

Research Article/Araştırma Makalesi

MEDITERRANEAN AGRICULTURAL SCIENCES (2020) 33(3): 405-410 DOI: 10.29136/mediterranean.780085

www.dergipark.org.tr/en/pub/mediterranean

SSR marker analysis of plant height in sweet sorghum [Sorghum bicolor (L.) Moench]

Şeker sorgumda [Sorgum bicolor (L.) Moench] bitki boyunun SSR marker analizi

Birgul GUDEN¹^(b), Engin YOL¹^(b), Cengiz ERDURMUS²^(b), Bulent UZUN¹^(b)

¹Akdeniz University, Faculty of Agriculture, Department of Field Crops, Antalya, Turkey ²West Mediterranean Agricultural Research Institute, Aksu, Antalya, Turkey

Corresponding author (Sorumlu yazar): B. Uzun, e-mail (e-posta): bulentuzun@akdeniz.edu.tr Author(s) e-mail (Yazar(lar) e-posta): birgulguden@akdeniz.edu.tr, enginyol@akdeniz.edu.tr, Cengiz.erdurmus@tarimorman.gov.tr

ARTICLE INFO

Received 13 August 2020 Received in revised form 23 August 2020 Accepted 23 September 2020

Keywords:

Bio-energy Biomass SSR QTL

ABSTRACT

Sorghum (Sorghum bicolor (L.) Moench) is one of the most promising bio-energy crops with the ability to produce high biomass with low input. Plant height that has a significant contribution to gain in bio-ethanol production is among the most important biomass yield components. In the present study, sorghum genotypes were screened with four SSR markers which are associated with plant height QTLs. The molecular assays were confirmed with two different environments in two consecutive years. In the first year of the study, molecular analyses were performed with a sorghum collection consisting of 551 accessions as well as plant height measurements were performed under field condition. In the second year, 53 out of 551 accessions were selected and further tests with nine controls were performed in Antalya (a lowland province) and Konya (a highland province) locations along with molecular marker analyses. The results indicated that four SSR markers efficiency were assessed as 38% at lowland and 39% at highland. Markers 40-9187 and 37-1740 were of more powerful to explain plant height QTLs than the other two markers at two environments. This study reported the successful application of the association between markers and plant height in two environments to identify valuable genetic resources for bio-energy production in sweet sorghum.

MAKALE BİLGİSİ

Alınış tarihi 13 Ağustos 2020 Düzeltilme tarihi 23 Ağustos 2020 Kabul tarihi 23 Eylül 2020

Anahtar Kelimeler:

Biyo-enerji Biyokütle SSR QTL

ÖZ

Sorgum (*Sorghum bicolor* (L.) Moench), düşük girdi ile yüksek biyokütle üretebilme yeteneğine sahip umut verici biyo-enerji bitkilerinden biridir. Biyoetanol üretiminde kayda değer katkıları olan bitki boyu, biyokütle verimini oluşturan en önemli bileşenler arasındadır. Bu çalışmada, sorgum genotipleri bitki boyu QTL'leri ile ilişkili dört SSR marker ile taranmıştır. Moleküler analizler, ardışık 2 yıl ve 2 farklı ortamda doğrulanmıştır. Çalışmanın ilk yılında 551 genotipten oluşan sorgum koleksiyonunda moleküler analizler ve tarla koşullarında bitki boyu ölçümleri yapılmıştır. İkinci yılda ise 551 genotipten 53'ü seçilerek, dokuz kontrol çeşit kullanılarak moleküler analizler ile birlikte Antalya (ova) ve Konya (yayla) lokasyonlarında ileri testler gerçekleştirildi. Sonuçlara göre; dört SSR markerin verimliliği ovada %38 ve yaylada %39'dur. 40-9187 ve 37-1740 markerleri, iki ortamda da diğer iki marköre göre bitki yüksekliği ile ilişkili QTL'lerin açıklanmasında daha güçlü olarak belirlenmiştir. Bu çalışma, şeker sorgumda biyo-enerji üretimi için değerli genetik kaynakları belirlemek adına iki ortamda da markerler ve bitki boyu arasındaki ilişkinin belirlenmesinde başarılı bir şekilde uygulandığının bildirilmesidir.

1. Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) has been recognized as 'smart' crop for ethanol production with high biomass production and high sugar concentration in its stalk (Rooney et al. 2007; Felderhoff et al. 2012; Han et al. 2012, 2013). Sorghum has an effective water usage which provides to be competitive against drought stress and high temperature

(Almodares et al. 2006; Rooney et al. 2007; Saballos 2008). Moreover, this crop stocks sugar in its stalk with a concentration of 8-20% (Rains et al. 1990). Comparing with the other crops like; wheat, sugarcane and maize which are used for human and animal consumption, all these benefits make sorghum a potential crop for bio-energy (Murray et al. 2008). To increase biomass production, the alteration of plant architecture is among the most important breeding purposes. Plant height is a significant component of structure that is positively and strongly correlated r= 0.68-0.7 (Murray et al. 2008) r= 0.355 (Ritter et al. 2008) with biomass productivity (Salas Fernandez et al. 2008; Zhao et al. 2009). Although taller genotypes are likely to lodge and can mature late (not always), these varieties have more advantages to produce more biomass with higher sugar content (Ritter et al. 2008; Murray et al. 2009). Because of significant correlation between height and regrowth fresh biomass, better ratoon is produced in taller genotypes (Murray et al. 2008) and less grain mould is seen on taller genotypes (Klein et al. 2001).

In sorghum, four major loci; *Dw*1, *Dw*2, *Dw*3 and *Dw*4 that regulate plant height by modifying internodes length, have been characterized (Quinby and Karper 1954). The first cloned plant height gene was *DW*3 (*SbPGP1*) in sorghum (Multani et al. 2003). This gene, located on chromosome 9, has associated with reduced lower internodes length and its role is an auxin efflux transporter (Multani et al. 2003). On chromosome 7, *SbPGP1* localizes with a height QTL (Murray et al. 2008; Brown et al. 2006). *Dw1* affected internodes length and contribute to the variation in stem weight, located on SBI-09 (Hilley et al. 2016). Moreover, *dw1* has diminished the cell proliferation activity in internodes (Yamaguchi et al. 2016). *Dw2*, located on SBI-06, is linked to the major photoperiod-sensitivity locus, *Ma*1 (Quinby 1967; Lin et al. 1995; Klein et al. 2008).

Advances in molecular technology have provided valuable tools for breeding implementations such as genetic diversity, linkage map, QTL mapping and marker assisted selection. Use of marker systems for quantitative traits which have economic importance supplies an opportunity to develop genotypes with desirable trait(s). Since sorghum is becoming crucial as a bioenergy crop, several studies have been carried out linked to the genetic characterization of plant height (Multani et al. 2003; Feltus et al. 2006; Brown et al. 2008; Mace and Jordan 2010; Wang et al. 2012; Morris et al. 2013; Upadhyaya et al. 2013; Reddy et al. 2013; Hilley et al. 2016; Yamaguchi et al. 2016; Shuklaa et al. 2017). Although plenty of markers have been improved for most of crop, SSR markers have been used extensively for application in breeding program (Wang et al. 2012). Moreover. these markers have low development/detection cost and high reproducibility (Wang et al. 2012; Madhusudhana 2015). In conjunction with molecular analysis, further field studies are needed to confirm markers associated with plant height that is affected by many QTLs (Quinby and Karper 1954; Multani et al. 2003).

In the present study, the sorghum collection consisting of 560 genotypes including sorghum mini core collection were screened with SSR markers linked to the plant height QTLs and those validity and efficiency were revealed with phenotyping in both lowland and highland conditions.

2. Materials and Methods

2.1. Genetic materials

The genetic material consisted of 560 sorghum genotypes. Of the 560 sorghum genotypes, 309 were provided by USDA (United States Department of Agriculture) and 242 were from ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) gene banks. Nine cultivars registered in Turkey were also the genetic material of the study.

