Mapping QTLs for spring green-up, plant vigor, and plant biomass in two lowland switchgrass populations

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Abstract Switchgrass (Panicum virgatum L.) is an important perennial C4 species due to its large potential for cellulosic bioenergy feedstock production. Identification of quantitative trait loci (QTL) controlling important developmental traits is valuable to understanding the genetic basis and using marker-assisted selection (MAS) in switchgrass breeding. One F₁ hybrid population derived from NL94 (♀)×SL93 (♂) and one S₁ (first-generation selfed) population from NL94 were used in this study. Both the populations showed significant variations for genotype and genotype by environment interactions for three traits studied: plant vigor, spring green-up, and plant biomass. Plant vigor had strong and positive correlations with plant biomass in both populations. Broad-sense heritability estimates for plant vigor ranged from 0.46 to 0.74 and 0.45 to 0.74 in the hybrid and selfed population, respectively. Spring green-up had similar heritability estimates, 0.42–0.78 in the hybrid population, and 0.47–0.82 in the selfed population. Heritability of plant biomass was 0.54–0.64 in the hybrid population and 0.64–0.74 in the selfed population. Fifteen QTLs for spring green-up, 6 QTLs for plant vigor, and 3 QTLs for biomass yield were detected in the hybrid population, whereas 4 QTLs for spring green-up, 4 QTLs for plant vigor, and 1 QTL for biomass yield were detected in the selfed population. Markers associated with these QTLs can be used in MAS to accelerate switchgrass breeding program. This study provided new information in understanding the genetic control of biomass components and demonstrated substantial heterotic vigor that could be explored for breeding hybrid cultivars in switchgrass.

Keywords Switchgrass · Spring green-up · Plant vigor · Plant biomass · Heritability · QTL

Introduction

Switchgrass (Panicum virgatum L.) is a warm-season C4 grass native to North America with a wide geographical distribution range (Bhandari et al. 2010; Wullschleger et al. 2010). The species has been targeted as a predominant bioenergy crop starting in the 1990s due to its high biomass yield potential, wide adaptability to marginal land, fast growth, and
low cost in management (Lynd et al. 1991; Sander-
son et al. 1996; Bouton 2007; Wang et al. 2010).
Substantial genetic diversity exists among and within
different ecotypes/cultivars, which provide enor-
mous potential towards improving biomass yield
through enhancing its component traits (Bouton
2007; Bhandari et al. 2010). The genome sequence
of switchgrass shed lights on genetic mechanisms that
have enabled the ancestors of this valuable biomass
crop to adapt to cycles of climate warming and cool-
ing (Lovell et al. 2021). Although high biomass yield
is the most important breeding objective in develop-
ing switchgrass as a biofuel cellulosic crop (Sladden
et al. 1991; Walsh et al. 2003; Rose et al. 2008; Casler
2010), biomass yield is a complex trait influenced by
many component traits that are controlled by numer-
ous genetic loci (Redfearn et al. 1997; Chang et al.
2016). It is challenging to improve switchgrass bio-
mass yield through traditional breeding methods
based on phenotypic or genotypic selection that needs
multiple years of breeding and testing cycles.

Climate-gene-biomass associations vary consider-
ably among diverged switchgrass gene pools. Low-
land ecotype has great biomass yield potential but is
winterkill susceptible (Lovell et al. 2021). Perennial
grasses such as switchgrass undergo seasonal cycling
through winter dormancy and spring regrowth (Sar-
ath et al. 2014). The onset of flowering and seed
development before killing frost induce senescence of
aboveground tissues to avoid adverse environmental
conditions. Photosynthates cumulated during a grow-
ing season are partly remobilized to belowground
organs such as rhizomes, which serve as storage for
nutrients to promote regrowth of shoots from rhi-
zome meristems in the following spring. Therefore,
the cyclical transition between winter dormancy and
spring regrowth is a fundamental developmental
trait in the perennial grass. While successful survival
from winter dormancy is important, and how well the
survived plants perform during vegetative growing
season is highly relevant to biomass yield. Vigorous
plants with a high volume of foliage and fast growth
rate are likely to produce a higher biomass yield com-
pared to plants that lack such characteristics. There-
fore, phenotypes of the overall robustness of plants in
early spring could be important indicators of biomass
yield potential.

Spring green-up and plant vigor are two impor-
tant developmental traits related to plant biomass
yield in switchgrass (Chen et al. 2012; Sadeghpour
et al. 2014a). Plant vigor reflects the overall growth
capacity and yield in morphology. Spring green-
up is a measure of the transition from winter dor-
mancy to active spring regrowth. Early green-up
switchgrass takes advantage of the rising tempera-
ture and daylength in spring for photosynthesis, and
thereby could increase biomass yield with a relatively
longer growing season than late green-up genotypes
(Bhandari et al. 2010). In addition, a long dormancy
period over winter and high dormancy rate in early
spring could lead to weak plant vigor and slow spring
green-up, and potentially reduce biomass yield (Sad-
eghpour et al. 2014a, b; Munshaw et al. 2006; Rimi
et al. 2011; Curran et al. 2011). Spring regrowth,
stem thickness, and biomass yield were studied in
lowland switchgrass, demonstrating that variations
in these traits were influenced by genetic and environ-
mental factors (Bhandari et al. 2011). However, the
genetic bases of spring green-up and plant vigor in
switchgrass remain underexplored (Sadeghpour et
al. 2014b), and the extent to which these two traits relate
to in-season plant biomass is also lacking. Although
switchgrass plots are able to maintain productivity for
a decade or longer, its establishment is slow (Parrish
and Fike 2005; Clifton-Brown et al. 2019). Stands of
switchgrass typically produce stable phenotypes in
the second year and succeeding years post establish-
ment. Spring green-up was reported to have a high
heritability indicating that this trait could be used
in phenotypic selection in improving biomass yield
(Bhandari et al. 2010).

