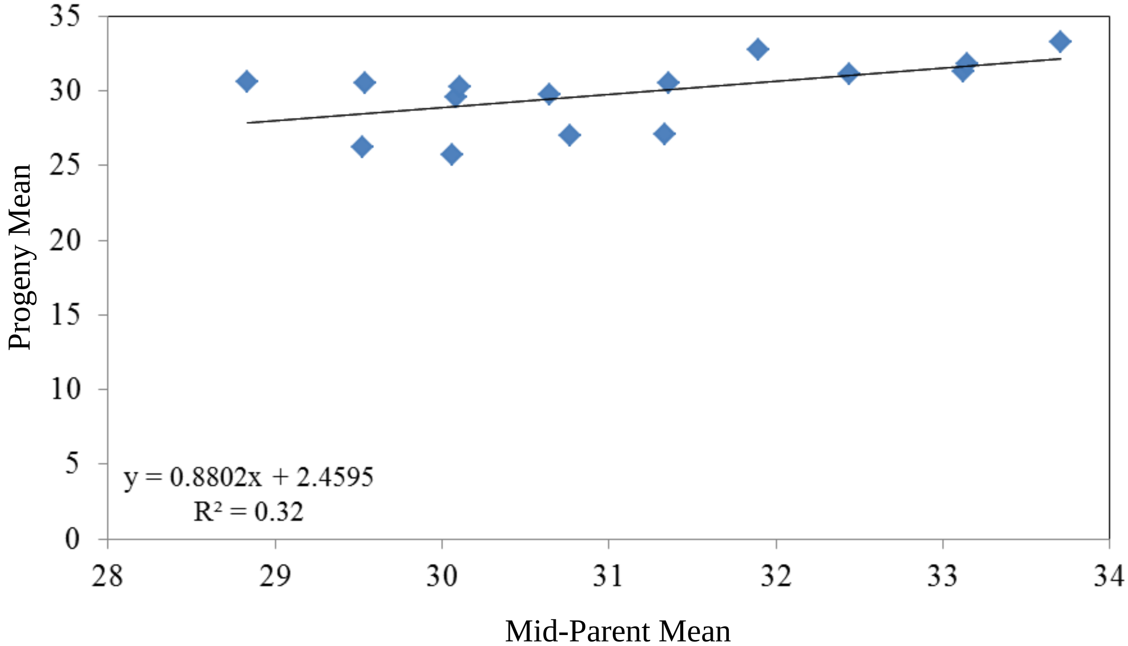
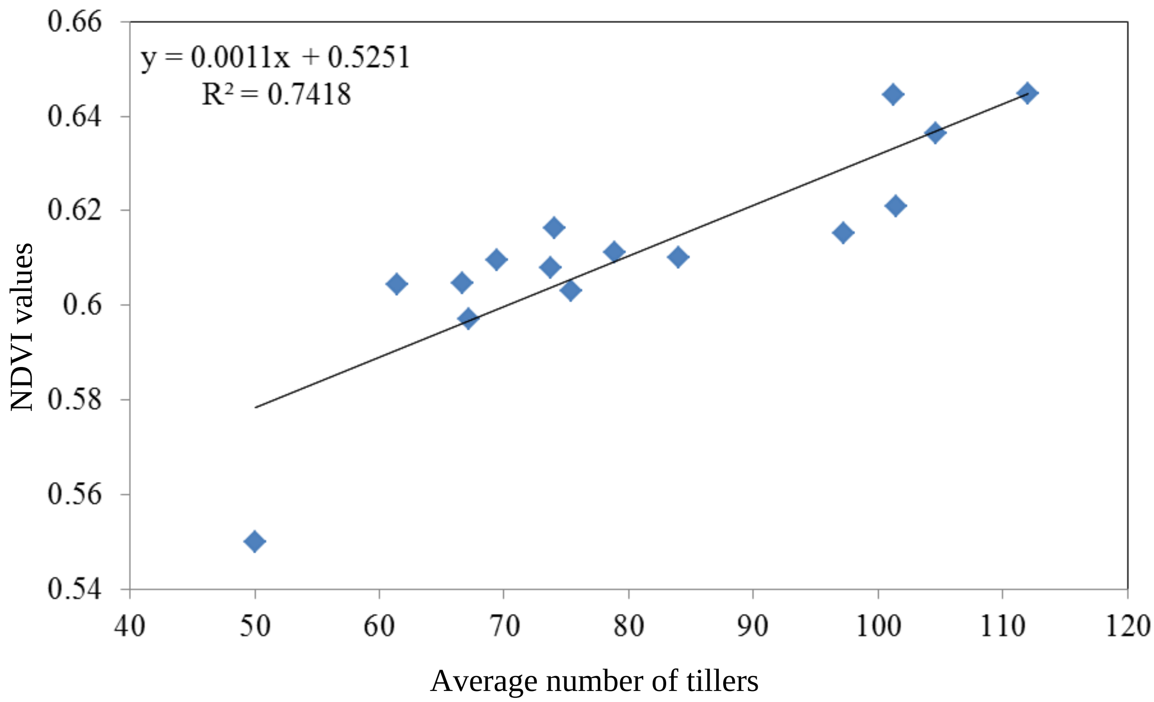


Figure 2.5: Correlation between the rapid tillering (no. of tillers per 7.62 cm plug) and NDVI evaluated in a mowed spaced planting in Adelphia, NJ in 2011.



CHAPTER 3

Estimating Genetic Effects of Tillering Rate and Rhizome Formation using Polycross Method in Tall Fescue

INTRODUCTION

A polycross mating design is useful in perennial cross-pollinated grasses because it determines the genotypes of mother parents by studying the progenies after inter-pollinate in isolation (Wellensiek, 1952). A polycross mating design is relatively simpler than a diallel mating design or factorial mating design because a large number of of parents can be used and an adequate amount of seeds can easily be produced through this mating design (Nguyen and Sleper, 1983). Additionally many cultivars have been developed using polycross mating scheme so the results obtain from this method would be truer to the performance of the cultivar. Hittle (1954) described the purpose of the polycross mating design was to provide an equal opportunity for each parent to be inter-pollinated in the polycross nursery. The randomization of the parental clones in polycross nursery provided each parent to be inter-pollinated uniformly in the polycross nursery. When the progenies obtained from the selected clones of parents differ in their performance, such differences are usually considered due to variations in the ability of maternal parents to transmit their alleles to their progeny and/or due in part to non-random pollination or different male effects (Hittle, 1954).

In a polycross mating design, randomization of the plants leads to uniform pollination and apparently plants combined with all or most of other plants; and expected to have same proportion in the progenies. The combination of each plant will then be evaluated for quantitative genetic information about important agronomic traits (Wit, 1952). Polycross mating is one of several mating designs which produces half –sibs and on which progeny testing is performed to evaluate the general combining ability of parental lines (Simmonds, 1979). The deviations of each half-sib progeny from population mean estimates the general combining ability (GCA) (de Araujo and Coulman, 2002 and Wrick and Weber, 1986) and GCA is an indicative of additive gene action (Nguyen and Sleper, 1995). The selection should be made for the high combining genetic components and continues as long as considerable genetic variation exists which utilize in the development of synthetic cultivars or hybrid production (Tysdal and Crandall, 1948).

Narrow sense heritability can be estimated using parent-progeny regression analysis in the polycross mating system to evaluate the performance of the parents. The narrow sense heritability provides the measure of additive gene effects, responsible for the inheritance of the traits from the parents to the offspring (Poelhman and Sleper, 1995). The parent-progeny regression analysis is used to estimate narrow sense heritability where the means of half-sib progeny would be regressed against the mean of parents, and the regression coefficient is one-half of the narrow sense heritability (Fehr, 1987, Falconer, 1981). Lush (1940) and Kneebone (1958) indicated that heritability estimates aid the breeder in planning efficient breeding programs. In cross pollinated crops, narrow sense heritability estimates h^2 = 2b, if offspring are regressed on the maternal parent.

The estimation of narrow sense heritability determines the proportion of additive gene effects influencing the total genetic variance. The knowledge of additive genetic variance with respect to the total genetic variance is important in the breeding of perennial grasses because additive genetic variance is transmitted to the next generation as compared to non-additive genetic variance (Hill, 1977). Hallauer (1981) illustrated that phenotypic recurrent selection which is common in forage breeding, utilizes additive and additive x additive type of epistatic genetic variance. In perennial forage grasses, additive genetic action has been reported to be the major force behind genetic variation in the agronomic traits (Breese and Hayward 1972, Burton 1989, Meyer and Funk 1989). If the trait influenced highly by the environmental conditions, it would be difficult to improve trait by selection as compare to if the environmental influence is smaller as than genetic variance, selection will be effective (Briggs and Knowles, 1967). The lower heritability estimates for plant spread in meadow bromegrass (*Bromus biebersteinii*) indicated that phenotypic selection would be difficult to improve the trait. Low variation in plant spread of bromegrass was suggested due to short rhizome formation in the single plant nursery than in mowed turf plots (de Araujo et al., 1983).