2.2. Field trials

Field experiments were conducted in Konya (a highland province) and Antalya (a lowland province) locations in the growing seasons of 2013 and 2014. Five hundred fifty one sorghum genotypes and 9 cultivars were grown at the West Mediterranean Agricultural Research Institute's fields of Antalya, Turkey on 19 May. With the presence of desirable banding pattern which showing close association with the plant height QTLs, 53 genotypes were selected. These genotypes and nine cultivars were planted in a randomized complete blocks design with three replications on 14 May in the highland (37°34'N and 32°47'E, 1016 m above sea level) and on 21 May in lowland (36°52'N and 30°50'E, 41 m above sea level) locations in 2014. Each plot consisted of four rows of 5 m long with a row spacing of 70 cm.

2.3. Phenotyping and classification

Three representative plants of each plot were measured for plant height as the distance between ground and the top of the panicle after full panicle emergence in all the years. The average plant height was calculated for each genotype in all locations. The genotypes were classified as tall if plant height was over 2 m (Wang et al. 2012).

2.4. Molecular analyses

2.4.1. DNA isolation

Young leaves of every genotype grown in each year and location were sampled for DNA isolation. Genomic DNA was isolated from leaf tissues following the CTAB protocol (Doyle and Doyle 1990) with minor modifications. The quality and quantity of DNAs were controlled with a λ DNA in 1% agarose gel electrophoresis.

2.4.2. SSR marker analyses linked to the plant height QTLs

A total of four SSR markers, 44-2080, 40-1897, 37-1740 and 23-1062, reported by Wang et al. (2012) were used to screen the sorghum collection for the plant height QTLs. PCR amplifications were performed in a 20 μ L reaction containing 2 μ L of 10x PCR buffer, 0.4 mM of dNTPs mix, 2.5 mM of MgCl₂, 10 μ M forward and reverse primers (Wang et al. 2012) 1 unit of Taq DNA polymerase, 2 μ L genomic DNA template and Milli-Q water, using thermo cyclers (Thermo Fisher, TCA0096, Finland). The protocol was initiated with 95°C for 5 min, 30 cycles of 95°C for 20 s 56°C for 20 s, 72°C for 1 min and final extension of 72°C for 7 min. A total of 12 μ L PCR products were used to separate on 2.5% agarose gel with ethidium bromide in electrophoresis at 75 V for 3 h. Different bands grouped according to respective size comparison with 100 bp ladder DNA size markers.

3. Results

3.1. QTL analyses

Four SSR markers, 44-2080, 40-1897, 37-1740 and 23-1062 associated with the plant height QTLs were used to evaluate genotypes in agarose gel after PCR amplification. Analysis of four SSR markers for each genotype was classified into two groups as tall and short plant height based on the report presented by Wang et al. (2012). The 40-1897 marker produced 264 bp allele in 431 genotypes indicated that they were of the related plant height allele while 244 bp band pattern associated

with short height were identified in 88 genotypes. 30 genotypes produced no amplification with this marker. 446 and 473 genotypes were amplified with the 37-1740 and 44-2080 markers, respectively showing that short plant height alleles were presence.

In the second year, molecular analysis was performed with the use of selected 53 genotypes and nine sorghum cultivars for both locations. 39 genotypes and 3 cultivars showed the tall plant height amplification with 264 bp in the analysis of 40-1897 marker for both locations (Fig. 1). The 44-2080 marker was observed in 62 genotypes in both locations. The 37-1740 marker produced no band in 30 and 32 genotypes in the lowland and highland locations, respectively meaning that they had the tall plant height allele (Fig. 1). For all the locations and years, the tall plant height allele was presented in higher frequency than the short height allele.

3.2. Phenotyping

All the genotypes were grouped based on the height data (tall versus short) for all the environments and years. Wide variation for plant height was observed in the sorghum collection; starting from 94 to 380 cm. While 352 genotypes which were determined 256 cm in the average of height were classified as tall group, 197 genotypes (two genotypes did not germinate) were grouped as short.