Quantitative trait loci (QTL) mapping is an impor-
tant technique that connects phenotypic data and
genomic loci in plant genetic research and that has
the potential to expedite genetic improvement and
enhance genetic gain per breeding cycle through
MAS, which can be especially valuable for breeding
perennial crop such as switchgrass that has multi-
year selection cycles. To date, QTL mapping studies
on biomass yield and adaptive traits have been con-
ducted in switchgrass (Dong et al. 2015; Lowry et al.
2015; Serba et al. 2015; Chang et al. 2016; Makaju
et al. 2018; Tornqvist et al. 2018; Taylor et al. 2018,
2019; Ali et al. 2019; Lowry et al. 2019). Reproduc-
tive maturity was a trait closely related to biomass
yield. Multiple genomic regions were detected for
this trait in two lowland switchgrass populations
(Dong et al. 2015). Serba et al. (2015) identified
QTLs for biomass yield in a heterozygous pseudo-F1 population and found four stable QTLs across ten environments, which explained 4.9–12.4% of phenotypic variation. Chang et al. (2016) investigated six tillering-related traits in two lowland switchgrass populations (the same populations as in this study), and two stable QTLs for biomass-related traits were detected in multiple environments. Taylor et al. (2019) found significant QTLs for plant height, crown diameter, and plant biomass in different environments in a pseudo-F2 population. However, few studies have been focused on spring green-up and plant vigor in switchgrass. Ali et al. (2019) reported 35 QTLs for spring green-up in a lowland (cv “Alamo”) by upland (cv “Summer”) switchgrass population, providing valuable knowledge of this developmental trait. A critical issue in the use of QTLs in breeding programs is that they can only be assumed a priori to be relevant to the cross and environment in which they were mapped (Feltus et al. 2006; Yu et al. 2008). Genetic mapping in different populations often results in distinct sets of QTLs due to genetic heterogeneity. For example, in Miscanthus, another well-known bioenergy biomass crop, substantial phenotypic variations of overwintering ability (i.e., transition from winter dormancy to spring regrowth, a trait analogous to spring green-up in this study) have been reported in a large M. sinensis germplasm panel (Dong et al. 2019a), and QTL mapping across multiple populations revealed numerous QTLs that are unique to specific populations (Dong et al. 2018, 2019b). Therefore, more genetic mapping studies are needed to understand the rich genetic diversity underlying agronomic traits in switchgrass, particularly the unexplored yet important traits such as spring green-up and plant vigor. The objectives in this study were to (1) evaluate phenotypic and genotypic variation for spring green-up, plant vigor, and plant biomass; (2) investigate correlations between the traits; and (3) identify QTLs for the traits.

Materials and methods

Plant materials and field management

One lowland switchgrass hybrid population encompassing 176 progeny from a cross between “NL94 LYE 16×13” (NL94) and “SL93 7×15” (SL93) and one lowland selfed population consisting of 265 progeny from NL94 were used in this study (Liu and Wu 2012; Liu et al. 2012; Dong et al. 2015). The parental plants NL94 and SL93 were chosen in 2007 from the Oklahoma State University (OSU) northern lowland (NL) breeding population growing in a low yield environment (LYE) selection nursery and the OSU southern lowland (SL) breeding population, respectively (Liu and Wu 2012). Prior to the initiation of flowering, one potted plant of NL94 and another of SL93 were transferred into a large growth chamber in the OSU Controlled Environmental Research Laboratory. Processed seeds from mature inflorescences from the respective plants were germinated in spring 2009. A total of 456 and 44 progeny were obtained for NL94 and SL93, respectively (Liu and Wu 2012). All of SL93 progeny were removed in subsequent genetic research due to the small number. Finally, 456 progeny from NL94 were divided into two populations based on 12 SSR markers: an NL94 selfed population of 279 progeny and one hybrid population (NL94×SL93) of 177 progeny (Liu and Wu 2012). The parents and progeny of the two populations were vegetatively propagated in a greenhouse at Oklahoma State University (OSU). Two field trials were established in 2011, one at the OSU Agronomy Farm (36° 12′ N Lat., 97° 08′ W Long), Stillwater, and the other at Cimarron Valley Research Station (35° 59′, 97° 03′), near Perkins, OK. Soil types were Kirkland silt loam in Stillwater and Teller fine sandy loam in Perkins, respectively. A randomized complete block design with three replications was arranged at each of the two locations. Within each block at each field trial, the 441 progeny (265 selfed and 176 hybrid progeny) and two parental genotypes were randomly assigned to 3.21 m×1.07 m plots with three clonal plants per plot.

Field management protocols have been described by Dong et al. (2015) and Chang et al. (2016). Briefly, irrigation was provided to two field trials after transplanting to improve establishment. Pre-emergence herbicides including 1.12 kg atrazine (6-chloro-N-ethyl-N-isopropyl-1,3,5-triazine-2,4-diamine) and 1.12 kg surflan (Oryzalin: 3,5-dinitro-N4N4–dipropylsulfanilamide) active ingredient per hectare were sprayed before spring green-up of switchgrass plants in the following 4 years (2012–2015). Urea was applied with a rate
of 67.2 kg/ha N when switchgrass plants started to grow vigorously in each growing season. Hand weeding was implemented as needed.

Phenotypic data collection and analysis

Phenotypic data were collected in the spring of 2012 (Yr 2) to 2015 (Yr 5). In early April, spring green-up was visually scored for each plant based on a 0–100% scale with 10% increment to evaluate the percentage of green-up tillers covering the whole plant stand area, in which 0 indicated no green tillers and 100% represented green tillers covering the whole plant stand base. Plant vigor data were collected based on visual scoring in May to June of 2012 to 2015. An ordinal scale from 1 to 9 was used to evaluate plant vigor by focusing on plant size (plant width and height), with 1 being the least vigorous (<10 tillers and short), and 9 being the most vigorous plants. Plant biomass data were collected from December to the following January in 2012 and 2013. Plants were cut at 10 cm above ground, and the three clonal plants within each plot were weighed together, and the average was used for plant biomass of each genotype.