Tall fescue has been reported to produce short rhizomes (Porter, 1958) and exhibited lateral growth through the rapid production of tillers (Saxena et al., 2013). However, tall fescue has been cited as bunch type, perennial, cool season, and self-incompatible turfgrass (Buckner and Cowan, 1973). Polycross mating design haven't been used to study the inheritance of different growth habits: rhizome formation, rapid tillering and bunch types, in tall fescue simultaneously. Therefore, it is important to evaluate the general combining ability of parents with different growth habits using the polycross mating design since this method is used frequently in cultivar development. This project was conducted to evaluate the role of gene effects and inheritance of different growth habits: rhizome formation, tiller density and bunch types in tall fescue genotypes.

The objectives of this study were to evaluate parents and polycross progenies for rhizome formation, tiller density and ground coverage in tall fescue to (*i*) estimate heritability and gain from selection, (*ii*) evaluate general combining ability of parental clones, and (*iii*) determine the most effective selection program.

MATERIAL AND METHODS

Fourteen plants were selected in the summer of 2009 based on their growth habits: bunch types (four different genotypes), rhizome types (five different genotypes) and rapid tillering types (five different genotypes). These genotypes were selected from the germplasm maintained at the New Jersey Agriculture Experiment Station (NJAES), NJ. These genotypes had gone through repeated cycles of selection and hybridization for improved quality and disease resistance. The parents chosen were previously described (Saxena et al., 2013) based on their ability to produce rhizomes. The bunch type parents produce more erect tillers and covered less ground area (Saxena et al., 2013) whereas rapid lateral tillering types produce a lateral tillers and covered more ground surface. Each parent plant was clonally propagated and planted in the field in the fall 2009 to be vernalized. The clones were then brought back into the greenhouse during April and were placed under long photoperiod (18 H) using extra overhead lighting to induce flowering. The plants were matched based on their flowering timing and two clones of each genotype were randomized in a block to inter-pollinate in an isolated spot in the greenhouse. The pollen flow was facilitated by the manually tapping the parents. A few inflorescences from each parent were covered with white paper bags to determine if any self-pollination occurs. The seeds harvested from these inflorescences did not produce any viable seeds. The seeds were harvested from each parent from the controlled crosses and dried and sown into the seed trays and placed in alternate cold and warm conditions treated with 2% KNO_3 to break the seed dormancy (Bush et al., 2000). One hundred seedlings were randomly selected from the each parent used in the cross after dormancy was broken. The seedlings were kept in the greenhouse before establishing the field trial.

The field experiment was established at the Rutgers, Plant Science Research and Extension Farm, Adelphia, NJ. The soil type was a Freehold sandy-loam (fine-loamy, mixed, active, mesic Aquic Hapludult). The progenies were planted along with the parents in a randomized complete block design with four replications on October 24th, 2010. Each replication contained 24 individual plants from each cross planted with12 plants in each row at the spacing of 0.46 meter spacing along with three clones of each parent in each replication. The plants were mowed with a Toro Groundmaster (Toro Corp. Bloomington, MN) twice a week during the growing season at a height of 6 cm. In 2011 and 2012 an application of 9-0-18 (N: P: K) fertilizer was applied during the months of April, May and October, respectively, at a rate of 0.4 g N m^{-2}. Brown patch was controlled with an application of Heritage (Azoxystrobin) at the prescribed labeled rates. Annual weeds were controlled with Acclaim (fenoxaprop-p-ethyl) at labeled rates and broad leaf weeds were controlled with 2, 4 D and Banvel (3, 6-dichloro-o-anisic acid) @ 2240 g ha^{-1} and 560 g ha^{-1}, respectively.

Statistical Analysis

Rhizome formation (number of rhizomes per plant), tiller density (number of tillers per 7.62 cm plug) and ground coverage (average of length and breadth (cm)) were collected on each individual progeny and parent plants. The numbers of rhizomes were counted by hands on each individual plant intact in the field in May 2012. The rhizomes which were >2 cm apart from the mother plant were only counted. The tiller counting was done at the end of the trial in September 2012 because it required destruction by cutting 7.62 cm size plug from each individual plant and manually counting tillers. Ground coverage was calculated by measuring the length (cm) and breadth (cm) and averaged on each individual plant in June 2012 and June 2013.

Narrow- sense heritability was estimated using parent progeny regression analysis with the mean of the half-sib progeny regressed against the mean of the parents. The regression coefficient (b) is equal to half of the narrow sense heritability and therefore multiplying it by 2 will provides the estimation of narrow sense heritability (Fehr, 1987) using the polycross mating design. The value obtained for narrow sense heritability can be used to calculate the gain from selection ($Gs = i\sigma p h^2$) where, Gs = genetic gain from selection, *i* is a constant based on selection intensity, σp is the standard deviation of the phenotypic variance, and h^2 is the narrow-sense heritability (Poehlman and Sleper, 1995). General combing ability was calculated for each parent as the deviation of each half-sib progeny from the population mean (de Araujo and Coulman, 2002). Pearson correlation coefficient was calculated using Sigma Plot software 12.2 (Systat Software Inc. San Jose, CA) to evaluate correlation between tiller density, rhizome formation and ground coverage in tall fescue.

All data were analyzed using analysis of variance by the PROC GLM procedure of SAS (SAS Institute Inc., Cary, NC, USA) and means separation was calculated based on Fisher's LSD.

RESULTS

Rhizome Formation (Number of rhizomes per plant)

Significant genotypic differences were found among the parents and half-sib progenies for the rhizome formation in tall fescue (Table 1 and 2). Parents selected for increased rhizome formation had higher mean values for rhizome formation (Table 3). Half-sibs progenies produced from the rhizome parents (R1, R2 and R5) and rapid tillering type (T2) have exhibited statistically significant higher mean values for rhizome formation, whereas the half-sib progenies of rapid tillering types (T3 and T4) and bunch types (B1) showed the least rhizome formation in tall fescue. Significant positive GCA estimates were found in the rhizome parents (R1 and R2). The significant negative GCA estimates were found in rapid tillering types (T5) and bunch type parent (B2), respectively (Table 3). Predicted gain from selection was 0.26 for rhizome formation at 5% selection intensity. Low narrow sense heritability estimates (h^2 = 0.25) was calculated using parent progeny regression analysis (Table 4).

Tiller Density (Number of Tillers per 0.76 cm plug)

Significant genotypic differences were found among the parents and half-sib progenies for the tiller density in tall fescue (Table 5 and 6). Bunch type parents (B3, B2 and B1) and rapid tillering type parents (T4, T1 and T2) had the highest tiller density in tall fescue (Table 7). The half-sibs produced from the bunch type parent (B3 and B4), rapid tillering type (T1 and T4) and rhizome type (R4) has shown the greatest mean value for the tiller density. The lowest mean value for tillering rate was found in the half-sib progenies obtained from the rhizome type parents (R1, R2 and R3). The half-sib progenies produced from the rhizome type parent R4 had significantly higher tiller per plant than other rapid tillering type half-sibs (T2 and T3) (Table 7).

Significant positive GCA estimates were found for tiller density in bunch type parents (B3, B2 and B4) and rapid tillering type parents (T4, T1 and T5). However, significant negative GCA estimates were found in the rhizome parents (R2, R3, R1 and R5) and rapid tillering type parent (T2) (Table 7). Predicted gain from selection for number of tillers per plant was 37.8 at 5% selection intensity (Table 4). Moderate narrow sense heritability estimates (h^2 = 0.51 ± 0.098) was calculated based on the phenotypic mean value of the parents and the progenies using parent-progeny regression analysis (Table 4).

Ground Coverage

Significant genotypic and environment differences were found among the parents and half-sib progenies in tall fescue (Table 8 and 9). Rapid tillering type parents exhibited highest mean value for ground coverage followed by rhizome type parents (R2 and R5) and bunch type parents (B2 and B4) (Table 10). Half-sib progenies of rapid tillering types (T1-T5) followed by rhizome type (R5 and R2) and bunch types (B1-B5) exhibited the highest ground coverage values. Whereas the lowest mean values were obtained for rhizome type (R1, R3 and R4) progenies (Table 10). The significant year effect was found in the parents and half-sib progenies; however the genotype x year effect was insignificant (Table 8 and 9). The analysis of variance showed significant genetic differences and year effect (Fig. 1) for ground coverage but no significant G x E interaction indicating that the individual plant's growth was based on their genetic effect not due to their genetic interaction with environmental conditions (Fig. 1).

