# ESTIMATION OF GENETIC PARAMETERS

# IN SEVERAL SWITCHGRASS

## (Panicum virgatum L.) POPULATIONS

By

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# IN SEVERAL SWITCHGRASS (Panicum

Virgatum L.) POPULATIONS

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## CHAPTER I

#### INTRODUCTION

#### THE RESEARCH PROBLEM

Switchgrass (*Panicum virgatum* L.) is a warm-season, perennial, determinate species indigenous to the precolonial tall grass prairies east of the Rocky Mountains (Hopkins et al., 1995). It is a bunchgrass that assimilates carbon via the C<sub>4</sub> photosynthetic pathway (Sanderson, 1992). Currently, the major uses of the crop are for livestock feed and soil stabilization.

Over the past decade, switchgrass has been the focus of a national research effort to develop a herbaceous energy crop (HEC). The potential of switchgrass for that purpose derives from its broad geographic adaptation, ability to grow on non-crop soils, and high biomass production with minimal inputs (McLaughlin et al., 1999). A portion of the developmental effort with switchgrass as a HEC involves the breeding of cultivars adapted to specific environments and having enhanced biomass yield. One of the breeding programs is located at Oklahoma State University (OSU). Other institutions involved in this collaborative research effort (launched by the United States Department of Energy through its Biomass Feedstock Development Program) are Auburn University (cultural practices), Texas A&M University (cultural practices), Virginia Tech University (cultural

practices), University of Tennessee (tissue culture), and Oak Ridge National Laboratory (physiology).

In support of the overall goal of developing switchgrass into a profitable HEC, the breeding project at OSU seeks to develop cultivars with enhanced biomass yield capabilities within a specific target region; the central and southern Great Plains (Taliaferro, 2002). Objectives of the breeding program are collection and evaluation of switchgrass germplasm for its performance, characterization of breeding behavior, determination of biosystematic relationships between ecotypic or ploidy forms, and estimation of genetic parameters for performance traits.

Recurrent selection for general combining ability to increase biomass production is currently underway in three genetically broad-based switchgrass populations. Associated research seeks to gain information regarding the kinds and relative magnitudes of heritable variation in those populations as well as in switchgrass generally. This information should provide more accurate estimates of selection response and could help identify improvements in current breeding procedures.

Recurrent selection is a conventional breeding procedure designed to provide improvement in quantitative characters (e.g. biomass yield) of plant populations by increasing the frequency of genes conditioning the trait of interest. Effective recurrent selection changes the mean of a population while maintaining genetic variation (Poehlman and Sleper, 1995).

A related part of this study seeks to discover what effects, if any, environment has upon selection for biomass yield and ultimately upon the performance of

cultivars emanating from that selection process. It was also desirable to identify predictable environmental variation so that the size of genotype-by-environment (GE) interactions could be reduced (Yau et al., 1991). Significant GE interactions for a quantitative trait reduce the usefulness of means over all environments for selection and advancing superior genotypes to the next stage of selection. Furthermore, GE interactions reduce the correlation between phenotypic and genotypic values and reduce the progress from selection (Pham and Kang, 1988).

Cultivars developed in high-yield environments may not perform well when grown in low-yield environments and vice versa. A successful switchgrass cultivar used as a HEC would likely be grown in a wide range of yield environments. Thus, it is important to know if the yield environment under which breeding is conducted will result in cultivars that perform well only in the same (or similar) yield environments after release.

#### LITERATURE REVIEW

Switchgrass is polymorphic and allogamous, as are most forage grass species, due to the presence of varying levels of self-incompatibility within the species (Nguyen and Sleper, 1983). Asexual seed production in the species has not been determined to date within the germplasm collection housed at OSU (McLaughlin et al., 1996). Outcrossing in switchgrass is achieved via wind

pollination and reinforced by considerable self-incompatibility (C.M. Taliaferro, personal communication).

In general, forage crops represent unique components in multipurpose cropping systems in that they can be used for soil conservation, livestock feed, a cash crop, wildlife habitat, and an aesthetic component to the landscape (Sanderson et al., 1996). Switchgrass may be employed for each of the aforementioned functions.

Two major ecotypic forms, lowland and upland, have been recognized based on morphology and habitat preference (Porter, 1966). Plants of lowland ecotypes are typically more robust, exhibiting coarser and thicker stems than their upland counterparts. The lowland ecotypes are tall-growing and are adapted to relatively wet growing sites. Plants of upland ecotypes are generally shorter with finer stem and leaf characters and are more adapted to drier habitats and more marginal soils. Extensive variation exists within each of those ecotypes for a variety of characters.

Upland ecotypes are preferred over lowland ecotypes for grazing and for forage production because of their finer stems and because they are significantly more tolerant of droughty conditions. Upland ecotypes are generally capable of providing abundant forage during hot summer months when cool-season grasses are generally unproductive (Vogel et al., 1979).

Switchgrass constitutes a polyploid series with reported chromosome numbers ranging from 2n = 2x = 18 to 12x = 108 (Nielson, 1944; Henry and Taylor, 1989). All confirmed lowland ecotypes have been tetraploids (2n = 4x = 36) and most

upland ecotypes are octoploids (2n = 8x = 72) (Hopkins et al., 1996). However, it is common for upland types to be hexaploid (2n = 6x = 54) (Sanderson et al., 1996). Allozyme inheritance studies have suggested that the inheritance mode of the species is disomic as opposed to polysomic (Taliaferro, 2002).

Genetic variation within switchgrass is generally thought to be considerable, and studies estimating the heritabilities of several traits within that variation that have been conducted or are currently underway. However, information on the inheritance of biomass yield and yield components in switchgrass is limited. In general, most currently published studies of genetic variation in switchgrass address the enhancement of forage quality, resistance to pathogens, and seedling establishment.

Talbert et al. (1983) reported narrow-sense heritability  $(h_n^2)$  estimates of 0.25 and 0.59 based on individual half-sib (HS) progeny means, respectively, for plant dry weight in lowland switchgrass populations. Eberhart and Newell (1959) reported broad-sense heritability  $(h_b^2)$  estimates of 0.78 for plant yield in an upland switchgrass population derived from strains endemic to Nebraska. Newell and Eberhart (1961) also reported heritability estimates for upland switchgrass from Nebraska and northern Kansas separated into "small bluegreen", "medium blue-green", and "tall green" plant populations. They evaluated 133 and 119 clones of "small blue-green" and "medium-tall blue-green" types, respectively, for several characters in replicated trials. Their estimates of  $h_b^2$  for biomass yield on a single plant basis were 0.23 and 0.19 for the "small bluegreen" and "medium-tall blue-green" types, respectively. Estimates of  $h_b^2$  on a

clonal mean basis were 0.42 and 0.45 for the two types, respectively. Several clones were selected based on superior performance for several characters in each of the three types. They reported  $h_b^2$  estimates using variance component analysis of the selected clones from two of the types and  $h_n^2$  estimates from the parent-offspring regression for each of the three types. Estimates of  $h_n^2$  for "small blue-green" and "medium-tall blue-green" populations were 0.57 and 0.40, respectively. The  $h_n^2$  estimates were 0.18, 0.52, and 0.05 for the three types, respectively.

Van Esbroeck et al. (1998) investigated variation for time-to-panicle emergence (i.e. maturity) in 'Alamo' switchgrass as a potential means to enhance biomass yield; the presumption was that later flowering plants would accumulate more biomass than those that headed earlier. Plants selected for early vs. late maturity differed in heading date by 22 d (10 d earlier compared to 12 d later than the mean heading date) and produced subsequent populations that also differed from the reference population mean. Postestablishment year realized heritability estimates from field study were 1.00 for early heading and 0.92 for late heading. Realized heritability estimates from field and greenhouse studies were lower for early heading (greenhouse, 0.21; field, 0.33) and higher for late heading (greenhouse 1.9; field, 1.75). Those differences relative to the later results were attributed to differential development of parent and progeny plants started from clones vs. seedlings, respectively. Talbert et al. (1983) also reported high  $h_n^2$ estimates (0.91 to 1.49) for heading date in lowland switchgrass. They concluded that selection could be used to either hasten or delay the trait.

Hopkins and Taliaferro (1997) reported minimal variation and low, nonsignificant  $h_n^2$  estimates for acid soil tolerance in the seedling stage of 'Kanlow' and 'Blackwell' switchgrass, lowland and upland ecotypes, respectively.

Heritability estimates for forage yield and yield components have been reported in several other grass species. Ross et al. (1975) reported a  $h_n^2$ estimate of 0.68 for forage yield in big bluestem (Andropogon gerardii Vitman). Vogel et al. (1981) reported an average  $h_n^2$  estimate of 0.43 for forage yield in two populations of indiangrass [Sorghastrum nutans (L.) Nash]. Barker et al. (1989) reported  $h_b^2$  estimates of 0.71, 0.84, 0.95, and 0.78 for forage yield in crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Shult.], intermediate wheatgrass [Thinopyrum intermedium (Host) Barkworth and Dewey], western wheatgrass [Pacopyrum smithii Rybd. (Löve)], and reed canarygrass (Phalaris arundinacea L.), respectively. Based on HS progeny means, Ray et al. (1997) reported  $h_n^2$  estimates of 0.52, 0.63, 0.15, 0.68, 0.49, 0.59, 0.36, and 0.70 for forage dry matter yield, tiller height, first-cut vigor, regrowth vigor, proline content, spikes per spike, anthocyanine pigmentation of stem nodes, and flag leaf pubescence, respectively, in diploid crested wheatgrass. Casler (1988) reported  $h_{p}^{2}$  estimates of 0.30 to 0.42 for forage yield within eight populations originating from smooth bromegrass (Bromus inermis Leyss. ), orchardgrass (Dactylis glomerata L)., and ryegrass (Lolium perene L. and L. hybridium Hausskm.).

Results from studies on the effects of variable yield environment on selection and cultivar performance vary from crop to crop. Gotoh and Osania (1959) reported that selection for increased grain yield in wheat (*Triticum aestivium* L.)

was more effective under a low-yield environment than under a high-yield environment. Conversely, Allen et al. (1978) found that selection for grain yield traits in soybean [*Glycine max* (L.) Merr.] and wheat were more effective under high-yield environments than under low-yield environments. Vela-Cardenas and Frey (1972) reported equal effectiveness in selection for seed weight in oat (*Avena sativa* L.) under low- vs. high-yield environments. Whitehead and Allen (1990) concluded that the low-stress environments commonly used in soybean breeding should provide high probabilities for selecting superior lines for performance in both low- and high-stress edaphic conditions.

The studies presented in the following chapters of this dissertation are intended to further the overall goal of development of switchgrass cultivars with enhanced biomass yield potential. Studies were conducted to estimate heritabilities for enhanced biomass yield and to determine if the yield environment under which breeding was conducted influenced the selection of parental plants and ultimately the yield level and stability of the derived commercial cultivars. Specific objectives were to estimate genetic variances, heritabilities, and genetic gain from selection for increased biomass yield within two lowland and two upland switchgrass populations and, to determine the effects of high- vs. low-yielding environments on the selection of switchgrass plants for enhanced biomass yield.

#### REFERENCES

- Allen, F.L., R.E. Comstock, and D.C. Rasmusson. 1978. Optimal environments for yield testing. Crop Sci. 18:747-751.
- Barker, R.E., A.B. Frank, and J.D. Berdahl. 1989. Cultivar and clonal differences for water-use efficiency and yield in four forage grasses. Crop Sci. 29:58-61.
- Casler, M.D. 1988. Performance of orchardgrass, smooth bromegrass, and ryegrass in binary mixtures with alfalfa. Agron. J. 80:509-514.
- Eberhart, S.A., and L.C. Newell. 1959. Variation in domestic collections of switchgrass, *Panicum virgatum* L. Agron. J. 51:613-616.
- Gotoh, K., and Osania. 1959. Efficiency of selection for yield under different fertilizer levels in a wheat cross. Jpn. J. Breed. 9:173-178.
- Henry, D.S., and T.H. Taylor. 1989. Registration of KY 1625 switchgrass germplasm. Crop Sci. 29:1096.
- Hopkins, A.A. and C.M. Taliaferro. 1997. Genetic variation within switchgrass populations for acid soil tolerance. Crop Sci. 37:1719-1722.
- Hopkins, A.A., C.M. Taliaferro, C.D. Murphy, and D. Christian. 1996. Chromosome number and nuclear DNA content of several switchgrass populations. Crop Sci. 36:1192-1195.
- Hopkins, AA., K.P. Vogel, K.J. Moore, K.D. Johnson and I.T. Carlson. 1995. Genotypic variability and genotype x environment interactions among switchgrass accessions from the midwestern USA. Crop Sci. 35:565-571.
- McLaughlin, S.B., R. Samson, D. Bransby, and A. Wiselogel. 1996. Evaluating physical, chemical, and energetic properties of perennial grasses as biofuels [Online]. In Proc. BIOENERGY '96, The Seventh National Bioenergy Conference: Partnerships to Develop and Apply Biomass Technologies. p. 15-20 Sept. 1996. Nashville, TN. Available at <u>http://bioenergy.ornl.gov/papers/bioen 96/mclaugh.html</u> (modified 11 Nov. 1999; accessed 27 Feb. 2002.)
- McLaughlin, S., J. Bouton, D. Bransby, B. Conger, W. Ocumpaugh, P. Parrish, C. Taliaferro, K. Vogel, and S. Wullschleger. 1999. Developing switchgrass as a bioenergy crop. p. 282-299. *In* J. Janick (ed.), Perspectives on new crops and new uses. ASHS Press, Alexandria, VA.

- Newell, L.C. and S.A. Eberhart. 1961. Clone and progeny evaluation in the improvement of switchgrass, Panicum virgatum L. Crop Sci. 1:117-121.
- Nguyen, H.T., and D.A. Sleper. 1983. Theory and application of half-sib matings in forage grass breeding. Theor. Appl. Genet. 64:187-196
- Nielson, E.L. 1944. An on-farm test of perennial forage grass varieties under management intensive grazing. J. Agron. Res. 69:327-353.
- Pham, H.N. and M.S., Kang. 1988. Interrelationships among and repeatability of several stability statistics estimated from international maize trials. Crop Sci. 28:925-928.
- Poehlman, J.M. and D.A. Sleper. 1995. Breeding field crops. 4th ed. Iowa State Univ. Press, Ames.
- Porter, C.L., Jr. 1966. An analysis of variation between upland and lowland switchgrass, Panicum virgatum L., in central Oklahoma. Ecology 47:980-992.
- Ray, I.M., A.B. Frank, and J.D. Berdahl. 1997. Genetic variances of agronomic and morphological traits of diploid crested wheatgrass. Crop Sci. 37:1503-1507.
- Ross, J.G., R.T. Thaden, and W.L. Tucker. 1975. Selection criteria for yield and quality in big bluestem grass. Crop Sci. 15:303-306.
- Sanderson, M.A. 1992. Morphological development of switchgrass and kleingrass. Agron. J. 84:415-419.
- Sanderson, M.A., L.R. Reed, S.B. McLaughlin, S.D. Wullschleger, B.V. Conger, D.J. Parrish, D.D. Wolf, C. Taliaferro, A.A. Hopkins, W.R. Ocumpaugh, M.A. Hussey, J.C. Read, and C.R. Tischler. 1996. Switchgrass as a sustainable bioenergy crop. Bioresour. Technol. 56:83-93.
- Talbert, L.E., D.H. Timothy, J.C. Burns, J.O. Rawlings, and R.H. Moll. 1983. Estimates of genetic parameters in switchgrass. Crop Sci. 23:725-728.
- Taliaferro, Charles M. 2002. Breeding and selection of new switchgrass varieties for increased biomass production. Oak Ridge Natl. Lab. Available at http://www.ornl.gov/~webworks/cppn/y2001/rpt/116285.pdf. (accessed 20 Apr.2005.)

- Van Esbroeck, G.A., M.A. Hussey, and M.A. Sanderson. 1998. Selection response and developmental basis for early and late panicle emergence in Alamo switchgrass. Crop Sci. 38:342-346.
- Vela-Cardenas, M., and K.J. Frey. 1972. Optimum environments for yield testing. Iowa State J. Sci. 46:381-394.
- Vogel, K.P., F.A. Haskins, and H.J. Gorz. 1979. Improving switchgrass, Panicum virgatum, as a forage crop. p. 8. In Proc. of the Grass Breeders Work Planning Conf.
- Vogel, K.P., H.J. Gorz, and F.A. Haskins. 1981. Heritability estimates for height, color, erectness, leafiness, and vigor in indiangrass. Crop Sci. 21:734-736.
- Whitehead, W.F., and F.L. Allen. 1990. High- vs. low-stress yield test environments for selecting superior soybean lines. Crop Sci. 30:912-918.
- Yau, S.K., G. Ortiz Ferrara, and J.P. Srivastava. 1991. Classification of diverse bread wheat-growing environments based on differential yield responses. Crop Sci. 31:571-576.

## CHAPTER II

# HIGH- VS. LOW-YIELD ENVIRONMENTS ON BIOMASS SELECTION WITHIN A LOWLAND SWITCHGRASS POPULATION

#### ABSTRACT

Switchgrass (*Panicum virgatum* L.) breeding objectives commonly include the enhancement of biomass yield in cultivars amenable for use in pasture and range plantings and as a herbaceous energy crop. No information is currently available on the effects of different environments on switchgrass plant selection. This study was conducted to assess the effects of high-yield environment (HYE) and low-yield environment (LYE) on plant selection in a lowland switchgrass (NL-94) population when subjected to recurrent selection for general combining ability (RSGCA). The top 22% of NL-94  $C_0$  parent plants were selected on the basis of biomass yield performance of clonal sets of half-sib (HS) progeny grown under HYE conditions. The same was done under LYE conditions. Selected plants were intercrossed to produce NL-94 HYE and NL-94 LYE  $C_1$  populations. The HS  $C_1$  progeny families (60 NL-94 HYE and 65 NL-94 LYE) were evaluated for dry biomass yield performance for 3-yr (2002-2004) under HYE and LYE conditions. The HYE produced about three times higher HS

biomass yields than the LYE. Nine of the 14 NL-94 C<sub>0</sub> parent plants selected under the HYE were also selected in the LYE. Biomass yield differences of C<sub>1</sub> HS progeny were attributable to year\*environment, year, family groups (S<sub>HYE</sub> vs S<sub>LYE</sub>) and family within groups. Yields of HS C<sub>1</sub> LYE families were significantly higher than the corresponding HYE families in both test environments all 3-yr. The 3-yr mean C<sub>1</sub> HS HYE and LYE yields indicated selection sets of C<sub>1</sub> parents with 43 and 1% congruence for 30 and 16% selection intensities, respectively. The results suggest greater yield gains from RSGCA conducted under LYE compared to HYE conditions.

#### INTRODUCTION

Switchgrass (*Panicum virgatum* L.) is a warm-season, perennial, determinate species indigenous to the precolonial tall grass prairies east of the Rocky Mountains (Hopkins et al., 1995). It is a bunchgrass that assimilates carbon via the C<sub>4</sub> photosynthetic pathway (Sanderson, 1992). Traditional uses for switchgrass are as livestock herbage and for soil stabilization. In the early 1990s switchgrass was chosen by the US Department of Energy through its Biomass Feedstock Development Program as a model species on which to focus research aimed at developing a herbaceous energy crop (HEC) (McLaughlin et al., 1999). Switchgrass was chosen because of its broad geographic adaptation, ability to grow on noncrop soils, and high biomass production capability with minimal inputs (McLaughlin et al., 1999).