The average height of the selected material and nine cultivars was 241 cm at highland and 276 cm at lowland (Table 1). Only one genotype, BSS376 was classified as short plant height with measurements of 146 cm and 169 cm in highland and lowland, respectively whereas the remains were classified as tall plant height. This result indicated the power and accuracy of the selection made for plant height character. BSS532 and BSS336 were identified as the tallest genotypes in both locations.

3.3. QTL markers efficiency for plant height

Significant associations were observed between the marker scores and the phenotypic data. The 23-1062 marker explained 48.09% of the height variance in the sorghum collection. The 37-1740 and 40-1897 markers were more efficient than the other two markers with the explained height variance of 54.08% and 56.99%, respectively (Table 2). The overall marker efficiency was 49.86% in the entire sorghum collection.

In the selected material, 44-2080 marker was the least association with the height data with a value of 8.06% for highland and 16.12% for lowland. In consistency with the previous year results, 37-1740 and 40-1897 had the strongest association in both locations, which were 43.54% and 62.90% for highland, 50% and 72.58% for lowland, respectively (Table 2).

4. Discussion

The first step of genetic improvement of sorghum for bioenergy is to enhance its biomass (Murray et al. 2008). Plant height in sorghum, after it was determined that highly positive correlated with biomass (Murray et al. 2008; Ritter et al. 2008; Zhao et al. 2009; Burks et al. 2015) has become the main aim of selection/breeding for bio-energy resource.

The genome of Sorghum bicolor is approximately 730 Mbp (Paterson et al. 2009). Its genome is relatively smaller than other important crops such as wheat (approximately 17000 Mbp. (Zhang et al. 2012)) and sugarcane (2547-3605 Mbp, (Bowers et al. 2003)), except rice (389 Mbp, The international rice genome project). Plant height, however, is a complicated trait controlled by major QTLs, and progress in improving plant height through traditional breeding has been slow, but molecular markers based breeding can achieve rapid genetic gains in plant height. To date, some important molecular markers associated with height have been identified for molecular breeding in sorghum. For example, Xgap72, pSB0945, Xtxp343, pSB0301 and Xtxp265 height markers identified by Murray et al. (2009) using with 125 genotypes with the aid of 47 SSR and 322 SNP markers. Among these, Xgap72, pSB0945and Xtxp265 were in line with other previous published QTL studies (Lin et al. 1995; Feltus et al. 2006; Brown et al. 2006; Pereira and Lee 1995). Ongom and Ejeta (2018) on chromosome 6, identified a new quantitative trait locus for plant height using with multi-parent advanced generation intercross (MAGIC) population. Bai et al. (2017) evaluated RIL (Recombinant Inbreed Line) population including 189 genotypes and identified 6 QTLs for plant height.

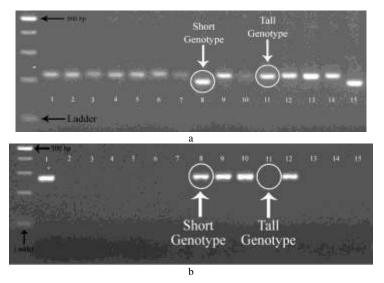


Figure 1. Agarose gel showing the amplification products of a number of accessions using the QTL markers, 40-1897 (a), 37-1740 (b).

Table 1. Plant height measurements of the selected genotypes and nine sorghum cultivars at the highland and lowland locations.