Significant positive GCA estimates were obtained in the rapid tillering type parents (T1, T3 and T5), whereas significant negative GCA estimates was found in rhizome parents (R1, R3 and R4) and bunch type parent (B1) (Table 10). Predicted gain from selection was low 6.13 (2011) and 7.06 (2012) at 5% selection intensity (Table 9). Narrow sense heritability estimate was moderate for the ground coverage in 2011 (h^2 = 0.57 ± 0.098) and in 2012 (h^2 = 0.62 ± 0.098) using parent- progeny mean regression analysis (Table 4).

Correlation between Tiller density, Rhizome Formation and Ground Coverage

Highly significant negative correlation coefficients were found between tiller density and rhizome formation between half-sib progenies (r = -0.72) and between parents (r = -0.63). There was also a significant negative correlation coefficient was found between rhizome formation and ground coverage between parents (r = - 0.58) only.

DISCUSSION

The results obtained from this experiment showed that genetic variation existed in tall fescue for the different growth habits: rhizome type, rapid tillering type, and bunch type. The highest mean values for the rhizome formation were found in the half-sib progenies from parents selected for rhizome production. This suggested that the inheritance of the rhizome formation is influenced mostly by the alleles carried by the maternal rhizome parents. Rapid tillering types and bunch type parents showed very low number of rhizomes or no rhizomes in their half-sib progenies indicating that they contributed least to rhizome formation in tall fescue. This might be due to the absence or low frequency of favorable alleles for the rhizome formation in rapid tillering type parents and bunch type parents. The half-sib progenies obtained from the bunch type parents and rapid tillering types produced significantly higher number of tillers than rhizomes in tall fescue, indicating higher tiller density and vigor. The variation in the tillering rate between rapid tillering type and bunch type half-sib progenies was indicated by the number of tillers counted in the 7.62 cm plug size which determined the tillering density, however not the spreading ability of the plants. The ground coverage measurements were done to determine the spreading ability of the individual plants in the mowed-spaced planting.

The general combining ability of the rhizome parents (R1, R2 and R3) and rapid tillering type parent (T2) were significantly positive for the rhizome formation, but rhizome parent (R4), rapid tillering type parent (T5) and bunch type parent (B2) had negative GCA indicating that these parents did not combine with other parents to enhance the rhizome production in tall fescue. R4 parent was selected for increased have shown rhizome formation, though when it inter-pollinated with other parents did not produce higher numbers of rhizomes in the progeny.

The significant positive GCA estimates for tillering rate were found in the bunch type parents indicating their ability to improve the traits when inter-pollinated with other parents. The GCA estimates showed that rapid tillering types (T3 and T1) had higher combining ability to enhance tiller density and ground coverage in tall fescue. Rhizome type (R1 and R3) parents showed significant negative GCA estimates for ground coverage indicating that they don’t contribute in improving the trait and if crossed with other parent may reduce the trait. The analysis of combining abilities of the selected genotypes was performed to evaluate their ability to produce superior progenies when crossed with other parents. This combining ability is useful in the breeding of cross-pollinating perennial forage grasses to develop synthetic cultivars (de Ajour 2002).

The narrow sense heritability estimate was low for rhizome formation indicating more non-additive gene effects and/or environmental effect than additive gene effects. Narrow sense heritability for the rhizome formation was reported by Bouton et al. (1992), range from 0.38 (individual plant basis) to 0.88 (averaged across replications) and to increase the number of rhizomes in tall fescue using selection, sufficient additive genetic variance would be required. D'Uva et al. (1982) reported the insignificant genotype x location interaction for the rhizome formation in tall fescue. Bouton et al. (1992) suggested that rhizome formation could be improved by using recurrent selection at a single location.

The moderately high estimates of narrow sense heritability for tillering rate indicated that tillering rate is inheritable and additive gene effects are responsible for the transmission of trait from the parents to offspring. However, non-additive gene effects and/or environmental effect may have an influence on the inheritance of the trait. This was supported by the moderately high narrow sense heritability estimates of the ground coverage: h^2 = 0.56 (± 0.098) (2011) and h^2 = 0.67 (± 0.098) (2012, respectively. The two years evaluation of ground coverage measurement showed significant differences in the increase of spreading ability of tall fescue. The rapid tillering types covered more ground than bunch types and rhizomes types, indicating the role of extended lateral tillers produced by the rapid tillering types in improving the spreading ability of tall fescue. This was supported by the highest mean values of half-sib progenies produced from the rapid tillering types which had significantly higher tillering rate, ground coverage and turf density (unpublished data). The bunch types produced more number of vertical tillers in limited 7.62 cm size plug than rapid tillering types but could not exhibit extended spreading ability. The bunch types have an ability to produce vertical tillers whereas rapid tillering types produced lateral tillers which cover more ground surface than bunch type and accentuated the lateral spread of the plants. This suggests that rapid tillering types enhance the lateral spread of tall fescue as compared to bunch types and rhizome types.

Highly significant negative correlation coefficient between tiller density and rhizome formation showed that tiller density decreased with increased in rhizome formation in tall fescue. This is supported by the fact that rhizomatous tall fescue plants are less dense and have the lowest number of tillers/plant. On the other hand, rapid tillering types produced higher number of tillers/plant with high density and vigor but no or lesser number of rhizomes/plant in tall fescue. The requirement of tiller density and rhizome formation in tillering rate is considered essential as it allow tall fescue to persist under competition, temperature extremes, provide tolerance to wear and traffic. This research showed that rhizome formation and tillering rate are significant negatively correlated, therefor consistent and effective breeding selection methods would be required to enhance rhizome and tillering traits in tall fescue and could produce improved cultivars with significant rhizome formation without compromising tillering rate and spreading ability of tall fescue.

Polycross is an effective mating design to utilize large number of genotypes and evaluate quantitative information about the selected parents and estimating their contribution based on progeny performance, for their selection in the breeding program to enhance the expression of trait(s) (Poehlman and Sleper, 1995). The polycross mating design is more effective when there is minimum pollen differential and parents were replicated multiple times (Hittle, 1954). Employing a polycross mating design in this current project was useful in providing relevant information about the performance of the selected genotypes and their combining abilities which could be further utilized for tall fescue improvement.

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Table 3.1: Analysis of variance of number of rhizomes of fourteen tall fescue parents crossed in polycross design and evaluated in mowed spaced planting in Adelphia, NJ in 2012.

Source of variation	Df	Mean square	F value
Parents	13	30.42	35.99***
Replication	3	4.97	5.88
Parents x Replication	39	3.47	4.11
Error	112	0.85	

***Significant at the 0.05 probability level

Table 3.2: Analysis of variance of number of rhizomes fourteen tall fescue half-sibs crossed in polycross design and evaluated in mowed spaced planting in Adelphia, NJ in 2012.

Source of Variation	Df	Mean Square	F value
Half-sibs	13	8.66	18.11***
Replication	3	2.33	4.86
Half-sibs x Replication	39	0.55	1.15
Error	2611	0.48	

***Significant at the 0.05 probability level

Table 3.3: Means of parents, progeny, and GCA estimates for fourteen parental tall fescue genotypes for rhizome formation evaluated in mowed spaced planting in Adelphia, NJ in 2012.

Parent Genotype	Parent Mean	Progeny Mean	GCA
R1	4.25	0.441	0.25***
R2	3.67	0.791	0.604***
R3	3.83	0.267	0.082
R4	0.67	0.098	-0.088
R5	1.58	0.209	0.023
T1	0	0.105	-0.081
T2	0.25	0.2656	0.079
T3	0.67	0.0052	-0.182
T4	0.17	0.00521	-0.180
T5	0	0.0681	-0.12***
B1	0	0.0314	-0.156
B2	0	0.075	-0.11***
B3	0	0.057	-0.13
B4	0.25	0.203	0.016
LSD (0.05)	0.74	0.14	

***Significant at the 0.05 probability level

Table 3.4: Narrow-sense heritability and predicted gain from selection for ground coverage (2011 and 2012), tillering rate (2012), and number of rhizomes per plant (2012) from a polycross design of tall fescue genotypes.

Traits	Parent Progeny Regression			Expected Gain from Selection
	b	r	h^2	(i) 5%
Ground coverage (2011)	0.284	0.26	0.568	6.13
Ground coverage (2012)	0.314	0.49	0.628	7.06
Tillering rate	0.253	0.004	0.506	37.8
Rhizome formation	0.121	0.55	0.242	0.26

***Significant at the 0.05 probability level

Table 3.5: Analysis of variance of tiller density of fourteen tall fescue parents crossed in polycross design and evaluated in mowed spaced planting in Adelphia, NJ in 2012.

Source of variation	Df	Mean square	F value
Genotypes	13	21855.85	22.97***
Replication	3	5694.96	5.99
Half-sibs x Replication	39	1389.8	1.46
Error	112	951.4	

***Significant at the 0.05 probability level

Table 3.6: Analysis of variance of tiller density of fourteen tall fescue half-sibs crossed in polycross design and evaluated in mowed spaced planting in Adelphia, NJ in 2012.