The strategy to develop switchgrass as a HEC crop includes breeding to enhance biomass yield and provide cultivars with adaptation to specific environments. The breeding method commonly used to improve quantitatively inherited traits (such as biomass yield) in populations of outcrossing species (such as switchgrass) is RSGCA (Poehlman and Sleper, 1995). The response to selection is contingent on the magnitude of genetic variation within the breeding population for the selection trait(s), its heritability, and the selection intensity utilized. Little information is known on the response of switchgrass to selection for increased biomass production. Information is also needed on the effects, if any, of yield environment on selection and ultimately on the performance of cultivars derived from that selection. Cultivars developed from selection in highyield environments (HYE) may not perform well when grown in low-yield environments (LYE) and vice versa. A successful switchgrass cultivar used as a HEC would likely be grown in a wide range of yield environments. Thus, it is important to know if the yield environment under which the breeding was conducted affects the performance level and stability of derived cultivars.

Results from studies on the effects of variable yield environment on selection and cultivar performance vary from crop to crop. Gotoh and Osania (1959) reported that selection for increased grain yield in wheat (*Triticum aestivum* L.), was more effective under a LYE than under a HYE. Conversely, Allen et al. (1978) found that selection for grain yield in soybean and wheat were more effective under a HYE than under a LYE. Vela-Cardenas and Frey (1972) reported equal effectiveness in selection for seed weight in oat, (*Avena sativa* L.)

under HYE and LYE. Whitehead and Allen (1990) concluded that low-stress environments commonly used in soybean breeding should provide high probabilities for selecting superior lines for performance in both low- and highstress edaphic conditions.

The objectives of this study were to determine the effects of HYE and LYE on the selection of parent plants in a  $C_0$  switchgrass lowland population and to assess the relative biomass yields of half-sib (HS) families from parental plants selected under those respective environments.

#### MATERIALS AND METHODS

#### Population Formation and Experimental Design

To test the effects of HYE and LYE on plant selection, identical (clonal) sets of HS progeny were grown in two environments. In 1996, HS seed were collected from 65 randomly selected, spaced (1.1 m) plants from a lowland switchgrass population (925 plants total) designated as 'NL-94'. The NL-94 population resulted from two cycles of Restricted Recurrent Phenotypic Selection for biomass yield within 'Kanlow' at a selection intensity of approximately 20%. For the purposes of this study the NL-94 population is considered the initial C<sub>0</sub> generation used for recurrent selection based on HS progeny evaluation. Eight HS plants were grown from seed harvested from each of the 65 randomly selected parents. Four clonal plants were then produced from each of the 520 HS plants. Those plants were used to establish HYE and LYE yield tests in spring 1997. The HYE and LYE tests were located near Stillwater, OK (36.16°N.

Lat., 97.09°W. Long.) on Oklahoma Agricultural Experiment Station sites approximately 2 km apart. The soils for the HYE and LYE were a Kirkland silt loam (fine, mixed, superactive, thermic Udertic Paleustolls) and a less productive Huska silt loam (fine, mixed, superactive, thermic Mollic Natrustalfs), respectively. To further enhance the yield environment on the HYE site, fertilizer (71 kg N ha <sup>-1</sup> yr <sup>-1</sup> plus P and K as indicated by soil test) was applied annually in the spring, irrigation was supplied as needed to prevent severe stress, and weeds were controlled by herbicide application. The LYE test received no fertilizer or supplemental water.

The experimental design in each test was a randomized complete block design (RCBD) with four replications. Each HS plant was replicated four times (clonal plants) in each experiment. Plants were taken from the greenhouse to the field and transplanted on 1.1 m centers. A row of plants, not harvested for biomass yield data, was planted around each test to guard against border effects. HS plant dry biomass yields were measured near the end of the 1998, 1999, and 2000 growing seasons. The HYE and LYE progeny biomass yield data in 1998 were used to choose the top 14 (22%) of the 65 original selected plants in the NL-94 nursery as parents.

Parent plants selected on the basis of HS performance were intercrossed in 1999 (14\*14 Latin square design, 1 block, field isolation) to produce new cyclic populations designated as NL-94 HYE  $C_1$  and NL-94 LYE  $C_1$ . The NL-94 HYE  $C_1$  and NL-94 LYE  $C_1$  selection nurseries, each comprising 1020 plants (1.1 m spacing, 12\*85 rows/columns), were established in early spring 2000. HS seed

was collected by hand stripping from 200 visually selected plants within the respective nurseries in fall 2000. That visual selection was on the basis of plant vigor and apparent seed production. The hand stripped HS seed were processed to near 100% pure seed and planted in rows (1 row/plant) in greenhouse flats containing a standard soil mix. Not all of the 200 plants in the respective nurseries produced adequate clean seed and seed of some plants exhibited poor germination. In spring 2001, 125 HS progeny families (60 from the NL-94 HYE C<sub>1</sub> and 65 from the NL-94 LYE C<sub>1</sub>) were planted in HYE and LYE tests at Stillwater, OK. Plant families were assigned to yield groups (S<sub>HYE</sub> or  $S_{LYE}$ ) based on the environment in which their parents were selected in the  $C_0$ population. The HYE test was on a relatively fertile Port silt loam soil (fine-silty, mixed, superactive, thermic Cumulic Haplustolls) while the LYE test was on the same site and under the same conditions as described for the C<sub>0</sub> HS families. The HYE test received the same cultural practices as previously described. A RCBD with four replications was used for both tests. Plant spacing was 1.06 m. An individual plot consisted of three HS plants. Individual plants of the two HS trials were harvested in the fall of 2002, 2003, and 2004 using a one-row, tractormounted flail chopper. Aliquot biomass samples were dried for approximately 1 wk to determine dry matter concentration and convert total wet plant weights to dry weights. Each of the tests were harvested in the fall of 2002, 2003, and 2004.

## Statistical Procedures

Data were analyzed in each year and over years using ordinary least squares in the PROC GLM procedure of SAS (SAS Inst., 1999). For the combined analysis, the data were arranged as a split plot in space and time. A four-factor analysis of variance was performed on data collected for all environments and years employing the following statistical model:

$$Y_{ijklm} = \mu + \alpha_i + \beta_{j(i)} + \tau_k + \gamma_{l(k)} + \delta_m + \alpha \tau_{ik} + \alpha \delta_{im}$$

$$+\beta\tau_{jk(i)}+\beta\delta_{jm(i)}+\tau\delta_{km}+\alpha\tau\delta_{ikm}+\beta\tau\delta_{jkm(i)}+e_{n(ijklm)}$$

Where:

μ	=	overall mean of biomass yield,
$\alpha_{i}$	=	fixed effect of group <i>i</i> ,
${m eta}_{{}_{j(i)}}$	=	fixed effect of family (genotype) <i>j</i> within group <i>i</i> ,
${ au}_k$	=	fixed effect of environment k,
$\gamma_{l(k)}$	=	fixed effect of replication / within environment k,
$\delta_{\scriptscriptstyle m}$	=	fixed effect of year <i>m</i> ,
$lpha au_{_{ik}}$	=	fixed interaction effect of group <i>i</i> and environment <i>k</i> ,
$lpha \delta_{_{im}}$	=	fixed interaction effect of group <i>i</i> and year <i>m</i> ,
$eta au_{_{jk(i)}}$	=	fixed interaction effect of family <i>j</i> and environment <i>k</i> within group <i>i</i> ,
$\beta \delta_{jm(i)}$	=	fixed interaction effect of family <i>j</i> and year <i>m</i> within group <i>i</i> ,
$ au \delta_{\scriptscriptstyle km}$	=	fixed interaction effect of environment <i>k</i> and year <i>m</i> ,
$lpha  au \delta_{_{ikm}}$	=	fixed interaction effect of group $i$ , environment $k$ , and year $m$ ,

$$\beta \tau \delta_{jkm(i)}$$
 = fixed interaction effect of family *j*, environment *k*, and year *m* within group *i*, and

 $e_{n(ijklm)}$  = experimental error, mean 0, variance  $\sigma^2$ .

Estimation of GE interaction was also accomplished via Spearmans Rank Correlation in the PROC CORR procedure (SAS Inst., 1999).

Because of significant disparity between variances with respect to the HYE and LYE environments as determined via F-test (P<0.0001), the data were transformed via square roots for all analyses conducted.

#### RESULTS AND DISCUSSION

#### C<sub>0</sub> Parental Selection

Mean dry biomass yields of  $C_0$  clonal HS families differed significantly in HYE vs. LYE tests, demonstrating the substantial differences (Table 2.1). Selections from the NL-94  $C_0$  population used to form the NL-94 HYE and NL-94 LYE  $C_1$  populations were based upon 1998 mean dry weight biomass yields of HS plant families tested within the HYE and LYE, respectively. Nine of 14 parents were common to the two groups selected based on HS progeny testing under HYE and LYE. Selection of parent plants based on 3-yr mean HS yield data would have resulted in slight changes in the array of selected plants. Eleven and nine of the 14 parent plants selected on the basis of 1998 HS family mean yields would also have been selected based on 3-yr mean yields of the HS families in HYE and LYE, respectively. However, based on LSD values of 0.587 and 0.278

for HS families in the HYE and LYE, respectively, only one selection in the HYE and two in the LYE were significantly different for 1998 means versus the 3-yr mean yields. Spearman's Rank Correlation coefficients of r = 0.830 in the HYE and r = 0.843 in the LYE (P<0.0001 for both) were obtained when comparing all family ranks for 1998 vs. the 3-yr mean yields.

#### C<sub>1</sub> Half-sib Family Yield Performance

Mean dry biomass yields of  $C_1$  HS families differed significantly (P<0.001) between the HYE and LYE tests, again substantiating the differences in the yield environments (Tables 2.2 and 2.3). Mean per plant HYE yields were approximately three times greater than those for the LYE. Family groups differed significantly within each year for each test. Mean yields of HS families from the  $S_{LYE}$  group were consistently greater than those from the  $S_{HYE}$  group in both the HYE and LYE tests (Table 2.3). The family nested within group [family (group)], environment, and year effects were also highly significant (P<0.0001). The environment\*family (group) and the environment\*year fixed interaction effects were also highly significant (P<0.0001). The environment\*family (group) interaction means that families failed to respond similarly with respect to different environments, a measure of genotype by environment (GE) interaction. Fig. 2.1 provides a visual assessment of the environment\*family (group) interaction indicating that the interaction results from greater variability present for biomass yield in the HYE in comparison with the LYE. Yields from plant families in the LYE were plotted in ascending order of magnitude, yields from plant families in

the HYE were plotted relative to corresponding families within the LYE. No crossover-type GE interactions were manifested in Figure 2.1. A significant environment\*year interaction means that biomass yield performance per environment was dissimilar across all years of the trial. Fig. 2.2 provides a visual assessment of the environment\*year interaction indicating the source to be failure of the mean yields of the respective tests to perform similarly in 2002.

Plants that would be selected from the C<sub>1</sub> parent nursery on the basis of C<sub>1</sub> HS performance under HYE and LYE is of interest. Based on 3-yr least square means yield and a 30% selection intensity (40 of 125 plants), 17 C<sub>1</sub> parent plants would be in common to the 40 plants selected based respectively on HYE and LYE performance. Twenty-six and 14 of 40 plants would trace respectively to the S<sub>LYE</sub> and S<sub>HYE</sub> protocols. For a 16% selection intensity (20 plants), only 2 C<sub>1</sub> parent plants would be common to the two groups. A Spearman's Rank Correlation of r = 0.139 was calculated for HS family biomass yields from the HYE and LYE tests. This lack of correlation and the significant family\*environment interaction from the ANOVA are indicative of the differential effects of yield environment on HS family biomass yields.

The results from this study indicate that yield environment may be important in breeding switchgrass for higher biomass yield.  $C_0$  parent plants selected on the basis of HS progeny yield performance (after one post establishment year) under HYE and LYE exhibited 64% congruence (9 of 14). Had selection of  $C_0$  plants been on the basis of 3-yr mean yields, the congruence would have been 50% (7 of 14). A congruence of 30% was indicated for  $C_1$  parent plants selected (30%

selection intensity: 40 of 125 plants) on the basis of 3-yr mean HS progeny performance under HYE and LYE. Mean biomass yields of C<sub>1</sub> HS families from parent plants selected under the  $S_{LYE}$  protocol consistently had higher yields than C<sub>1</sub> HS families from plants selected under the  $S_{HYE}$  protocol. The results suggest that selection under LYE would produce higher yielding populations grown under either HYE or LYE conditions.

#### REFERENCES

- Allen, F.L., R.E. Comstock, and D.C. Rasmusson. 1978. Optimal environments for yield testing. Crop Sci. 18:747-751.
- Gotoh, K., and Osania. 1959. Efficiency of selection for yield under different fertilizer levels in a wheat cross. Jpn. J. Breed. 9:173-178.
- Hopkins, A.A., K.P. Vogel, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1995. Genotypic variability and genotype x environment interactions among switchgrass accessions from the midwestern USA. Crop Sci. 35:565-571.
- McLaughlin, S., J. Bouton, D. Bransby, B. Conger, W. Ocumpaugh, P. Parrish, C. Taliaferro, K. Vogel, and S. Wullschleger. 1999. Developing switchgrass as a bioenergy crop. P. 282-299. In J. Janick (ed.) Perspectives on new crops and uses. ASHS Press, Alexandria, VA.
- Poehlman, J.M. and D.A. Sleper. 1995. Breeding field crops. 4th ed. Iowa State Univ. Press, Ames.
- Sanderson, M.A. 1992. Morphological development of switchgrass and kleingrass. Agron. J. 84:415-419.
- SAS Institute. 1999. SAS system for Windows. v. 8.2. SAS Inst., Cary, NC.
- Vela-Cardenas, M., and K.J. Frey. 1972. Optimum environments for yield testing. Iowa State J. Sci. 46:381-394.
- Whitehead, W.F., and F.L. Allen. 1990. High- vs. low-stress yield test environments for selecting superior soybean lines. Crop Sci. 30:912-918.

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- Table 2.3. Mean (range) dry biomass yield of NL-94 LYE and NL-94 HYE switchgrass C<sub>1</sub> half-sib families tested under a low-yield environment (LYE) and a high-yield environment (HYE) at Stillwater, OK, 2002-2004.

Year	LYE	HYE	P-value	
1998	0.82 (0.04 – 3.36 )	kg plant <sup>-1</sup> 1.22 (0.04– 3.32)	<0.0001	
1999	1.76 (0.05 – 6.17)	3.77 (0.05 – 9.15)	<0.0001	
2000	0.98 (0.08 – 4.86)	2.76 (0.15 – 6.62)	<0.0001	

Table 2.1. Mean (range) dry biomass yield of NL-94 LYE and NL-94 HYE switchgrass C<sub>0</sub> half-sib families tested under a low-yield environment (LYE) and a high-yield environment (HYE) at Stillwater, OK, 1998-2000.

			LYE		HYE				Over Yr and
Source	2002	2003	2004	Over Yr	2002	2003	2004	Over Yr	Environ.
Group (G) <sup>†</sup>	0.1325**	0.0250**	0.4949*	0.3925**	0.8938**	0.5844*	0.8409*	0.7730**	0.5828**
Family (F)/G	0.0627**	0.0516**	0.1403	0.0249**	0.1094*	0.1042**	0.2792**	0.1643**	0.1246**
Environ. (E)	-	-	-	-	-	-	-	-	858.5808**
Year (Y)	-	-	-	16.0563**	-	-	-	20.3157**	18.1860**
G*E	-	-	-	-	-	-	-	-	0.0980
G*Y	-	-	-	0.0093	-	-	-	0.0114	0.01004
F <sub>/G</sub> *E	-	-	-	-	-	-	-	-	0.2779**
F <sub>/G</sub> *Y	-	-	-	0.0460	-	-	-	0.0264	0.0362
E*Y	-	-	-	-	-	-	-	-	5.0815**
G*E*Y	-	-	-	-	-	-	-	-	0.0007
F <sub>/G</sub> *E*Y	-	-	-	-	-	-	-	-	0.0367**
Residual	0.1941	0.1781	0.5445	0.3261	0.40541	0.3611	0.8294	0.5460	0.0286

Table 2.2. Mean squares from ANOVA of dry biomass yield of NL-94 LYE and NL-94 HYE switchgrass C<sub>1</sub> half-sib (HS) families tested under a low-yield environment (LYE) and a high-yield environment (HYE) at Stillwater, OK, 2002-2004.

<sup>†</sup>HS families grouped according to LYE or HYE origin. <sup>\*\*\*</sup> Significant at the 0.05 and 0.01 probability levels, respectively.

	LYE				HYE			
Half-sib group <sup>†</sup>	2002	2003	2004	Over Yr	2002	2003	2004	Over Yr
				ka r	olant⁻¹			
$S_{\text{LYE}}$	0.60 (0.28 – 0.92)	0.70 (0.52 – 0.93)	0.99 (0.72 – 1.47)	0.76 (0.28 – 1.47)	1.84 (1.45 – 2.20)	1.66 (1.35 – 1.97)	2.03 (1.28 – 2.63)	1.84 (1.28 – 2.63)
S <sub>HYE</sub>	0.54 (0.35 – 0.90)	0.65 (0.41 – 0.93)	0.92 (0.54 – 1.27)	0.70 (0.35 – 1.27)	1.75 (1.19 – 2.09)	1.60 (1.35 – 2.06)	1.94 (1.48 – 2.51)	1.76 (1.19 – 2.51)
$\overline{x}$	0.56 (0.28 – 0.92)	0.67 (0.35 – 0.93)	0.96 (0.35 – 1.47)	0.73 (0.28 – 1.47)	1.79 (1.19 – 2.20)	1.63 (1.35 – 2.06)	1.99 (1.28 – 2.63)	1.80 (1.19 – 2.63)
P value	0.0011	0.0094	0.0364	<0.0001	0.0012	0.0053	0.0272	<0.0001

Table 2.3. Mean (range) of dry biomass yield of NL94 LYE and NL-94 HYE switchgrass C1 half-sib families tested under a low-yield environment (LYE) and a high-yield environment (HYE) at Stillwater, OK, 2002-2004.

<sup>†</sup> Grouped according to the LYE or HYE original selection environment.

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- Fig. 2.1. Visual assessment of the high-yield environment (HYE) and low-yield environment (LYE)\*family (group) interaction within the NL-94 C<sub>1</sub> population. Yields from plant families in the LYE were plotted in ascending order of magnitude, yields from plant families in the HYE were plotted relative to corresponding families within the LYE.
- Fig. 2.2. Graphical depiction of the significant interaction of the fixed effects of high-yield environment (HYE) and low-yield environment (LYE)\*year. Estimates on the ordinate are over plant families.

Fig. 2.1. Visual assessment of the high-yield environment (HYE) and low-yield environment (LYE)\*family (group) interaction within the NL-94 C<sub>1</sub> population. Yields from plant families in the LYE were plotted in ascending order of magnitude, yields from plant families in the HYE were plotted relative to corresponding families within the LYE.