Accession No.	USDA/ ICRISAT ID -	Plant Height (cm)	
		Highland	Lowland
BSS5	PI 144134	248	291
BSS27	PI 154988	198	240
BSS46	PI 170787	286	306
BSS47	PI 175919	286	314
BSS55	PI 196049	222	229
BSS57	PI 196598	139	221
BSS58	PI 217691	289	317
BSS59	PI 218112	243	278
BSS62	PI 255239	247	279
BSS67	PI 273465	270	364
BSS69	PI 273969	254	304
BSS73	PI 533998	194	287
BSS78	PI586541	292	299
BSS79	PI 641807	256	266
BSS80		249	237
	PI 641810		
BSS81	PI 641815	264	260
BSS82	PI 641817	265	295
BSS83	PI 641821	263	273
BSS84	PI 641834	271	267
BSS85	PI 641835	161	224
BSS86	PI 641862	211	239
BSS91	PI 651495	220	361
BSS100	PI155746	275	317
BSS246	PI 330128	254	252
BSS312	PI646858	261	283
BSS314	IS 602	265	260
BSS320	IS 1212	279	324
BSS325	IS 2389	255	268
BSS325 BSS331		233	264
	IS 2902		
BSS332	IS 3121	232	248
BSS336	IS 4092	303	322
BSS359	IS 7957	268	250
BSS367	IS 9113	282	325
BSS376	IS 11619	146	169
BSS402	IS 15744	257	269
BSS402 BSS410	IS 18039	204	20) 275
BSS422	IS 20632	231	356
BSS423	IS 20679	245	260
BSS424	IS 20697	272	381
BSS429	IS 20816	260	325
BSS456	IS 24453	267	317
BSS473	IS 26222	255	284
BSS475 BSS474	IS 26484	223	258
		224 290	314
BSS496	IS 29187		
BSS497	IS 29233	237	283
BSS505	IS 29358	208	265
BSS507	IS 29441	280	274
BSS508	IS 29468	295	332
BSS510	IS 29565	293	312
BSS515	IS 29654	289	300
BSS515 BSS517	IS 29714	226	318
BSS518	IS 29733	184	266
BSS532	IS 30466	307	363
ROX	-	214	243
Aldari	-	121	162
Akdari	-	113	112
Beydari	_	129	161
Ogretmenoglu		133	144
	-		
E. S.	-	230	248
Gozde 80	-	301	315
Leoti	-	232	267
Nes		251	281

-: Sorghum cultivars are registered in Turkey.

% variance explained			
Entire collection (2013)	*Selected materials (2014)		
	Highland	Lowland	
48.09	24.19	25.80	
54.08	43.54	50.00	
56.99	62.90	72.58	
40.29	8.06	16.12	
	48.09 54.08 56.99	Entire collection (2013) *Selected ma 48.09 24.19 54.08 43.54 56.99 62.90	

Table 2. Association between the SSR markers and plant height in the sorghum collection and the selected materials in two environments.

*Selected materials: selected fifty three genotypes and nine cultivars.

Using sorghum mini core collection with 703 SSR markers and phenotypic information, Upadhyaya et al. (2012) was developed a marker, 39-1833, which was 84 kb distance from photoperiod response gene (Ma/SbPRR37), associated with height and maturity. Moreover, Upadhyaya et al. (2013) were determined height SNP linked to peroxidase gene, Prx53, regulates plant height through its auxin metabolism. Wang et al. (2012) were defined four SSR markers related to plant height QTLs in sorghum with using sorghum mini core collection developed by Upadhyaya et al. (2009). These four markers were of a valuable tool to perform this research. We report here that both 40-9187 and 37-1740 SSRs had a powerful marker to find out genotypes which have a tall genetic background. Those markers efficiency was confirmed with selected genotypes in all the environments. The results agrees with Wang et al. (2012) study which reported marker 40-9187 had the strongest effect on plant height with 26.5% in ICRISAT and 13.9% in UL Lafayette.

Origin of sorghum is African, but the domestication may have been occurred elsewhere (Kimber 2000). The five basic races (bicolor, guinea, caudatum, kafir and durra) were described in sorghum (Harlen and De Wet 1972; Mann et al. 1983). Moreover, there are ten intermediate races (guineaguinea-caudatum, guinea-kafir, bicolor. guinea-durra, caudatum-bicolor, kafir-bicolor, durra-bicolor, kafir-caudatum, kafir-durra, and durra-caudatum) seen on different parts of the world. In this study, genotypes confirmed by molecular markers as a tall were identified predominantly durra which is generally tall with a good quality (Hariprasanna and Patil 2015) and caudatum which is usually medium to tall with high yield (Mann et al. 1983).