Source of Variation	df	Mean Square	F Value
Half-sibs	13	42410.27	31.42***
Replication	3	9247.59	6.83
Half-sibs x Replication	39	3749.77	2.77
Error	2602	1354.15	

***Significant at the 0.05 probability level

Table 3.7: Means of parents, progeny, and GCA estimate for fourteen parental tall fescue genotypes for tiller density evaluated in mowed spaced planting in Adelphia, NJ in 2012.

Parent Genotype	Parent Mean	Progeny Mean	GCA
R1	56	86.97	-16.42***
R2	56.92	77.68	-25.71***
R3	61.33	86.8	-16.59***
R4	91.67	100.72	-2.67
R5	80.58	95.64	-7.75***
T1	119.33	111.84	8.45***
T2	101.58	95.74	-7.65***
T3	86.25	99.29	-4.09
T4	130	113.68	10.29***
T5	71.75	109.29	5.90***
B1	122.67	103.87	0.48
B2	127.67	116.23	12.84***
B3	220.17	135.80	32.41***
B4	98.3	114.74	11.36***
LSD	24.95	7.41	

***Significant at the 0.05 probability level

Table 3.8: Analysis of variance of ground coverage of fourteen tall fescue parents evaluated in mowed spaced planting in Adelphia, NJ in 2011-2012.

Source of Variation	Df	Mean Square	F value
Parent	13	644.31***	110.65***
Year	1	3601.19***	618.45***
Rep(Year)	7	99.1	17.01
Parent x Year	13	19.71	3.39
Parent x Rep(Year)	39	5.07	0.87
Error	224	5.82	

***Significant at the 0.05 probability level

Table 3.9: Analysis of variance of ground coverage of fourteen tall fescue half-sibs crossed in polycross design and evaluated in mowed spaced planting in Adelphia, NJ in 2011-2012.

Source of Variation	df	Mean Square	F value
Half-sibs	13	1844.89	71.47***
Year	1	65905.64	2553.33***
Rep(Year)	6	313.45	12.14
Half-sibs x Year	13	72.39	2.80
Half-sibs x Rep(Year)	78	105.30	4.08
Error	5231	25.81	

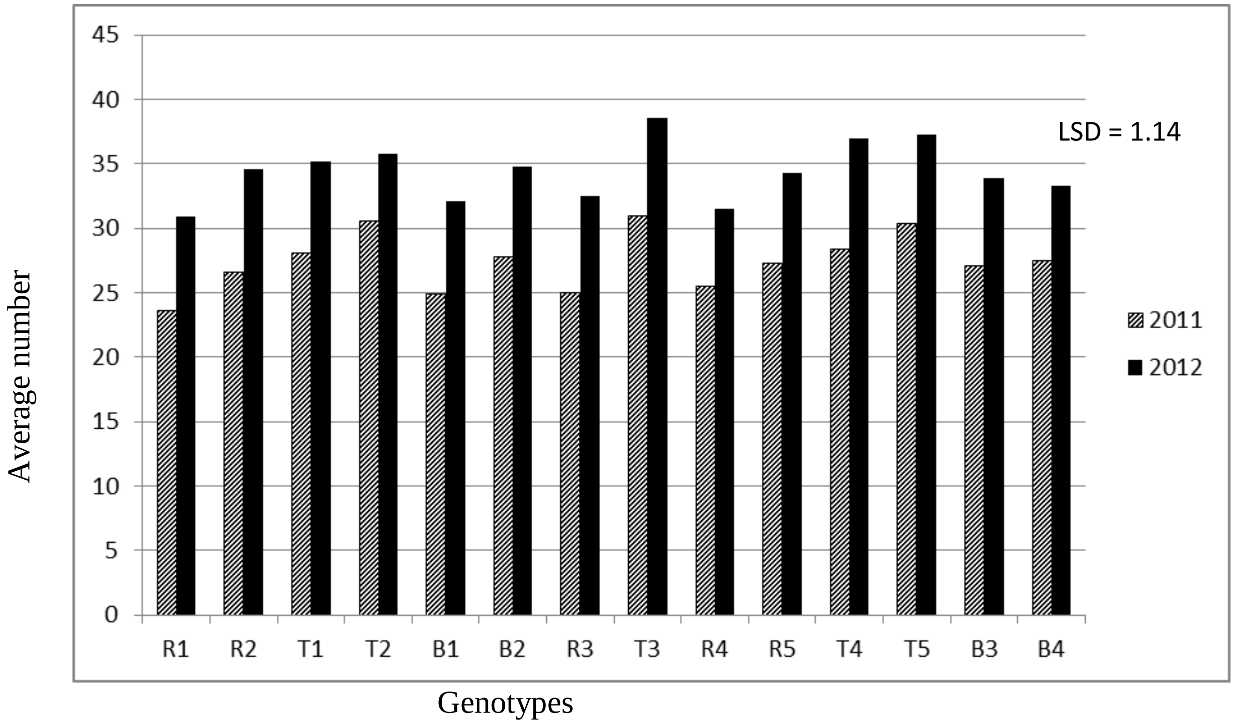
***Significant at the 0.05 probability level

Table 3.10: Means of parents, progeny, and GCA estimate for fourteen parental tall fescue genotypes for ground coverage evaluated in mowed spaced planting in Adelphia, NJ in 2011-2012.

Parent Genotype	Parent Mean	Progeny Mean	GCA
R1	21.58	26.973	-3.92***
R2	32.5	30.62	-0.27
R3	10.85	28.29	-2.60***
R4	29.83	28.46	-2.43***
R5	33.14	30.6	-0.28
T1	36.7	33	2.11***
T2	25.68	31.47	0.58
T3	37.52	34.73	3.84***
T4	34.87	32.68	1.79
T5	38.92	33.66	2.77***
B1	25.54	28.34	-2.54***
B2	30.43	30.21	0.68
B3	29.31	30.47	-0.42
B4	31.71	30.36	0.53
LSD (0.05)	1.37	0.721	

***Significant at the 0.05 probability level

Figure 3.1: Effect of genotypes on the ground coverage over two years (2011 and 2012)



CHAPTER 4

Comparisons between commercial cultivars and experimental breeding populations for rhizome formation and rapid tillering rate in tall fescue

INTRODUCTION

Tall fescue [*Lolium arundinaceum*, (Schreb.) Darbysh.] (2n = 6x = 42) is one of the most widespread cool season, perennial, turfgrasses in the Northern United States and was introduced to U.S. from Europe in mid 1800s as a forage grass (Hoveland, 2009; and Buckner and Cowan, 1973). It is used in golf course roughs, sports fields, home and public lawns, recreational fields (Watkins and Meyer, 2004), low maintenances turfgrass in northern half of US, transition zone and parts of California (Bonos et al, 2006), Tall fescue is native to most of Europe, Mediterranean region (North Africa, parts of Middle East, central Asia), and Siberia (Hopkins et al., 2009). Two major gene pools (Continental type and Mediterranean type) were reported by Hopkins et al. (2009) to characterize tall fescue genotypes. A third gene pool was also reported and named as "Rhizomatous" type which originated from northwest Spain and Portugal (Borrill et al., 1971) and produce rhizomes. de Brujin (2004) reported that germplasm originated from Iberian Peninsula produced prevalent and longer rhizomes. Continental germplasm originated from central and northern Europe and from a portion of Asia whereas Mediterranean germplasm originated from southern Europe, Middle East and North Africa (Hopkins et al., 2009). Continental type is characterized as winter hardy and summer active and often has coarser leaf texture; such as Kentucky-31 (Hopkins et al., 2009); and some plants were reported to produce rhizomes (Jernstedt and Bouton, 1985; Bouton et al., 1989 and Bouton et al., 1992). Rhizomatous types are not as winter hardy as Continental types (Diesburg and Carlson, 1983). Mediterranean types are less winter hardy (Burner et al., 1988) and more winter active and often bear narrower leaves than Continental types. Tall fescue accessions from North Africa were found to be very stiff, and have wiry leaves during spring and summer (Hopkins et al., 2009). Turf type tall fescue were defined as plants with finer leaves, upright, short stature, dense tillering and dark green color and are developed mostly from Continental germplasm (Hopkins et al., 2009).

Tall fescue has gained increased attention as turfgrass type after the release of first commercial turf type tall fescue cultivar “Rebel” in 1980 (Funk et al., 1982). Since then consistent efforts have continued to improve tall fescue for disease and insect resistance, drought tolerance, turf quality, turf density, growth habit, through cycles of selection and hybridization (Morris et al., 2006; Saxena et al., 2011). Recently released cultivars have exhibited superior performances and outperformed the old cultivars (Watkins and Meyer, 2004). Developed tall fescue cultivars are expected to have desirable characteristics such as disease resistance, stress resistance and quality that would favor growers for production and finance (Brilman, 1998).