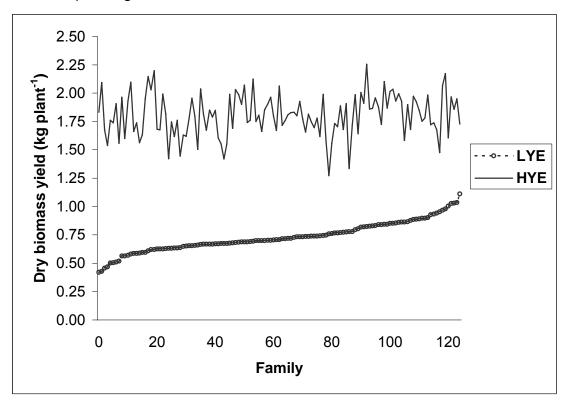
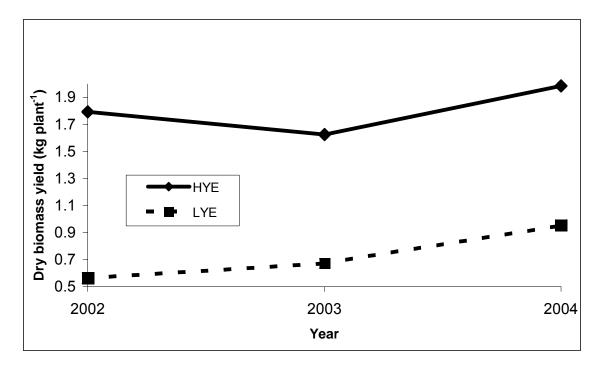


Fig. 2.2. Graphical depiction of the significant interaction of the fixed effects of high-yield environment (HYE) and low-yield environment (LYE)\*year. Estimates on the ordinate are over plant families.



### CHAPTER III

# GENETIC PARAMETERS FOR BIOMASS YIELD IN TWO POPULATIONS OF LOWLAND SWITCHGRASS

#### ABSTRACT

Breeding for increased biomass yield in switchgrass populations using recurrent selection techniques requires substantial resources in time and capital. Information on heritability and predicted gains from selection for increased yield in switchgrass is limited and may vary among populations, particularly those artificially synthesized for breeding improvement. Accordingly, studies were conducted to estimate amounts of heritable variation and predicted gains from selection for higher biomass yield within two lowland ecotype switchgrass populations,'Southern Lowland 93'(SL-93) and 'Northern Lowland 94' (NL-94), to determine the potential effectiveness of recurrent selection.

Half-sib (HS) progeny families from 130 and 125 randomly selected plants from the SL-93 and NL-94 populations, respectively, were evaluated for biomass yield in replicated trials (2002-2003 for SL-93; 2002-2004 for NL-94). For the NL-94 population, 60 and 65 Hs families were chosen respectively from parent plants emanating from previous selection under high (HYE) and low (LYE) environments. The 125 NL-94 HS progeny families were evaluated in HYE and LYE tests. Clonal parent plants were evaluated for biomass yield in separate

environments to provide unbiased estimates from progeny-parent regression. Yield differences were significant for SL-93 HS progenies within and over years and for NL-94 HS progenies within environment within and over years. The 2<sup>nd</sup> order interaction involving environments, years, and HS families was highly significant for the SL-93 population and for the NL-94 population within HYE and LYE environments. For SL-93,  $h_n^2$  estimates were 0.123 and 0.276 based respectively on individual plant and phenotypic family mean (PFM) selection. Variance component estimates of  $h_n^2$  were 0.521 and 0.872 based respectively on individual plant and PFM selection. Significant additive genetic variation was not detected within the NL-94 population when analyzed over HYE and LYE, but was present based on analyses within the respective environments. Estimates of  $h_{n}^{2}$  from progeny-parent regression were low (-0.027 to 0.050), but variance component estimates were high (0.574 to 0.848). The magnitudes of the estimates of additive genetic variation and the  $h_n^2$  estimates from variance components suggest that selection for higher biomass yield should be possible within the SL-93 and NL-94 populations.

## INTRODUCTION

Switchgrass (*Panicum virgatum*, L.) is a warm-season, perennial, determinate species, indigenous to the precolonial tall grass prairies east of the Rocky Mountains (Hopkins, et al., 1995). It is a bunchgrass and assimilates carbon via the C<sub>4</sub> photosynthetic pathway (Sanderson, 1992). It is currently used as livestock forage and for soil stabilization.

Switchgrass is polymorphic and allogamous. Cross-pollination in the species is reinforced by strong genetic self-incompatibility (Talbert et al., 1983; C.M. Taliaferro, personal communication, Martinèz-Reyna and Vogel, 2002). Two major ecotypes, lowland and upland, have been recognized based upon morphology and edaphic conditions (Porter, 1966). Plants of lowland ecotypes are typically more robust, exhibiting stems that are more coarse and thicker in diameter than their upland counterparts. The lowland ecotypes are tall-growing, at times in excess of 3 m and are well adapted to alluvial soils and sites that are relatively wet (C.M. Taliaferro, personal communication). Plants of upland ecotypes are generally shorter and finer with respect to stem and leaf characters and are better adapted to drier habitats, droughty conditions, and marginal, traditionally noncrop soils than their lowland counterparts. Extensive variation exists within each of these two major ecotypes for a number of traits of interest.

Over the past decade, switchgrass has been the focus of a multi-institutional, collaborative research effort to develop it as a herbaceous energy crop (HEC). The potential of switchgrass as a HEC derives mainly from its broad geographic adaptation, ability to grow on noncrop soils, and high biomass production capability with minimal inputs (McLaughlin et al., 1999). A portion of the developmental effort with switchgrass as a HEC involves the breeding of cultivars with adaptations for specific environments and enhanced biomass yield capability. One of the breeding programs involved in the collaborative research effort is located at Oklahoma State University. RSGCA for increased biomass

production is currently underway in two genetically broad-based populations of lowland ecotype switchgrass, SL-93 and NL-94.

Few studies have been conducted to estimate genetic parameters for biomass yield in lowland switchgrass. Talbert et al. (1983) reported estimates of genetic parameters in a population of lowland switchgrass for *in vitro* dry matter disappearance, percent N dry weight, and dry weight. They reported  $h_n^2$ estimates of 0.25 and 0.59 for dry weight on an individual plant and family basis, respectively. Van Esbroeck et al. (1998) calculated realized heritability estimates of 1.0 and 0.92 for early and late panicle emergence, respectively in 'Alamo' switchgrass; the assumption being that late panicle emergence could be used to increase above-ground biomass yield. Hopkins and Taliaferro (1997) reported  $h_n^2$  estimates ranging from 0.06 to 0.18 for acid soil tolerance at the seedling stage in 'Kanlow' switchgrass.

Heritability estimates for forage yield and yield components have been reported in several other grass species. Ross et al. (1975) reported a  $h_n^2$ estimate of 0.68 for forage yield in big bluestem (*Andropogon gerardii* Vitman). Vogel et al. (1981) reported an average  $h_n^2$  estimate of 0.43 for forage yield in two populations of indiangrass [*Sorghastrum nutans* (L.) Nash]. Barker et al. (1989) reported  $h_b^2$  estimates of 0.71, 0.84, 0.95, and 0.78 for forage yield in crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Shult.], intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkworth and Dewey], western wheatgrass [*Pacopyrum smithii* Rybd. (Löve)], and reed canarygrass (*Phalaris arundinacea* L.), respectively. Based on HS progeny means, Ray et al. (1997)

reported  $h_n^2$  estimates of 0.52, 0.63, 0.15, 0.68, 0.49, 0.59, 0.36, and 0.70 for forage dry matter yield, tiller height, first-cut vigor, regrowth vigor, proline content, spikes per spike, anthocyanine pigmentation of stem nodes, and flag leaf pubescence, respectively, in diploid crested wheatgrass. Casler (1988) reported  $h_n^2$  estimates of 0.30 to 0.42 for forage yield within eight populations originating from smooth bromegrass (*Bromus inermis* Leyss. ), orchardgrass (*Dactylis glomerata* L)., and ryegrass, (*Lolium perene* L. and L. hybridium Hausskm.).

Estimates of heritable genetic variation and gains from selection within breeding populations are helpful to breeding program managers in determining the probable effectiveness of pursuing the breeding process over time. Accordingly, the objectives of this study were to estimate genetic variances,  $h_n^2$ , and  $\Delta G$  for increased biomass yield within the SL-93 and NL-94 populations of lowland switchgrass.

#### MATERIALS AND METHODS

Plant materials consisted of HS families and clonal parent plants from the SL-93 and NL-94 switchgrass populations. The SL-93 base population was synthesized in 1993 from plants of the 'Alamo' and 'PMT-279'. The population providing plant materials for this study resulted from two cycles of Restricted Recurrent Phenotypic Selection (RRPS) for higher biomass yield. In the spring of 2001, 130 HS families from plants in an SL-93 selection nursery were planted in a replicated field trial at the Perkins Research Station (35.57°N. Lat., 97.01°W. Long.) to assess biomass yield performance. The 130 HS families were from

randomly selected plants within the selection nursery that contained a total of 1020 plants. A randomized complete block design (RCBD) with four replications was used. Greenhouse grown plants were transplanted on 1.06 m centers. Individual plots consisted of three HS progeny plants. The soil type was a Teller loam (fine, loamy, mixed, active, thermic, Udic Argiustolls).

So that unbiased estimates of  $h_n^2$  could be obtained (Casler, 1982) via progeny-parent regression, a replicated trial consisting of clonal parents of the HS families was planted in the spring of 2002 on the Agronomy Research Station, Stillwater, OK (36.16°N. Lat., 97.09°W. Long.). A RCBD with three replications was used. Greenhouse grown plants were transplanted on 1.06 m centers. Individual plots consisted of one clonal parent plant. The soil type was a Kirkland silt loam (fine, mixed, superactive, thermic, Udertic Paleustolls).

Both of the trials received annual early spring applications of N in the amount of 90 kg ha<sup>-1</sup>. Phosphorus and potash were applied in early spring when needed in amounts recommended by soil test results. Surflan<sup>®</sup> herbicide (oryzalin: 3,5dinitro-N<sup>4</sup>, N<sup>4</sup>-dipropysulfanilamide) was applied annually in early spring at the rate of 2.24 kg ha<sup>-1</sup> to prevent establishment of volunteer switchgrass and to control weeds. Individual plants of the HS progeny trial were harvested in the fall of 2002 and 2003, the clonal parent test was harvested in the fall of 2003 and 2004. Aliquot biomass samples were dried for approximately 1 wk to determine dry matter (dm) concentration and convert total wet plant weights to dry weights.

The NL-94 population from which plant materials were obtained resulted from two cycles of RRPS for biomass yield within 'Kanlow'. In 1997, 65 plants from

the RRPS C<sub>3</sub> selection nursery were randomly selected to form a new population for RSGCA under a high-yield environment (HYE) and low-yield environment (LYE). Clonal sets of HS progeny from each of the 65 plants were evaluated under a HYE and a LYE in 1998. Parent plants selected on the basis of HS performance under HYE and LYE were intercrossed in 1999 to produce new cyclic populations designated NL-94 HYE C<sub>1</sub> and NL-94 LYE C<sub>1</sub>. Selection nurseries (1020 plants) of each were established in spring 2000, and seed was harvested from 240 randomly selected plants in fall 2000. In spring 2001, 125 HS families (60 from the NL-94 HYE C<sub>1</sub> and 65 from the NL-94 LYE C<sub>1</sub>) were planted in HYE and LYE yield tests. The HYE trial was on the Agronomy Research Station, Stillwater, OK (36.16°N. Lat., 97.09°W. Long.). The soil was a Port silt loam (fine, silty, mixed, superactive, thermic Cumulic Haplatstolls). The experimental design was a RCBD with four replications. Greenhouse grown plants were transplanted to the field on 1.06 m centers. A row of plants was planted on all sides of the test to guard against border effects. The test received annual early spring applications of 90 kg ha<sup>-1</sup> N plus P and K as indicated by soil test recommendations. The test was irrigated as needed to maintain good growing conditions. Surflan<sup>®</sup> herbicide (oryzalin: 3,5-dinitro-N<sup>4</sup>, N<sup>4</sup>dipropysulfanilamide) was applied annually in early spring at the rate of 2.24 kg ha<sup>-1</sup> a.i. to prevent volunteer switchgrass and control weeds. The LYE was also located at Stillwater, OK, approximately 2 km distance from the HYE test on a less productive Huska silt loam (fine, mixed, superactive, thermic Mollic Natrustalfs) soil. The experimental design of the LYE was the same as for the

HYE. A border row of plants was planted on all sides of the test. The LYE received no fertilizer or irrigation. Surflan<sup>®</sup> herbicide was applied annually at 2.24 kg ha<sup>-1</sup> a.i. Individual plants of each test were harvested in the fall of 2002, 2003, and 2004. Aliquot biomass samples were dried for approximately 1 wk to determine dm concentration and convert total wet plant weights to dry weights. Plant families were assigned to groups (S<sub>HYE</sub> or S<sub>LYE</sub>) designating the yield environment under which their respective parents were selected.

So that unbiased estimates of  $h_n^2$  could be obtained (Casler, 1982) via progeny-parent regression methods, NL-94 HYE C<sub>1</sub> and NL-94 LYE C<sub>1</sub> clonal parent plants were planted into a replicated field trial in the spring of 2003. The test was on the Perkins Research Station near Perkins, OK (35.57°N. Lat., 97.01°W. Long.). The soil type was a Teller loam (fine-loamy, mixed, active, thermic, Udic Argiustolls). The experimental design was a RCBD with three replications. Individual plots consisted of a single clonal plant. Fertilizer and herbicide were applied annually as per the HYE HS progeny test. A row of plants was planted on all sides of the test to guard against border effects. Individual plants were harvested in the autumn of 2003 and 2004.

Table 3.1 shows the expected mean squares, degrees of freedom (df) and sources thereof associated with the analysis of a trial consisting of families tested across multiple years. Table 3.2 shows the expected mean squares, df, and sources thereof associated with the analysis of a trial consisting of families tested within multiple selection groups, and across multiple years and environments.

For the SL-93 population, the data were analyzed using generalized least squares (SAS Inst., 1999). Statistical analyses of the SL-93 population were conducted on a whole experiment basis (across years) and within each year (2002 and 2003). A two-factor analysis of variance was conducted on data collected for all environments and years employing the following statistical effects model:

$$Y_{ijklm} = \mu + \alpha_i + \beta_j + \tau_k + \beta \tau_{jk} + e_{m(ijk)}$$

Where:

μ	=	overall mean of biomass yield,
$lpha_i$	=	random effect of replication <i>i</i> ,
${m eta}_j$	=	random effect of plant family (genotype) j,
${ au}_k$	=	fixed effect of year k,
$eta  au_{_{jk}}$	=	random interaction effect of plant family $j$ and year $k$ , and
$e_{m(ijk)}$	=	experimental error, mean 0, variance $\sigma^2$ .

For the NL-94 population, the data were analyzed using generalized least squares (SAS Inst., 1999). A four-factor analysis of variance was performed on data collected for all environments and years employing the following statistical effects model:

$$Y_{ijklm} = \mu + \alpha_i + \beta_{j(i)} + \tau_k + \gamma_l + \delta_m + \alpha \tau_{ik} + \alpha \delta_{im}$$

$$+ \beta \tau_{jk(i)} + \beta \delta_{jm(i)} + \tau \delta_{km} + \alpha \tau \delta_{ikm} + \beta \tau \delta_{jkm(i)} + e_{n(ijklm)}$$

Where:

μ	=	overall mean of biomass yield,
$lpha_i$	=	fixed effect of group <i>i</i> ,
${m eta}_{{}_{j(i)}}$	=	random effect of family (genotype) <i>j</i> within group <i>i</i> ,
${oldsymbol  au}_k$	=	fixed effect of environment k,
$\gamma_{l(k)}$	=	random effect of replication <i>I</i> within environment <i>k</i> ,
$\delta_{\scriptscriptstyle m}$	=	fixed effect of year <i>m</i> ,
$lpha au_{_{ik}}$	=	fixed interaction effect of group <i>i</i> and environment <i>k</i> ,
$lpha \delta_{_{im}}$	=	fixed interaction effect of group <i>i</i> and year <i>m</i> ,
$eta  au_{_{jk(i)}}$	=	random interaction effect of family <i>j</i> and environment <i>k</i> within group <i>i</i> ,
$\beta \delta_{jm(i)}$	=	random interaction effect of family <i>j</i> and year m within group <i>i</i> ,
$ au \delta_{\scriptscriptstyle km}$	=	fixed interaction effect of environment <i>k</i> and year <i>m</i> ,
$lpha au\delta_{_{ikm}}$	=	fixed interaction effect of group $i$ , environment $k$ , and year $m$ ,
$eta au\delta_{jkm(i)}$	=	random interaction effect of family <i>j</i> , environment <i>k</i> , and year <i>m</i> within group <i>i</i> , and
$e_{n(ijklm)}$	=	experimental error, mean 0, variance $\sigma^2$ .

Estimation of  $h_n^2$  was conducted in two ways. The first estimation was via progeny-parent regression via generalized least squares (SAS Inst., 1999)

Estimates of  $h_n^2$  were calculated as follows:

**2**\*β<sub>1</sub>

Where:

 $\beta_1$  = the linear regression coefficient of progeny-parent regression The regression coefficient is derived as described and presented by Casler (1982) as follows:

$$h_n^2 = 2 \frac{\sigma_{P_{PO}}}{\sigma_p^2}$$

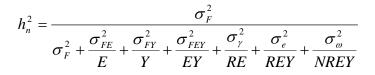
Where:

- $\sigma_{\rm P_{PO}}$  = phenotypic covariance between parental values and progeny values, and
- $\sigma_{P}^{2}$  = phenotypic variance among parental means.

Estimates of  $h_n^2$  were calculated in this manner on both an individual plant and phenotypic family mean (PFM) basis.

Estimates of  $h_n^2$  were also obtained via a variance component method as described by Nguyen and Sleper, (1983). The variance component method based on the analysis of variance procedures provides the greatest flexibility for predicting the effectiveness of alternative selection procedures (Fehr, 1987).

Estimates of  $h_n^2$  on an individual plant basis, in general, were derived as follows:



Estimates of  $h_n^2$  on a PFM basis were calculated as follows:

$$h_n^2 = \frac{\sigma_F^2}{\sigma_F^2 + \frac{\sigma_{FE}^2}{E} + \frac{\sigma_{FY}^2}{Y} + \frac{\sigma_{FEY}^2}{EY} + \frac{\sigma_\gamma^2}{RE} + \frac{\sigma_e^2}{REY}}$$

For analyses within a particular environment, the genetic variance term corresponding to the family\*environment and family\*environment\*year components of variance and their associated divisors were omitted from the formula.

Where:

tion
1

The formulae above provide an estimate of  $h_n^2$  since the genetic variance among HS families represents primarily the additive genetic variance contained in the phenotypic variance among HS plot family means and among individual plants (Nguyen and Sleper, 1983). In addition to estimates of  $h_n^2$ , the 95% confidence intervals (CIs) were calculated corresponding to each  $h_n^2$  estimate. Concerning the variance component calculation method, standard errors of  $h_n^2$ estimates were obtained via the method described theoretically by Nelder (1953).