Further field studies in different locations for plant height controlled more than one major QTL and significantly affected by environment were needed to confirm genetic evaluations. The plant height QTLs were therefore comparatively analyzed with the real field data in two different environments. However, the markers efficiency in lowland (38%) was almost the same comparing with the highland (39%). This result obviously showed the stability of the QTL markers used in the study.

It is also important to mention here the powerful selection performed for plant height character in the study. Within the 53 selected genotypes with regard to plant height character using both genotypic and phenotypic data, only one genotype (BSS376) was classified as short plant stature in both locations while the remains were of tall plant height.

5. Conclusion

Measurement of plant height and thus determining tall plants in sorghum seem to be possible by basic phenotyping. Nevertheless, plant height is strongly influenced by environment as in many other QTLs. Hence, the related QTL(s) for plant height in sorghum could be masked or overreacted by environment. Molecular marker confirmation is therefore an effective way to plant height characterization. In this study, two QTL markers (40-9187 and 37-1740) were of high and consistent efficiency in all environments for plant height characterization. Fifty three genotypes that were selected with the QTL markers and evaluated at two different environments might be used as a gene pool to improve bio-energy types in sweet sorghum and these two QTL markers will be complement to achieve gains in DNA level for plant height beyond traditional breeding approaches.

Acknowledgements

This study was supported by the Scientific and Technological Research Council of Turkey (TUBITAK) [grant number 1130092].We are grateful to International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Gene bank, Hyderabad, India and United States Department of Agriculture (USDA), Gene bank, USA, and West Mediterranean Agricultural Research Institute (BATEM), Antalya, Turkey for providing genetic material.

References

- Almodares A, Mostafafi Darany SM (2006) Effects of planting date and time of nitrogen application on yield and sugar content of sweet sorghum. Journal of Environmental Biology 27: 601-605.
- Bai C, Wang C, Zhu Z, Cong L, Li D, Liu Y, Zheng W, Lu X (2017) QTL mapping of agronomically important traits in sorghum (Sorghum bicolor L.). Euphytica 213(285).
- Bowers JE, Abbey C, Anderson S, Chang C, Draye X, Hoppe AH, Jessup R, Lemke C, Lennington J, Li Z, Lin YR, Liu SC, Luo L, Marler BS, Ming R, Mitchell SE, Qiang D, Reichmann K, Schulze SR, Skinner DN, Wang YW, Kresovich S, Schertz KF, Paterson AH (2003) A high-density genetic recombination map of sequencetagged sites for sorghum, as a framework for comparative structural and evolutionary genomics of tropical grains and grasses. Genetics 165: 367-386.
- Brown PJ, Klein PE, Bortiri E, Acharya CB, Rooney WL, Kresovich S (2006) Inheritance of inflorescence architecture in sorghum. Theoretical and Applied Genetics 113: 931-942.
- Brown PJ, Rooney WL, Franks C, Kresovich S (2008) Efficient mapping of plant height quantitative trait loci in a sorghum association population with introgressed dwarfing genes. Genetics 180: 629-637.
- Burks PS, Kaiser CM, Hawkins ME, Brown PJ (2015) Genomewide association for sugar yield in sweet sorghum. Crop Science 55: 2138-2148.
- Doyle JJ, Doyle JL (1990) A rapid total DNA preparation procedure for fresh plant tissue. Focus 12: 13-15.
- Felderhoff TJ, Murray SC, Klein PE, Sharma A, Hamblin MT, Kresovich S, Vermerris W, Rooney WL (2012) QTLs for energyrelated traits in a sweet x grain sorghum *[Sorghum bicolor* (L.) Moench] mapping population. Crop Science 52: 2040-2049.
- Feltus FA, Hart GE, Schertz KF, Casa AM, Kresovich S, Abraham S, Klein PE, Brown PJ, Paterson AH (2006) Alignment of genetic

maps and QTLs between inter- and intra-specific sorghum populations. Theoretical and Applied Genetics 112: 1295-1305.