Commonly, tall fescues is knows as bunch type which primarily grow by vertical tillers and have limited spreading ability (Buckman and Cowan, 1973and Beard, 1973). The genotypic variations in the growth habits of tall fescue genotypes were known with the first report of the short rhizome formation (Porter 1958). The variability in tillering rate was also observed which allow the plants to spread laterally through the production of lateral tillers. The ability of tillers develops rapidly which allows turfgrass to spread laterally with continuous replacement, and cover more ground with uniform density and vigor. The perennial life cycle continuously replaces older tillers with new ones (Robson, 1968). High tiller density is one of the important characteristics of turfgrasses to be utilized as these are necessary for smooth ball roll and to resist weed infestation (Cattani and Struik, 2001). Tillers are the above ground stems that develop within the leaf sheath of adjacent tillers; they have shorter internodes than rhizomes (De Battista and Bouton, 1990). A perennial turfgrass is defined as a dynamic population of tillers, some of which die within a few weeks and some survive for more than a year; thus, the plant is perennial, but tillers are short lived (Robson, 1968). Friend (1965) suggested that tillering rate was influenced by environment and genetic factors. Tillering rate is directly affected by leaf formation interval in grasses; for example, tall fescue has a slower tillering rate than orchard grass (*Dactylis glomerata*) and timothy (*Phleum pratense*).

Rhizomes are vegetative structures that grow horizontally underground, and bear nodes that are separated by internodal connectors (De Battista and Bouton, 1990). Rhizomes originate from the crown as rhizome bud and develop into lateral stem beneath the soil surface, bearing roots and shoots at the nodes. Evans and Ely (1935) suggested that rhizomes enhance competitiveness and persistence in a competitive sward; for example, rhizomes improve the survival of Kentucky bluegrass (*Poa pratensis*) in marginal areas (Moser et al., 1968) and enhance persistence under high temperature and drought stress conditions by serving as a storage organ for carbohydrates (Weaver, 1963; De Battista and Bouton, 1990). Rhizomes also assist in filling bare spots, allow close knitting of turfgrass in sods, fill the gaps and improve traffic tolerance, re-establish turf in open area (Bouton et al., 1992; Brilman, 1998). However it has been reported that those tall fescues with extensive rhizomes have poor turf quality and seed yield (Brilman, 1998). The mixture of tall fescue and Kentucky bluegrass provide the good traffic tolerance of tall fescue and higher recuperative ability of Kentucky bluegrass due to formation of rhizomes in Kentucky bluegrass (Turgeon, 2008).

Traditional tall fescue (non-rhizomatous type) have been reported to have slow recovery from damage and bunchy or clumpy growth when not over-seeded (Brilman, 1998). Turf researches are going on to improve tall fescue with higher rhizome formation with other agronomically important traits in tall fescue. Tall fescue cultivars recently developed have more and longer rhizomes than traditional cultivars (which have shown some short rhizome formation) in tall fescue (Brilman, 1998). With advancement in breeding programs, large number of improved and high performing tall fescue cultivars continues to be released. These cultivars provide a wide range of morphological differences and utility purposes which can be utilized in different regions. Watkins and Meyer (2004) reported that commercial cultivars have exhibited morphological differences when planted in a breeding nursery and characterized turf type tall fescues into semi dwarf, early semi-dwarf, dwarf, standard and forage groups. The semi-dwarf group consists of most cultivars such as Rembrandt, Millennium which have medium height, medium maturity and finer leaves than forage standard and early semi-dwarf groups. Standard group is characterized by the medium leaf width and medium maturity. Dwarf types cultivars have finer leaf texture, highest turf density compared to other groups and are generally late maturing. Kentucky -31 was categorized into

Forage/standard group which has the lowest turf quality, poorest density and wider leaves than other commercial cultivars (Watkins et al., 2003).

Bowman and Macaulay (1991) reported that increase in popularity of tall fescue is due to the improvement in turf quality, disease resistance, turf density, and mowing qualities. Rodney et al., (2009) reported that blend of rhizomatous and non-rhizomatous tall fescue cultivars are available in the market. After comparing the pure stands and blends of rhizomatous and non-rhizomatous turf type tall fescue cultivars, Rodney et al., (2009) reported the establishment rate and lateral spread of rhizomatous type cultivars were slow in both pure stand and in blend as compare to other traditional or non-rhizomatous tall fescue cultivars.

Comparing the commercial cultivars with Rutgers's populations and Moroccan accessions for the different growth habits in tall fescue would provide more information about the genetic variation existing within the species which could be used to evaluate the range of improvement required to enhance the rhizome formation and rapid tillering rate in tall fescue. The objectives of this project were to: (i) compare turf type tall fescue cultivars, Rutgers's populations and Moroccan accessions for the rhizome formation, rapid tillering and ground coverage (ii) estimate Pearson correlation coefficient between rhizome formation, rapid tillering and ground coverage.

MATERIAL AND METHODS

Forty eight tall fescue entries were selected based on their tillering ability and rhizome formation. These entries consist of: nineteen commercial cultivars (Table 1); eight Rutgers's populations (Table 2) and twenty one introduced Moroccan accessions from

Africa (Table 3). The Rutgers's populations were selected from the germplasm collected and maintained at Rutgers, Plant Science and Extension Research Station, Adelphia, NJ. The commercial cultivars were selected based on their reported tillering rate and rhizome formation ability. The accessions from Morocco, Africa were introduced to the United States in 2010 and twenty one accessions were selected based on the rhizome production ability. Seeds from each entry were sown in a pot in the greenhouse in winter 2010 and sixty seedlings were randomly selected from each pot and planted in the randomized complete block design in the field on June 3rd, 2011. The seedlings were kept in the greenhouse before establishing the field trial. The field experiment was designed and established at Rutgers, Plant Science Research and Extension Farm, Adelphia, NJ. The soil type of the field was sandy-loam. The experimental design was composed of five replications and each replication was consisted of 12 individual plants from each entry in a single row at spacing of 0.46 meters. The plants were mowed with a Toro Groundmaster (Toro Corp. Bloomington, MN) twice a week during growing season at the height of 6 cm. In 2011, 2012 and 2013, the application of 9-0-18 (N: P: K) fertilizer was done during the months of May, October and April respectively, at the rate of 0.4 g N m^{-2}. Brown patch was controlled by the spray of Heritage , as labeled (Syngenta, Greensboro, NC), annual weeds with Acclaim as labeled (Bayer Environmental Science, NC) and broad leaf weeds by spraying 2,4 D and Banvel (Du Pont, DE) @ 32 oz. acre and 8 oz/ acre, respectively.

The plants were maintained for a year to grow and produce tillers and rhizomes in the field. The data was collected for the rhizome formation (number of rhizomes per plant), rapid tillering rate (number of tillers per 7.62 cm plug size) and ground coverage (average of length and breadth) in summer 2012 and 2013. The tiller counting was done at the end of the trial in August 2013 because it required the destruction of each individual plant by cutting the 7.62 cm size plugs and counting tillers manually. This method took two weeks to complete counting the tillers. The numbers of rhizomes were counted by hand on each individual plant in the field in June, 2012 and June 2013, respectively. The rhizomes which were >2 cm apart from the mother plant were only counted. Ground coverage was calculated by measuring the length (cm) and breadth (cm) and averaged on each individual plant in June 2012 and June 2013.

Turf color, quality and density ratings were recorded on each individual plant in the nursery in summer 2012-2013. The rating was done on the scale of 1 to 9, where 9 was highest result for density and quality; for leaf color, 9 was the darkest green leaf color.

Statistical Analysis

All the values were averaged over five replications and 2012- 2013 years. The observations were collected on each individual plant for tillering rate (number of tillers per 7.62 cm plug size), rhizome formation (number of rhizomes per plant) and ground cover (cm). All data were analyzed using analysis of variance by the PROC GLM procedure of SAS (SAS Institute Inc., Cary, NC, USA) (Table 2 and 3) and means separation was calculated based on Fisher's LSD.

Pearson correlation coefficient estimation was done using Sigma Plot software 12.2 (Systat Software Inc. San Jose, CA) to determine correlation coefficients between rapid tillering rate, rhizome formation and ground coverage in tall fescue. Pearson correlation coefficient ranges from +1 (absolute positive correlation between two variables) to -1 (absolute negative correlation between two variables).

RESULTS

Rhizome formation (number of rhizomes per plant)

Analysis of variance has shown that significant differences were exhibited by the entries for the rhizome formation in tall fescue (Table 4). The highest rhizome formations were found in the Moroccan accessions, followed by Rutgers's population: PSG 8Az Rh and cultivars: Ky-31, Grande and Jaguar 3 in tall fescue. The lowest mean value for the rhizome formation was found in Turbo TF, Shenandoah III, and CCRI (Table 5).