 $\Delta G$  per cycle of selection was also calculated on both an individual plant and PFM basis as described by Nguyen and Sleper (1983).

 $\Delta G$  per cycle of individual plant selection can be predicted as follows:

$$\Delta G = ckh_{ph}^2 \sigma_{ph} = ck \frac{\sigma_F^2}{\sigma_p}$$

 $\Delta G$  per cycle of selection based on a PFM basis can be estimated as follows:

$$\Delta G = ckh_{pfm}^2 \sigma_{pfm} = ck \frac{\sigma_F^2}{\sigma_{pfm}}$$

Where:

С	=	parental control factor
k	=	standardized selection differential
$h_{\scriptscriptstyle ph}^2$	=	narrow-sense heritability on an individual plant basis
$\sigma_{_{ph}}$	=	phenotypic standard deviation from individual plant analysis
$h_{\scriptscriptstyle pfm}^2$	=	narrow-sense heritability on a PFM basis
$\sigma_{\scriptscriptstyle p\!f\!m}$	=	phenotypic standard deviation from PFM analysis
$\sigma_{\scriptscriptstyle F}^2$	=	variance attributable to plant families

Here, c = 2 and k = 1.16.

#### **Results and Discussion**

#### SL-93 Population

Significant variation (P<0.0001) was detected among HS families of the SL-93 population for dry biomass yield in both years (2002-2003) and for the combined analysis over years. In the combined analysis, the fixed main effect of years was highly significant (P<0.0001). The year\*family interaction effect was not significant (P=1.000). Table 3.3 lists estimated variance components and their associated standard errors for the HS progeny and clonal parental trials of the SL-93 population. The variance components due to HS families and parent plants were relatively small but significantly greater than 0 (Table 3.3). The year\*family component was negative indicating lack of GE interaction. In order to further substantiate the absence of significant GE interaction, the solution vectors for the family component of the mixed model equations for the analysis of the data within years of the trial were obtained, ranked corresponding to magnitude of their estimate, and a Spearman's Rank Correlation was calculated for the association between family rankings for 2002 and 2003. A Spearman's Rank Correlation coefficient of r = 0.76801 (P<0.0001) was obtained. Furthermore, the raw ranks of the families within each year of the study were examined. Based upon a 30% selection intensity, 39 parent plants would be selected based on their HS family performance. Twenty-seven of the 39 parent plants were synonymous to both years.

Estimates of  $h_n^2$  and  $\Delta G$  varied with method of computation (Table 3.4). For the progeny-parent regression method, estimates of  $h_n^2$  were 0.123 and 0.276

based on PFM and individual plant selection, respectively. Neither estimate was significantly greater than 0 as indicated by the 95% CIs. The 95% CIs for PFM and for individual plants from estimates  $h_n^2$  obtained from variance component calculation techniques did not contain 0, indicating that both estimates were significantly greater than 0. Predicted  $\Delta G$  values per selection cycle ranged from 0.097 to 0.697 (Table 3.4). Estimates derived from parent-progeny regression analysis (0.097 for PFM and 0.244 for individual plant selection) were lower than those derived from variance component analysis (0.697 for PFM and 0.476 for individual plant selection). Gains from selection based on progeny-parent regression are considered less reliable than those based on variance components because  $h_n^2$  estimates of the former were not significantly different from 0.

#### **NL-94** Populations

Statistical analyses of data from the NL-94 population study were conducted on a whole experiment basis and within each environment across all years of the trial. The whole experiment analysis indicated that environment, group, year, and environment\*year effects were highly significant (P<0.01). Therefore, inference drawn with respect to the fixed effects of environments and years singly is not valid. Neither the environment\*group interaction nor the year\*group interaction was significant, (P=0.5557 and P=0.6130, respectively). Significant additive genetic variation as estimated via the family nested within group [family (group)] component of variance (0.0004) was not significant (P=0.2830). The GE

interaction, as determined by the environment\*family (group) component of variance, (0.0067), was highly significant (P<0.0001). Table 3.5 provides the estimates of variance components and their associated standard errors for the HS progeny and clonal parental trials for the combined analysis of the NL-94 population.

A significant environment\*year interaction means that plant families fail to respond similarly at each environment across all years of the trial. Figure 3.1 provides a visual assessment of the significant interaction. Examination of the graph evinces that the nature of the interaction, in large part, can be accounted for from the first year (2002) of data collection.

The analysis of the HYE across years of the trial showed that the fixed effects of year and group were highly significant (P<0.01). The year\*group interaction was not significant (P=0.8063). Hence, inference drawn with respect to fixed effects individually is valid. The variance corresponding to the family (group) component (0.1437) was found to be highly significant (P<0.0001) while the variance associated with the year\*family (group) interaction (-0.08080) was nonsignificant (P=1.000).

The LYE analysis across all years of the trial indicated that the fixed effects of years (P<0.0001) and groups (P=0.0183) were significant. The year\*group interaction was nonsignificant (P=0.6502). Thus, inference drawn with respect to the fixed effects individually is valid. The variance associated with the family (group) component (0.07094) was highly significant (P<0.0001), while the variance associated with the year\*family (group) interaction (-0.04945) was

nonsignificant (P=1.000). Tables 3.5, 3.6, and 3.7 list the variance component estimates and their associated standard errors for the HS progeny NL-94 HYE  $\pm$  LYE, HYE, and LYE tests, respectively, and also for the NL-94 clonal parental trial.

Table 3.8 lists  $h^2_n$  estimates and associated 95% CIs and  $\Delta G$  per cycle of selection and per year based on progeny-parent regression estimation methods for PFM. The  $h^2_n$  estimates ranged from –0.011 for the S<sub>HYE</sub> group within the LYE to 0.050 for the S<sub>LYE</sub> group within the LYE. A  $\Delta G$  of 0.012 kg dm per cycle of selection and of 0.002 kg dm per year were calculated for the S<sub>LYE</sub> group within the LYE. Examination of the 95% CIs for the  $h^2_n$  estimates reveals that each CI is inclusive of 0. Hence, no estimate of  $h^2_n$  obtained via the progeny-parent regression method for PFM was significantly greater than 0.

Table 3.9 lists  $h_n^2$  estimates and their associated 95% CIs and  $\Delta G$  per cycle of selection and per year based on progeny-parent regression estimation methods for individual plant selection. The  $h_n^2$  estimates ranged from –0.115 for the combined analysis to 0.017 for the S<sub>LYE</sub> group within the HYE. No  $\Delta G$  per cycle of selection was found to be greater than 0.01 kg dm for the individual plant analysis. Examination of the 95% CIs of the  $h_n^2$  estimates for individual plants calculated via this method shows no interval that does not contain 0.

Table 3.10 lists  $h_n^2$  estimates and their associated 95% CIs and  $\Delta G$  per cycle of selection and per year based on the variance component estimation method for PFM. Estimates of  $h_n^2$  ranged from 0.048 for the S<sub>HYE</sub> group across both the HYE and LYE to 0.881 for the S<sub>HYE</sub> group within the HYE. Estimates of  $h_n^2$ 

calculated via the variance component method for PFM produced no values from analyses across both the HYE and LYE that failed to contain 0 within the 95% CI. However, all estimates of  $h_n^2$  calculated from analyses within either the HYE or the LYE alone were considered to be high (range 0.749 – 0.881) and were each found to be significantly greater than 0.

Table 3.11 lists  $h_n^2$  estimates and their associated 95% CIs and  $\Delta G$  per cycle of selection and per year pertaining to the variance component estimation method for individual plant selection. Estimates of  $h_n^2$  obtained by this method ranged from 0.055 for the S<sub>HYE</sub> group across both the HYE and LYE to 0.601 for the S<sub>HYE</sub> group within the HYE. Estimates of  $h_n^2$  obtained via the variance component method for individual plant selection produced no estimate from analyses across both the HYE and LYE that failed to contain 0 within the 95% CI. As with the variance component PFM analysis, estimates of  $h_n^2$  for analyses within either the HYE or LYE were generally considered to be high (range 0.519 – 0.601) and were all found to be significantly greater than 0.

Significant genetic variation was found for biomass yield in the SL-93 switchgrass population via the family component in analyses for the years 2002 and 2003 as well as in the analysis across both years of the study. In the combined analysis, significant GE interaction was not detected. Lack of GE interaction was further substantiated by a high Spearman's Rank Correlation coefficient and considerable homology for plant family ranks among years as ascertained by examination of the plant family solution vectors obtained from the mixed model equations in the analysis.

The SL-93 estimates of  $h_n^2$  obtained from the progeny-parent regression method were low and moderate for PFM and individual plant selection, respectively. Although the 95% CIs for both PFM and individual plant selection  $h_n^2$  estimates obtained from progeny-parent regression techniques are both inclusive of 0, it is important to note that the CIs for both estimates are extremely wide. Estimates of  $h_n^2$  obtained from the variance component method for both PFM and individual plant selection (0.872 and 0.521, respectively) provide 95% CIs that are not inclusive of 0. The results suggest that the magnitude of additive genetic variance for biomass yield within the SL-93 population is sufficient to provide positive response to selection based either on HS PFM or HS individual plant performance. The greatest potential progress would most likely be realized via PFM selection techniques.

Significant genetic variation was not found within the NL-94 population for biomass yield via the family (group) component of variance in the analysis that spanned both the HYE and LYE across all years of the study. In the same analysis, significant GE interaction was detected for the environment\*family (group) random effect. GE interaction, especially the environment\*family (group) effect, is considered to be a major cause of the extremely low estimates of  $h^2_n$ , from both progeny-parent regression and variance component methods of estimation in the overall analysis. Accordingly, plant selection based on the mean performance of HS progeny evaluated in divergent environments would likely not be effective in improving biomass yield within the population.

Significant additive genetic variation was detected within the NL-94 C<sub>1</sub> population via the family (group) component of variance when assayed per yield environment (HYE or LYE). Furthermore, estimates of  $h_n^2$  obtained from the variance component method of calculation for both PFM and individual plant selection (Tables 10 and 11) indicate that the genetic variation within the NL-94 population for enhanced dry biomass yield is potentially exploitable via RSGCA breeding procedures.

## REFERENCES

- Barker, R.E., A.B. Frank, and J.D. Berdahl. 1989. Cultivar and clonal differences for water-use efficiency and yield in four forage grasses. Crop Sci. 29:58-61.
- Casler, M.D. 1982. Genotype x environment interaction bias to parent-offspring regression heritability estimates. Crop Sci. 22:540-542.
- Casler, M.D. 1988. Performance of orchardgrass, smooth bromegrass, and ryegrass in binary mixtures with alfalfa. Agron. J. 80:509-514.
- Fehr, W.R. 1987. Principles of cultivar development: Theory and technique. Vol. 1. McGraw-Hill, Inc. New York.
- Hopkins, A.A., K.P. Vogel, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1995. Genotypic variability and genotype x environment interactions among switchgrass accessions from the midwestern USA. Crop Sci. 35:565-571.
- Hopkins, A.A. and C.M. Taliaferro. 1997. Genetic variation within switchgrass populations for acid soil tolerance. Crop Sci. 37:1719-1722.
- Martinèz-Reyna, J.M., and K.P. Vogel. 2002. Incompatibility systems in switchgrass. Crop Sci. 42:1800-1805.
- McLaughlin, S., J. Bouton, D. Bransby, B. Conger, W. Ocumpaugh, P. Parrish, C. Taliaferro, K. Vogel, and S. Wullschleger. 1999. Developing switchgrass as a bioenergy crop. p. 282-299. *In* J. Janick (ed.) Perspectives on new crops and uses. ASHS Press, Alexandria, VA.
- Nelder, J.A. 1953. Statistical models in biometrical genetics. Heredity 7:111-119.
- Nguyen, H.T., and D.A. Sleper. 1983. Theory and application of half-sib matings in forage grass breeding. Theor. Appl. Genet. 64:187-196.
- Porter, C.L., Jr. 1966. An analysis of variation between upland and lowland switchgrass, *Panicum virgatum* L., in central Oklahoma. Ecology 47:980-992.
- Ray, I.M., A.B. Frank, and J.D. Berdahl. 1997. Genetic variances of agronomic and morphological traits of diploid crested wheatgrass. Crop Sci. 37:1503-1507.
- Ross, J.G., R.T. Thaden, and W.L. Tucker. 1975. Selection criteria for yield and quality in big bluestem grass. Crop Sci. 15:303-306.

- Sanderson, M.A. 1992. Morphological development of switchgrass and kleingrass. Agron. J. 84:415-419.
- SAS Institute. 1999. SAS system for Windows. v. 8.2. SAS Inst., Cary, NC.
- Talbert, L.E., D.H. Timothy, J.C. Burns, J.O. Rawlings, and R.H. Moll. 1983. Estimates of genetic parameters in switchgrass. Crop Sci. 23:725-728.
- Taliaferro, Charles M. 2002. Breeding and selection of new switchgrass varieties for increased biomass production. Oak Ridge Natl. Lab. Available at <u>http://www.ornl.gov/~webworks/cppn/y2001/rpt/116285.pdf</u>. (accessed 20 Apr. 2005.)
- Van Esbroeck, G.A., M.A. Hussey, and M.A. Sanderson. 1998. Selection response and developmental bias for early and late panicle emergence in Alamo switchgrass. Crop Sci. 38:342-346.
- Vogel, K.P., H.J. Gorz, and F.A. Haskins. 1981. Heritability estimates for height, color, erectness, leafiness, and vigor in indiangrass. Crop Sci. 21:734-736.

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Source	df	Expected mean squares
Rep (R)	(r-1)	$\sigma^2$ + fy $\sigma^2_r$
Year (Y)	(y-1)	$\sigma^2$ + $r\sigma^2_{fy}$ + f $\sigma^2_{ry}$ + $\theta^2_y$
Family (F)	(f-1)	$\sigma^2$ + $r\sigma^2_{fy}$ + $ry\sigma^2_{f}$
F*Y	(f-1)(y-1)	$\sigma^2 + r\sigma^2_{fy}$
Error	n-model df	$\sigma^2$
Total	rfy-1	

Table 3.1. ANOVA for the SL-93 switchgrass half-sib families evaluated for biomass yield at Perkins, Oklahoma, 2002-2003.

Source	df	Expected mean squares
Group (G	6) (g-1)	$\sigma^{2} + r\sigma^{2}_{f(g)ey} + re\sigma^{2}_{f(g)y} + ry\sigma^{2}_{f(g)e} + re\sigma^{2}_{f(g)}$ $+ re\sigma^{2}_{f(g)} + \theta^{2}_{e} + \theta^{2}_{eg} + \theta^{2}_{yg} + \theta^{2}_{eyg}$
Family (F	$(f/g_1-1) + (f/g_2-1)$	$\sigma^2 + r\sigma^2_{f(g)ey} + re\sigma^2_{f(g)y} + ry\sigma^2_{f(g)e} + rey\sigma^2_{f(g)} + re\sigma^2_{f(g)}$
Environm	nent (E) (e-1)	$ \begin{array}{l} \sigma^2 + r \sigma^2_{f(g)ey} + r y \ \sigma^2_{f(g)e} + f y \ \sigma^2_{r(e)} + \theta^2_e + \\ \theta^2_{eg} + \theta^2_{ey} + \theta^2_{eyg} \end{array} $
Rep (R)/ <sub>E</sub>	e(r-1)	$\sigma^2$ + fy $\sigma^2_{r(e)}$
Year	(y-1)	$\sigma^{2} + r\sigma^{2}_{f(g)ey} + re\sigma^{2}_{f(g)y} + \theta^{2}_{y} + \theta^{2}_{ey} + \theta^{2}_{yg} + \theta^{2}_{eyg}$
G*E	(g-1)(e-1)	$\sigma^2$ + $r\sigma^2_{f(g)ey}$ + $ry \sigma^2_{f(g)e}$ + $\theta^2_{eg}$ + $\theta^2_{eyg}$
G*Y	(g-1)(y-1)	$\sigma^{2} + r\sigma^{2}_{f(g)ey} + re\sigma^{2}_{f(g)y} + \theta^{2}_{yg} + \theta^{2}_{eyg}$
F/ <sub>G</sub> *E	$e[(f/g_1-1) + (f/g_2-1)]$	$\sigma^2$ + $r\sigma^2_{f(g)ey}$ + $ry \sigma^2_{f(g)e}$
F/ <sub>G</sub> *Y	$y[(f/g_1-1) + (f/g_2-1)]$	$\sigma^2$ + r $\sigma^2_{f(g)ey}$ + re $\sigma^2_{f(g)y}$
E*Y	(e-1)(y-1)	$\sigma^2$ + $r\sigma^2_{f(g)ey}$ + $\theta^2_{ey}$ + $\theta^2_{eyg}$
G*E*Y	(g-1)(e-1)(y-1)	$\sigma^2$ + $r\sigma^2_{f(g)ey}$ + $\theta^2_{eyg}$
F/ <sub>G</sub> *E*Y	$(f/g_1-1) + (f/g_2-1)(e-1)(y-1)$	$\sigma^2$ + r $\sigma^2_{f(g)ey}$
Error	n-model df	$\sigma^2$
Total	rfey-1	

Table 3.2. ANOVA for the NL-94 switchgrass half-sib families evaluated for biomass yield at Stillwater, OK, 2002-2004.

Table 3.3. Estimates of variance components and their associated standard errors for the SL-93 switchgrass half-sib (HS) families evaluated for biomass yield at Perkins, OK, 2002-2003 and SL-93 clonal parents evaluated for biomass yield at Stillwater, OK, 2003-2004.

	Population			
Variance Component	SL-93 HS Progeny	SL-93 Clonal Parents		
Family $(\sigma^2_F)$	0.1034 ± 0.0282**	0.2132 ± 0.0405**		
Family*Year ( $\sigma^2_{FY}$ )	-0.0095 ± -	0.0239 ± 0.0096*		
Residual $(\sigma_e^2)$	0.3046 ± 0.0171	0.2685 ± 0.0186		

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 3.4. Estimates of narrow-sense heritability  $(h_n^2)$  for biomass yield, 95% confidence intervals (CIs) of those  $h_n^2$  estimates, and predicted genetic gains  $(\Delta G)$  per cycle of selection (5 years per cycle) and per year for the SL-93 population based on calculations from progeny-parent regression and variance component methods for phenotypic family means (PFM) and for individual plant selection.

Population	h² <sub>n</sub> Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	$\Delta G$ Year (kg dm)
SL-93 PFM (ProgPar. Reg.)⁺	0.123	(-0.051, 0.297)	0.097	0.019
SL-93 PFM (Var. Comp. Anal.) <sup>††</sup>	0.872	(0.847, 0.896)	0.697	0.139
SL-93 Individual Plants (ProgPar. Reg.) <sup>†</sup>	0.276	(-0.104, 0.655)	0.244	0.049
SL-93 Individual Plants (Var. Comp. Anal.) <sup>††</sup>	0.521	(0.476, 0.566)	0.461	0.092

<sup>†</sup> Progeny-Parent regression method of  $h_n^2$  estimation. <sup>††</sup> Variance component method of  $h_n^2$  estimation.