Phenotypic data analyses were conducted using R (version 3.6.0) (R Core Team 2019). Pearson’s correlations between the traits studied were calculated using cor function. To assess the significance of location (STW and PKS), year (2012–2015), genotype, and their interactions, analyses of variance (ANOVAs) were conducted for each trait in each population using the following linear mixed model in lme4 package (Bates et al. 2015).

\[
Y_{ijkl} = \mu + L_i + G_j + B(L)_{ik} + LAG_{ijk} + \epsilon_{ijkl}
\]

where \( Y \) represents the raw phenotypic data, \( \mu \) is the grand mean, \( L \) represents location, \( A \) represents year, \( G \) represents genotype, \( B(L) \) represents block within location, \( LA \) represents location by year interaction, \( LG \) represents year by genotype interaction, \( AG \) represents year by genotype interaction, and \( \epsilon \) is the random error. Broad-sense heritability (\( H \)) was then calculated using the aforementioned model by fitting all model terms as random effects. Variance components were estimated based on the restricted maximum likelihood (REML) method. Equation of \( H \) calculation is as follows:

\[
H = \frac{V_G^2}{V_G^2 + \frac{V_{AG}^2}{2} + \frac{V_{LG}^2}{4} + \frac{V_{\epsilon}^2}{24}}
\]  

Since perennial grass such as switchgrass undergoes an establishment phase, we were also interested in the year-by-year heritability to assess the temporal stability of phenotypes. Therefore, we conducted a second round of ANOVAs for each trait under single-year scenario following model:

\[
Y_{ijk} = \mu + L_i + G_j + B(L)_{ik} + LG_{ij} + \epsilon_{ijk}
\]

where model terms are defined in Eq. 1. Single-year heritability was then calculated following Eq. 4:

\[
H = \frac{V_G^2}{V_G^2 + \frac{V_{LG}^2}{2} + \frac{V_{\epsilon}^2}{6}}
\]

Genotypic data collection and QTL mapping

The preexisting genetic maps of these two populations developed by Liu et al. (2012) and Dong et al. (2015) only included 139 and 132 individuals of the selfed and hybrid population, respectively. In order to increase the statistical power in QTL analysis, marker data of previously un-genotyped individuals were obtained as follows. Initially, QTL mapping for plant vigor, spring green-up, and plant biomass were performed on the two preexisting linkage maps (Liu et al. 2012; Dong et al. 2015). Once significant QTLs were identified, SSR markers flanking the QTLs were selected to genotype the remaining 126 individuals of the selfed population and 44 individuals of the hybrid population. Then, a second round QTL mapping was conducted by including the marker information of these newly genotyped individuals. We employed this strategy based on two considerations: (1) to assess the stability of identified QTLs and (2) to expedite genotyping work by focusing on the statistically significant genomic regions.

QTL detection was conducted using MapQTL 6.0 (Van Ooijen 2009). Genotype file, map file, and phenotype files were prepared following the software user manual. Interval mapping (IM) was used to do initial genome-wide scan, and then significant markers detected in IM were used as cofactors in a Multiple-QTL model (MQM) to scan additional QTLs.
QTLs with the LOD threshold above 3.5 were recorded based on the 1000-permutation test (Churchill and Doerge 1994). QTL mapping for spring green-up and plant vigor were both conducted under separate environment (individual combinations of year and location; e.g., 2012STW represents data collected in 2012 at Stillwater field) and across environments (i.e., based on trait least squared means across four years and two locations). Additive allelic effect is of great interest to plant breeding. Given that switchgrass is a tetraploid, up to four distinct alleles could segregate in a bi-parental population such as the hybrid population in this case (i.e., locus heterozygous in both parents). Genotype codes for such scenario would be $ab \times cd$, resulting in four possible genotypes in progeny: $ac$, $ad$, $bc$, and $bd$ (refer to Tables 4, 5 in JoinMap manual: https://www.kyazma.nl/docs/JM5Manual.pdf). Then, QTL additive effects were estimated based on the deviation from the $ac$ genotype (refer to page 41 in MapQTL 6 manual: https://www.kyazma.nl/docs/MQ6Manual.pdf). In contrast, only two alleles were segregating in the selfed population, and QTL additive effects were estimated as the traditional method.

Genetic maps of these two populations used molecular markers developed from multiple sources (Tobias et al. 2008; Okada et al. 2010; Wang et al. 2011). Relationship between the linkage groups and the subgenome designations (N and K) in the switchgrass genome remains unknown. Therefore, primer sequences of mapped markers were retrieved from the respective sources and were compared to switchgrass reference genome (Lovell et al. 2021) using BLASTN 2.6.0+ with an E-value threshold of 0.1.

Results

Phenotypic variation and broad-sense heritability

In most individual environments (location and year combinations), plant vigor in the hybrid population exhibited left skewed distributions whereas the distributions in the selfed population were slightly right skewed (Figs. 1 and 2). Normally distributed patterns or right-skewed distributions were showed for plant biomass in the hybrid population. Large phenotypic variation existed for spring green-up in the two populations. Genotype mean values spanned a wide range in all environments (e.g., 1–100% in 2015PKS: Table 1). Population means also varied considerably across environments, ranging from 35 to 81% and 17 to 44% in the hybrid population and the selfed population, respectively (Figs. 1 and 2; Table 1). For plant vigor, substantial variations were observed among genotypes within each environment, whereas population means were generally similar across environments (6–8 in hybrid population, 3–4 in selfed population: Table 1). For plant biomass, obvious heterosis and selfing depression for the two populations can be found crossing all individual environments (Table 1).

ANOVA indicated that significant effects of genotype, year, and location×year for spring green-up, plant vigor, and plant biomass in both populations (Table 2). Significant genotype×location interactions were detected for plant vigor in both populations and plant biomass in the selfed population, but slightly significant genotype×year interactions were showed in the hybrid population. Significant genotype×year interactions were found for spring green-up in both populations and marginally significant ($P=0.0036$ in the selfed population) or non-significant ($P=0.0518$ in the hybrid population) for plant vigor (Online Resource 1). However, non-significant genotype×year interactions were detected for plant biomass in both populations.