Rapid Tillering (number of tillers per 7.62 cm plug)

Significant differences for the rapid tillering rate were found between the entries (Table 6). Tall fescue cultivars: Turbo TF, Falcon V, Shenandoah III, Six point, Traverse SRP, Falcon IV, and Firenza and; Rutgers's populations: CCRI, LSD comp, Regenerate and TPC Comp have shown significantly higher rapid tillering in tall fescue whereas the lowest tillering rate was found in the Moroccan accessions: 48944-10, 48980-10, 49851-10 and Ky-31 (Table 5).

Ground Coverage

Analysis of variance showed significant differences between entries and years (Table 7). The entry x year effect was insignificant for ground coverage. Rutgers's populations: LSD Comp, TPC, ATF- 1224, have shown maximum ground coverage followed by the commercial cultivars: Turbo TF, 2nd Millennium, Rhambler SRP, Grande II, Shenandoah

III, Cezanne Rz, Falcon V and Turbo Rz. The smallest ground coverage was shown by the Moroccan accessions (Table 5).

Pearson correlation coefficient

Pearson correlation coefficient was estimated by using Sigma Plot Software between rapid tillering rate, rhizome formation and ground coverage in tall fescue (Table 8). Significant negative correlation was found (r = -0.406 and P value = 0.106×10^{-6}) between rapid tillering rate and rhizome formation in tall fescue. Significant negative correlation coefficient (r= -0.83 and P value = 0.614×10^{-3}) was found between rhizome formation and ground coverage. However, significantly positive correlation (r = 0.73, P = 0.0131×10^{-6}) between tillering rate and ground coverage was obtained in tall fescue.

Turf color, quality and density

Cultivar Turbo TF, Flacon V, Shenandoah III, Six point, Rhambler SRP, Firenza; and Rutgers's populations: LSD Comp, TPC, CCRI, Regenerate, and ATF -1224 have higher turf quality and density. Higher rating for turf color was shown by the cultivars and Rutgers's populations. Moroccan accessions, Rutgers's populations: PSG 8Az Rh and cultivars: Ky-31, Grande and Jaguar 3 have lower ratings for turf color, turf quality and density (Table 9).

DISCUSSION

The results obtained showed that genotypic and phenotypic variations were found in tall fescue commercial cultivars, Rutgers's populations and Moroccan accessions for rhizome formation, rapid tillering and ground coverage. The significant year effect was found for the ground coverage indicating increment in the lateral growth with every year. The lateral spread of the plants is proportionate to the rapid tillering of the plant. Lateral tillers in tall fescue provided uniform ground coverage and reduce clumpy growth appearance. This was supported by the results of this investigation that higher ground coverage was exhibited by the entries which also exhibited higher rapid tillering in tall fescue. On the other hand, rhizomes are also important for the plant spread though it does not provide density and vigor as tillers does but filling the bare spots by colonizing the tillers developed from the rhizomes (Bouton et al., 1992). Moroccan accessions were prolific rhizome producers and hence contain open canopy and poor turf density in the mowed spaced planted nursery. Moroccan accessions have shown higher number of rhizomes per plant which were distributed around the mother plants and length of rhizome ranged from ≥ 2 cm and in some plants to ≥ 20 cm distant from the mother plant in tall fescue. The low turf color, quality and density ratings for Moroccan accessions indicated coarser leaf texture, low shoot density and lighter green leaf color. The similar leaf texture and wiry and stiff leaves were found during spring and summer growth in Mediterranean germplasm originated from North Africa as reported earlier (Hopkins et al., 2009).

The commercial cultivars and Rutgers's populations exhibited significantly higher rapid tillering, ground coverage, high turf quality, density ratings and darker turf color. All these characteristics indicated that cultivars and Rutgers's population were improved through cycles of selections and recombination. Hopkins et al., (2009) reported that source of most of all the tall fescue genotypes in Northern United States was Continental germplasm originating from central and Northern Europe eastward and some part of Asia.

The different growth habits are important for tall fescue improvement and could extend its utility and adaptability to different regions. The results obtained showed that rapid tillering and rhizome formation were negatively correlated and could not be increased simultaneously in the same plant. Similarly, rhizome formation and ground coverage were negatively correlated. This was supported by the data we obtained on each individual plants that cultivars and Rutgers's populations have higher rapid tillering and ground coverage but no or little rhizome formation, whereas Moroccan accessions and cultivars: Jaguar 3 and Ky-31 have higher rhizome formation but lower rapid tillering and ground coverage in the mowed spaced planted nursery.

Some commercially available tall fescue cultivars have shown short rhizome formation and even the first turf type tall fescue cultivar "Rebel" had shown rhizome formation in few plants (Brilman, 1998). Singh et al. (2005) reported that in rhizomatous type tall fescue, not all the plants in the seed lot were capable of producing rhizomes. On the other hand, in non-rhizomatous types fewer plants showed rhizome formation. He also reported that in rhizomatous tall fescue cultivar Labarinth, 88% of plants produced rhizomes, whereas in other (non-rhizomatous) cultivars 16 to 42% of plants showed rhizome formation. Malik et al., (1967); and Hunt and Sleper (1989) reported the meiotic irregularity occurred during the crossing of continental (Central and Northern Europe) and Mediterranean germplasm (North Africa). Similarly, sterile hybrids were obtained when rhizomatous germplasm was crossed with Continental or Mediterranean germplasm. Saxena et al. (2013) reported significant increase in rhizome formation in tall fescue genotypes when grew under long photoperiod (18 H) and significantly higher rapid tillering when treated with low temperature treatment (day/night temperature: 15/10

C), indicating environmental conditions also influence the tiller production and rhizomes formation in tall fescue.

As mentioned by Dunn et al. (2002), rhizome formation is considered necessary in Kentucky bluegrass for sod production and harvesting. Likewise, increase in rhizome formation in tall fescue would enhance the strength of tall fescue sod and its market value. The rhizome formations in the released rhizomatous commercial cultivars were lower than reported by the companies in the spaced planted nursery. Rutgers' populations were mostly tillering types except PSG 8Az Rh which have shown significant rhizome formation. Moroccan accessions were prominently rhizomatous and have produced vigorous number of rhizomes in the mowed spaced planted nursery. Tall fescue cultivars with superior characteristics, lateral spread and increased rhizome formation would aid in the plant's ability to withstand traffic, recover from injury, and good sod strength. Efficient and organized breeding methods could aid development of improved tall fescue synthetic cultivars with significant rhizome formation without compromising rapid tillering and ground coverage in tall fescue.

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Table 4.1: List of tall fescue commercial cultivars evaluated in a mowed spaced planted nursery in Adelphia, NJ, 2012-2013.

Cultivars	Company	Information
Grande II	Seed Research of Oregon	http://www.sroseed.com/Products/PDF/grande_II_ts.pdf
Turbo Rz	Burlingham Seeds	http://www.burlinghamseeds.com/userfiles/products/docs/Turbo-RZ-TF-flyr.pdf
Millennium	Turf Merchants, Inc.	http://www.turfmerchants.com/turf_type_tall_fescue/millenium.php
Shenandoah III	ProSeeds Marketing	http://proseedsmarketing.com/tech-sheets/TF/Shenandoah3-TF.pdf
SR 8650	Seed Research of Oregon	http://www.sroseed.com/Products/PDF/sr8650_ts.pdf
2nd Millennium	Turf Merchants, Inc.	http://www.turfmerchants.com/turf_type_tall_fescue/2nd-millenium.php
Grande	Seed Research of Oregon	http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1489132
Cezanne Rz	Lebanon Seaboard Corp.	http://www.lebanonturf.com/products/items/5866903/index.aspx
Six point	Proseeds Marketing	http://proseedsmarketing.com/tech-sheets/TF/Six_Point.pdf
Turbo TF	Burlingham Seeds	http://www.burlinghamseeds.com/userfiles/products/docs/Turbo-TF-flyr.pdf
Jaguar 3	Jacklin seeds	http://techsheets.simplot.com/Jacklin/jaguar3.pdf
Rhambler SRP	Turf Merchants, Inc.	http://www.turfmerchants.com/turf_type_tall_fescue/rhambler-srp.php
Ky-31	Standard Entry	http://ntep.org/data/tf06/tf06_12-10f/tf0612ftent.txt
Rhizing star	DLF international Seeds	http://www.dlfis.com/upload/rhizing_star_ts_new.pdf
Falcon V	ProSeeds Marketing	http://proseedsmarketing.com/tech-sheets/TF/Falcon-V-TF.pdf
Rembrandt	Lebanonturf	http://www.lebanonturf.com/products/items/5866804/index.aspx
Traversa SRP	Turf Merchants, Inc.	http://www.turfmerchants.com/turf_type_tall_fescue/traverse-srp.php
Firenza	Integra Seeds	http://www.integraturf.com/uploads/1/9/7/8/19785133/firenza_website.pdf

Table 4.2: List of the tall fescue selections from Rutgers, Plant Science Research and Extension Farm, evaluated in mowed spaced planted nursery in Adelphia, NJ, 2012-2013.