Table 3.5. Estimates of variance components and their associated standard errors for the NL-94 switchgrass half-sib (HS) families evaluated for biomass yield at Stillwater, OK, 2002-2004 and NL-94 clonal parents evaluated for biomass yield at Perkins, OK, 2003-2004.

	Population		
Variance Component	NL-94 HS Progeny	NL-94 Clonal Parents	
Family/ $_{G^{\dagger}}(\sigma^{2}_{F})$	0.0004 ± 0.0018	0.0719 ± 0.0240**	
Environment (E)*Family/ <sub>G</sub> <sup>†</sup> ( $\sigma^2_{FL}$ )	0.0067 ± 0.0052**	-	
Year (Y)*Family/ $_{G}^{\dagger}$ ( $\sigma^{2}_{FY}$ )	-0.0004 ± -	0.1921 ± 0.0277**	
E*Y*Family/ $_{G}^{\dagger}$ ( $\sigma^{2}_{FLY}$ )	-0.0049 ± -	-	
Residual $(\sigma_e^2)$	0.0286 ± 0.0031	0.1829 ± 0.0156	
*,** Significant at the 0.05 and 0.01 probability levels, respectively. $^{\dagger}$ Fixed effect of yield group (S <sub>HYE</sub> and S <sub>LYE</sub> ).			

Table 3.6. Estimates of variance components and their associated standard errors for the NL-94 high-yield environment (HYE) switchgrass half-sib (HS) families evaluated for biomass yield at Stillwater, OK, 2002-2004 and NL-94 clonal parents evaluated for biomass yield at Perkins, OK, 2003-2004.

	Population			
Variance Component	NL-94 HYE HS Progeny	NL-94 Clonal Parents		
$Family_{G^{\dagger}}(\sigma^{2}{}_{F})$	0.1437 ± 0.0339**	0.0719 ± 0.0240**		
Year*Family/ $_{G^{\dagger}}(\sigma^{2}_{FY})$	-0.0808 ± -	0.1921 ± 0.0277**		
Residual $(\sigma_e^2)$	0.5460 ± 0.0191	0.1829 ± 0.0156		

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively. <sup>†</sup> Fixed effect of yield group ( $S_{HYE}$  and  $S_{LYE}$ ).

Table 3.7. Estimates of variance components and their associated standard errors for the NL-94 low-yield environment (LYE) switchgrass half-sib (HS) families evaluated for biomass yield at Stillwater, OK, 2002-2004 and NL-94 clonal parents evaluated for biomass yield at Perkins, OK, 2003-2004.

	Population			
Variance Component	NL-94 LYE HS Progeny	NL-94 Clonal Parents		
Family/ $_{\rm G}^{\dagger}(\sigma^2_{\rm F})$	0.0709 ± 0.0238**	0.0719 ± 0.0240**		
Year*Family/ $_{G^{\dagger}}(\sigma^{2}_{FY})$	-0.0495 ± -	0.1921 ± 0.0277**		
Residual ( $\sigma_e^2$ )	0.3261 ± 0.0147	0.1829 ± 0.0156		

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.  $^{\dagger}$  Fixed effect of yield group (S\_{HYE} and S\_{LYE}).

Table 3.8. Estimates of narrow-sense heritability $(h_n^2)$ for biomass yield, 95% confidence intervals (CIs) of those $h_n^2$ estimates, and predicted genetic gains
( $\Delta G$ ) per cycle of selection (5 years per cycle) and per year for the NL-94
high-yield environment (HYE) and low-yield environment (LYE) C1
populations based on progeny-parent regression estimation techniques using
phenotypic family means.

Population	<i>h<sup>2</sup>n</i> Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	$\Delta G$ Year (kg dm)
Combined Analysis	0.033	(-0.057, 0.123)	0.005	0.001
S <sub>HYE</sub> Group Over Environments	0.011	(-0.154, 0.177)	0.002	0.000
S <sub>LYE</sub> Group Over Environments	0.044	(-0.065, 0.152)	0.008	0.001
HYE	0.030	(-0.105, 0.152)	0.007	0.001
LYE	0.031	(-0.073, 0.134)	0.007	0.001
S <sub>HYE</sub> Group Within HYE	0.025	(-0.232, 0.183)	0.006	0.001
S <sub>HYE</sub> Group Within LYE	-0.011	(-0.191, 0.169)	-0.002	0.000
S <sub>LYE</sub> Group Within HYE	0.035	(-0.125, 0.138)	0.007	0.001
S <sub>LYE</sub> Group Within LYE	0.050	(-0.080, 0.181)	0.011	0.002

Table 3.9. Estimates of narrow-sense heritability  $(h^2_n)$  for biomass yield, 95% confidence intervals (CIs) of those  $h^2_n$  estimates, and predicted genetic gains( $\Delta G$ ) per cycle of selection (5 years per cycle) and per year for the NL-94 high-yield environment (HYE) and low yield-environment (LYE) C1 populations based on progeny-parent regression estimation techniques for individual plant selection.

Population	<i>h<sup>2</sup>n</i> Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	% $\Delta G$ Year (kg dm)
Combined Analysis	-0.115	(-0.104, 0.074)	-0.035	-0.007
S <sub>HYE</sub> Group Over Environments	-0.021	(-0.016, 0.114)	-0.004	-0.001
S <sub>LYE</sub> Group Over Environments	-0.006	(-0.125, 0.113)	-0.001	0.000
HYE	-0.005	(-0.148, 0.138)	-0.001	0.000
LYE	-0.021	(-0.080, 0.074)	-0.005	-0.001
S <sub>HYE</sub> Group Within HYE	-0.023	(-0.239, 0.194)	-0.054	-0.001
S <sub>HYE</sub> Group Within LYE	-0.010	(-0.153, 0.133)	-0.002	0.00
S <sub>LYE</sub> Group Within HYE	0.017	(-0.172, 0.206)	0.004	0.001
S <sub>LYE</sub> Group Within LYE	-0.027	(-0.157, 0.102)	-0.006	-0.001

Table 3.10. Estimates of narrow-sense heritability  $(h_n^2)$  for biomass yield, 95% confidence intervals (CIs) of those  $h_n^2$  estimates, and predicted genetic gains  $(\Delta G)$  per cycle of selection (5 years per cycle) and per year for the NL-94 high-yield environment (HYE) and low-yield environment (LYE) C<sub>1</sub> populations based on calculations from variance components using phenotypic family means.

Population	<i>h<sup>2</sup>n</i> Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	$\Delta G$ Year (kg dm)
Combined Analysis	0.087	(-0.077, 0.252)	0.014	0.003
S <sub>HYE</sub> Group Over Environments	0.048	(-0.020, 0.116)	0.008	0.002
S <sub>LYE</sub> Group Over Environments	0.118	(-0.182, 0.418)	0.019	0.004
HYE	0.848	(0.838, 0.858)	0.079	0.016
LYE	0.749	(0.715, 0.784)	0.165	0.033
S <sub>HYE</sub> Group Within HYE	0.881	(0.832, 0.931)	0.197	0.039
S <sub>HYE</sub> Group Within LYE	0.726	(0.712, 0.739)	0.160	0.032
S <sub>LYE</sub> Group Within HYE	0.800	(0.759, 0.831)	0.168	0.034
S <sub>LYE</sub> Group Within LYE	0.768	(0.714, 0.823)	0.287	0.057

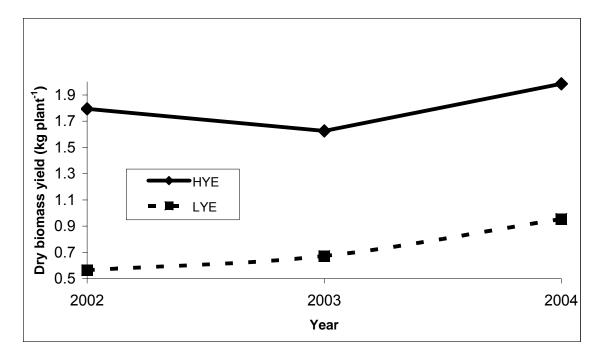
Table 3.11. Estimates of narrow-sense heritability  $(h^2_n)$  for biomass yield, 95% confidence intervals (CIs) of those  $h^2_n$  estimates, and predicted genetic gains  $(\Delta G)$  per cycle of selection (5 years per cycle) and per year for the NL-94 high-yield environment (HYE) and low-yield environment (LYE) C<sub>1</sub> populations based on calculations from variance components for individual plant selection.

Population	<i>h<sup>2</sup>n</i> Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	$\Delta G$ Year (kg dm)
Combined Analysis	0.072	(-0.062, 0.207)	0.012	0.002
S <sub>HYE</sub> Group Over Environments	0.055	(-0.140, 0.250)	0.010	0.002
S <sub>LYE</sub> Group Over Environments	0.083	(-0.143, 0.309)	0.014	0.003
HYE	0.574	(0.483, 0.666)	0.131	0.026
LYE	0.579	(0.544, 0.615)	0.135	0.027
S <sub>HYE</sub> Group Within HYE	0.601	(0.525, 0.678)	0.142	0.028
S <sub>HYE</sub> Group Within LYE	0.574	(0.554, 0.594)	0.133	0.027
S <sub>LYE</sub> Group Within HYE	0.519	(0.460, 0.570)	0.117	0.023
S <sub>LYE</sub> Group Within LYE	0.583	(0.522, 0.643)	0.135	0.003

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Fig. 3.1. Graphical depiction of the significant interaction of the fixed effects of high-yield environment (HYE) and low-yield environment (LYE)\*year. Estimates on the ordinate are over plant families.

Fig. 3.1. Graphical depiction of the significant interaction of the fixed effects of high-yield environment (HYE) and low-yield environment (LYE)\*year. Estimates on the ordinate are over plant families.



#### CHAPTER IV

## GENETIC PARAMETERS FOR BIOMASS YIELD IN TWO POPULATIONS OF UPLAND SWITCHGRASS

#### ABSTRACT

Breeding for increased biomass yield in switchgrass populations using recurrent selection techniques requires substantial resources in time and capital. Information on heritability and predicted gains from selection for increased yield in switchgrass is limited and may vary among populations, particularly those artificially synthesized for breeding improvement. Accordingly, studies were conducted to estimate amounts of heritable variation and predicted gains from selection for higher biomass yield within two upland ecotype switchgrass populations, SNU-EM and SNU-LM, to determine the potential effectiveness of recurrent selection.

For the respective populations, half-sib (HS) progeny from 100 randomly selected plants and the respective clonal parents were evaluated for biomass yield in replicated trials at different environments in 2003 and 2004. Estimates of  $h_n^2$  and predicted gains from selection were estimated using variance component and progeny-parent regression procedures. For each population, year and year\*HS family effects were highly significant (P<0.01) and the effect due to HS families was nonsignificant (P>0.05). HS family effects were significant within

respective years. HS family variance components were low and nonsignificant while family\*year components were higher and significant for both populations. Estimates of  $h_n^2$  derived from progeny-parent regression analysis were similar for the populations, ranging from 0.444 to 0.471. Predicted genetic gains ( $\Delta G$ ) per selection cycle using these  $h_n^2$  values ranged from 0.097 to 0.120. Estimates of  $h_n^2$  (0.043 to 0.108) and  $\Delta G$  (0.012 to 0.028) from variance components were similar for the two populations and much lower than those from progeny-parent regression. The large effect of environment on biomass yields and the failure of families to respond similarly over years stresses the importance of adequately testing through time to assess yield quantity and stability.

#### INTRODUCTION

Switchgrass (*Panicum virgatum*,L.) is a polymorphic, warm-season (C<sub>4</sub>), determinate, perennial bunchgrass indigenous to much of the contiguous United States east of the Rocky Mountains (Hitchock and Chase, 1951). It was an integral component of the precolonial North American tall grass prairie (Moser and Vogel, 1995; Hopkins, et al. 1995; Sanderson 1992). Switchgrass has been classified into upland and lowland ecotypes based on soil preference and morphology (Porter, 1966). Upland ecotypes are generally shorter growing, have leaves and stems that are finer in texture, and are better adapted to drier habitats and less fertile soils than their lowland counterparts.

Switchgrass constitutes a polyploid series with reported chromosome numbers ranging from 2n = 2x = 18 to 2n = 12x = 108 (Nielson, 1944; Henry and

Taylor, 1989). All confirmed lowland ecotypes have been tetraploids (2n = 4x = 36) and most upland ecotypes are octoploids (2n = 8x = 72) (Hopkins, et al., 1996). Switchgrass is cross-pollinated and out-crossing in enforced by a gametophytic self-incompatibility system that is similar to the S-Z incompatibility system found in other Poaceae (Martinèz-Reyna and Vogel, 2002).

Switchgrass is used in pasture and rangeland plantings as a monoculture and in a mixture with other grasses and in conservation plantings Moser and Vogel, 1995). Additionally, it has potential as a biomass energy crop (McLaughlin et al., 1999). The potential of switchgrass as such derives from its broad geographic adaptation, ability to grow on noncrop soils, and high biomass production capability with minimal inputs (McLaughlin, et al., 2000). Increased biomass yield is an important breeding objective for switchgrass but information concerning the magnitude of genetic variation for the trait in the upland ecotype is limited. Eberhart and Newell (1961) reported a broad-sense heritability ( $h_b^2$ ) estimate of 0.78 for plant yield in an upland switchgrass population from Nebraska. Newell and Eberhart (1961) reported narrow-sense heritability ( $h_n^2$ ) estimates of 0.18, 0.52, and 0.05 for "small blue-green", "medium-tall bluegreen", and "tall-green" plant populations derived from germplasm from Nebraska and northern Kansas.

The objectives of this study were to estimate genetic variances,  $h_n^2$ , and genetic gain from selection ( $\Delta G$ ) for increased biomass yield within two upland switchgrass populations.

#### MATERIALS AND METHODS

Plant materials used in this study comprised 100 HS families and their respective clonal maternal parent from each of two upland switchgrass populations. The two populations, 'Southern Upland Northern Upland – Early Maturing' (SNU-EM) and 'Southern Upland Northern Upland – Late Maturing' (SNU-LM), were synthesized respectively from late maturing and early maturing plants from two populations designated as 'Southern Upland' (SU) and 'Northern Upland' (NU) and from Oklahoma switchgrass accessions SWG001, SWG006, and SWG068. The original SU population was synthesized in 1993 from 'Caddo' and 'Blackwell'. Switchgrass accessions SWG001, SWG006, and SWG068 were subsequently merged into the SU population. The original NU population was synthesized in 1993 from 'Nebraska 28', 'Pathfinder', and 'Cave-in-Rock'. In 1998, isolated polycross nurseries were planted to form two populations designated as SNU-EM and SNU-LM populations. A total of 56 clonal parent plants from the SU and NU populations were included in each polycross. Parent plants used in the respective polycross synthesis nurseries were selected for flowering date compatibility. Seed  $(C_0)$  was harvested from each polycross nursery in 1999. In 2000, 1020  $C_0$  plants of each population were space planted (1.06 m) for purposes of selection and estimating genetic variation in the populations. For this study, HS seed was harvested from 130 randomly selected plants from each nursery in fall of 2001.

In spring 2002, 100 HS C<sub>0</sub> families from each population were established in replicated tests at the Perkins Research Station, Perkins, OK (35.57°N. Lat.,

97.01°W. Long.) using plants started in the greenhouse. The experimental design for each test was a randomized complete block design (RCBD) with four replications. Individual plots consisted of four HS progeny. Greenhouse grown plants were transplanted on 1.06 m centers. A row of plants, not harvested for biomass yield data, was established around the respective tests to protect against border effects. The soil type for both tests is a Teller loam (fine-loamy, mixed, active, thermic Udic Argiustolls).

So that unbiased estimates of  $h_n^2$  could be obtained via progeny-parent regression methods (Casler, 1982), clonal parent plants of each HS progeny family from the respective populations were established in field tests in spring 2002. Parent-offspring regression is a commonly used technique for estimating  $h_n^2$  of quantitative characters in crop species (Casler, 1982). This technique, however, may lead to biased estimates of  $h_n^2$  as a result of GE interactions and error covariances between parents and offspring. Furthermore, if these covariances are positive, the resulting positive bias to  $h_{p}^{2}$  will result in overly optimistic expected genetic advances (Casler, 1982). To compensate for that error, progeny plot mean and progeny individual plant biomass yield was regressed onto parent means from a separate environment and year utilizing generalized least squares analysis, (SAS Inst., 1999). A RCBD with three replications was used for both tests. Individual plots consisted of one plant. Greenhouse grown clonal plants of each parent were transplanted on 1.06 m centers. A row of plants, not harvested for biomass yield data, was established around the respective tests to protect against border effects. The clonal parental

trials were placed on the Agronomy Research Station, Stillwater, OK (36.16°N. Lat., 97.09°W. Long.). The soil corresponding to the two tests is a Kirkland silt loam (fine, mixed, superactive, thermic Udertic Paleustolls).

All tests were fertilized annually in early spring with 90 kg ha<sup>-1</sup> N. Surflan<sup>®</sup> herbicide was applied to the tests early each spring at a rate of 1.7 kg ha<sup>-1</sup> a.i. to prevent switchgrass seedling emergence and to control other weeds.

Table 4.1 provides the expected mean squares, degrees of freedom (df) and sources thereof of a study consisting of plant families tested across multiple years. The data were analyzed using generalized least squares (SAS Inst., 1999). A combined three-factor analysis of variance was performed on data collected for all environments and years employing the following statistical effects model:

$$Y_{ijklm} = \mu + \alpha_i + \beta_j + \tau_k + \alpha \beta_{ij} + e_{l(ijk)}$$

Where:

μ	<ul> <li>overall mean of biomass yield,</li> </ul>
$\alpha_{i}$	= random effect of family (genotype) <i>i</i> ,
${m eta}_j$	= fixed effect of year <i>j</i> ,
$ au_k$	= random effect of replication <i>k</i> ,
$lphaeta_{ij}$	= random interaction effect of group <i>i</i> and year <i>j</i> , and
$e_{l(ijk)}$	= experimental error, mean 0, variance $\sigma^2$ .

Estimates of  $h_n^2$  were derived in two ways. The first estimation was via progeny-parent regression via generalized least squares (SAS Inst., 1999) [citation=SAS online doc, Version 8. SAS Institute, Inc. Cary, NC].

Estimates of  $h_n^2$  can thus be calculated as follows:

**2**\*β<sub>1</sub>

Where:

 $\beta$ 1 = the linear regression coefficient of progeny-parent regression The regression coefficient is derived as described and presented by Casler (1982) as follows:

$$h_n^2 = 2 \frac{\sigma_{P_{PO}}}{\sigma_p^2}$$

Where:

 $\sigma_{\rm P_{\rm Po}}$  = phenotypic covariance between parental values and progeny

values, and

 $\sigma_{P}^{2}$  = phenotypic variance among parental means.

Estimates of  $h_n^2$  were calculated in this manner on both an individual plant and a phenotypic family mean (PFM) basis. Estimates of  $h_n^2$  were also obtained via a variance component method as described by Nguyen and Sleper (1983) and by Fehr (1987).