- Han KJ, Pitman WD, Alison MW, Harrell DL, Viator HP, McCormicks ME, Gravois KA, Kim M, Day DF (2012) Agronomic considerations for sweet sorghum biofuel production in the South-Central USA. Bioenergy Research 5: 748-758.
- Han KJ, Pitman WD, Kim M, Day DF, Alison MW, McCormick ME, Aita G (2013) Ethanol production potential of sweet sorghum assessed using forage fiber analysis procedures. GCB Bioenergy 5: 358-366.
- Hariprasanna K, Patil JV (2015) Sorghum: Origin, classification, biology and improvement. In: Madhusdhana R, Rajendrakumar P, Patil JV (Eds), Sorghum molecular breeding, Springer, India, pp. 3-19.
- Harlen JR, De Wet JMJ (1972) A simplified classification of cultivated sorghum. Crop Science 12: 172-176.
- Hilley J, Truong S, Olson S, Morishige D, Mullet J (2016) Identification of *Dw*1, a regulator of sorghum stem internode length. Plos One 11: e0151271.
- Kimber CT (2000) Origins of domesticated sorghum and its early diffusion to India and China. In: Smith CW, Frederiksen RA (Eds), Sorghum: origin, history, technology, and production, Wiley Series in Crop Science, New York, pp. 3-96.
- Klein RR, Rodriguez-Herrera R, Schlueter JA, Klein PE, Yu H, Rooney WL (2001) Identification of genomic regions that affect grainmould incidence and other traits of agronomic importance in sorghum. Theoretical and Applied Genetics 102: 307-319.
- Klein C, Chan A, Kircher L, Cundiff AJ, Gardner N, Hrovat Y, Scholz A, Kendall BE, Airame S (2008) Striking a balance between biodiversity conservation and socioeconomic viability in the design of marine protected areas. Conservation Biology 22: 691-700.
- Lin YR, Schertz KF, Paterson AH (1995) Comparative analysis of QTLs affecting plant height and maturity across the poaceae, in referecence to an interspecific sorghum population. Genetics 141: 391-411.
- Mace E, Jordan D (2010) Location of major effect genes in sorghum (Sorghum bicolor (L.) Moench). Theoretical and Applied Genetics 121: 1339-1356.
- Madhusudhana R (2015) Application of DNA Markers for Genetic Improvement. In: Madhusudhana R, Rajendrakumar P, Patil JV (Eds), Sorghum molecular breeding, Springer, India, pp. 71-99.
- Mann JA, Kimber CT, Miller FR (1983) The origin and early cultivation of sorghums in Africa. Texas: Texas Agricultural Experiment Station.
- Morris GP, Ramu P, Deshpande SP, Hash CT, Shah T, Upadhyaya HD, Riera-lizarazu O, Brown PJ, Acharya CB, Mitchell SE, Harriman J, Glaubitz JC, Buckler ES, Kresovich S (2013) Population genomic and genome-wide association studies of agroclimatic traits in sorghum. Proceedings of the National Academy of Sciences of the United States of America 110: 453-458.
- Multani DS, Briggs SP, Chamberlin MA, Blakeslee JJ, Murphy AS, Johal GS (2003) Loss of an MDR transporter in compact stalks of maize br2 and sorghum dw3 mutants. Science 302: 81-84.
- Murray SC, Sharma A, Rooney WL, Klein PE, Mullet JE, Mitchell SE, Kresovich S (2008) Genetic improvement of sorghum as a biofuel feedstock: I. QTL for stem sugar and grain nonstructural carbohydrates. Crop Science 48: 2165-2179.
- Murray SC, Rooney WL, Mitchell SE, Kresovich S (2009) Sweet sorghum diversity and association mapping for Brix and height. Plant Genome 2: 48-62.
- Ongom PO, Ejeta G (2018) Mating design and genetic structure of a multi-parent advanced generation intercross (MAGIC) population of sorghum (*Sorghum bicolor* (L.) Moench). G3-Genes Genomes Genetics 8: 331-341.

- Paterson AH, Bowers JE, Bruggmann R et al. (2009) The Sorghum bicolor genome and the diversification of grasses. Nature 457: 551-556.
- Pereira MG, Lee M (1995) Identification of genomic regions affecting plant height in sorghum and maize. Theoretical and Applied Genetics 90: 380-388.
- Quinby JR, Karper RE (1954) Inheritance of height in sorghum. Agronomy Journal 46: 211-216.
- Quinby JR (1967) The maturity genes of sorghum. In: Norman A (Ed), Advances in agronomy XIX, Academic Press, New York, pp. 267-305.
- Rains GC, Cundiff JS, Vaughan DH (1990) Development of a wholestalk sweet sorghum harvester. Transactions of the ASAE 33: 56-62.
- Reddy DS, Bhatnagar-Mathur P, Cindhuri KS, Sharma KK (2013) Evaluation and validation of reference genes for normalization of quantitative real-time PCR based gene expression studies in peanut. Plos One 8: e78555.
- Ritter KB, Jordan DR, Chapman SC, Godwin ID, Mace ES, McIntyre CL (2008) Identification of QTL for sugar related traits in a sweet 9 grain sorghum (*Sorghum bicolor* L. Moench) recombinant inbred population. Molecular Breeding 22: 367-384.
- Rooney WL, Blumenthal J, Bean B, Mullet JE (2007) Designing sorghum as a dedicated bioenergy feedstock. *Biofuel* Bioproducts Biorefining 1: 147-157.
- Saballos A (2008) Development and utilization of sorghum as a bioenergy crop. In: Vermerris W (Ed), Genetic improvement of bioenergy crops, Springer Science and Business Media, New York, pp. 211-248.
- Salas Fernandez MG, Becraft PW, Yin Y, Lubberstedt T (2009) From dwarves to giants? Plant height manipulation for biomass yield. Trends in Plant Science 14: 454-461.
- Shuklaa S, Felderhoff TJ, Saballos A, Vermerris W (2017) The relationship between plant height and sugar accumulation in the stems of sweet sorghum (*Sorghum bicolor* (L.) Moench). Field Crops Research 203: 181-191.
- Upadhyaya HD, Pundir RPS, Dwivedi SL, Gowda CLL, Reddy VG, Singh S (2009) Developing a mini core collection of sorghum for diversified utilization of germplasm. Crop Science 49: 1769-1780.
- Upadhyaya HD, Wang YH, Sharma S, Singh S (2012) Association mapping of height and maturity across five environments using the sorghum mini core collection. Genome 55: 471-479.
- Upadhyaya HD, Wang YH, Gowda CLL, Sharma S (2013) Association mapping of maturity and plant height using SNP markers with the sorghum mini core collection. Theoretical and Applied Genetics 126: 2003-2015.
- Wang YH, Bible P, Loganantharaj R, Upadhyaya HD (2012) Identification of SSR markers associated with height using pool based genome-wide association mapping in sorghum. Mol Breeding 30: 281-292.
- Yamaguchi M, Fujimoto H, Hirano K, Araki-Nakamura S, Ohmae-Shinohara K, Fujii A, Tsunashima M, Song XJ, Ito Y, Nagae R, Wu J, Mizuno H, Yonemaru J, Matsumoto T, Kitano H, Matsuoka M,

Kasuga S, Sazuka T (2016) Sorghum Dw1, an agronomically important gene for lodging resistance, encodes a novel protein involved in cell proliferation. Scientific Reports 6: 28366.

- Zhang L, Zhao YL, Gao LF, Zhao GY, Zhou RH, Zhang BS, Jia JZ (2012) *TaCKX6-D1*, the ortholog of rice *OsCKX2*, is associated with grain weight in hexaploid wheat. New Phytologist 195: 574-584.
- Zhao YL, Dolat A, Steinberger Y, Wang X, Osman A, Xie GH (2009) Biomass yield and changes in chemical composition of sweet sorghum cultivars grown for biofuel. Field Crops Research 111: 55-64.