Correlations among spring green-up, plant vigor, and plant biomass in the hybrid and selfed populations are presented in Table 2. Only data collected in 2012 and 2013 were used in correlation analysis as plant biomass data were not available in 2014 and 2015. The correlation between spring green-up and plant biomass was marginally positive (0.09) in the selfed population while it was negative ($-0.07$) in the hybrid population (Table 2). Plant vigor was positively correlated with plant biomass in both the hybrid population (0.30) and the selfed (0.26). Between spring green-up and plant vigor, significant positive correlation was found in the selfed population (0.31), while non-significant correlation was found between these two traits in the hybrid population (Table 2).

Broad-sense heritabilities of spring green-up and plant vigor were estimated under both single-year (i.e., based on single-year data across two locations) and joint environments (i.e., based on multiple year data across two locations). For spring green-up, the highest single-year heritabilities were found in 2012, with the value of 0.78 and 0.82 in the hybrid
population and selfed population, respectively (Online Resource 2). In subsequent years (2013 to 2015), heritabilities of spring green-up were moderate, ranging from 0.42 to 0.59 in the hybrid population and 0.47 to 0.57 in the selfed population (Online Resource 2). Under joint environments, the heritability of spring green-up was 0.51 in the hybrid population and 0.63 in the selfed population (Table 3). For plant vigor, the highest single-year heritabilities in the two populations were both detected in 2013 with both the value of 0.74 (Online Resource 2). Moreover, the lowest heritabilities of plant vigor in the hybrid population and selfed population were 0.46 in 2015 and 0.45 in 2014, respectively (Online Resource 2). Based on the joint environment analysis, a high heritability (0.80) for plant vigor was observed in the hybrid population, and a moderately high heritability (0.69) was found in the selfed population (Table 3). As the trait plant biomass, single-year heritability ranged from 0.54 to 0.74 in the hybrid and selfed populations (Online Resource 2). For the joint environments, the heritability of plant biomass was 0.63 in the hybrid population and the same in the selfed population (Table 3).

Spring green-up QTL detection

In the hybrid population, a total of 15 QTLs for spring green-up were detected on seven LGs across individual environments (Table 4). Specifically, four QTLs were discovered in 2012STW and three QTLs in each of 2013PKS, 2014PKS, and 2015STW. The QTLs of 2012STW, 2013PKS, 2014PKS, and 2015STW cumulatively explained 29.9, 27.4, 27.5, and 24.4% of the phenotypic variance, respectively. Only one QTL was identified on LG 2a in the joint environment of 2012PKS, 2014STW, and 2015PKS, explaining 9.6, 11.8, and 9.9% of the phenotypic variance (Table 4). However, only one QTL was identified on LG 2a in the joint environment.
environment analysis (Table 4). The significant QTL between markers sww-532 and nfsg-052 on LG 2a was identified in 2014PKS and 2015PKS as well as the joint environment (Table 4; Fig. 3). The consistent results in multiple environments indicated that this significant QTL was stably expressed. The effects for the genotypes AD, BC, and BD were positive for the QTLs on LGs 2b, 9a, and 1a in 2015STW while significant QTLs mapped on LGs 1a, 5a, and 6b in 2012STW and 2a in 2014PKS, 2015PKS, and the joint environments had negative effects (Table 4).

In the selfed population, four significant QTLs for spring green-up were identified on three LGs based on individual environments and one significant QTL on LG 6b-1 based on the joint environment (Table 4). Two QTLs in 2012STW, one QTL in each of 2012PKS, 2015PKS and 2015STW explained 18.5, 6.3, 7.1 and 7.1% phenotypic variance, respectively (Table 5). No significant QTL was detected at the two locations in 2013 and 2014 (Table 5). The QTL between PVAAG-3017/3018 and PVGA-1115/1116 on LG 6b-1 was detected in 2012PKS and 2012STW and the joint environment analysis (Table 5; Fig. 3). The additive effects for spring green-up ranged from –5.76 to 5.96 and only one single QTL located on LG 9a in 2015PKS had the positive effect, and other QTLs had negative effects (Table 5).

Plant vigor QTL detection

Six significant QTLs for plant vigor with LOD scores from 3.81 to 6.01 and one QTL with an LOD value of 4.7 were discovered in individual environments and the joint environment in the hybrid population (Table 4). In the selfed population, four QTLs from individual environments were detected with LOD values from 3.54 to 4.77 and one QTL from the joint-environment analysis with an LOD value...
Table 1  Mean and variation parameters of spring green-up and plant vigor in two switchgrass mapping populations