Estimates of  $h_n^2$  on an individual plant basis were derived as follows:

$$h_n^2 = \frac{\sigma_F^2}{\sigma_F^2 + \frac{\sigma_{FY}^2}{Y} + \frac{\sigma_\gamma^2}{R} + \frac{\sigma_e^2}{RY} + \frac{\sigma_\omega^2}{NRY}}$$

Estimates of  $h_n^2$  on a plant family mean basis were derived as follows:

$$h_n^2 = \frac{\sigma_F^2}{\sigma_F^2 + \frac{\sigma_{FY}^2}{Y} + \frac{\sigma_\gamma^2}{R} + \frac{\sigma_e^2}{RY}}$$

Where:

$\sigma_{\scriptscriptstyle F}^{\scriptscriptstyle 2}$	= variance attributable to plant families,
$\sigma^2_{\scriptscriptstyle FY}$	<ul> <li>variance attributable to family*year interaction,</li> </ul>
$\sigma_{\gamma}^2$	<ul> <li>variance attributable to replications,</li> </ul>
$\sigma_{_e}^2$	= experimental error, mean 0, variance $\sigma^2$ ,
$\sigma^2_{\scriptscriptstyle \omega}$	= variance attributable to individual within plots,
Y	= number of years,
R	<ul> <li>number of replications, and</li> </ul>
Ν	= number of plants per plot.

The formulae provide an estimate of  $h_n^2$  since the genetic variance among HS families represents primarily the additive genetic variance contained in the phenotypic variance among HS plot family means and among individual plants (Nguyen and Sleper, 1983). In addition to estimates of  $h_n^2$ , the 95% confidence intervals (CIs) were calculated corresponding to each  $h_n^2$  estimate. Concerning

the variance component calculation method, standard errors of  $h^2_n$  estimates were obtained via the method described theoretically by Nelder (1953).

 $\Delta G$  per cycle of selection was also calculated on both an individual plant and PFM basis as described by Nguyen and Sleper (1983).

 $\Delta G$  per cycle of individual plant selection can be predicted as follows:

$$\Delta G = ckh_{ph}^2 \sigma_{ph} = ck \frac{\sigma_F^2}{\sigma_{ph}}$$

 $\Delta G$  of selection based on a PFM basis can be estimated as follows:

$$\Delta G = ckh_{pfm}^2 \sigma_{pfm} = ck \frac{\sigma_F^2}{\sigma_{pfm}}$$

Where:

С	=	parental control factor,
k	=	standardized selection differential,
$h_{\scriptscriptstyle ph}^2$	=	narrow-sense heritability on an individual plant basis,
$\sigma_{_{ph}}$	=	phenotypic standard deviation from individual plant analysis,
$h_{\scriptscriptstyle pfm}^2$	=	narrow-sense heritability on a PFM basis,
$\sigma_{{}_{p\!f\!m}}$	=	phenotypic standard deviation from PFM analysis, and
$\sigma_{\scriptscriptstyle F}^2$	=	variance attributable to plant families.

Here, the parental control factor (c) = 2 and the standardized selection differential

(*k*) = 1.16.

#### **Results and Discussion**

In both the SNU-EM and SNU-LM populations, analysis of variance of HS family biomass yields over years indicated significant differences (P<0.01) due to years and the family\*year interaction, but not families (P>0.05) (Table 4.2). Yield differences among HS families in both populations were significantly different during each of the two years (data not presented). For the SNU-EM population 2-yr mean yield per plant for the HS families was 0.55 + 0.02 kg dm. The biomass yield of HS families ranged from 0.38 to 0.80 kg dm. For the SNU-LM population 2-yr mean yield per plant for the HS families was 0.76 ± 0.02 kg dm. The mean biomass yield of HS families ranged from 0.49 to 1.02 kg dm. The failure of HS families in both populations to respond similarly in biomass yield to different years masked differences evident within individual years. In both populations, yield differences among parent plants were significantly different each year and over years (data not presented). Estimates of variance components for biomass yield of HS progeny families and clonal parents of the SNU-LM and SNU-EM populations are given in Tables 4.3 and 4.5. Estimates for family (additive genetic) variance ( $\sigma_F^2$ ) of HS progeny were small in both populations and were not significant based on the significance as determined by an F-test. The family variance estimate for clonal parents and the family\*year variance ( $\sigma_{_{FY}}^2$ ) estimates for HS families and clonal parents were significant. For HS families the magnitude of the family variance estimate is much lower than that of the family\*year estimate, while the clonal parent variance estimate is

considerably higher than the family\*year estimate. The results indicate that differential genotypic yield response to environment is large and that testing over years is required to evaluate switchgrass genotypes for quantity and stability of biomass yield

Estimates of  $h_n^2$  from progeny-parent regression were of similar magnitude for the two populations (0.444 to 0.471) and higher than corresponding estimates from variance component analysis (0.043 to 0.108) (Tables 4.4 and 4.6). The confidence intervals for all variance component derivative  $h_n^2$  estimates are inclusive of zero (0). The individual plant vs. PFM  $h_n^2$  estimates from progenyparent regression were nearly identical, while the variance component derivative estimates were higher when based on PFM.

Estimates of  $\Delta G$  were patterned after the  $h_n^2$  estimates (Tables 4.4 and 4.6). Predicted yield gains per selection cycle from progeny-parent regression ranged from 0.097 to 0.122 while those from variance component analysis ranged from 0.012 to 0.028.

Estimates of  $h_n^2$  calculated from variance component methods of estimation were found to be low and not significantly greater than 0 for both the SNU-EM and SNU-LM populations. These findings are attributable to the low magnitude of the family (group) component of variance, which is an estimate of additive genetic variance within the population, coupled with the highly significant estimates of variance corresponding to the year\*family component of variance, which is an estimate of GE interaction. Conversely, the progeny-parent regression method of  $h_n^2$  calculation provided more optimistic estimates of the

amount of heritable variation for enhanced dry biomass yield present in both of the reference populations. The disparity between the estimates of  $h^2_n$  obtained from the progeny-parent regression and variance component methods of estimation suggest that the sparse variance estimates of biomass yield within both populations is nearly 50% attributable to genetic factors. The higher  $h^2_n$  estimates were for PFM selection in the SNU-EM population and for individual plant selection within the SNU-LM population.

Despite the favorable estimates of heritable variation within both of the reference populations for enhanced dry biomass yield from progeny-parent regression techniques, significant additive genetic variation was not detected in either the SNU-EM or SNU-LM via HS analysis employing generalized least squares (SAS Inst., 1999). Heritability can be defined as the ratio of genetic variance to total phenotypic variance within a population (Fehr, 1987);  $h_n^2$  is the ratio of additive genetic variance to phenotypic variance within a population. Hence, from examination of formulae provided in the materials and methods section of this report, it can readily be seen that a formidable and significant estimate of  $h^2$  is not contingent upon a significant level of additive genetic variation being present within the reference population. Such is the case for both reference populations in this study.

Based upon the aforementioned findings, it is concluded that breeding for enhanced dry biomass yield production may not be practical without introduction of new genetic material into both the SNU-EM and SNU-LM populations.

#### REFERENCES

Casler, M.D. 1982. Genotype x environment interaction bias to parent-offspring regression heritability estimates. Crop Sci. 22:540-542.

Fehr, W.R. 1987. Principles of cultivar development: Theory and technique. Vol. 1. McGraw-Hill, Inc. New York.

- Henry, D.S., and T.H. Taylor. 1989. Registration of KY 1625 swichgrass germplasm. Crop Sci. 29:1096.
- Hitchock, A.S. 1951. Manual of the grasses of the United States. USDA Misc. Publ. 200. 2nd ed. U.S. Gov. Print. Office, Washington, DC.
- Hopkins, A.A., C.M. Taliaferro, C.D. Murphy, and D. Christian. 1996. Chromosome number and nuclear DNA content of several switchgrass populations. Crop Sci. 36:1192-1195.
- Hopkins, A.A., K.P. Vogel, K.J. Moore, K.D. Johnson, and I.T. Carlson. 1995. Genotypic variability and genotype x environment interactions among switchgrass accessions from the midwestern USA. Crop Sci. 35:565-571.
- Martinèz-Reyna, J.M., and K.P. Vogel. 2002. Incompatibility systems in switchgrass. Crop Sci. 42:1800-1805.
- McLaughlin, S., J. Bouton, D. Bransby, B. Conger, W. Ocumpaugh, P. Parrish, C. Taliaferro, K. Vogel, and S. Wullschleger. 1999. Developing switchgrass as a bioenergy crop. P. 282-299. *In J. Janick* (ed.) Perspectives on new crops and uses. ASHS Press, Alexandria, VA.
- Moser, L.E., and K.P. Vogel. 1995. Switchgrass, big bluestem and indiangrass. p. 409-420. *In* R.F. Barnes et al. (ed.) Forages Vol. 1: An introduction to grassland agriculture. 5th ed. Iowa State Univ. Press, Ames.
- Nelder, J.A. 1953. Statistical models in biometrical genetics. Heredity 7:111-119.
- Nguyen, H.T., and D.A. Sleper. 1983. Theory and application of half-sib matings in forage grass breeding. Theor. Appl. Genet. 64:187-196.
- Nielson, E.L. 1944. An on-farm test of perennial forage grass varieties under management intensive grazing. J. Agron. Res. 69:327-353.

- Porter, C.L., Jr. 1966. An analysis of variation between upland and lowland switchgrass, *Panicum virgatum* L., in central Oklahoma. Ecology 47:980-992.
- Sanderson, M.A. 1992. Morphological development of switchgrass and kleingrass. Agron. J. 84:415-419.

SAS Institute. 1999. SAS system for Windows. v. 8.2. SAS Inst., Cary, NC.

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population	51		
Source	df	Expected mean squares	
Year (Y)	(y-1)	$\sigma^2$ + r $\sigma^2_f$ + $\theta^2_y$	
Rep (R)	(r-1)	$\sigma^2$ + fy $\sigma^2_r$	
Family (F)	(f-1)	$\sigma^2$ + $r\sigma^2_{fy}$ + $ry\sigma^2_{f}$	
F*Y	(f-1)(y-1)	$\sigma^2 + r\sigma^2_{fy}$	
Error	n-model df	$\sigma^2$	
Total	rfy-1		

Table 4.1. Sources, degrees of freedom (df), and expected mean squares for half-sib progeny analysis of the SNU-EM and SNU-LM switchgrass populations.

Table 4.2. ANOVA of biomass yield for half-sib (HS) progeny and clonal parent
plants of SNU-EM and SNU-LM switchgrass populations tested in 2003 and
2004. HS progeny and clonal parent plants were respectively tested at
Perkins and Stillwater, OK.

		SNU	-EM	SNU	-LM
Source	df	HS Prog.	Parents	HS Prog.	Parents
			Mean	squares	
Family (F)	99	0.0676	1.2792**	0.0972	1.0243**
Rep (R)	3 (2 parents)	0.1489**	0.7409**	0.2544**	0.4786
Year (Y)	1	24.0964**	2.6838**	21.4108**	0.4209
F*Y	99	0.0607**	0.2403**	0.0864**	0.3457*

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 4.3. Estimates of variance components and their associated standard errors for the SNU-EM half-sub (HS) progeny and clonal parental populations tested at Perkins and Stillwater, OK, respectively, 2003-2004.

	Population		
Variance Component	SNU-EM HS Progeny	SNU-EM Clonal Parents	
Family $(\sigma^2_F)$	$0.0009 \pm 0.0030$	0.1743 ± 0.0417**	
Family*Year ( $\sigma^2_{FY}$ )	0.0097 ± 0.0070**	0.0406 ± 0.0142**	
Residual ( $\sigma_{e}^{2}$ )	0.02248 ± 0.0053	0.1195 ± 0.0141	

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 4.4. Narrow-sense heritability estimates  $(h^2_n)$  for biomass yield, 95% confidence intervals (CIs) of those  $h^2_n$  estimates, and predicted genetic gains  $(\Delta G)$  per cycle of selection (5 years per cycle) and per year for the SNU-EM population based on progeny-parent regression and variance component estimation methods for phenotypic family means (PFM) and individual plant selection.

Population	<i>h<sup>2</sup>n</i> Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	$\Delta G$ Year (kg dm)
SNU-EM – PFM (ProgPar. Reg.) <sup>†</sup>	0.446	(0.303, 0.589)	0.097	0.019
SNU-EM - Indiv. Plnt. (ProgPar. Reg.) <sup>†</sup>	0.444	(0.302, 0.587)	0.121	0.025
SNU-EM – PFM (Var. Comp.) <sup>††</sup>	0.093	(-0.168, 0.372)	0.022	0.004
SNU-EM - Indiv. Plnt (Var. Comp.) <sup>††</sup>	0.043	(-0.023, 0.109)	0.012	0.002

<sup>†</sup> Progeny-Parent regression method of  $h_n^2$  estimation. <sup>††</sup> Variance component method of  $h_n^2$  estimation.

Table 4.5. Estimates of variance components and their associated standard errors for the SNU-LM half-sib (HS) progeny and clonal parental populations. tested at Perkins and Stillwater, OK, respectively, 2003-2004.

	Population		
Variance Component	SNU-LM HS Progeny	SNU-LM Clonal Parents	
Family $(\sigma^2_F)$	0.0014 ± 0.0037	0.1517 ± 0.0389**	
Family*Year ( $\sigma^2_{FY}$ )	0.0129 ± 0.0080**	0.0338 ± 0.0130*	
Residual $(\sigma_e^2)$	$0.0348 \pm 0.0066$	0.2459 ± 0.0175	

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 4.6. Narrow-sense heritability estimates  $(h_n^2)$  for biomass yield, 95% confidence intervals (CIs) of those  $h_n^2$  estimates, and predicted genetic gains  $(\Delta G)$  per cycle of selection (5 years per cycle) and per year for the SNU-LM population based on progeny-parent regression and variance component estimation techniques for phenotypic family means (PFM) and for individual plant selection.

Population	h <sup>2</sup> n Estimate	95% C.I.	$\Delta G$ Sel. Cycle (kg dm)	% ∆ <i>G</i> Year (kg dm)
SNU-LM - PFM (Prog. – Par. Reg.) <sup>†</sup>	0.464	(0.295, 0.632)	0.120	0.024
SNU-LM - Indiv. PInt. (Prog. – Par. Reg.) <sup>†</sup>	0.471	(0.308, 0.634)	0.122	0.024
SNU-LM – PFM (Var. Comp.) <sup>††</sup>	0.108	(-0.027, 0.250)	0.028	0.006
SNU-LM – Indiv. Plnt. (Var. Comp.) <sup>††</sup>	0.047	(-0.004, 0.099)	0.016	0.003

<sup>†</sup>Progeny-Parent regression method of  $h_n^2$  estimation. <sup>††</sup> Variance component method of  $h_n^2$  estimation.

## APPENDIX TABLES

	2002, 2003, 2004,		o youro.		Over
$Family^\dagger$	$Location^{\dagger\dagger}$	2002	2003	2004	2002-2004
				g plant⁻¹	
S <sub>HYE</sub> 02-03	CCB	1.53	1.31	1.49	1.44
S <sub>HYE</sub> 02-07	CCB	1.56	1.33	1.37	1.42
S <sub>HYE</sub> 06-02	CCB	2.02	1.81	2.48	2.10
S <sub>HYE</sub> 08-05	CCB	1.76	1.55	1.89	1.73
S <sub>HYE</sub> 09-02	CCB	1.94	1.72	1.97	1.88
S <sub>HYE</sub> 09-06	CCB	1.65	1.52	1.88	1.68
S <sub>HYE</sub> 10-10	CCB	1.93	1.91	2.44	2.10
S <sub>HYE</sub> 11-02	CCB	1.70	1.60	1.81	1.70
S <sub>HYE</sub> 11-06	CCB	1.96	1.61	1.98	1.85
S <sub>HYE</sub> 11-08	CCB	1.77	1.60	1.85	1.74
S <sub>HYE</sub> 11-09	CCB	1.66	1.39	1.60	1.55
S <sub>HYE</sub> 12-10	CCB	1.58	1.41	1.82	1.60
S <sub>HYE</sub> 13-07	CCB	1.56	1.37	1.88	1.61
S <sub>HYE</sub> 14-02	CCB	1.65	1.50	1.87	1.68
S <sub>HYE</sub> 15-05	CCB	1.63	1.53	1.82	1.66
S <sub>HYE</sub> 15-08	CCB	1.94	1.79	2.14	1.95
S <sub>HYE</sub> 16-01	CCB	1.62	1.48	1.56	1.55
S <sub>HYE</sub> 17-04	CCB	1.19	1.22	1.40	1.27
S <sub>HYE</sub> 17-07	CCB	1.79	1.65	1.94	1.79
S <sub>HYE</sub> 18-06	CCB	1.83	1.69	1.79	1.77
S <sub>HYE</sub> 18-08	CCB	1.88	1.64	2.09	1.87
S <sub>HYE</sub> 18-09	CCB	1.85	1.61	1.99	1.81
S <sub>HYE</sub> 21-03	CCB	1.62	1.45	1.60	1.56
S <sub>HYE</sub> 21-04	CCB	1.81	1.55	1.92	1.76
S <sub>HYE</sub> 21-05	CCB	1.67	1.58	2.00	1.75
S <sub>HYE</sub> 22-06	CCB	1.86	1.54	2.03	1.81
S <sub>HYE</sub> 22-09	CCB	1.59	1.48	1.90	1.66
S <sub>HYE</sub> 23-06	CCB	1.77	1.72	2.23	1.91
S <sub>HYE</sub> 24-09	CCB	1.89	1.73	2.09	1.90
S <sub>HYE</sub> 25-04	CCB	1.63	1.53	1.85	1.67
S <sub>HYE</sub> 25-10	CCB	1.86	1.69	2.15	1.90
S <sub>HYE</sub> 26-06	CCB	1.61	1.48	1.64	1.58
S <sub>HYE</sub> 26-07	CCB	1.97	1.67	2.14	1.93
S <sub>HYE</sub> 26-10	CCB	1.62	1.59	1.80	1.67
S <sub>HYE</sub> 28-07	CCB	1.89	1.98	2.35	2.07
S <sub>HYE</sub> 29-01	CCB	1.65	1.54	2.04	1.74
S <sub>HYE</sub> 30-02	CCB	1.72	1.58	1.86	1.72
S <sub>HYE</sub> 30-07	CCB	1.63	1.56	1.88	1.69
S <sub>HYE</sub> 30-09	CCB	1.72	1.55	1.94	1.74
S <sub>HYE</sub> 30-12	CCB	1.72	1.45	1.85	1.68
S <sub>HYE</sub> 31-06	CCB	1.60	1.49	1.84	1.64

Table A.1. Mean dry matter (dm) yield of NL-94 HYE and LYE population plant families for 2002, 2003, 2004, and across years.