Rutgers's populations
TPC Comp
CCRI
LSD Comp
FSD Comp
Regenerate
ATF- 1224
PSG 8Az Rh
A08-88

Table 4.3: List of the accessions introduced from Morocco, Africa evaluated in mowed spaced planted nursery in Adelphia, NJ, 2012-2013.

Moroccan Accessions	Location
48919-10	Touama
48924-10	Immouzer
48933-10	Aquelmorys
48938-10	Aquelmorys
48944-10	Achaoud
48945-10	Achaoud
48947-10	Achaoud
48951-10	Achaoud
48952-10	Achaoud
48953-10	Achaoud
48959-10	Achaoud
48960-10	Achaoud
48973-10	Ibel Quanzel
48980-10	Ibel Quanzel
48981-10	Ibel Quanzel
48985-10	Ibel Quanzel
48988-10	Ibel Quanzel
49012-10	Ibel Quanzel
49016-10	Ibel Quanzel
49107-10	Cathechale
49112-10	Et Tnine

Table 4.4: Analysis of variance of rhizome formation for the forty eight entries of tall fescue evaluated in a mowed spaced planted nursery in Adelphia, NJ in 2012-2013.

Source of variation	df	Mean square
Entry	47	3280.48***
Year	1	13905.38***
Replication (Year)	4	3.45
Entry x Year	47	26.35
Entry x Replication	188	6.64
Entry x Year x Replication	188	8.55
Error	5080	12.48

***Significant at the 0.05 probability level

Table 4.5: Mean value of rapid tillering (number of tillers per 7.62 cm plug), rhizome formation (no. of rhizome per plant), and ground coverage (cm) of entries of tall fescue evaluated in a mowed spaced planted nursery in Adelphia, NJ in 2012-2013.

Entry	Rapid tillering	Rhizome formation	Ground Coverage
Turbo TF	92.61	0.197	30.1
Turbo Rz	64.62	0.56	28.96
Traverse SRP	74.94	0.36	28.03
TPC Comp	70.55	0.75	30.28
SR 8650	51.3	0.27	28.94
Six point	75.44	0.34	28.35
Shenandoah III	74.62	0.10	29.81
Rhizing star	43.68	0.61	25.7
Rhambler SRP	63.75	0.46	29.70
Rembrandt	48.43	0.73	28.3
Millennium	52.41	0.62	28.93
2nd Millennium	58.93	0.39	29.91
Regenerate	72.6	0.48	28.76
LSD Comp	79.92	0.95	31.22
Ky-31	21.44	2.29	24.53
Jaguar 3	43.91	1.097	28.74
Grande II	58.66	0.40	29.52
Grande	39.76	1.22	28.71
FSD Comp	62.20	0.83	28.52
Firenza	67.12	0.22	28.63
Falcon V	83.23	0.87	29
Falcon IV	69.95	0.57	28.94
Cezanne Rz	55.69	0.94	29.33
CCRI	80.11	0.08	28.91

ATF- 1224	61.04	0.33	29.94
PSG 8Az Rh	41.48	5.62	23.73
A08- 88	51.99	0.45	29.08
49112-10	23.34	7.6	27.25
49107-10	25.82	5.41	26.62
49016-10	27.18	8.63	24.7
49012-10	29.33	8.52	24.44
48988-10	30.7	4.41	23.55
48985-10	23.53	8.95	24.31
48981-10	26.71	6.28	24.18
48980-10	21.95	10.9	22.60
48973-10	22.72	7.5	23.73
48960-10	23.05	17.7	22.26
48959-10	27.26	14.65	23.69
48953-10	24.37	11.76	21.39
48952-10	28.76	13.94	22.08
48951-10	21.81	13.33	20.54
48947-10	31.37	14.15	22.85
48945-10	30.84	14.7	21.86
48944-10	21.22	13.5	22.50
48938-10	26.4	6.3	23.88
48933-10	23.63	9.51	24.91
48924-10	32.81	7.34	25.74
48919-10	28.88	5.2	25.3
LSD (5%)	6.67	0.91	0.85

Table 4.6: Analysis of variance of tillering rate for the forty eight entries of tall fescue evaluated in a mowed spaced planted nursery in Adelphia, NJ in 2013.

Source of variation	df	Mean square
Entry	47	26211.95***
Replication	5	6184.14
Entry x Replication	188	3783.2
Error	2541	334.96

***Significant at the 0.05 probability level

Table 4.7: Analysis of variance of ground coverage for the forty eight entries of tall fescue evaluated in a mowed spaced planted nursery in Adelphia, NJ in 2012-2013.

Source of variation	df	Mean square
Entry	47	1017.65***
Year	1	46506.01***
Replication (Year)	4	108.82
Entry x Year	47	201.41
Entry x Replication	188	52.99
Entry x Year x Replication	188	14.95
Error	5086	10.95

***Significant at the 0.05 probability level

Table 4.8: Correlation between rapid tillering, rhizome formation and ground coverage for tall fescue cultivars, Rutgers's population and Moroccan accessions evaluated in mowed spaced planted nursery in Adelphia, NJ in 2011-2012.

Traits	Entries
rapid tillering vs rhizome formation	-0.406***
rapid tillering vs ground coverage	0.734***
rhizome formation vs ground coverage	-0.833***

***Significant at the 0.05 probability level

Table 4.9: Mean values of turf color, quality and density for tall fescue cultivars, Rutgers's population and Moroccan accessions evaluated in a mowed spaced planted nursery in Adelphia, NJ in 2012-2013.

Entry	Turf Color	Turf Quality	Turf density
Turbo TF	7.17	6.89	7.06
Turbo Rz	6.73	5.45	5.70
Traverse SRP	6.81	5.54	6.08
TPC	6.88	6.15	6.78
SR 8650	6.90	5.27	5.53
Six point	7.12	5.85	5.88
Shenandoah III	6.73	6.47	6.95
Rhizing star	5.78	5.08	5.42
Rhambrandt	6.09	4.47	4.35
Rhambler SRP	6.65	5.87	6.65
Millennium	6.57	4.48	4.90
2nd Millennium	6.83	5.12	5.76
Regenerate	6.68	5.58	6.28
LSD Comp	7.10	7.77	7.40
Ky-31	3.84	3.05	2.54
Jaguar 3	5.53	3.35	4.57
Grande II	6.65	5.79	6.47
Grande	5.47	4.95	5.37
FSD Comp	6.85	5.17	5.48
Firenza	7.00	6.05	6.41
Falcon V	7.14	6.61	6.71
Falcon IV	6.58	5.53	6.14
Cezanne Rz	6.43	5.05	5.10
CCRI	6.66	5.76	6.38

ATF 1224	6.88	5.50	5.62
A08-88	6.85	5.44	6.08
PSG 8Az Rh	3.96	3.19	3.21
49112-10	3.71	2.48	4.00
49107-10	3.21	2.67	3.66
49016-10	3.36	2.38	3.21
49012-10	3.03	2.39	3.56
48988-10	2.87	2.46	3.59
48985-10	3.03	2.03	3.95
48981-10	2.92	2.02	3.90
48980-10	3.25	2.10	3.02
48973-10	3.17	2.15	3.31
48960-10	3.20	2.32	3.07
48959-10	3.19	2.37	3.46
48953-10	3.24	2.19	2.62
48952-10	3.09	2.44	3.25
48951-10	3.35	2.02	3.02
48947-10	3.17	2.52	3.20
48945-10	3.36	2.26	3.79
48944-10	3.08	2.18	3.77
48938-10	3.41	2.49	3.42
48933-10	3.48	2.33	3.98
48924-10	3.41	2.33	3.59
48919-10	3.85	2.34	3.63
LSD (5%)	1.20	1.32	1.15

CHAPTER 5

Conclusion of Dissertation

The improvement in tall fescue has been astronomical since the development of first forage type cultivars “Alta” and ‘Kentucky-31” in United States. After the release of first land mark turf type cultivar “Rebel”, the standard for the development of superior and high performing tall fescue cultivars was established. The current varieties such as Regenerate, Falcon V, Grande 3, Shenandoah III, SR 8650, and Traverse SRP showed high turf quality, disease resistance, turf density, drought and heat tolerance. However most of the commercial tall fescue cultivars lack lateral spreading ability and rhizome production.

In this research, the genetic control of different growth habits was studied to understand to the inheritance of rhizome formation and rapid tillering rate in tall fescue. The genetic information obtained should assist breeders to enhance the rhizome production and rapid lateral tillering rate in tall fescue that would improves the utility, adaptability and market value of tall fescue in the turfgrass industry.

The role of environmental conditions were evaluated in the experiment using growth chambers with different photoperiod and temperature combinations; and found that long photoperiod (18 H) influenced the rhizome formation; and low temperature (day night 10/15 C) increased the tillering rate in selected tall fescue genotypes.

Diallel and polycross mating designs were employed to analyze the combining abilities of the selected genotypes. The results showed that additive gene effects controlled the rapid tillering and ground coverage in tall fescue. For rhizome formation, both additive and non-additive gene effects were significant. This indicated that a recurrent selection breeding program should be effective in aggregating additive alleles that will be fixed in the experimental breeding population which may develop into advanced populations to be use in synthetic cultivar development. Recurrent selection could be effective in improving the rapid tillering and bunch type growth habits in tall fescue, whereas rhizome formation could be improved by employing reciprocal recurrent selection breeding program in tall fescue. The results indicated that genetic effects were the major forces influencing the phenotypic expression in tall fescue. Maternal and reciprocal effects were also observed in the results for the tiller density and to evaluate their roles similar studies should be conducted at multiple locations for multiple years.

The correlation between rhizome formation and rapid tillering was negatively significant indicating with increase in rhizome formation the rapid tillering may not increase significantly. On the other hand, rapid tillering and ground coverage were positively correlated indicating that with increase in rapid tillering, ground coverage may increase significantly. The rapid tillering and bunch type showed higher tiller density in a 7.62 cm plug indicating their ability to exhibit rapid tillering however lower ground coverage values of bunch types suggested compact and limited spreading ability as compare to rapid tillering types (Fig. 5.1 and 5.2).

To estimate an increase in biomass as a measure of turf density, remote sensing technique (Multisprectral Radiometry) was utilized and Normalized Difference Vegetative Index (NDVI) was calculated (in 2011). In the following year (2012) the tillers were counted in the field in a 7.62 cm plug and correlation was estimated between the tiller density and NDVI values. High correlation was found between tiller density and

NDVI, indicating that tiller density was consistently increasing in rapid tillering and bunch type; and can be estimated without destructing plants and labor intensive method instead using remote sensing techniques.

The rhizome formation was observed in the crosses between non-rhizomatous parents (T1 x B2) indicating phenotypic plasticity may be due to the environmental influence (Fig. 5.3). It is important to evaluate rhizome formation and tillering traits at multiple locations for multiple years to estimate effects of environment and genotypic variations influencing growth habits in tall fescue. The rhizomes were developed around the mother parent ≥ 2cm distant. The area between the mother parent and rhizome was covered mostly by the aerial tillers produced from rhizomes (Fig. 5.4).

Both rapid tillering and greater ground coverage were referred to “rapid lateral tillering type growth habit” of tall fescue whereas the ability of tall fescue plants to produce higher number of tillers without significant lateral spread was referred to as “bunch type growth habit” in tall fescue; and rhizomes production with lower number of tillers referred to “rhizome type”, respectively. Rapid tillering genotype T2 showed both rhizome formation and rapid tillering in the mowed-spaced planting. The significant rhizome production was observed in the parental clones as well in the rhizome parents (R1, R2) x T2 (including reciprocals). The significant tillering rate was found in the crosses between the rapid tillering parents T1 x T2 and T2 x T1, respectively. This indicated parent T2 may considered as an intermediate type parent.

The rhizome types may be linked to coarser leaf texture and open turf canopy as most of the plant storage carbohydrates were assimilated to rhizome production or into tiller production. This was supported by the negatively correlation obtained using Pearson Correlation Coefficient. Therefore it is important to evaluate the relationship between carbon assimilation, rhizome formation, and tillering rate in tall fescue to predict the development of different growth structures in tall fescue.

The research conducted on the commercial tall fescue cultivars and experimental breeding populations elucidated that introduced Moroccan accessions collected from Africa produced very high number of rhizomes and exhibited coarser texture and poor tiller density. On the contrary, most of the commercial cultivars and Rutgers's population showed little or no rhizome formation but high tillering exhibited high turf density and fine texture in the mowed- spaced planted nursery. The rhizomatous cultivars reported earlier as rhizomatous types did not show high rhizome formation as expected. This field experiment suggested the requirement of developing new cultivars which produce significant number of rhizomes and higher tillering rate in tall fescue.

From this research project we can conclude that selection of superior genotypes based on their combining abilities (such as R1, R2, T1 and B2) and employing efficient breeding method (recurrent selection) are the important factors to improve the rhizome formation without compromising the tillering rate in tall fescue; and to enhance its utility, adaptability and market value.

Further research would also require evaluating tall fescue at multiple locations for more than one year to estimate the influence of environmental, maternal and reciprocal effects on rhizome and tillering traits which would provide breeders with relevant information about the genetic factors as well as the environmental conditions influencing the rhizome formation and rapid tillering rate in tall fescue. The obtained information would help in selecting the superior genotypes for breeding program and development of cultivar(s) outperforming the older cultivars. The development of a genetic linkage map of tall fescue and the subsequent identification of putative QTLs associated with rhizome and tillering traits in tall fescue would enhance the knowledge about the expression of different growth habits.

Figure 5.1: Bunch type growth habit exhibited by progenies in mowed tiller plots obtained from the cross between bunch type parents (B1 x B2) in studies at the Adelphia Research farm, Adelphia, NJ.

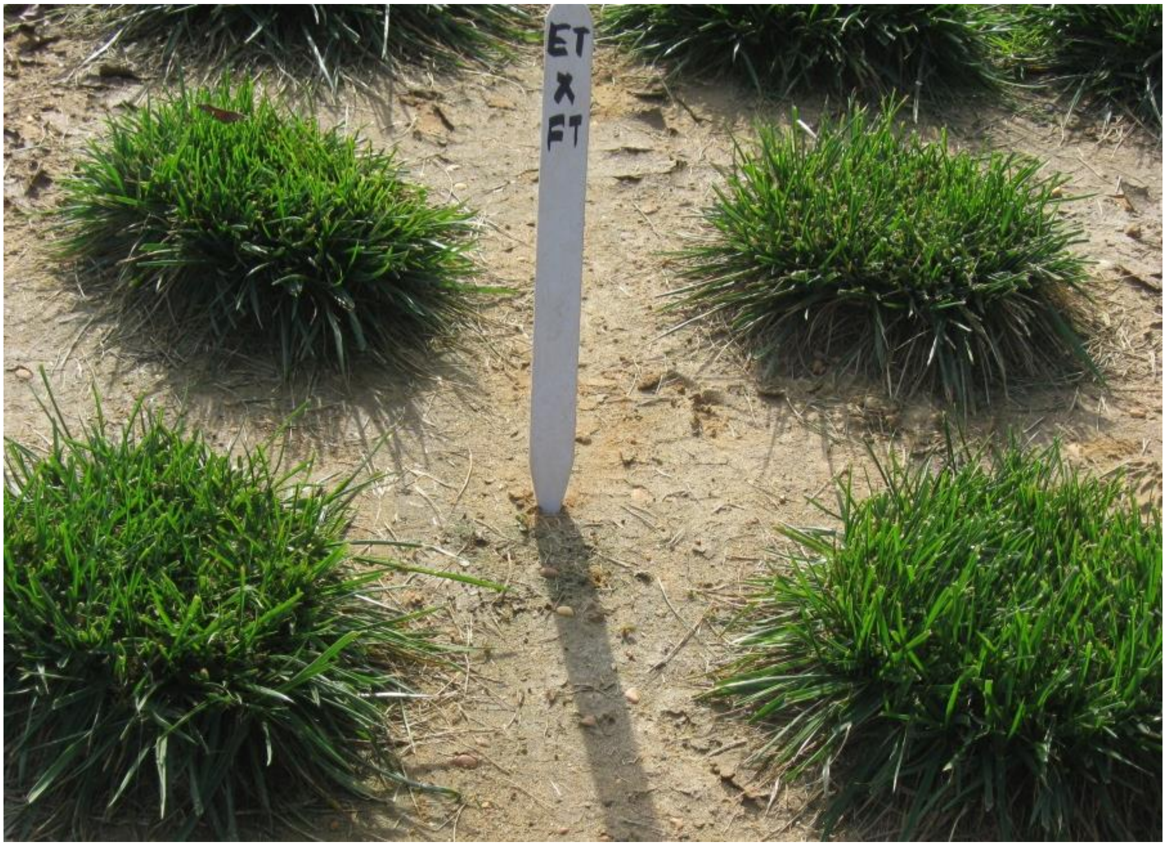

Figure 5.2: lateral spread exhibited by progenies progenies in mowed tiller plots obtained from the cross between rapid tillering type parents (T1 x T2) in studies at the Adelphia Research farm, Adelphia, NJ.

Figure 5.3: The rhizome formation in mowed tiller plots in the cross between rapid tillering and bunch type parents (T1 x B2) at at the Adelphia Research farm, Adelphia, NJ.

Figure 5.4: Rhizome production in R1 x R2 and aerial tillers developed from the rhizomes in the mowed tiller plots at the Adelphia Research farm, Adelphia, NJ.