| Population | Environment | Spring green-up | Plant vigor | Plant biomass (g/plant) |
|------------|-------------|----------------|-------------|------------------------|
|            |             | NL94 | SL93 | Mean | Min | Max | SD | NL94 | SL93 | Mean | Min | Max | SD | NL94 | SL93 | Mean | Min | Max | SD |
| Hybrid     | 2012PKS     | 69   | 92   | 81   | 10  | 100 | 14.36 | 5    | 7    | 7    | 2   | 9   | 1.44 | 943.67 | 1377 | 1383.10 | 4.00 | 3223.00 | 539.25 |
|            | 2012STW     | 67   | 90   | 78   | 12  | 100 | 17.32 | 5    | 6    | 7    | 2   | 9   | 1.31 | 865.33 | 976.33 | 1407.24 | 11.00 | 2870.00 | 480.56 |
|            | 2013PKS     | 90   | 13   | 56   | 5   | 100 | 20.50 | 5    | 7    | 8    | 1   | 9   | 1.58 | 843 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2013STW     | 57   | 63   | 67   | 5   | 100 | 21.12 | 5    | 7    | 8    | 1   | 9   | 1.47 | 1267 | 1220.33 | 1393.80 | 126.00 | 4246.00 | 626.70 |
|            | 2014PKS     | 32   | 30   | 35   | 10  | 90  | 12.25 | 5    | 7    | 8    | 1   | 9   | 1.55 | 943 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2014STW     | 37   | 43   | 37   | 1   | 90  | 15.52 | 5    | 7    | 6    | 2   | 9   | 1.63 | 843 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2015PKS     | 42   | 35   | 50   | 1   | 100 | 18.56 | 5    | 7    | 7    | 2   | 9   | 1.45 | 943 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2015STW     | 32   | 38   | 36   | 1   | 95  | 16.11 | 5    | 7    | 7    | 1   | 9   | 1.45 | 943 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
| Selfed     | 2012PKS     | 69   | –    | 44   | 5   | 100 | 20.01 | 5    | -4   | -4   | 1   | 8   | 1.54 | 943 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2012STW     | 67   | –    | 37   | 2   | 100 | 21.87 | 5    | -3   | -3   | 1   | 7   | 1.11 | 865.33 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2013PKS     | 90   | –    | 29   | 5   | 90  | 20.11 | 5    | -3   | -3   | 1   | 9   | 1.33 | 843 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2013STW     | 57   | –    | 31   | 5   | 100 | 21.33 | 5    | -3   | -3   | 1   | 8   | 1.11 | 1267 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2014PKS     | 32   | –    | 20   | 1   | 80  | 12.26 | 5    | -3   | -3   | 1   | 9   | 1.57 | 1267 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2014STW     | 37   | –    | 17   | 1   | 70  | 10.47 | 5    | -3   | -3   | 1   | 8   | 1.11 | 1267 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2015PKS     | 42   | –    | 27   | 1   | 90  | 18.92 | 5    | -4   | -4   | 1   | 9   | 1.35 | 1267 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
|            | 2015STW     | 32   | –    | 17   | 1   | 70  | 12.43 | 5    | -4   | -4   | 1   | 9   | 1.23 | 1267 | 1460.67 | 1768.43 | 110.00 | 4611.00 | 797.15 |
The phenotypic variance was explained from 7.7 to 12.6% in the hybrid population and from 5.5 to 8.3% in the selfed population (Tables 4 and 5). Among all the significant QTLs in the hybrid population, the QTL between PVGA-1813/1814 and PVGA-1357/1358 on LG 5a was stably expressed in 2014STW, 2015PKS, and the joint environment, which accounted for 34.5% of the total phenotypic variance, and the additive effects of the three genotypes AD, BC, and BD for this QTL ranged from $-0.65$ to $0.93$ (Table 4; Fig. 3). The QTL between PVCA-815/816 and nfsg-50 was also detected in three environments, 2013PKS, 2014STW, and the joint environment, accounting for 18.7% phenotypic variance in the selfed population, with the additive effects ranging from 0.03 to 0.14 (Table 5; Fig. 3).

### Plant biomass QTL detection

In the hybrid population, interesting findings showed in individual environments and joint-environments, all of the significant QTLs were focused on LG 5a with the LOD values ranging from 3.75 to 5.69 (Fig. 3). Identical QTLs (e.g., the QTL between PVGA-1971/1972 and PVCAG-2197/2198) and adjacent QTLs (e.g., the QTL between PVCAG-2389/2390 and PVCAG-2167/2168 and the QTL between PVCAG-2167/2168 and PVGA-1971/1972) were found between plant biomass and spring green-up or plant biomass and plant vigor. In the selfed population, only one QTL between sww-1622 and sww-2501 was found on LG 2a with the LOD value 4.15 (Fig. 3).

### Correspondence between linkage groups and switchgrass genome

High correspondence was found between the nomenclature of genetic linkage groups (a and b) and the subgenome designations (N and K) in the switchgrass genome (Online Resource 3). For both populations, clear correspondences are as follows: LG 1a–Chr 01 K, LG 1b–Chr 01 N, LG 2a–Chr 02 N, LG 2b–Chr 02 K, LG 3a–Chr 03 K, LG 3b–Chr 03 N, LG 4a and 4b–Chr 04 N and 04 K, LG 5a–Chr 05 K, LG 5b–Chr 05 N, LG 6a–Chr 06 N (the selfed population only), LG 6b–Chr 06 K, LG 7a–Chr 07 K, LG 7a–Chr 07 N, LG 8a–Chr 08 N, LG 8b–Chr 08 K, LG 9a–Chr 09 K, LG 9b–Chr 02 N. However, LG 6a in the hybrid population largely matched with Chr 07 N, indicating the lack of marker coverage on this group. Moreover, LG 7b only contained 3 and 4 markers in the hybrid and selfed population, respectively, and these markers did not correspond to the expected Chr 07 N. This is also likely due to the low marker density.

### Table 2  Correlation coefficients among traits in a hybrid population (above diagonal) and a selfed population (below diagonal) in lowland switchgrass

| Trait             | Spring green-up | Plant vigor | Biomass yield |
|-------------------|----------------|-------------|---------------|
| Spring green-up   | –              | 0.05NS†     | –             |
| Plant vigor       | 0.31****       | –           | 0.30****      |
| Biomass yield     | 0.09****       | 0.26****    | –             |

†Non-significant at 0.05 level, ****P<0.0001; **P<0.01; *P<0.05

### Table 3  Broad-sense heritability of spring green-up and plant vigor across joint environments in two lowland switchgrass populations

| Variance and heritability estimation | Hybrid population | Selfed population |
|-------------------------------------|-------------------|------------------|
|                                     | Spring green-up   | Plant vigor      | Plant biomass   | Spring green-up   | Plant vigor      | Plant biomass   |
| $\sigma^2_G$                        | 19.22             | 0.51             | 215,342         | 34.02             | 0.33             | 55,114          |
| $\sigma^2_{G\times A}$              | 32.18             | 0.03             | 5279            | 38.72             | 0.03             | 1351            |
| $\sigma^2_{G\times L}$              | 1.70              | 0.11             | 213,163         | 1.19              | 0.18             | 54,561          |
| $\sigma^2_E$                        | 231.40            | 1.56             | 215,342         | 234.54            | 1.24             | 55,119          |
| $H$                                 | 0.51              | 0.80             | 0.63            | 0.63              | 0.69             | 0.63            |

$G$ genotype, $G\times A$ genotype by year interaction, $G\times L$ genotype by location interaction, $E$ error
Table 4  QTL detection for spring green-up and plant vigor in a hybrid population in lowland switchgrass

| Trait | Environment | LG | Position (cM) | LOD | Marker interval | AD  | BC  | BD  | PVE (%) |
|-------|-------------|----|---------------|-----|-----------------|-----|-----|-----|---------|
| Spring green-up | 2012PKS | 9a | 21.98 | 4.90 | nfg-137 | PVAAG-3091/3092 | 11.38 | 9.84 | 2.17 | 9.6 |
| | 2012STW | 1a | 78.64 | 4.19 | sww-1615 | sww-333 | -16.78 | -3.84 | -4.99 | 6.5 |
| | 2012STW | 5a | 42.44 | 3.84 | PVGA-1971/1972 | PVCAG-2197/2198 | -7.94 | -1.09 | -5.87 | 6.0 |
| | 2012STW | 6b | 15.16 | 4.77 | sww-1813 | sww-1749 | -13.46 | -9.36 | -6.21 | 7.5 |
| | 2012STW | 9a | 15.98 | 5.98 | sww-463 | nfg-137 | 3.02 | 10.20 | 3.35 | 9.9 |
| | 2013PKS | 2b | 24.05 | 5.23 | PVE-413/414 | PVCAG-2197/2198 | 4.39 | 12.77 | 10.73 | 9.5 |
| | 2013PKS | 5a | 6.00 | 5.26 | PVCA-2389/2390 | PVCAG-2197/2198 | 2.69 | -6.67 | 7.10 | 9.6 |
| | 2014PKS | 2b | 33.05 | 5.64 | PVE-1143/1144 | sww-2662 | -7.42 | 0.63 | -3.28 | 11.1 |
| | 2014STW | 1a | 43.92 | 5.10 | PVGA-2107/2108 | PVCAG-2197/2198 | 3.78 | -1.89 | 8.62 | 11.8 |
| | 2015PKS | 2a | 36.49 | 4.37 | PVE-1143/1144 | nfg-052 | -13.40 | -9.73 | -13.78 | 9.9 |
| | 2015STW | 1a | 13.81 | 3.64 | PVGA-1253/1254 | sww-1615 | 4.53 | 9.43 | 0.15 | 7.0 |
| | 2015STW | 1b | 62.21 | 4.76 | PVCA-1401/1402 | PVCAG-2197/2198 | 16.22 | -1.34 | 16.32 | 9.3 |
| | 2015STW | 2a | 73.15 | 4.13 | PVGA-2107/2108 | PVCAG-2197/2198 | -4.04 | 1.23 | -7.76 | 8.1 |
| | 2015STW | 5a | 34.46 | 3.80 | PVGA-1971/1972 | PVCAG-2197/2198 | -0.81 | 1.46 | -0.15 | 8.3 |
| | 2015STW | 5a | 62.31 | 5.70 | PVCAG-2357/2358 | PVGA-1813/1814 | 0.28 | 0.93 | 0.82 | 12.1 |
| Plant vigor | 2014PKS | 2a | 40.49 | 3.70 | PVGA-1971/1972 | nfg-052 | -6.24 | -2.42 | -3.66 | 7.2 |
| | 2014STW | 1a | 0.00 | 3.92 | PVGA-1813/1814 | PVCAG-2197/2198 | -0.92 | 0.06 | 0.31 | 12.0 |
| | 2014STW | 5a | 61.96 | 5.58 | PVGA-1813/1814 | PVCAG-2197/2198 | 0.92 | 0.42 | 0.15 | 9.0 |
| | 2014STW | 9a | 44.53 | 4.41 | PVGA-1971/1972 | PVCAG-2197/2198 | -1.75 | -0.26 | -0.61 | 7.7 |
| | 2015STW | 1a | 39.68 | 3.81 | PVGA-1813/1814 | PVCAG-2197/2198 | -0.07 | 0.54 | 0.45 | 9.8 |
| | 2015STW | 5a | 60.96 | 4.70 | PVE-1361/1362 | PVCAG-2197/2198 | -0.07 | 0.54 | 0.45 | 9.8 |
| | 2015STW | 5a | 47.37 | 5.69 | PVCA-2389/2390 | PVCAG-2197/2198 | -33.69 | 136.75 | 21.08 | 13.8 |
| | 2015STW | 5a | 38.44 | 4.21 | PVCA-1971/1972 | PVCAG-2197/2198 | -89.47 | 191.37 | 125.27 | 9.9 |
| | 2015STW | 5a | 41.44 | 3.75 | PVCA-1971/1972 | PVCAG-2197/2198 | -181.66 | 49.64 | 222.22 | 8.2 |
| | 2015STW | 5a | 34.46 | 3.80 | PVCAG-2197/2198 | PVCAG-1971/1972 | 38.05 | 209.82 | 233.74 | 7.7 |
| | 2015STW | 5a | 34.46 | 5.53 | PVCAG-2197/2198 | PVCAG-1971/1972 | -117.14 | 155.53 | 183.36 | 13.4 |

AD, BC, BD represent the additive effects of the deviation between genotype AD, BC, or BD and genotype AC. Position represents the peak of QTL.

PVE phenotypic variance explanation, JE joint environments.
**Fig. 3** Significant QTLs for spring green-up, plant vigor, and plant biomass in the hybrid population and selfed population of lowland switchgrass.

**Table 5** QTL detection for spring green-up and plant vigor in a selfed population in lowland switchgrass

| Trait          | Environment | LG  | Position (cM) | LOD   | Marker interval           | Additive | PVE (%) |
|----------------|-------------|-----|---------------|-------|---------------------------|----------|---------|
| Spring green-up| 2012PKS     | 6b-1| 37.44         | 3.53  | PVAAG-3017/3018 PVGA-1115/1116 | −5.30    | 6.3     |
|                | 2012STW     | 6b-1| 38.44         | 9.16  | PVAAG-3017/3018 PVGA-1115/1116 | −5.76    | 12.7    |
|                | 2012STW     | 9a  | 64.10         | 4.24  | PVCAG-2487/2488 PVCA-19/20 | 5.96     | 7.1     |
|                | 2015PKS     | 9a  | 79.39         | 4.35  | PVCAG-2487/2488 PVCA-19/20 | −3.06    | 7.1     |
|                | 2015STW     | 2b  | 35.18         | 4.23  | sww-2501 PVCA-597/598     | 5.37     | 5.8     |
|                | JE          | 6b-1| 38.44         | 5.25  | PVAAG-3017/3018 PVGA-1115/1116 | −3.79    | 8.3     |
| Plant vigor    | 2012PKS     | 2b  | 57.75         | 3.94  | sww-83 M PVCAG-2647/2648  | 0.14     | 7.4     |
|                | 2013PKS     | 2a  | 20.00         | 4.02  | PVCA-815/816 nfsg-50      | 0.08     | 6.7     |
|                | 2014PKS     | 2b  | 25.34         | 4.77  | sww-2545 sww-1622         | 0.01     | 8.3     |
|                | 2014STW     | 2a  | 17.00         | 3.54  | PVCA-815/816 nfsg-50      | 0.14     | 5.5     |
|                | 2015STW     | 9b  | 40.96         | 3.62  | PVAAG-2901/2902 sww-166_200 | −0.19   | 6.1     |
|                | JE          | 2a  | 20.00         | 4.39  | PVCA-815/816 nfsg-50      | 0.03     | 6.5     |
| Plant biomass  | 2013PKS     | 2b  | 31.63         | 4.15  | sww-1622 sww-2501         | 10.64    | 7.9     |

Position represents the peak of QTL

PVE phenotypic variance explanation, JE joint environments
Discussion

Heterosis is one of the primary biological phenomena extensively explored for the success of plant breeding endeavors in many species (East 1936; Gallais 1988; Lippman and Zamir 2007). Both the frequency distributions and population means for the three traits in individual environments indicated heterosis in the hybrid population and inbreeding depression in the selfed population (Figs. 1 and 2; Table 1). The hybrid progeny means were between or higher than the two parents for these three traits. The hybrid progeny means were higher than the two parents in all individual environments for plant biomass, in the individual environments 2013STW, 2014PKS, and 2015PKS for spring green-up and in the individual environments 2012STW, 2013PKS, 2013STW, and 2014PKS for plant vigor, indicating substantial transgressive segregation for these two traits. Heterosis in switchgrass was also observed in the study that spring green-up showed transgressive segregation in a hybrid population derived from crossing by AP13 (lowland) and VS16 (upland) (Ali et al., 2019). Different genetic segregations were reported in the full-sib family due to the high heterozygosity between the two parents during meiosis (Lowry et al. 2019). The recombined hybrids surpassed both parents for the traits studied. The transgressive segregation may be derived from the cumulative and complementary effects of favorable genes from both parents. Similarly, the inbred progeny derived from selfing NL 94 parent were segregating. As expected, inbreeding depression for the three traits was observed in the selfed population. Interestingly, some selfed progeny of NL 94 were more vigorous than the parent, providing an opportunity to select for better progeny with increased homozygosity. Vigorous progeny have high potential for the development of advanced inbreds.

Although heterosis is common in crops, the genetic architecture underlying this phenomenon remains elusive due to its complexity. Huang et al. (2016) examined tens of thousands of F₂ rice lines of three genetic groups and identified a small number of loci from female parents explaining a large portion of the yield advantage of hybrids. However, no heterosis-associated loci were shared across all lines. Moreover, heterosis is an environmentally modified quantitative phenotype (Williams 1959; Griffing 1990; Schnell and Cockerham 1992). Genetic and genomic analysis such as genetic mapping, genomic sequencing, and transcriptomics will not suffice. An integrated framework composed of genomic tools, QTL-based phenotyping, and map-based cloning should be employed to understand the role of heterosis in plant breeding and evolution (Lippman and Zamir 2007). As a largely outcrossing species, switchgrass enjoys wide geographical distribution and rich genetic diversity. The highly heterozygous tetraploid genome of switchgrass renders the genetic study of heterosis a challenging task. The availability of rare self-compatible genotype (i.e., NL94 in this study) provided a valuable resource for the development of inbred lines to assist the study of heterosis in switchgrass. Moreover, climate-associated adaptation has resulted in divergence between the northern upland and southern lowland ecotypes that is exemplified by divergent whole-plant morphologies and distinct overwintering ability (Lovell et al. 2021). It is likely that the genetic architectures for heterosis would also be different between ecotypes as that observed in different rice genetic pools (Huang et al. 2016). Therefore, more populations of diverse genetic backgrounds and coordinated long-term study are needed to better understand heterosis in switchgrass.

Marginal correlation coefficients between spring green-up and plant biomass indicated that spring green-up could be a relatively independent trait for plant biomass. A previous study reported that spring green-up showed no correlation with plant biomass resulted from a half-sib family (Bhandari et al. 2010). The correlation analysis between plant vigor and plant biomass indicated that selection for plant vigor during the early stages of growing season may result in a higher plant biomass (Table 2). The consistent results suggested plant vigor could be recommended as an indirect selection criterion for biomass yield. Mature lowland switchgrass plants can grow 2–3 m in height. Phenotyping plant vigor on large mature plants is not readily feasible due to high amounts of foliage and tillers. The results of this study suggest that selection in early stage is a sound alternative. The different correlation results between the spring green-up and plant vigor based on the two populations suggested that the genetic background of the populations is an important factor influencing correlations between the traits.

Heritability estimates varied in different environments obviously demonstrated that environments across years and locations are necessary for evaluating heritable
traits and providing sufficient information for selection. Broad-sense heritability is statistically higher than narrow-sense heritability because the dominance and epistatic genetic effects are not parsed out from additive effects in calculations. However, it is not easy to obtain accurate genetic effects for the three components. In addition, dominance effects and the epistatic effects are indeed complicated and less readily maneuvered than additive effects in applied breeding programs. Consequently, broad-sense heritability was selected as a method to evaluate the genetic proportion controlling total phenotypic variation. Heritability of the three traits was moderate to high in both the hybrid (Online Resource 2 and Table 3) and selfed populations (Online Resource 2 and Table 3) across years, indicating strong influence of environmental effects as evidenced in the ANOVA analysis (Online Resource 1). A high heritability of 0.82 for spring green-up was reported based on a half-sib family in lowland switchgrass, which could be accounted for more additive effects produced from half-sib family (Bhandari et al. 2010). Plant vigor and spring green-up are dynamic traits reflecting the active growth in spring. It has become widely recognized that the dynamic nature of traits explains the different heritability estimates between environments and populations (Würschum et al. 2014; Pauli et al. 2016). With the advancement in high-throughput phenotyping technologies (HTP), there is a trend to treat heritability as a function across development rather than a fixed time point (Xu et al. 2021). Application of HTP in switchgrass could provide novel insights into the dynamic response to the ever-changing ambient environment in different genotypes and could enable us to estimate heritability at a finer scale along the temporal dimension.

In this study, the QTLs detected for the three traits were distributed unevenly in the linkage groups, and some linkage groups exhibited clusters of QTLs while other linkage groups contained just one QTL or no QTL. In these two populations, the QTLs associated with the three traits were mainly distributed on LGs 1a, 2a, 2b, 5a, and 9a. The variability of QTL distribution could be partially explained by the significant genotype by environment effects in the ANOVA analysis (Online Resource 1). The dynamic nature of traits also imposed an inherent factor influencing trait expressions under different environments, and thereby resulted in distinct sets of QTLs. In the QTL analysis, adjacent QTLs were found for spring green-up (the QTLs around nfsg-137, PVAAG-3091/3092, PVCAG-2517/2518, PVE-1143/1144, and sww-1615), plant vigor (the QTL around PVGA-1513/1514), and plant biomass (the QTL around PVGA-1971/1972 and PVCAG-2197/2198) in the hybrid population (Tables 4 and 5), which suggested that quantitative traits were controlled by multiple closely located genes and (or) influenced by the strong genetic linkage among these QTLs. An in-depth examination on these QTL hot-spot regions may reveal more detailed genetic mechanisms controlling agronomic traits in switchgrass, but this requires a sufficiently large population size and high-density genetic maps, as genetic linkage could often yield synthetic associations in genetic mapping studies. From the perspective of applied plant breeding, identifying the exact location of QTLs or candidate genes is perhaps less important than finding the significant genomic regions that can be used to introduce favorable alleles through marker-assisted selection. Moreover, in the hybrid population, the QTLs between PVGA-1971/1972 and PVCAG-2197/2198 were detected for spring green-up associated with 2012STW, plant vigor associated with 2012STW and 2014PKS, and plant biomass with 2012STW and 2013PKS. Common genomic regions controlling multiple traits simultaneously in this study suggested that this interval could have a pleiotropic effect or harbor multiple genes, and these three traits may be related in genetic control mechanism despite no significant correlation was detected between spring green-up and plant vigor in the hybrid population (Table 2). Although these two populations share a common parent NL94, the commonality of QTLs was not evident between these two populations, which may be caused by the unique polymorphism in SL93 of the hybrid population.

Compared with previous QTL research of switchgrass, we found identical marker intervals and a few markers shared by different traits in the two populations. For example in the hybrid population of this study, the QTL for spring green-up in single environment located in the marker intervals of nfsg-137 and PVAAG-3091/3092, sww-463 and nfsg-137, PVCAG-2389/2390 and PVCAG-2167/2168, PVAAG-3091/3092 and PVCAG-2517/2518, and sww-1667 and PVCA-1253/1254 were also detected for biomass-related traits (i.e., plant base size, tillering ability, node numbers, and tiller dry weight) in previous research (Chang et al. 2010).
The QTL for plant biomass between PVCAG-2197/2198 and PVGA-1649/1650 was the same as the QTL for plant girth in PKS12 and 13. In the selfed population, the QTLs found in this study between sww-2285 and PVGA-1405/1406 and sww-2501 and PVCA-597/598 for spring green-up, as well as PVCA-815/816 and nfsg-50 for plant vigor just appeared in the previous study referring to those biomass-related traits (Chang et al. 2016). We also found QTLs flanked by common markers in these two studies (i.e., PVCAG-2197/2198, PVCA-179/180, sww-463, nfsg-13, PVGA-1813/1814, and PVCA-2167/2168) (Chang et al. 2016). These repeated QTLs and common markers could be of great interest in MAS to improve biomass breeding in switchgrass. Moreover, some novel QTLs were found in this study (i.e., QTLs between sww-1615 and sww-333, PVE-413/414 and PVE-1143/1144 and the QTL between sww-532 and nfsg-052 for spring green-up, the QTL between PVE-1361/1362 and PVGA-2107/2108 for plant vigor detected in the hybrid population, QTLs between PVAA-3017/3018 and PVGA-1115/1116 for spring green-up, the QTL between sww-2545 and sww-1622 for plant vigor, and the QTL between sww-1622 and sww-2501 for plant biomass detected in the selfed population), which expanded our knowledge in understanding the genetics of biomass and biomass-related traits in switchgrass.

QTL mapping studies on yield and yield-related traits in switchgrass are increasing, but still largely rely on single environment and (or) single population. Evaluation of multiple populations under multi-environments is necessary to provide information in plant breeding, particularly in perennial crops such as switchgrass, which is expected to have multiple years of growth for biomass production (Lowry et al. 2019; Lovell et al. 2021). Indeed, maintenance of large-scale multi-year multi-environment field trials is cost prohibitive and labor intensive. Coordinated agricultural projects such as Lovell et al. (2021) and Zhang et al. (2020) laid the cornerstone for a comprehensive understanding of this important bioenergy biomass crop.

Conclusions

This study characterized phenotypic variations and identified QTLs for spring green-up, plant vigor, and plant biomass in two populations of lowland switchgrass. Both the hybrid and selfed populations showed significant variations for genotype by year or genotype by location interactions. Heterosis in the hybrid population and inbreeding depression in the selfed population indicated the genetic potential in the development of hybrid cultivars in lowland switchgrass. Adjacent and common QTLs detected in the three traits suggested SSR markers flanking the significant QTLs are valuable for marker-assisted selection in lowland switchgrass. The findings in this study will extend the knowledge base of QTLs for biomass components in the species.

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Author contribution D. Chang carried out the experiment, data analysis, and writing of the manuscript, H.X. Dong conducted data analysis and writing of the manuscript, S.Q. Bai designed and supervised the experiment, and Y.Q. Wu conceived and supervised the experiment, wrote, and finalized the manuscript.

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Declarations

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