	Location <sup>**</sup>	2002	2003	2004	Over 2002-2004
Family <sup>†</sup>	Location	2002			2002-2004
0 24 40		4 40	K(	g plant <sup>-1</sup>	1 50
S <sub>HYE</sub> 31-10	CCB	1.48	1.35	1.68	1.50
S <sub>HYE</sub> 32-11	CCB	1.94	1.76	2.03	1.91
S <sub>HYE</sub> 33-10	CCB	2.01	1.85	2.43	2.09
S <sub>HYE</sub> 34-06	CCB	1.52	1.42	1.48	1.47
S <sub>HYE</sub> 36-09	CCB	2.09	1.78	2.09	1.99
S <sub>HYE</sub> 36-12	CCB	1.94	2.06	2.51	2.17
S <sub>HYE</sub> 37-06	CCB	1.75	1.43	1.69	1.62
S <sub>HYE</sub> 38-11	CCB	1.91	1.60	1.98	1.83 2.03
S <sub>HYE</sub> 39-10	CCB	1.91	1.82	2.36	
S <sub>HYE</sub> 41-06	CCB	1.79	1.73	2.02	1.85
S <sub>HYE</sub> 41-12	CCB	1.90	1.77	2.29	1.99
S <sub>HYE</sub> 44-08	CCB	1.80	1.45	1.64	1.63
S <sub>HYE</sub> 46-01	CCB	1.97	1.73	2.20	1.96
S <sub>HYE</sub> 49-04	CCB	1.82	1.73	2.47	2.01
S <sub>HYE</sub> 51-02	CCB	1.68	1.43	1.74	1.62
S <sub>HYE</sub> 52-06	CCB	1.66	1.57	2.06	1.76
S <sub>HYE</sub> 54-05	CCB	1.47	1.38	1.77	1.54
S <sub>HYE</sub> 56-01	CCB	1.91	1.78	2.03	1.91
S <sub>HYE</sub> 57-02	CCB	1.71	1.49	1.95	1.72
S <sub>LYE</sub> 03-05	CCB	1.53	1.44	1.70	1.56
S <sub>LYE</sub> 04-10	CCB	2.00	1.81	1.96	1.92
S <sub>LYE</sub> 04-30	CCB	1.75	1.65	2.04	1.81
S <sub>LYE</sub> 04-32	CCB	2.05	1.80	2.07	1.97
S <sub>LYE</sub> 05-15	CCB	1.75	1.69	2.16	1.87
S <sub>LYE</sub> 05-32	CCB	1.98	1.96	2.43	2.12
S <sub>LYE</sub> 06-05	CCB	1.73	1.56	2.04	1.78
S <sub>LYE</sub> 08-13	CCB	1.87	1.79	2.31	1.99
S <sub>LYE</sub> 08-23	CCB	2.13	1.95	2.36	2.15
S <sub>LYE</sub> 09-20	CCB	1.87	1.63	1.88	1.80
S <sub>LYE</sub> 09-24	CCB	1.82	1.86	2.44	2.04
S <sub>LYE</sub> 09-25	CCB	1.97	1.78	2.21	1.99
S <sub>LYE</sub> 10-09	CCB	2.01	1.66	2.23	1.97
S <sub>LYE</sub> 10-22	CCB	1.68	1.53	1.97	1.72
S <sub>LYE</sub> 10-28	CCB	1.84	1.58	2.07	1.83
S <sub>LYE</sub> 11-07	CCB	1.80	1.54	1.90	1.75
S <sub>LYE</sub> 11-15	CCB	1.83	1.53	1.68	1.68
S <sub>LYE</sub> 11-16	CCB	1.77	1.47	1.80	1.68
S <sub>LYE</sub> 11-31	CCB	2.01	1.80	1.97	1.93
S <sub>LYE</sub> 12-13	CCB	1.86	1.79	2.12	1.93
S <sub>LYE</sub> 12-26	CCB	2.09	1.63	1.86	1.86
S <sub>LYE</sub> 12-27	CCB	1.68	1.57	2.00	1.75
S <sub>LYE</sub> 12-33	CCB	1.46	1.35	1.46	1.42

Table A.1. Continued.

	Location <sup>**</sup>	2002	2002	2004	Over
Family <sup>†</sup>	Location	2002	2003	2004	2002-2004
C 12 15	ССВ	 1.88	K( 1 70	g plant <sup>-1</sup>	1 00
S <sub>LYE</sub> 13-15 S <sub>LYE</sub> 13-27	CCB		1.79 1.55	2.28 1.97	1.98 1.76
S <sub>LYE</sub> 13-27 S <sub>LYE</sub> 14-16	ССВ	1.75 1.82	1.55	2.31	2.01
S <sub>LYE</sub> 14-10 S <sub>LYE</sub> 15-06	CCB	1.62	1.38	1.79	1.58
S <sub>LYE</sub> 17-26	CCB	1.88	1.64	2.02	1.85
S <sub>LYE</sub> 17-20 S <sub>LYE</sub> 17-30	CCB	2.20	1.04	2.62	2.2
S <sub>LYE</sub> 17-30 S <sub>LYE</sub> 17-32	CCB	1.72	1.93	2.03	1.78
S <sub>LYE</sub> 18-27	CCB	1.72	1.64	2.15	1.86
S <sub>LYE</sub> 19-06	CCB	1.92	1.84	2.13	2.03
S <sub>LYE</sub> 19-00	CCB	2.08	1.71	2.04	1.95
$S_{LYE}$ 20-05	CCB	1.93	1.88	2.39	2.07
S <sub>LYE</sub> 20-05	CCB	1.84	1.59	1.72	1.72
S <sub>LYE</sub> 20-18	CCB	1.93	1.61	1.90	1.82
$S_{LYE}$ 20-24	CCB	1.99	1.74	2.16	1.96
S <sub>LYE</sub> 21-28	CCB	1.74	1.62	2.13	1.83
S <sub>LYE</sub> 22-12	CCB	1.56	1.49	1.85	1.63
S <sub>LYE</sub> 22-14	CCB	1.62	1.43	1.74	1.60
S <sub>LYE</sub> 23-05	CCB	1.84	1.53	1.86	1.74
S <sub>LYE</sub> 23-32	CCB	1.65	1.50	1.54	1.56
S <sub>LYE</sub> 23-34	CCB	1.80	1.61	1.87	1.76
S <sub>LYE</sub> 24-12	CCB	1.70	1.47	1.91	1.70
S <sub>LYE</sub> 24-28	CCB	1.84	1.76	2.20	1.93
S <sub>LYE</sub> 24-29	CCB	1.72	1.46	1.67	1.62
S <sub>LYE</sub> 25-01	CCB	1.70	1.68	2.02	1.80
S <sub>LYE</sub> 25-09	CCB	1.95	1.77	2.25	1.99
S <sub>LYE</sub> 25-13	CCB	1.45	1.27	1.28	1.33
S <sub>LYE</sub> 25-24	CCB	1.76	1.56	1.65	1.66
S <sub>LYE</sub> 25-34	CCB	1.69	1.56	1.78	1.68
S <sub>LYE</sub> 26-08	CCB	1.83	1.71	2.17	1.90
S <sub>LYE</sub> 26-09	CCB	1.72	1.62	1.99	1.78
S <sub>LYE</sub> 26-14	CCB	2.11	1.85	2.13	2.03
S <sub>LYE</sub> 26-29	CCB	1.84	1.62	2.10	1.85
S <sub>LYE</sub> 26-34	CCB	2.16	1.92	2.52	2.20
S <sub>LYE</sub> 27-24	CCB	1.69	1.62	1.93	1.75
S <sub>LYE</sub> 28-10	CCB	1.97	1.84	2.18	2.00
S <sub>LYE</sub> 28-20	CCB	1.96	1.75	2.48	2.06
S <sub>LYE</sub> 28-29	CCB	1.81	1.64	1.98	1.81
S <sub>LYE</sub> 29-21	CCB	1.73	1.65	1.80	1.73
S <sub>LYE</sub> 29-25	CCB	1.82	1.71	2.32	1.95
S <sub>LYE</sub> 29-31	CCB	2.04	1.75	1.87	1.89
S <sub>LYE</sub> 30-22	CCB	1.97	1.53	1.87	1.79
S <sub>LYE</sub> 30-33	CCB	1.86	1.78	2.23	1.96

Table A.1. Continued.

					Over
Family <sup>†</sup>	Location <sup>††</sup>	2002	2003	2004	2002-2004
			k(	g plant⁻¹	
S <sub>HYE</sub> 02-03	HORT	0.54	0.60	0.78	0.64
S <sub>HYE</sub> 02-07	HORT	0.55	0.62	0.86	0.67
S <sub>HYE</sub> 06-02	HORT	0.46	0.82	1.25	0.84
S <sub>HYE</sub> 08-05	HORT	0.58	0.72	1.00	0.77
S <sub>HYE</sub> 09-02	HORT	0.59	0.78	1.15	0.84
S <sub>HYE</sub> 09-06	HORT	0.5	0.56	0.77	0.63
S <sub>HYE</sub> 10-10	HORT	0.35	0.58	0.81	0.58
S <sub>HYE</sub> 11-02	HORT	0.69	0.67	0.93	0.77
S <sub>HYE</sub> 11-06	HORT	0.60	0.60	0.81	0.67
S <sub>HYE</sub> 11-08	HORT	0.70	0.88	1.22	0.93
S <sub>HYE</sub> 11-09	HORT	0.52	0.58	0.92	0.67
S <sub>HYE</sub> 12-10	HORT	0.81	0.93	1.28	1.00
S <sub>HYE</sub> 13-07	HORT	0.56	0.61	0.84	0.67
S <sub>HYE</sub> 14-02	HORT	0.38	0.45	0.54	0.46
S <sub>HYE</sub> 15-05	HORT	0.50	0.63	0.97	0.70
S <sub>HYE</sub> 15-08	HORT	0.48	0.58	0.89	0.65
S <sub>HYE</sub> 16-01	HORT	0.54	0.61	0.86	0.67
S <sub>HYE</sub> 17-04	HORT	0.63	0.74	0.90	0.76
S <sub>HYE</sub> 17-07	HORT	0.47	0.69	0.96	0.71
S <sub>HYE</sub> 18-06	HORT	0.63	0.70	0.87	0.73
S <sub>HYE</sub> 18-08	HORT	0.55	0.81	1.17	0.84
S <sub>HYE</sub> 18-09	HORT	0.48	0.61	0.80	0.63
S <sub>HYE</sub> 21-03	HORT	0.46	0.48	0.61	0.52
S <sub>HYE</sub> 21-04	HORT	0.42	0.62	0.97	0.67
S <sub>HYE</sub> 21-05	HORT	0.58	0.62	0.90	0.70
S <sub>HYE</sub> 22-06	HORT	0.48	0.68	0.95	0.70
S <sub>HYE</sub> 22-09	HORT	0.48	0.65	1.08	0.74
S <sub>HYE</sub> 23-06	HORT	0.51	0.43	0.59	0.51
S <sub>HYE</sub> 24-09	HORT	0.52	0.72	0.87	0.70
S <sub>HYE</sub> 25-04	HORT	0.51	0.58	1.04	0.71
S <sub>HYE</sub> 25-10	HORT	0.74	0.91	0.95	0.87
S <sub>HYE</sub> 26-06	HORT	0.53	0.64	1.07	0.75
S <sub>HYE</sub> 26-07	HORT	0.67	0.74	1.16	0.86
S <sub>HYE</sub> 26-10	HORT	0.43	0.61	0.97	0.67
S <sub>HYE</sub> 28-07	HORT	0.53	0.66	0.88	0.69
S <sub>HYE</sub> 29-01	HORT	0.45	0.44	0.62	0.51
S <sub>HYE</sub> 30-02	HORT	0.76	0.80	1.23	0.93
S <sub>HYE</sub> 30-07	HORT	0.47	0.65	0.92	0.68
S <sub>HYE</sub> 30-09	HORT	0.46	0.52	0.77	0.59
S <sub>HYE</sub> 30-12	HORT	0.45	0.61	0.82	0.63
S <sub>HYE</sub> 31-06	HORT	0.46	0.78	1.18	0.80
S <sub>HYE</sub> 31-10	HORT	0.45	0.60	0.92	0.66

Table A.1. Continued.

Table A.T. Con					Over
Family <sup>†</sup>	Location <sup>††</sup>	2002	2003	2004	2002-2004
			k(	g plant⁻¹	
S <sub>HYE</sub> 32-11	HORT	0.67	0.74	1.05	0.82
S <sub>HYE</sub> 33-10	HORT	0.31	0.41	0.57	0.43
S <sub>HYE</sub> 34-06	HORT	0.90	0.84	1.13	0.95
S <sub>HYE</sub> 36-09	HORT	0.50	0.69	0.87	0.69
S <sub>HYE</sub> 36-12	HORT	0.91	0.84	1.19	0.98
S <sub>HYE</sub> 37-06	HORT	0.51	0.61	0.78	0.64
S <sub>HYE</sub> 38-11	HORT	0.47	0.70	1.01	0.73
S <sub>HYE</sub> 39-10	HORT	0.35	0.70	0.99	0.68
S <sub>HYE</sub> 41-06	HORT	0.42	0.66	0.93	0.67
S <sub>HYE</sub> 41-12	HORT	0.54	0.62	0.87	0.68
S <sub>HYE</sub> 44-08	HORT	0.52	0.63	0.79	0.65
S <sub>HYE</sub> 46-01	HORT	0.42	0.54	0.73	0.56
S <sub>HYE</sub> 49-04	HORT	0.56	0.67	1.22	0.82
S <sub>HYE</sub> 51-02	HORT	0.61	0.68	0.94	0.74
S <sub>HYE</sub> 52-06	HORT	0.37	0.45	0.69	0.50
S <sub>HYE</sub> 54-05	HORT	0.32	0.42	0.66	0.47
S <sub>HYE</sub> 56-01	HORT	0.66	0.64	1.03	0.78
S <sub>HYE</sub> 57-02	HORT	0.49	0.68	0.98	0.72
S <sub>LYE</sub> 03-05	HORT	0.62	0.66	1.00	0.76
S <sub>LYE</sub> 04-10	HORT	0.67	0.81	1.18	0.89
S <sub>LYE</sub> 04-30	HORT	0.67	0.64	0.90	0.74
S <sub>LYE</sub> 04-32	HORT	0.68	0.80	1.18	0.88
S <sub>LYE</sub> 05-15	HORT	0.65	0.76	1.08	0.83
S <sub>LYE</sub> 05-32	HORT	0.56	0.58	0.94	0.69
S <sub>LYE</sub> 06-05	HORT HORT	0.56	0.59	0.81	0.65
S <sub>LYE</sub> 08-13		0.56	0.67	1.01	0.75
S <sub>LYE</sub> 08-23	HORT	0.52 0.53	0.59	0.72	0.61
S <sub>LYE</sub> 09-20	HORT HORT		0.61 0.64	0.82	0.66
S <sub>LYE</sub> 09-24		0.56		0.80 1.08	0.66
S <sub>LYE</sub> 09-25 S <sub>LYE</sub> 10-09	HORT HORT	0.62 0.70	0.69 0.91	1.08	0.80 1.03
$S_{LYE}$ 10-09 S <sub>LYE</sub> 10-22	HORT	0.70	0.91	1.47	0.84
S <sub>LYE</sub> 10-22 S <sub>LYE</sub> 10-28	HORT	0.08	0.73	0.99	0.72
S <sub>LYE</sub> 11-07	HORT	0.48	0.69	0.99	0.63
S <sub>LYE</sub> 11-15	HORT	0.55	0.39	0.70	0.03
S <sub>LYE</sub> 11-16	HORT	0.83	0.73	1.06	0.88
S <sub>LYE</sub> 11-31	HORT	0.83	0.74	1.00	0.87
$S_{LYE}$ 12-13	HORT	0.09	0.83	0.99	0.73
S <sub>LYE</sub> 12-15	HORT	0.49	0.70	1.02	0.83
S <sub>LYE</sub> 12-20	HORT	0.70	0.82	1.16	0.90
S <sub>LYE</sub> 12-33	HORT	0.52	0.65	0.72	0.63
S <sub>LYE</sub> 13-15	HORT	0.80	0.00	1.13	0.90
OLIE IO IO		0.00	0.70	1.10	0.00

Table A.1. Continued.

Family <sup>†</sup>	Location <sup>**</sup>	2002	2003	2004	Over 2002-2004
T anniy	Location	2002		g plant <sup>-1</sup>	2002 2004
S <sub>LYE</sub> 13-27	HORT	0.51	0.68	0.97	0.72
S <sub>LYE</sub> 14-16	HORT	0.64	0.80	1.11	0.85
S <sub>LYE</sub> 15-06	HORT	0.69	0.79	1.12	0.86
S <sub>LYE</sub> 17-26	HORT	0.73	0.76	1.19	0.89
S <sub>LYE</sub> 17-30	HORT	0.58	0.80	1.10	0.82
S <sub>LYE</sub> 17-32	HORT	0.66	0.81	1.22	0.90
S <sub>LYE</sub> 18-27	HORT	0.82	0.92	1.35	1.03
S <sub>LYE</sub> 19-06	HORT	0.68	0.71	1.17	0.85
S <sub>LYE</sub> 19-10	HORT	0.74	0.93	1.44	1.04
S <sub>LYE</sub> 20-05	HORT	0.79	0.85	1.26	0.97
S <sub>LYE</sub> 20-16	HORT	0.71	0.70	0.93	0.78
S <sub>LYE</sub> 20-18	HORT	0.57	0.58	0.86	0.67
S <sub>LYE</sub> 20-24	HORT	0.60	0.67	0.83	0.70
S <sub>LYE</sub> 21-28	HORT	0.28	0.43	0.55	0.42
S <sub>LYE</sub> 22-12	HORT	0.46	0.58	0.74	0.59
S <sub>LYE</sub> 22-14	HORT	0.36	0.57	0.76	0.57
S <sub>LYE</sub> 23-05	HORT	0.49	0.66	0.92	0.69
S <sub>LYE</sub> 23-32	HORT	0.38	0.62	0.78	0.59
S <sub>LYE</sub> 23-34	HORT	0.59	0.64	0.84	0.69
S <sub>LYE</sub> 24-12	HORT	0.61	0.66	0.95	0.74
S <sub>LYE</sub> 24-28	HORT	0.50	0.54	0.68	0.57
S <sub>LYE</sub> 24-29	HORT	0.50	0.61	0.85	0.65
S <sub>LYE</sub> 25-01	HORT	0.49	0.75	0.96	0.73
S <sub>LYE</sub> 25-09	HORT	0.41	0.59	0.88	0.63
S <sub>LYE</sub> 25-13	HORT	0.62	0.72	0.99	0.78
S <sub>LYE</sub> 25-24	HORT	0.45	0.53	0.78	0.59
S <sub>LYE</sub> 25-34	HORT	0.76	0.86	1.21	0.94
S <sub>LYE</sub> 26-08	HORT	0.47	0.62	0.97	0.69 0.74
S <sub>LYE</sub> 26-09	HORT	0.52	0.71	0.99	••••
S <sub>LYE</sub> 26-14	HORT	0.59	0.59	0.68	0.62
S <sub>LYE</sub> 26-29	HORT	0.56	0.68	0.86	0.70
S <sub>LYE</sub> 26-34 S <sub>LYE</sub> 27-24	HORT HORT	0.51 0.68	0.54 0.63	0.81 0.91	0.62 0.74
S <sub>LYE</sub> 28-10	HORT	0.68	0.80	1.09	0.86
S <sub>LYE</sub> 28-10 S <sub>LYE</sub> 28-20	HORT	0.69	0.60	0.95	0.80
OLYEZO-ZO		0.04	0.05	0.95	0.71

Table A.1. Continued.

					Over
Family <sup>†</sup>	Location <sup>††</sup>	2002	2003	2004	2002-2004
			kg	g plant⁻¹	
S <sub>LYE</sub> 29-21	HORT	0.93	0.94	1.48	1.11
S <sub>LYE</sub> 29-25	HORT	0.41	0.53	0.84	0.59
S <sub>LYE</sub> 29-31	HORT	0.57	0.72	1.02	0.77
S <sub>LYE</sub> 30-22	HORT	0.59	0.58	0.84	0.67
S <sub>LYE</sub> 30-33	HORT	0.49	0.76	1.24	0.83
LSD (0.05)	-	0.25	0.24	0.38	0.17

Table A.1. Continued.

<sup>†</sup>Family prefix (S<sub>HYE</sub>, S<sub>LYE</sub>) designates the environment in which parental selection was conducted. <sup>††</sup>CCB corresponds to HYE, HORT corresponds to LYE.

2002, 2003, ar	id across years.		
Family	2003	2004	Over 2003 & 2004
ł		kg	
01-16	1.32	1.42	1.37
01-22	1.25	1.55	1.40
02-11	1.23	1.35	1.29
02-22	1.12	1.24	1.18
02-28	1.08	1.21	1.14
03-11	1.42	1.67	1.55
03-15	1.12	1.53	1.33
03-19	1.17	1.45	1.31
04-05	1.17	1.54	1.36
04-06	1.15	1.26	1.20
04-13	1.14	1.12	1.13
04-19	1.17	1.38	1.28
04-27	1.00	1.11	1.06
05-08	1.19	1.34	1.27
05-16	1.05	1.40	1.22
05-22	1.24	1.36	1.30
05-25	1.33	1.43	1.38
05-27	1.40	1.47	1.43
05-31	1.17	1.22	1.20
06-07	1.32	1.41	1.37
06-14	0.94	1.01	0.98
06-20	1.06	1.35	1.20
06-31	1.24	1.14	1.19
07-03	1.23	1.32	1.28
07-27	1.15	1.26	1.21
08-10	0.96	1.06	1.01
08-12	1.03	1.19	1.11
08-14	1.52	1.68	1.60
08-17	1.24	1.32	1.28
08-20	1.49	1.63	1.56
08-26	1.50	1.60	1.55
09-05	1.36	1.53	1.44
09-07	1.36	1.31	1.34
09-17	1.21	1.38	1.30
09-19	1.37	1.61	1.49
09-30	1.52	1.45	1.48
09-31	0.96	0.96	0.96
10-02	0.90	0.93	0.92
10-15	1.12	1.14	1.13
10-29	1.32	1.44	1.38

Table B.1. Mean dry matter (dm) yield of SL-93 population plant families for 2002, 2003, and across years.

			Over
Family	2003	2004	2003 & 2004
		kg	
11-01	1.12	1.34	1.23
11-08	1.11	1.17	1.14
11-12	1.20	1.39	1.30
12-08	1.49	1.51	1.50
12-09	1.09	1.27	1.18
12-13	1.27	1.46	1.37
12-14	1.41	1.47	1.44
12-16	1.07	1.20	1.14
12-28	1.35	1.65	1.50
13-01	1.16	1.13	1.14
13-05	1.18	1.24	1.21
13-11	1.30	1.45	1.37
13-14	1.25	1.47	1.36
13-20	1.02	1.26	1.14
13-22	0.99	1.22	1.11
14-02	1.24	1.28	1.26
14-20	1.24	1.26	1.25
15-04	1.21	1.37	1.29
15-06	1.18	1.36	1.27
15-17	1.32	1.42	1.37
16-01	1.43	1.47	1.45
16-08	1.42	1.65	1.53
16-13	0.94	1.25	1.10
16-14	1.30	1.44	1.37
17-03	1.24	1.40	1.32
17-10	1.04	1.23	1.14
17-16	1.34	1.40	1.37
17-27	0.99	1.22	1.10
18-01	1.55	1.73	1.64
18-03	1.37	1.46	1.42
18-08	1.38	1.47	1.43
18-23	1.35	1.26	1.30
18-26	1.19	1.33	1.26
19-07	1.29	1.41	1.35
19-09	1.24	1.17	1.21
19-15	1.32	1.50	1.41
19-18	1.28	1.45	1.37
19-26	1.58	1.55	1.56
19-29	1.25	1.28	1.26
20-07	1.47	1.47	1.47
20-09	1.36	1.46	1.41
20-10	1.28	1.22	1.25

Table B.1. Continued.

			Over
Family	2003	2004	2003 & 2004
		kg	
20-12	1.13	1.52	1.33
20-14	1.24	1.45	1.34
20-31	0.77	0.97	0.87
21-10	1.23	1.00	1.12
21-14	1.16	1.22	1.19
21-17	1.49	1.60	1.55
21-27	1.54	1.45	1.50
22-07	1.38	1.29	1.34
22-11	1.17	1.31	1.24
22-12	1.23	1.35	1.29
22-17	1.33	1.36	1.35
22-24	1.11	1.36	1.24
23-04	1.12	1.25	1.18
23-08	1.35	1.32	1.33
23-12	1.04	1.29	1.17
23-15	1.26	1.50	1.38
23-17	1.57	1.65	1.61
23-19	1.07	1.30	1.19
23-32	1.34	1.53	1.44
24-10	1.13	1.35	1.24
24-13	1.01	1.06	1.04
24-19	1.27	1.29	1.28
26-01	1.46	1.52	1.49
26-05	1.39	1.45	1.42
26-07	1.39	1.60	1.49
26-19	1.31	1.48	1.39
26-28	1.17	1.39	1.28
26-30	1.15	1.43	1.29
27-07	1.40	1.54	1.47
27-17	1.27	1.55	1.41
28-06	0.99	1.19	1.09
28-08	1.31	1.58	1.44
28-18	0.94	1.25	1.10
28-33	1.31	1.50	1.41
29-06	1.14	1.27	1.21
29-11	1.25	1.52	1.38
29-12	1.07	1.18	1.12
29-14	1.39	1.60	1.50
29-17	1.26	1.30	1.28
29-18	1.12	1.09	1.11
29-21	0.96	1.09	1.02
29-29	1.36	1.72	1.54

Table B.1. Continued.

			Over
Family	2003	2004	2003 & 2004
		kg	
30-01	1.18	1.31	1.25
30-03	1.63	1.71	1.67
30-07	1.22	1.31	1.27
30-10	1.35	1.58	1.46
30-16	1.24	1.47	1.35
30-31	1.27	1.39	1.33
LSD (0.05)	0.33	0.35	0.24

Table B.1. Continued.

	5, 2004, and 6ver years.		Over
$Family^\dagger$	2003	2004	2003 & 2004
		kg	
EM01-12	0.53	0.36	0.44
EM01-20	0.84	0.29	0.57
EM01-27	0.63	0.41	0.52
EM01-30	0.58	0.44	0.51
EM02-04	0.84	0.38	0.61
EM02-14	0.79	0.34	0.56
EM02-27	0.68	0.36	0.52
EM02-28	0.64	0.31	0.48
EM02-29	0.58	0.33	0.46
EM03-04	0.58	0.38	0.48
EM03-08	0.49	0.46	0.48
EM03-22	0.66	0.35	0.50
EM03-29	0.67	0.58	0.62
EM03-32	0.61	0.44	0.52
EM04-21	0.65	0.39	0.52
EM04-27	0.73	0.28	0.51
EM04-28	0.75	0.43	0.59
EM04-29	0.71	0.61	0.66
EM05-13	0.62	0.35	0.49
EM05-29	0.65	0.40	0.53
EM05-30	0.46	0.30	0.38
EM06-22	0.72	0.34	0.53
EM06-30	0.74	0.37	0.56
EM06-32	0.70	0.33	0.51
EM07-29	0.57	0.41	0.49
EM08-02	0.74	0.34	0.54
EM08-14	0.77	0.42	0.59
EM08-28	0.93	0.35	0.64
EM08-30	0.73	0.49	0.61
EM09-18	0.68	0.32	0.50
EM09-22	0.78	0.34	0.56
EM10-14	0.54	0.30	0.42
EM10-18	0.53	0.33	0.43
EM10-24	0.84	0.28	0.56
EM10-28	0.68	0.34	0.51
EM10-33	0.69	0.24	0.47
EM10-34	0.68	0.38	0.53
EM11-27	0.98	0.32	0.65
EM12-14	0.60	0.28	0.44
EM12-16	0.60	0.40	0.50

Table C.1. Mean Dry matter yield of SNU-EM and -EML population switchgrass families for 2003, 2004, and over years.

<b>Femilu</b> <sup>†</sup>	2002	2004	Over
Family <sup>†</sup>	2003	2004	2003 & 2004
		kg	
EM12-20	0.48	0.39	0.43
EM12-27	0.54	0.30	0.42
EM13-19	0.87	0.43	0.65
EM13-20	0.45	0.36	0.40
EM14-28	0.62	0.35	0.48
EM14-29	0.77	0.33	0.55
EM16-19	0.59	0.44	0.51
EM16-20	0.66	0.53	0.59
EM18-22	0.47	0.33	0.40
EM18-30	0.78	0.37	0.57
EM18-34	0.89	0.39	0.64
EM19-24	0.70	0.34	0.52
EM19-30	0.80	0.39	0.59
EM19-33	0.78	0.31	0.54
EM20-15	0.68	0.37	0.52
EM20-19	0.61	0.33	0.47
EM20-20	0.67	0.39	0.53
EM20-24	0.76	0.57	0.67
EM21-26	0.67	0.32	0.50
EM21-31	0.54	0.35	0.45
EM24-13	0.81	0.49	0.65
EM24-16	0.44	0.31	0.37
EM24-29	0.63	0.45	0.54
EM25-11	0.55	0.27	0.41
EM25-12	0.76	0.36	0.56
EM26-12	0.67	0.37	0.52
EM26-14	0.62	0.33	0.48
EM26-31	1.01	0.44	0.72
EM27-22	0.75	0.26	0.51
EM28-02	0.74	0.34	0.54
EM28-03	0.55	0.43	0.49
EM28-19	0.61	0.36	0.48
EM29-03	0.65	0.35	0.50
EM29-24	0.65	0.48	0.56
EM29-25	0.68	0.40	0.54
EM29-27	0.00	0.37	0.54
EM29-28	0.72	0.37	0.54
EM29-28 EM29-30	0.72	0.34	0.54
EM29-30 EM30-13	0.75	0.34	0.46
EM30-13 EM30-20	0.54	0.37	0.49
			0.49
EM30-21	0.66	0.41	
EM30-27	0.57	0.41	0.49

Table C.1. Continued.

			Over
Family <sup>†</sup>	2003	2004	2003 & 2004
		kg	
EM30-32	0.69	0.34	0.51
EML02-09	0.90	0.35	0.62
EML04-22	0.67	0.35	0.51
EML06-09	0.69	0.41	0.55
EML07-18	1.14	0.46	0.80
EML07-21	0.92	0.40	0.66
EML08-14	1.15	0.30	0.73
EML09-08	1.19	0.32	0.75
EML16-24	0.93	0.41	0.67
EML18-12	0.85	0.43	0.64
EML18-20	1.01	0.50	0.75
EML19-21	1.17	0.41	0.79
EML24-13	0.75	0.39	0.57
EML24-21	1.18	0.34	0.76
EML25-15	0.90	0.42	0.66
EML28-16	1.00	0.34	0.67
EML28-26	1.04	0.37	0.71
EML30-10	1.03	0.42	0.73
LSD (0.05)	0.26	0.16	0.15

Table C.1. Continued.

<sup>†</sup>EM and EML correspond to 'early maturing' and 'early maturing late' groups, respectively within the SNU-EM population.

			Over
Family <sup>†</sup>	2003	2004	2003 & 2004
		kg	
LM01-10	1.09	0.56	0.82
LM01-12	0.75	0.63	0.69
LM01-13	1.12	0.60	0.86
LM01-18	0.99	0.50	0.75
LM02-07	1.13	0.57	0.85
LM02-18	1.01	0.53	0.77
LM02-22	0.96	0.57	0.77
LM02-23	1.17	0.38	0.77
LM02-27	1.01	0.56	0.79
LM03-13	0.90	0.70	0.80
LM03-15	1.01	0.52	0.77
LM03-18	0.94	0.49	0.71
LM04-08	1.00	1.06	1.03
LM04-28	0.76	0.62	0.69
LM05-10	1.00	0.72	0.87
LM05-19	1.18	0.69	0.94
LM06-14	0.94	0.70	0.82
LM06-17	1.05	0.57	0.81
LM07-10	0.91	0.76	0.84
LM07-28	0.88	0.57	0.73
LM07-31	1.10	0.54	0.82
LM08-18	1.086	0.75	0.91
LM08-31	0.97	0.69	0.83
LM09-13	1.05	0.55	0.80
LM10-07	1.08	0.74	0.91
LM10-14	0.93	0.64	0.79
LM10-18	0.86	0.63	0.74
LM10-23	1.06	0.62	0.84
LM10-32	1.00	0.62	0.81
LM12-05	1.06	0.54	0.80
LM12-13	1.12	0.65	0.88
LM12-20	0.94	0.66	0.80
LM13-03	1.12	0.53	0.83
LM13-07	1.22	0.48	0.85
LM13-16	0.84	0.52	0.68
LM13-20	0.95	0.67	0.81
LM13-26	0.95	0.73	0.84
LM14-02	0.96	0.64	0.80
LM14-30	0.79	0.52	0.65
LM15-08	1.09	0.60	0.84

Table C.2. Mean dry matter yield of SNU-LM and -LME population switchgrass families for 2003, 2004, and over years.

			Over	
Family <sup>†</sup>	2003	2004	2003 & 2004	
		kg		
LM15-13	1.05	0.56	0.80	
LM15-23	1.16	0.52	0.84	
LM15-29	0.95	0.64	0.79	
LM16-19	0.92	0.65	0.79	
LM17-08	0.85	0.53	0.69	
LM18-19	1.12	0.52	0.82	
LM18-23	0.99	0.76	0.87	
LM18-26	0.99	0.57	0.78	
LM19-09	1.01	0.66	0.83	
LM19-11	0.85	0.63	0.74	
LM19-18	0.84	0.61	0.73	
LM20-17	1.12	0.66	0.89	
LM20-20	0.63	0.58	0.61	
LM21-08	0.83	0.53	0.68	
LM21-11	1.06	0.51	0.79	
LM21-23	1.10	0.51	0.81	
LM22-10	1.02	0.59	0.80	
LM22-18	0.99	0.68	0.84	
LM22-20	0.98	0.63	0.81	
LM23-03	1.05	0.70	0.87	
LM24-09	1.26	0.53	0.90	
LM24-11	0.95	0.60	0.78	
LM24-19	1.10	0.61	0.85	
LM25-18	1.02	0.56	0.79	
LM25-21	1.30	0.48	0.89	
LM25-23	1.18	0.63	0.90	
LM26-13	1.03	0.65	0.84	
LM26-18	0.90	0.54	0.72	
LM26-26	0.92	0.53	0.73	
LM27-12	1.01	0.63	0.82	
LM28-15	1.22	0.67	0.95	
LM29-31	1.04	0.62	0.83	
LM30-07	0.81	0.44	0.62	
LM30-08	0.99	0.64	0.82	
LM30-12	1.11	0.57	0.84	
LM30-21	1.30	0.62	0.96	
LME04-22	0.52	0.45	0.49	
LME04-23	0.65	0.62	0.63	
LME05-21	0.58	0.46	0.52	
LME06-29	0.65	0.57	0.61	
LME07-19	0.58	0.64	0.61	
LME07-24	0.71	0.75	0.73	

Table C.2. Continued.

Family <sup>†</sup>	2003	2004	Over 2003 & 2004
		kg	
LME11-26	0.70	0.55	0.62
LME14-18	0.73	0.50	0.61
LME15-21	0.63	0.56	0.59
LME15-31	0.83	0.59	0.71
LME17-22	0.59	0.66	0.62
LME17-29	0.62	0.60	0.61
LME18-29	0.76	0.51	0.63
LME19-27	0.73	0.55	0.64
LME21-27	0.87	0.54	0.71
LME22-23	0.57	0.58	0.57
LME23-21	0.62	0.55	0.59
LME23-23	0.68	0.62	0.65
LME24-19	0.75	0.59	0.67
LME25-29	0.82	0.68	0.75
LME26-23	0.50	0.53	0.52
LME29-14	0.40	0.59	0.49
LME29-23	0.61	0.62	0.61
LME29-32	0.71	0.50	0.60
LSD (0.05)	0.26	0.26	0.18

Table C.2. Continued.

<sup>†</sup>LM and LME correspond to 'late maturing' and 'late maturing early' groups, respectively within the SNU-LM population.

#### VITA

#### Louis Walker Rose IV

Candidate for the Degree of

Doctor of Philosophy

# Thesis: ESTIMATION OF GENETIC PARAMETERS IN SEVERAL SWITCHGRASS (*Panicum virgatum* L.) POPULATIONS

Major Field: Plant Science

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Date of Degree: May, 2005

Institution: Oklahoma State University

Location: Stillwater, OK

Title of Study:ESTIMATION OF GENETIC PARAMETERS IN SEVERAL<br/>SWITCHGRASS (Panicum virgatum L.) POPULATIONS

Pages in Study: 106 Candidate for the Degree of Doctor of Philosophy

Major Field: Plant Science

- Scope and Method of Study: The objectives of this study were to determine: 1) the effects of high-and low- biomass yield environments on plant selection in breeding switchgrass for enhanced biomass yield using recurrent selection, and 2) genetic variances, narrow-sense heritability  $(h_n^2)$ , and predicted genetic gain ( $\Delta G$ ) from selection procedures for increased biomass yield in two populations (SL 93 & NL 94) of lowland ecotype switchgrass and two populations (SNU-EM & SNU-LM) of upland ecotype switchgrass. For objective 1, Co parent plants were selected for biomass yield based on performance of their half-sib (HS) progeny evaluated under high- and lowyield environments for 1 year. Yield performance of C<sub>1</sub> HS families was assessed under both high-and low-biomass yield environments for 3 years. For objective 2, HS families and their clonal parent plants for the respective populations were evaluated in replicated field tests over 2 to 3 years. Genetic variance components for biomass yield were estimated for the respective populations and narrow-sense heritability  $(h_n^2)$  estimates were derived using variance component estimates and by progeny-parent regression.
- Findings and Conclusions: The results suggested that breeding gains may be higher when parent plant selection is based on HS progeny performance under a low yield environment. Significant magnitudes of genetic variation for biomass yield were found in the SL 93 and NL 94 populations, but not in the SNU-EM and SNU-LM populations. The  $h^2_n$  estimates varied in magnitude with population and method of calculation. Positive response to selection for higher biomass production was indicated in the NL 93 and NL 94 populations based on estimated magnitudes of genetic variation and  $h^2_n$ . Low amounts of genetic variation for biomass yield in the SNU-EM and SNU-LM populations predicted low, or no, response to selection, although some estimates of the additive genetic component of the available variation were of moderate to high magnitudes.

Advisors Approval: