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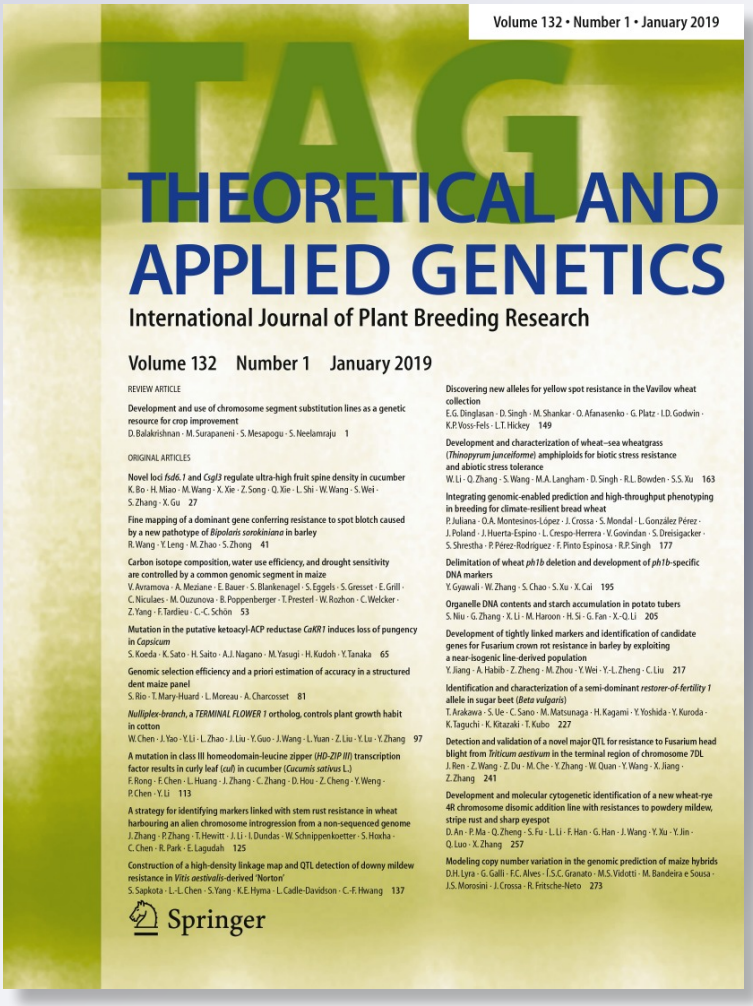
Theoretical and Applied Genetics
International Journal of Plant Breeding Research

ISSN 0040-5752
Volume 132
Number 1

Theor Appl Genet (2019) 132:1-25
DOI 10.1007/s00122-018-3219-y



Springer

Theoretical and Applied Genetics (2019) 132:1–25
https://doi.org/10.1007/s00122-018-3219-y

REVIEW ARTICLE

Development and use of chromosome segment substitution lines as a genetic resource for crop improvement

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Received: 4 December 2017 / Accepted: 24 October 2018 / Published online: 27 November 2018

Abstract

Key message **CSSLs are a complete library of introgression lines with chromosomal segments of usually a distant genotype in an adapted background and are valuable genetic resources for basic and applied research on improvement of complex traits.**

Abstract Chromosome segment substitution lines (CSSLs) are genetic stocks representing the complete genome of any genotype in the background of a cultivar as overlapping segments. Ideally, each CSSL has a single chromosome segment from the donor with a maximum recurrent parent genome recovered in the background. CSSL development program requires population-wide backcross breeding and genome-wide marker-assisted selection followed by selfing. Each line in a CSSL library has a specific marker-defined large donor segment. CSSLs are evaluated for any target phenotype to identify lines significantly different from the parental line. These CSSLs are then used to map quantitative trait loci (QTLs) or causal genes. CSSLs are valuable prebreeding tools for broadening the genetic base of existing cultivars and harnessing the genetic diversity from the wild- and distant-related species. These are resources for genetic map construction, mapping QTLs, genes or gene interactions and their functional analysis for crop improvement. In the last two decades, the utility of CSSLs in identification of novel genomic regions and QTL hot spots influencing a wide range of traits has been well demonstrated in food and commercial crops. This review presents an overview of how CSSLs are developed, their status in major crops and their use in genomic studies and gene discovery.

Abbreviations

CASLs	Chromosome arm substitution lines
CILs	Candidate introgression lines
CSILs	Chromosome segment introgression lines
NGNL	Next-generation NIL (near isogenic line) library
RCSLs	Recombinant chromosome substitution lines
SSCTI	Small-segment chromosome translocations and introgression
SSSL	Single-segment substitution lines
STAIRS	Stepped aligned inbred recombinant strains

Communicated by Rajeev K. Varshney.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00122-018-3219-y) contains supplementary material, which is available to authorized users.

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Introduction

Chromosome segment substitution lines (CSSLs) are genetic resource in which the whole genome of a specific donor genotype is represented segment wise (preferably overlapping) in the genetic background of usually an adapted variety. CSSLs were first reported as introgression lines in tomato (Eshed and Zamir 1994, 1995) followed by contig lines in rice (Ghesquire et al. 1997; Doi et al. 1997). Several populations of CSSLs were developed in model plants such as *Arabidopsis* and used for studies on epistatic interaction and heterosis (Koumproglou et al. 2002; Kubo et al. 2002; Keurentjes et al. 2007; Torjek et al. 2008; Fletcher et al. 2013; Goulet et al. 2017). CSSL libraries are developed by advanced backcross, marker-assisted selection (MAS) of

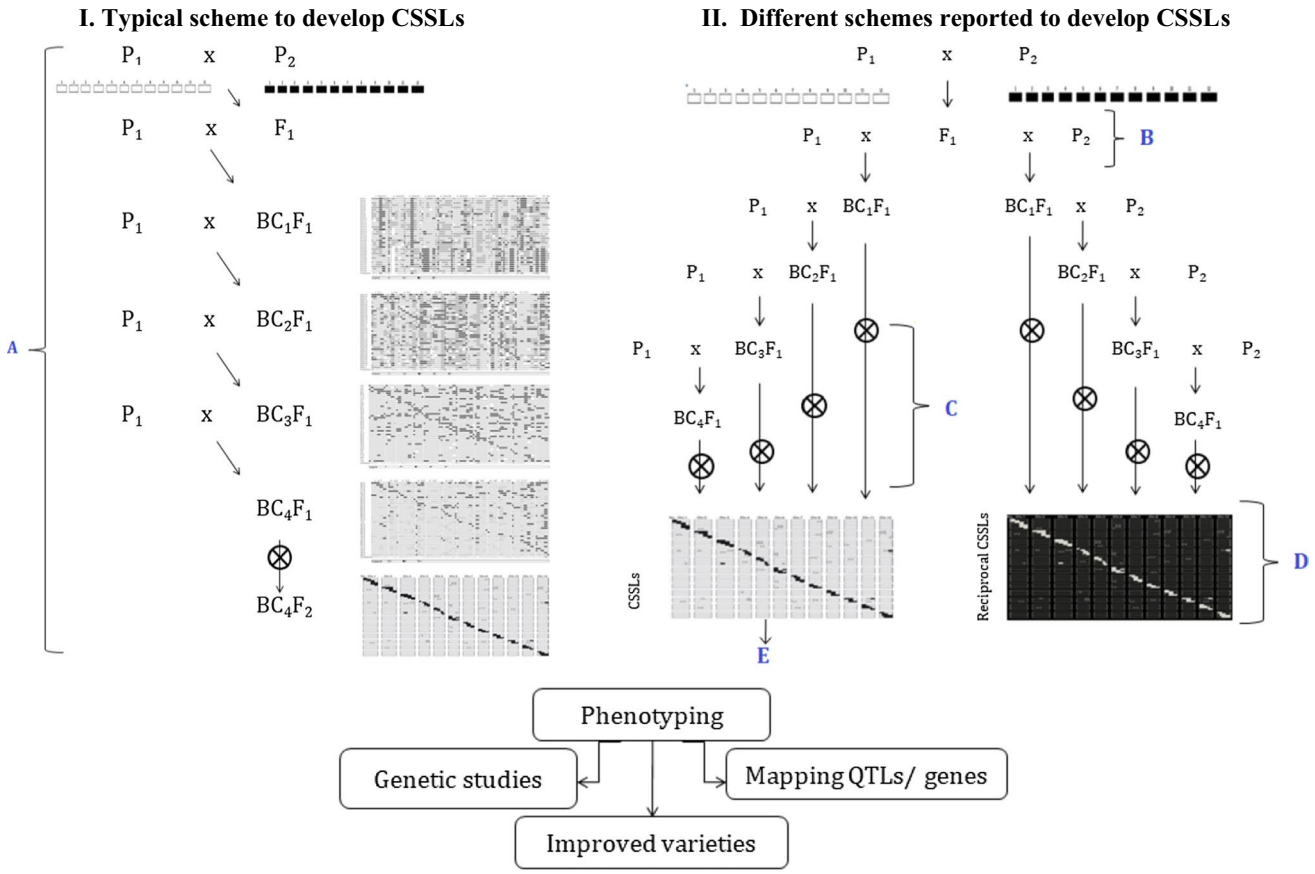
donor introgressions and selfing. Marker-assisted selection is either used in early generations of development (Torjek et al. 2008) or postponed to advanced backcross generations (Xi et al. 2006). Usually, selfing is done only after 3–4 backcrosses but Ebitani et al. (2005) developed novel rice CSSL population by selfing after each backcross. CSSLs can simplify the study of complex genetic traits such as yield, and they are valuable resources for the precise identification of QTL and genes (Ali et al. 2010). Whole-genome CSSL population are more effective recombinant populations for high-resolution mapping of major and minor QTL (Koumproglou et al. 2002; Subudhi et al. 2015) which are quite often masked in primary mapping populations (Ebitani et al. 2005; Tian et al. 2013). Accurate detection and validation of epistatic interactions are possible using reciprocal chromosome substitution sets, sub-CSSLs and secondary F_2 populations generated from CSSLs (Yano et al. 2000; Lin et al. 2000; Jacquemin et al. 2013; Xie et al. 2014; Chen et al. 2014).

Deployment of unexploited gene pool from distant and wild germplasm has emerged as an essential option for enhancement of genetic diversity. It employs the advantages of advanced backcross QTL mapping by bridging wild species and cultivars (Cavanagh et al. 2008). Wild *Oryza* species *O. rufipogon*, *O. glumaepatula*, *O. barthii*, *O. nivara*, *O. longistaminata* and *O. meridionalis* were used as the donor parent in backcross breeding programme to get CSSLs in rice (Qiao et al. 2016; Rangel et al. 2008; Ramos et al. 2016; Ma et al. 2016; Uehara et al. 2017; He et al. 2017). Similarly, interspecific crosses were utilized in other crops such as wheat (Gu et al. 2015), barley (Von Korff et al. 2006), brassica (Li et al. 2015), tomato (Monforte and Tanksley 2000) and cotton (Li et al. 2017). CSSLs are also good raw material to study the traits lost or retained during the process of evolution, domestication and selection. Thus, CSSLs are the pre-breeding material for simultaneous identification, transfer and pyramiding of key genes in crop improvement programs (Li 2001). The major advantages and disadvantages of CSSL over other mapping populations and in association mapping were detailed in previous reviews by Cavanagh et al. (2008) and Jacquemin et al. (2013). Ali et al. (2010) reviewed the status of wild introgression CSSLs and BILs in *Oryza* species and illustrated their significance in identifying new genes from wild relatives of rice. In this paper, we review the development and use of CSSLs in major crops.

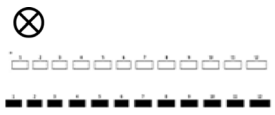
Development of CSSLs

An ideal CSSL population consists of a set of single chromosome segment substitution lines (SSSL), each carrying a different but single chromosome segment of donor parent and representing the whole donor genome in the recurrent parent background. Usually, lines are selected with overlapping segments to ensure all chromosomal regions of the donor are included resulting in some donor chromosome segments shared by two CSSLs. Finally, CSSLs have homozygous substitutions but heterozygous CSSLs were also reported (Yang et al. 2016). CSSLs are developed by continuous marker-assisted background selection with the aim of having only a specific donor segment in each SSSL. CSSL development strategies mainly involve two steps: i) backcross breeding between recurrent and donor parent and ii) genotyping the backcross progenies for tracking the donor chromosome segments in recurrent background. These two steps are conducted simultaneously, and finally a set of lines each with a specific target chromosome segment is selfed to create a complete CSSL library for further evaluation. In general, an advanced backcross breeding strategy is followed with minor deviations (Fig. 1).

CSSLs have been developed in several crops using intra- and interspecific donors and recipients (Table 1). Usually, an adapted or popular genotype is used as recurrent parent and unadapted, exotic or wild genotypes are used as donor parent. When both the parents in the breeding programme are adapted genotypes, reciprocal crosses can be made and two sets of CSSLs developed one in each background with the other parent as donor. Such reciprocal CSSLs are reported only in rice and *Arabidopsis* (Kubo et al. 2002; Hori et al. 2010; Torjek et al. 2008). Reciprocal CSSLs enable the evaluation of allelic effects variation of QTLs in both parental genetic backgrounds and help in fine mapping (Takai et al. 2014; Ookawa et al. 2016; Mulsanti et al. 2018). Epistatic interaction of QTL with background factors can be identified when a QTL shows a different gene activity in normal and reciprocal CSSL sets and vice versa. The QTLs detected in only one of the genetic backgrounds also suggest that these regions are under epistatic control with other gene(s) in the background. These reciprocal crosses can explain cytoplasmic and maternal effect from the female parents and nucleo-cytoplasmic interactions for expression of various traits. The recurrent parent or adapted genotype is used as female parent in the initial crosses to develop F_1s to avoid any adverse cytoplasm effect from the donor parent, especially when donor is a wild genotype (Ali et al. 2010). This strategy is followed throughout the backcross breeding programme and is useful in distinguishing a self and a backcross for precise genotyping. But when a wild or unadapted germplasm is used in the breeding programme, F_1s may have problems of sterility, lower number of spikelets, less pollen which becomes a constraint for being used as pollen donor. In such situations, F_1s and BC_1F_1s can be used as female parent instead of using the recurrent parent as female. For these reasons, recurrent parents were used as female only in F_1 development and as male in further backcrossing (Kubo



A. Typical method - Ramos et al, 2016, Li et al, 2016, Fonceka et al, 2012
B. F1 used as female parent - Kubo et al, 2002, Ando et al, 2008; Hao et al, 2009; Bian et al, 2010; Zhang et al, 2011
C. CSSLs pooled from different generations - Kumari et al, 2014; Li et al, 2015; Subudhi et al, 2016.
D. Reciprocal CSSLs - Kubo et al, 2012; Hori et al, 2010, Torjek et al, 2003
E. Secondary back crosses - Ando et al., 2008



: Selfing or doubled haploidization
: Representation of a recurrent/ female parent with 12 chromosomes
: Representation of a donor/ male parent with 12 chromosomes

Fig. 1 Schematic diagram on development of CSSLs

et al. 2002; Ando et al. 2008; Hao et al. 2009; Bian et al. 2010; Ali et al. 2010; Zhang et al. 2011).

A typical backcross scheme to develop CSSLs was proposed by Ali et al. (2010), and minor modifications have been reported (Fig. 1). The number of backcrosses, number of backcrossed lines in each generation and number of selfings varied in different CSSL construction programmes. These depend on the crop; crossing methodology; compatibility of genotypes; the type and number of markers used; and number or size of target chromosome segment introgressions. CSSL development usually involves backcrossing up to BC_3, BC_4 or even up to BC_5 to get maximum recurrent parent recovery and further selfing until the desired purity of phenotype or reduction of heterozygous segments is achieved. However, selfed progenies from just one backcross BC_1 (BC_1F_5) were also used in CSSL development from an interspecific cross in rice (Chen et al. 2006) and BC_2 in rye (Falke et al. 2008). The number of individuals used for genotyping needs to be increased in each backcrossing step. Since the donor segments segregate, the percentage of introgressed segments per plant decreases and frequency of plants with a specific chromosome segment is reduced with each generation advance. In previous studies, 35–200 lines constituted a complete set of CSSLs with more than 90%

Table 1 CSSLs developed in various crops

Crop	Recurrent	Donor	CSSLs developed	Generation	References
Rice *Oryza sativa* L. $2n=24$	***Indica***	***Japonica***			
	IR24	Asominori	70/888 CSSLs	BC_3F_1	Kubo et al. (2002)
	HJX74	IRAT 2612 *indica* and 4 *japonica*	217 CSSLs		Xi et al. (2006)
	Huajingxian 74	Six donors—Suyunuo, IR64, IRAT261, Lemont, IAPAR9 and Chenglongshuijingmi	86 SSSLs	BC_3F_2, BC_3F_3	He et al. (2005a, b, c)
	Zhenshan 97B	Nipponbare	88 CSSLs		Chen et al. (2007)
	9311	Nipponbare	128 CSSLs	BC_6F_2	Zhu et al. (2009) Xu et al. (2010) Lin et al. (2011)
	9311	C418	108 CSSL	BC_3F_8	Bian et al. (2010)
	Takanari	Koshihikari	39 CSSLs	BC_4F_2	Takai et al. (2014)
	IR64	Koshihikari	43 CSSLs	BC_4F_2	Ujiie et al. (2016)
	Takanari	Koshihikari	41 CSSLs	BC_1F_4	Ookawa et al. (2016)
	Japonica	***Indica***			
	Asominori	IR 24	91	BC_3F_2	Kubo et al. (2002)
	Koshihikari	Kasalath	39 CSSL	SBC_3F_3	Ebitani et al. (2005)
	Koshihikari	Nona Bokra	44CSSL	BC_3F_4	Takai et al. (2007)
	Sasanishiki	Habataki	39 CSSL	SBC_1F_2, SBC_1F_3, SBC_1F_4, SF_5	Ando et al. (2008)
	Koshihikari	Nona Bokra	154 CSSLs	BC_3F_2	Hao et al. (2009)
	Taichung 65	DV85	45 TA-CSSLs	BC_3F_5	Yasui et al. (2010)
	Taichung 65	ARC10313	44 TD-CSSLs	BC_3F_5	Yasui et al. (2010)
	Nipponbare	9311	57 CSSL	BC_5F_3	Zhang et al. (2011)
	Khao Dawk Mali 105	DHs from CT9993 × IR62266	90 CSSL	BC_5F_2,BC_5F_3	Kanjoo et al. (2012)
	Lemont	TeQing	123 TILs	BC_2, BC_4	Pinson et al. (2012)
	Koshihikari	Takanari	41 CSSLs	BC_4F_2	Takai et al. (2014)
	Kinandang Patong	IR64	26 CSSLs	BC_4F_4	Uga et al. (2015)
	Koshihikari	Takanari	37 Takanari CSSLs	BC_1F_4	Ookawa et al. (2016)
	Japonica	***Japonica***			
	Koshihikari	Nipponbare	48 N-CSS Ls	BC_4F_4	Hori et al. (2010)
	Nipponbare	Koshihikari	41 K-CSSLs	BC_4F_4	Hori et al. (2010)
	Indica	***Indica***			
	HJX74	Zihui100	123 CSSLs	BC_1F_1	Chen et al. (2014)
	93-11	Peiai64 s	156 CSSLs	BC_3F_4, BC_5F_3, SBC_1F_2, BC_4F_3, BC_5F_2	Liu et al. (2016)
	Indica	***Oryza glaberrima*** Steud.			
	IR64	*O. glaberrima*	100 CSSL	BC_nF_1	Ghesquire et al. (1997)

Table 1 (continued)

Crop	Recurrent	Donor	CSSLs developed	Generation	References
	V 20A	*O. glaberrima*	308CSSL	BC_3F_1	Li et al. (2004)
	Japonica	***Oryza glaberrima***			
	WAB 181-18	*O. glaberrima*	100CSSL	BC_nF_1	Ghesquire et al. (1997)
	Taichung 65	*O. glaberrima*	91	BC_3F_2	Doi et al. (1997)
	Caiapo	*O. glaberrima* MG12	64 CSSL	BC_3F_1	Gutierrez et al. (2010)
	Koshihikari	*O. glaberrima*	34 CSSL	BC_7F_7	Shim et al. (2010)
	Indica	**Wild species**			
	Teqing	*O. rufipogon* Griff.	133 CSSL	BC_3F_2	Hao et al. (2006)
	Guichao 2	*O. rufipogon*	159/214 CSSL	BC_4F_4	Tian et al. (2006)
	IR 24	*O. rufipogon* IRGC 105491	105CSSLs	BC_2F_5	Cheema et al. (2008)
	BG 90-2	*O. glumaepatula* Steud	35ILs	BC_2F_8	Rangel et al. (2008)
	IR24 (I)	*O. minuta* Presl.et Presl.	131 ILs	BC_4F_3	Guo et al. (2013)
	Bengal	PSRR-1 weedy rice	74 CSSLs	BC_3F_1, BC_3F_2, BC_3F_3	Subudhi et al. (2015)
	Dongnanihui 810	ZhangPu wild rice	146 CSSLs, 244 HCSSLs	BC_3F_3, BC_4F_2	Yang et al. (2016)
	Huajingxian 74	*O. meridionalis*	99 SSSLs	BC_4F_2, BC_5F_2, BC_5F_3 BC_6F_2, BC_7F_1, BC_7F_2	He et al. (2017)
	Japonica	**Wild species**			
	Taichung 65	*O. glumaepatula*	84/184	BC_4F_2	Sobrizal et al. (1999)
	Xieqingzao B	*O. rufipogon*	35/202 CSSL	BC_1F_5	Chen et al. (2006)
	Koshihikari	*O. rufipogon*	33 CSSLs	BC_7F_2	Furuta et al. (2014)
	Curinga	*O. meridionalis* Ng.-W2112	32 ILs	BC_3F_2 DH	Arbelaez et al. (2015)
	Curinga	*O. rufipogon* IRGC 105491	48 ILs	BC_3DH	Arbelaez et al. (2015)
	Koshihikari	*O. barthii* A. Chev.	38	BC_4F_1 and BC_5F_1	Uehara et al. (2017)
Wheat *Triticum aestivum* L. $2n=6x=42$	*T. aestivum* –Shi 4185	*T. aestivum* ssp. *yunnanense* –YN3 *T. aestivum* ssp. *tibetanum*—XZ-ZM19450 *T. aestivum* ssp. *Petropavlovskyi*-XJ5 Synthetic wheat, HC-XM1620	991 CSSL	BC_2F_3	Gu et al. (2015)
	Bethlehem	Wild emmer wheat TTD140	22 chromosome-arm substitution lines	BC_7	Millet et al. (2012)
	Chinese Spring	*Aegilops tauschii*	84 ILs	BC_1, BC_1F_2, BC_2, BC_2F_2	Pestsova et al. (2006)
	Laizhou953	Am3	97 CSSLs	BC_4F_3	Liu et al. (2006)
	T. aestivum cv. 'Chinese Spring'	*Aegilops tauschii*	36 ILs	BC_1, BC_1F_2	Pestsova et al. (2001)
	Chinese	Thatcher, Hope and Timstein	Three sets of substitution lines	–	Kuspira and Unrau (1957)

Table 1 (continued)

Crop	Recurrent	Donor	CSSLs developed	Generation	References
Maize *Zea mays* L. $2n=20$	Chang 72	1x9801	184 CSSLs	–	Wang et al. (2016)
	H21	Nongxi531	130 CSSLs	BC_4F_4	Li et al. (2014)
	Mi29	*Z. nicaraguensis*	45 CSSLs	BC_3F_4	Mano and Omori (2013)*
	Zheng58	Chang7-2	108 SSSLs	BC_5F_2, BC_6F_2, BC_7F_2	Lu et al. (2011)
	B73	Gaspe Flint	47 ILs	BC_5F_5, F_2,BC_1	Salvi et al. (2011)*
	Ye515	*Z. mays* ssp. *mexicana*	52 lines	BC_1, BC_2	Wang et al. (2008)
	Hengbai 522	87-1 and Zong 3	SSILs	BC_3	Wang et al. (2007)
	B73	Tx303	89	$BC_3F_{2:3}$	Szalma et al. (2007)*
Pearl millet *Pennisetum glaucum* L. $2n=14$	ICMB 841	863B	124 CSSLs	BC_5F_1 and BC_5F_3; BC_6F_1, BC_6F_3	Kumari et al. (2014)
Barley *Hordeum vulgare* L. $2n=14$	Haruna Nijo	Akashinriki	35 RCSL,	BC_3F_4	Sato et al. (2011)
	Haruna Nijo	H602, *H. vulgare* ssp. *spontaneum*	99 BC3F5 RCSLs	BC_3F_5	Sato and Takeda (2009)
	Scarlett	ISR42-8, *H. vulgare* ssp. *spontaneum*	59 ILs	BC_3S_6	Schmalenbach et al. (2008)*
	Scarlett	ISR42-8, *H. vulgare* ssp. *spontaneum*	301 CSSLs	BC_2DH	Von Korff et al. (2006, 2005)
	Haruna Nijo	H60, *Hordeum vulgare ssp. spontaneum*	134 RCSLs	BC_3F_2	Hori et al. (2005)
	Scarlett, S42 and Thuringia, T42	ISR42-8, *H. vulgare* ssp. *spontaneum*	49 and 43 pre-ILs	BC_2DH	von Korff et al. (2004)*
	H. vulgare subsp. *vulgare* Harrington	*H. vulgare* subsp. *spontaneum*, Caesarea 26-24	140 RCSL	BC_2F_6	Matus et al. (2003)
	H. vulgare ssp. *vulgare*	*H. v.* ssp. *Spontaneum*, ISR101-23	136 BC_2F_2 lines	BC_2F_2	Pillen et al. (2003)
Rye *Secale cereale* L. $2n=14$	Altevogt 14160	L2053-N	40 BC_2S_3 pre-ILs	BC_2S_3	Falke et al. (2008)*
Soybean *Glycine max* L. $2n=40$	ZYD00006 *Glycine max* (L.) Merrill	Suinong 14	194 CSSLs	BC_3F_2, BC_3F_3, BC_3F_4, BC_3F_5, BC_3F_6	Xin et al. (2016)
	NN1138-2 *Glycine soja* Sieb. Et Zucc.	N24852	151 CSSLs	$BC_1F_{2\text{-}3}$; $BC_2F_{2\text{-}3}$, F_5; BC_3F_4; BC_4F_4; BC_5F_2	Wang et al. (2013)
Peanut *Arachis hypogaea* L. $2n=40$	Fleur11	*A. ipaensis*×*A. duranensis*^{4x}	122 CSSLs	BC_4F_3	Fonceka et al. (2012)
Pea *Pisum sativum* L. $2n=14$	*P. sativum*	*Pisum fulvum* WL2140 or *Pisum elatius* L100	–	BC_2F_2, BC_2F_3	Svabova et al. (2016)
Rapeseed *Brassica napus* L. $2n=38$	Tapidor N-0-44b	Victor	74 lines	BC_3	Howell et al. (1996)*
	TapDH1	Victor	22 lines	BC_3S_1 and BC_4S_1	Burns et al. (2003)*
B. rapa L. $2n=20$	Express 617	RS239	15 ISL	BC_1	Ecke et al. (2015)*
B. juncea L. $2n=36$	Chiifu	49 Caixin	63 CSSLs	BC_4F_3, BC_5F_2	Li et al. (2015)
Cabbage *B. oleracea* L. $2n=18$	*B. napus*	*B. carinata*	C genome CSSLs	–	Gupta et al. (2016)
	B. oleracea var.italica	*B. oleracea var. alboglabra*	176 recombinant BC_1 lines, 18 BC_2	BC_1, BC_2, BC_2S and BC_2S_2	Ramsay et al. (1996)*

Table 1 (continued)

Crop	Recurrent	Donor	CSSLs developed	Generation	References
Tomato *Lycopersicum esculentum* Mill. (syn. *Solanum lycopersicum* L.) 2*n* = 24	*L. esculentum*	*S. lycopersicoides*	56 lines	F_2	Canady et al. (2005)
	L. esculentum cv E6206	*L. hirsutum LA1777*	99 lines	NILs, BCRILs	Monforte and Tanksley (2000)
	L. esculentum cv VF36	*S. lycopersicoides* LA2951	300 lines	BC_2	Chetelat and Meglic (2000)*
	L. esculentum cv E6203, E6203	*L. hirsutum* LA1777 *L. pimpinellifolium* LA1589	23 NILs	BC_3	Bernacchi et al. (1998)*
	L. esculentum	*L. pennellii* LA716	50 lines	BC_1S_2, BC_1S_6	Eshed and Zamir (1995)*
Lettuce *Lactuca sativa* L 2*n* = 18	*L. sativa* cv. Olof	*Lactuca saligna* CGN 5271	28 lines	BC_4S_1	Jeuken and Lindhout (2004)*
Melon *Cucumis melo* L 2*n* = 24	Songwhan Charmi	Piel de Sapo	57 NILs	BC_3S_1, BC_3S_2 BC_4S_1	Eduardo et al. (2007, 2005)*
Cucumber *Cucumis sativus* L 2*n* = 14	D8	JIN5-508	17 CSSLs	BC_{12}	Lin et al. (2012)
	D8	SSL508-28		Secondary BC CSSL	Xu et al. (2017)
Cotton *Gossypium hirsutum* L. 2*n* = 4*x* = 52	CCRI36 *G. hirsutum*	Hai1 *G. barbadense*	15 RNA-seq libraries	Secondary BC CSSL BC_5F_3	Li et al. (2017)
	CCRI36 *G. hirsutum*	Two ILs-MBI9749 and MBI9915		Secondary BC CSSL $BC_5F_{3:5}$	Guo et al. (2018)
	CCRI36 and CCRI45 *G. hirsutum*	Hai1 *G. barbadense*	658 Pop CCRI 36, 332 Pop CCRI 45	CCRI36 × Hai1 $BC_5F_{3:5}$ CCRI45 × Hai1 $BC_4F_{3:5}$	Li et al. (2016)
	CCRI36 *G. hirsutum*	Hai1 *G. barbadense*	236 introgression lines	CSSL × CCRI36, double-crossed F_1, F_2, $F_{2:3}$	Zhai et al. (2016)
	TX-1046	TX-256	115 ILs	BC_3F_2	Zhang et al. (2016)
	G. tomentosum	*G. barbadense*	34 interspecific CSSLs	BC_5F_1	Ulloa et al. (2016)
	Lumianyan28 Shannongmian6	*G. barbadense*		CSIL + F_2, $F_{2:3}$, BC_2F_3 lines	Guo et al. (2014)
	Xinluzao 26, XLZ41, XLZ42, 0768	4 CSILs with segments from Hai7124	Population from 40 BC2 plants	Cultivar × CSSL BC_2S_2	Cao et al. (2014)
	TM-1	Sub18	45 CSSL	–	Fu et al. (2013)
	TM-1	Hai7124	174 CSILs	$BC_5S_{1–4}$, $BC_4S_{1–3}$	Wang et al. (2012a)
	G. hirsutum	*G. barbadense*	50 CSSL	BC_4F_2 and BC_4F_3	Lan et al. (2011)
	CCRI36 *G. hirsutum*	Hai1 *G. barbadense*	CSSLs	BC_5F_3	Zhang et al. (2012)
	CCRI221 *G. hirsutum*	Hai1 *G. barbadense*	116 CSSLs	BC_4F_1	Yang et al. (2009)
Ryegrass *Lolium perenne* L. 2*n* = 4*x* = 28	*Lolium perenne*	*Festuca pratensis*	161 lines	BC_1	Harper et al. (2011)

*CSSLs are mentioned as ILs

of donor genome introgression represented in wheat (Gu et al. 2015), brassica (Li et al. 2015), cotton (Li et al. 2017), peanut (Fonceka et al. 2012) and pearl millet (Kumari et al. 2014). In general, more plants were required to make a complete CSSL library when more backcrosses ($\geq BC_4$) were made because donor segments segregate and recombine with each additional backcrossing.

A strategy which alternates, backcrossing and selfing, before each marker-assisted selection to minimize segregation and obtain a maximum number of homozygous

segments can help in developing precise CSSLs. The final CSSLs were either from one generation or pooled from different backcross generations as in rye, pearl millet and rapeseed to represent the whole set of donor genome segments in the background of an adapted variety (Falke et al. 2008; Kumari et al. 2014; Li et al. 2015). Secondary backcrosses were made after BC_2F_5 to increase recurrent parent genome recovery in CSSLs (Ando et al. 2008). Recovery of recurrent parent genome was more than 90% in most of the CSSL sets developed so far but percentage of donor parent genome introgressed in each SSSL varied from 67% (Tian et al. 2006) to 99% (Jie et al. 2006). This also depends on the backcross generation from which CSSLs were derived. Phenotypic selection is not exercised throughout to obtain an unbiased complete set of donor segments. Yet, CSSLs are not always complete and missing segments are reported (Furuta et al. 2014). These can be due to chromosome regions recalcitrant to recombination usually near the centromere, presence of gamete lethal genes, and genes involved in the reproductive barrier in these missing particular segments (Li et al. 2015), and fewer backcross progenies genotyped or due to some unintended selection exerted during backcrossing. Finally, selfed progenies of each line in the CSSL library can be evaluated for any trait to identify lines which are significantly different for a trait, and also for QTL mapping, gene discovery or use in breeding. Genotyping the backcross introgression lines is the most important step in CSSL development with an aim to track both the donor segment introgression and the recurrent parent genome recovery.

Cytogenetic methods such as chromosome banding and chromosome painting using fluorescent in situ hybridization were earlier used to identify large chromosomal introgressions from closely related species and wild relatives. CSSLs were thus generated using *Zea mays* ssp. mexicana as the female parent and cultivated maize inbred line Ye515 as the male parent, and genomic in situ hybridization (GISH) was used to prove chromosome segment introgression from wild species (Wang et al. 2008). Different cytogenetic techniques from a classical chromosomal staining to molecular cytogenetics were used as valuable tools for accurate diagnosis of gene transfer and establishment of gene introgression (Benavente et al. 2008). Whole chromosome substitutions were reported in wheat (Kuspira and Unrau 1957), cotton (Saha et al. 2012) and maize (Burnham 1966) by modification of the monosomic-type approach using TB interchanges. Instead of whole chromosome substitutions, only segments of chromosomes can be substituted. Substitution lines were produced in maize using multiple interchange stocks which differ from each other by the presence or absence of one chromosome in ring of ten interchange complexes (Burnham 1966). In wheat breeding, in addition to aneuploids, lines developed by replacing specific chromosomes or chromosome segments from related species helped in modifying particular traits (Allard 1960). Intergeneric BC2 and BC3 progenies generated between Badila (*Saccharum officinarum*) × HN 92–77 (*E. arundinaceus*) or HN 92–105 (*E. arundinaceus*) were studied using genomic in situ hybridization (GISH) technique (Huang et al. 2015). The progenies carried an intergeneric translocated chromosome, which occurred at a terminal fragment from the *E. arundinaceus* chromosome. Their findings suggest that terminal regions are more actively involved than centromeric regions in translocations of *E. arundinaceus or Saccharum* spp. Seven monosomic substitution lines were developed from *Lolium perenne* (perennial ryegrass)/*Festuca pratensis* (meadow fescue). Cytological observations at metaphase I of meiosis in substitution lines revealed the presence of a low level of interspecific chromosomal translocations between these species (Harper et al. 2011). Presence–absence variations and structural variations such as inversions and translocations (within a chromosome) have been reported between cultivated and wild species, and markers can be designed to target introgression of such variants and develop CSSLs which include structural variation in lines to see the effect of such variations (Hu et al. 2018).

Due to advent of molecular markers and their robustness in genotyping, majority of the CSSL development studies used various molecular marker systems for genotyping and genetic mapping of the developed populations. A set of markers which are polymorphic among parents with a genome-wide distribution is required for screening the backcross lines. The loci can be selected after a survey of parental polymorphism and identifying their chromosomal location for complete genome coverage and uniform distribution. An average distance of 1.5 Mb per marker was suggested in rice (Xu et al. 2010). STS and RAPD markers (Ghesquire et al. 1997), RFLP (Kubo et al. 2002; Ando et al. 2008), CAPS (Hao et al. 2006), SSRs (Hao et al. 2006; Chen et al. 2007; Tian et al. 2006; Zhu et al. 2009; Hao et al. 2009; Bian et al. 2010; Gutierrez et al. 2010; Xu et al. 2010; Shim et al. 2010; Yasui et al. 2010; Lin et al. 2011; Guo et al. 2013; Subudhi et al. 2015; Li et al. 2015), SNPs (Zhang et al. 2011; Furuta et al. 2014; Tao et al. 2016) and GBS (Arbelaez et al. 2015) were used for CSSL development.

In most of the studies, SSRs were preferred because of their genome-wide availability, codominant nature, high polymorphism, representation of small segments and ease of genotyping in large populations. In case of rice, a universal core genetic map by Orjuela et al. (2010) is useful in developing CSSL library where three sets of uniformly distributed SSRs covering whole rice genome are available. These SSRs are polymorphic within the AA genome and are able to distinguish cultivar and wild species (Ali et al. 2010), and this core set of markers was deployed in developing CSSLs in rice (Gutierrez et al. 2010; Arbelaez et al. 2015). More recently, SNP assays were used to genotype CSSLs. Use of

large number of SNPs and dense SNP maps can improve the scale and precision of genotyping CSSLs and avoid any false CSSLs due to double recombination events. Thus, they are helpful in rapid and accurate gene identification (Zhu et al. 2009; Tung et al. 2010; Ma et al. 2016; Qiao et al. 2016). High-throughput SNP arrays are now being deployed, for genotyping, tracking introgressions, and developing pre-breeding materials (Zhao et al. 2011; Chen et al. 2013; Singh et al. 2015; McCouch et al. 2016; Thomson et al. 2017). The high-density SNP-based genetic maps have greatly improved the high-throughput genotyping applications in terms of marker density and genome coverage in comparison with SSR-based maps. Sequencing-based CSSLs development involves the use of ultrahigh-quality physical maps and gives contig lines with an average resolution of 6.3 kb per SNP than the 1.46 Mb per marker obtained with PCR-based markers in rice (Xu et al. 2010). NGS technologies will be useful for development and confirming introgression lines for specific chromosome regions introgression from one cultivar to another (Varshney et al. 2009, 2014) and QTL mapping by genome-wide association studies (Hu et al. 2018). With several crops sequenced, NGS technologies for genotyping CSSLs will become more popular, provided the costs are not prohibitive for a large population size. Singh et al. (2013) compared SSR and SNP markers for genetic diversity estimation and population structure of Indian rice varieties and found SNP increased resolution of population structure but SSR was more efficient in case of diversity analysis with better grouping of genotypes correlating their phenotype. The purpose of developing CSSLs is to have a workable set of lines with large segments substituted with homologous donor segments such that these substitutions one by one in a background line make a difference in phenotype for agronomically useful traits. A practical strategy therefore is to use multi-allelic SSRs to track large substituted segments and bi-allelic SNP for further genomic studies.

After identification of polymorphic markers, marker-assisted selection is employed in each backcross generation so that complete donor genome introgression can be confirmed in the population and only the selected lines with desirable donor segments can be advanced by additional backcrossing. Large multiple donor segments with less recurrent parent genome are obtained when genotyping early backcross population but avoiding early-generation genotyping altogether may result in large or many missing segments in later generations. Kubo et al. (2002) constructed reciprocal sets of CSSLs and MAS was carried out in an early generation (BC_1F_1) in one set, while in the other set MAS was employed two generations later (BC_3F_1). Larger segments were obtained with few CSSLs in the first set but the restoration ratios of recurrent genome were almost the same in both the libraries. Though the precision is more by employing MAS in every backcross population, the second strategy of using MAS only in advanced generations can considerably reduce the time, cost and labor involved in genotyping hundreds of lines in each generation for tracking parental segments. When marker-assisted selection is employed only in the advanced backcross stages such as BC_3 or BC_4, early generations can be forwarded by bulk or single seed descent method and a larger population needs to be genotyped to obtain maximum donor introgressions. More backcrosses are then carried out to recover any of the missing donor segments in the later stages.

A middle approach while employing MAS could be that early generations can be surveyed with few markers and then more markers can be engaged in advance generations, but this strategy may result in identification of some false segments due to double crossover in early generations and missing segments in the later. It is therefore preferred to keep the number and markers the same in every generation for consistency in the segments being tracked. About 80–580 SSRs were used in genotyping CSSLs in different studies but using 80–120 markers equally distributed throughout the rice genome was adequate to obtain CSSLs with nearly complete donor segments (Subudhi et al. 2015; Li et al. 2015). However, the number of lines tracked for target markers should be increased at every successive backcross as the percentage of donor segments and large single segments gets reduced in advanced generations. Unidentified introgressions within marker tags and conserved regions with limited crossovers are the two major factors that reduce the efficiency of donor introgressions, especially when parents are of distant genetic background.

After selecting a set of CSSLs, selfing for few generations or development of doubled haploids may be required to maintain the homozygosity of these lines (Gutierrez et al. 2010). Utilization of doubled haploidy in the development process can accelerate CSSL development by reaching homozygosity of lines rapidly. This is all the more important in elite/wild crosses where stability of lines takes several generations. The advanced introgression lines can be fixed by doubled haploid (DH) method in place of selfing and single seed descent method so that any further segregation and heterozygosity can be avoided. DH can also be employed when large heterozygous segments persist in earlier generation to get fixed homozygous individuals. CSSLs are preferred to be homozygous for the substituted segments so that there is no segregation. However, if they are heterozygous, they can be considered akin to F_1 for target locus and the progeny akin to F_2 and used for fine mapping without having to cross a CSSL to parent and then mapping in F_2 (Yang et al. 2016). Thus, heterozygous CSSLs (HCSSLs) if available need to be maintained through vegetative propagation for further use in fine mapping significant QTL regions.

CSSL Finder (http://mapdisto.free.fr/CSSL Finder), R software (R Core Team 2013) and graphical genotyping

(GGT ver.2.0) are commonly used softwares in identifying the complete set of CSSLs from a huge genotypic data of a large population (Fonceka et al. 2012; van Berloo 2008). CSSL Finder software is designed to support selection of a set of CSSLs with maximum donor genome coverage and presence of minimum donor genome in individual background. It employs an Excel-VBA (Visual Basic for Applications) programming language and macros or programming code to read a matrix genotypic data of introgression lines. There are options provided for selecting a subset of markers for the analysis and inferring missing data points. Options are also provided to choose the segment size and whether to treat heterozygous segments as donor. Based on the options, a greedy algorithm finds the optimal lines for each segment in the order of markers in each linkage group until all markers are covered. The main constraint of this method is the number of lines to select the best and optimum lines gets reduced as it moves from first chromosome to last chromosome, thus making the selection biased (http://mapdisto.free.fr/CSSLFinder/). Ayling and Lorieux 2010 proposed a graph theoretic algorithm to improve the selection of CSSLs using an algorithm of single-source shortest path (SSSP) (Dijkstra 1959) and found that SSSP algorithm outperformed the original greedy heuristic, in terms of less number of lines covering more markers with reduced background donor segments and genomic extent. Falke et al. (2009) employed computer simulations to identify optimized procedure to develop complete introgression library in rye and showed that the breeding design, selection approach and the size of the population significantly influence the parental genome content in the introgression lines. Tang et al. (2012) proposed a bin-based model and analytical scheme to identify main and epistatic QTL effects separately using CSSLs.

CSSLs developed in major crops

CSSL libraries have been reported in a diverse range of crop species including major staple food crops and even commercial crops such as cotton and fodder crop *Lolium*. About 75 CSSLs in 17 major crops (Table 1) have been reported using both intraspecific and interspecific crosses, and many more are in pipeline at research stations around the world. Introgression line sets in crop plants were first developed in tomato (Eshed et al. 1992) and rice (Jena et al. 1992). In cereals, CSSLs were reported from rice, wheat, maize, barley, pearl millet and rye. CSSLs were constructed in soybean, peanut and rapeseed. CSSL libraries were developed in vegetable crops: brassicas, tomato, lettuce, melon, cucumber and commercial fiber crop, cotton. About 46 CSSL libraries were reported in rice in the last three decades. Most of the initial CSSLs developed in rice involved *indica/japonica* crosses with increased use of wild species as donor (Ali et al. 2010). There are CSSLs developed between *indica* and *japonica* subspecies of *Oryza sativa* by utilizing either *indica* (Kubo et al. 2002; Ebitani et al. 2005; Takai et al. 2007; Ando et al. 2008; Hao et al. 2009; Li et al. 2011; Yasui et al. 2010; Zhang et al. 2011; Lin et al. 2011; Kanjoo et al. 2012; Pinson et al. 2012; Zuo et al. 2014;Takai et al. 2014;Uga et al. 2015) or *japonica* as donor parent (Kubo et al. 2002; Xi et al. 2006; Chen et al. 2007; Zhu et al. 2009; Xu et al. 2010; Bian et al. 2010). To overcome the problems of sterility in early generation of *O. glaberrima*/*O. sativa* crosses, Ghesquire et al. (1997) initiated CSSL development in rice to produce a set of 100 'contig lines,' each one bearing an alien *O. glaberrima* chromosomal fragment of around 20 cM in the *O. sativa* (IR64 *indica* and WAB 181-18 *japonica*) genetic background. Doi et al. (1997), Gutierrez et al. (2010) and Shim et al. (2010) used *O. glaberrima* with different *japonica* lines, and Li et al. (2004) used *O. glaberrima* with *indica* lines to develop CSSLs. Subudhi et al. (2015) developed a set of CSSLs from weedy rice in the background of US rice cultivar Bengal with complete donor genome introgression except for a small portion in chromosome 4.

In hexaploid wheat, genotypic analysis of quantitative traits is more complex, due to polyploidy and presence of minor modifying genes. Yet, CSSL has been developed in wheat for QTL mapping and gene discovery. Kuspira and Unrau (1957) developed three sets of substitution lines from spring wheat variety Chinese Spring with chromosomes from three donor varieties, viz. Thatcher, Hope and Timstein, and these were used for genetic characterization of various traits. A set of 36 'Chinese spring' homozygous lines with introgression from *Aegilops tauschii* were developed (Pestsova et al. 2001). Also, 84 ILs were developed covering the entire D genome of common wheat using *Aegilops tauschii* as a donor parent and hexaploid wheat Chinese Spring as a recurrent parent. Fifty-two ILs were evaluated for six traits; flowering time, plant height, ear length, spikelet number, fertility and grain weight per ear and QTLs were identified (Pestsova et al. 2006). Gu et al. (2015) developed four sets of ILs to improve agronomic traits of wheat cultivar Shi 4185 with donor parents of Chinese endemic subspecies accessions: Yunnan wheat (*T. aestivum* ssp. *yunnanense*) YN3, Tibetan semi-wild wheat (*T. aestivum* ssp. *tibetanum*) XZ-ZM19450, Xinjiang wheat (*T. aestivum* ssp. *petropavlovskyi*) XJ5 and synthetic wheat HC-XM1620. In wheat, a series of 85 bread wheat ILs derived from the cross *T. aestivum*/*Aegilops tauschii* were developed for *Septoria tritici* blotch (*Mycosphaerella graminicola*) resistance. A subset of 13 chromosome 7D introgression lines were investigated along with the susceptible recipient, Chinese Spring (CS), and the resistant donor line, CS (Syn 7D).

CSSLs have been developed in maize with several parental combinations to detect QTL for flowering time, plant

height, ear height (Szalma et al. 2007; Bai et al. 2010; Lu et al. 2011) and kernel number across environments (Li et al. 2014). In comparison with hexaploid wheat, maize has a simpler genetic background and the specific introgressed segments compared to the recipient parent (Paterson et al. 2000; Kaeppler 1997; Szalma et al. 2007). Mano and Omori (2013) developed flooding-tolerant interspecific introgression lines carrying chromosome segments of teosinte (*Zea nicaraguensis*) in maize (*Zea mays* subsp. *mays*). In barley, recombinant chromosomal substitution lines (RCSLs) and DH populations were developed using *H. vulgare* ssp. *spontaneum* as donor (Hori et al. 2005; von Korff et al. 2004; Schmalenbach et al. 2008). Sato et al. (2011) developed a DH population derived from BC_3F_4 of the cross between Haruna Nijo and Akashinriki and obtained 98 RCSLs (recombinant chromosome substitution lines) that were genotyped with 1448 SNPs. Thirty-five selected RCSLs carried most of the Akashinriki barley genome, with only a few missing segments. There is only one report on CSSL in pearl millet (Kumari et al. 2014). CSSLs were developed in the genetic background of the recurrent parent ICMB841 with 863B as donor parent through marker-assisted backcrossing. In all, 1492 advanced backcross progenies were selected for genotyping at 74 polymorphic marker loci from each of the seven pearl millet linkage groups in BC_5F_2, BC_5F_3 and BC_6F_1 families. These CSSLs were developed to select new cultivars with high quality of grain and stover yield in pearl millet.

CSSLs were developed in different *Brassica* species. C genome chromosome substitution lines substituting B genome were found in the progenies of derived *B. juncea* synthesized through hybridization between *B. napus* and *B. carinata. Brassica* Illumina 60 K Infinium SNP array and SSRs were used for genotyping to confirm the presence of C genome chromosomes. High heterosis was observed in hybrid combinations of substitution lines with natural *B. juncea* (Gupta et al. 2016). A set of 63 CSSLs were developed using a marker-assisted backcrossing strategy for the introgression of chromosome segments of donor parent Chiifu into the genetic background of 49 Caixin. The total coverage of the substitution chromosome segments of the *B. rapa* genome was 269.61 Mb (Li et al. 2015). Intervarietal *B. napus* substitution lines were developed from a cross between varieties to identify the QTL for seed oil fatty acid composition and seed oil content (Howell et al. 1996; Burns et al. 2003) and to identify the genetic factors controlling embryogenic potential of substitution lines (Ecke et al. 2015).

Among the four cultivated cotton species, *G. hirsutum*, *G. barbadense*, *G. herbaceum* and *G. arboreum*, only Egyptian cotton *G. barbadense* produces high quality of fiber but it accounts for only 3–4% of the entire cotton production. Inter-mated CSSLs have been developed using both tetraploid species (Saha et al. 2012; Cao et al. 2014). Two sets of CSSL population were developed from CCRI36/Hai1 and CCRI45/Hai1 crosses. Genetic effects and heterosis of yield traits analyzed with additive-dominance genetic model showed that the yield traits of CSSLs were controlled by combined additive and dominance effects and lint percentage was primarily controlled by additive effects. Dominance effects were observed on boll weight, boll number, seed cotton yield and lint yield (Li et al. 2016). Transcriptome analysis was conducted between the two CSSLs MBI9915 and MBI9749 with substituted *G. barbadense* chromosome segments and the recurrent parent CCRI36, during the development stages of fiber elongation and secondary cell wall synthesis. This study offers novel insights into the molecular mechanism of fiber development in cotton (Li et al. 2017).

The primary gene pool of crop plants has limited genetic variability for several target traits so that breeders rely on the wild or distant relatives as an extended source of variability for crop improvement programs (Harlan 1976; Sharma et al. 2013). Domestication and trait-oriented breeding have led to the loss of many valuable genes in the cultivated rice compared to its wild progenitors, which harbor potentially useful genes that can help improve cultivars. Yield-enhancing QTLs have been mapped from wild species (Swamy and Sarla 2008), and there is an increased interest in wild relatives for crop improvement (Brozynska et al. 2016; Zhang et al. 2017). Much work is focused now on collecting and making available crop wild relatives (CWR) which are novel resources for alleles of economic importance. Almost 70% taxa associated with 63 crops were identified as high priority for collection, and 95% taxa were not well represented considering their geographical or ecological distribution (Castaneda-Álvarez et al. 2016). As more and more CSSLs are developed in different crops and used in both basic and applied studies, the value of the wild accessions is likely to be more appreciated.

Wild rice accessions from *O. rufipogon*, *O. glumaepatula*, *O.barthii*, *O. nivara* and *O. meridionalis* were used as donor parent in backcross breeding program to get contig lines. Hao et al. (2006), Chen et al. (2006), Tian et al. (2006), McCouch et al. (2007) and Furuta et al. (2014) developed CSSLs using *Oryza rufipogon* accession as donor. Rangel et al. (2008) developed CSSL in *indica* cultivar BG90-2 using *O. glumaepatula* as donor. In *O. longistaminata*, 40 CSSLs were developed in the background of Taichung 65 and evaluated for yield traits (Ramos et al. 2016). The International Center for Tropical Agriculture and Institute de Recherche pour le Developpement (CIAT/IRD) for rice genetics and genomics initiated Generation Challenge Project (GCP) for the development of four libraries of CSSLs in the genetic background of tropical *japonica* upland cultivar Curinga, using donor wild species, *O. barthii*, *O. glumaepatula*, *O. meridionalis* and *O. rufipogon*. In

this program, doubled haploids (DH) of BC_3F_1 plants from crosses of *O. sativa*/wild genotypes were used to generate BC_4F_2 population and further identify CSSL library (Ali et al. 2010). Arbelaez et al. (2015) developed two populations of interspecific introgression lines in cv. Curinga, using *O. meridionalis* and *O. rufipogon* representing 76.73–97.6% of donor genomes, respectively.

Domestication of barley has led to a substantial loss of allelic diversity in cultivated—spring barley *Hordeum vulgare* (Hv). *Hordeum spontaneum* (Hsp), the progenitor of barley, can be a possible source of novel alleles for yield-related traits and disease resistances in crop improvement programs. Introgression lines have been developed in the background of cultivated spring barley (Hv) with ancestral barley (Hsp). Brown et al. (1988) developed a set of 84 backcross introgressed lines bearing single homozygous chromosome segments of Hsp. Matus et al. (2003) generated 140 RCSLs (recombinant chromosome substitution lines) by introgressing Hsp alleles into Hv cv Harrington using two backcrosses, followed by six generations of selfing and genotyping with 47 SSR markers. In most RCSLs, on an average 12.6% of Hsp genome was introgressed with several Hsp segments. Similarly, Hori et al. (2005) developed 134 RCSLs, genotyped with 25 SSR and 60 EST markers which covered an average 12.9% of Hsp genome. Representative core set of 19 RCSLs carried the complete genome in each of the lines with one or several exotic introgressions. Likewise, von Korff et al. (2004) developed a complete IL set in barley. Two sets of candidate introgression lines (pre-ILs) were selected from two BC_2DH populations, using the Hsp accession ISR42-8 as donor and the spring barley cultivars Scarlett and Thuringia as recurrent parents. Sato and Takeda (2009) generated substituted segments of the wild barley H602 into cultivated Haruna Nijo. Sato et al. (2011) developed a DH population derived from BC_3F_4 cross between Haruna Nijo and Akashinriki and obtained 98 RCSLs that were genotyped with 1448 SNPs. Thirty-five selected RCSLs carried most of the Akashinriki barley genome, with only a few missing segments. Falke et al. (2008) developed two rye (*Secale cereale*) introgression libraries (A and B) and investigated per se performance of pentosan and starch content whose quantity and composition highly affect the baking quality of rye. A cross was made between inbred line L2053-N as recurrent parent and a heterozygous Iranian primitive line Altevogt 14160 as donor. Two backcrosses (BC_1 and BC_2) and three selfing generations (BC_2S_1, BC_2S_2 and BC_2S_3) were carried out to develop ILs by monitoring through 5–13 AFLP and 77–114 SSR markers at each generation. At BC_2S_3 generation, 40 progenies were selected per introgression library. The donor genome coverage was 74% for introgression library A and 59% for introgression library B.

Peanut (*Arachis hypogaea* L.) ($2n = 40$, AABB) is an allotetraploid tropical legume; since genetic barriers exist between wild and cultivated species, the use of wild diploid relatives was very limited in peanut breeding programs. The process of speciation was superimposed during domestication and resulted in narrowing of the genetic base of cultivated peanut. The wild relatives of peanuts were identified as an important source of interesting traits for abiotic and biotic stress tolerance (Holbrook and Stalker 2010; Simpson 2001). A total of 122 CSSLs were developed from cross between the cultivated variety Fleur11 and wild synthetic allotetraploid (*A. ipaensis* × *A. duranensis*). 122 CSSLs covered wild genome with target chromosome segments averaging 39.2 cM in length. Significant line × trait associations were assigned to 42 QTLs for growth habit, plant height, plant spread and flower color (Fonceka et al. 2012). CSSLs containing genomic segments of wild pea (*Pisum fulvum* WL2140 or *Pisum elatius* L100) in the cultivated pea (*P. sativum*) genetic background were developed (Svabova et al. 2016). In addition, complete or partial IL sets with marker-defined chromosome segment substitutions have been also developed in tomato (Monforte and Tanksley 2000), rice (Li et al. 2005), wheat (Pestsova et al. 2006), maize (Szalma et al. 2007), cotton (Li et al. 2017; Guo et al. 2014, 2018), melon (Eduardo et al. 2005), pearl millet (Kumari et al. 2014), soybean (Wang et al. 2013), peanut (Fonceka et al. 2012) and *Arabidopsis* (Keurentjes et al. 2007) even though the term CSSLs was not mentioned in these studies.

Utilization of CSSLs for crop improvement and gene identification

CSSL libraries are evaluated for significant difference in any phenotype. Effect of chromosome segment substitutions on phenotypic expression of any trait of interest is assessed as percentage deviation from the phenotype of the recurrent parent. In addition to bringing the desirable traits from donors, CSSLs can have tremendous novel variability when distant cultivars or wild species are involved in their development. Novel phenotypic variations observed in CSSLs are mainly due to introduction of new genomic segments, its interaction with background genome and reduced co-segregation of multiple genes (Xiao et al. 2010). Characterization of different morphological, physiological and biochemical traits of CSSLs can narrow down the chromosome regions affecting a trait (CRATs) (Ujiie et al. 2012; Ujiie and Ishimaru 2014). Reciprocal CSSLs are an excellent resource to compare parents for the genetic factors affecting any trait. A CSSL population allows one to understand the genetic architecture of complex traits and identification of consistent QTL across years and environments, QTL × environment (QE) interactions and epistatic interactions. Comparisons

of the specific segments between CSSLs and the recurrent parent can reveal the sequence and position of candidate genes. Sequencing, expression studies, functional annotations and high-throughput genomics analysis can accelerate allele mining for several traits in sets of CSSLs, significantly different for a trait compared to the recurrent parent or even two significantly different CSSLs. The secondary material derived from CSSLs with the desirable phenotype can be used for various genomics as well as expression studies.

CSSLs have been used in several crops for identification of agronomically important genomic regions as well as to identify lines with significant trait improvement over recurrent parent (Supplementary Table 1). Fifty-four CSSLs developed from the Nipponbare/Kasalath cross were compared for root system under non-stress and stress condition in hydroponics. A CSSL with more lateral roots than Nipponbare was identified under drought stress conditions, and another two CSSLs under stagnant-to-drought conditions (Suralta et al. 2008). A late heading CSSL of HJX74/Zihui100 was identified under both natural long-day and natural short-day conditions (Chen et al. 2014). The genetic basis for late heading was analyzed using F_2 population derived from CSSL5 × HJX74, and it was found that late heading was controlled by two novel epistatic loci LH8 and EH3 which delay flowering by inhibiting expression of Early heading date1 (Ehd1) by CCAAT-box-binding transcription factor Heading date1 (Hd1). Their study proved that CSSLs can be used in validation of interactions among genes or gene by environment. There is also interest in hybridization and introgression for the introduction of novel adaptive variation, and CSSLs can be used to address questions on genetic and epigenetic changes that occur due to introgression.

Koshihikari/*O. barthii* substitution lines were evaluated for flag leaf morphology and other agronomical traits. A total of 66 significant lines were identified, of which 28 exhibited positive and 38 showed negative values compared to Koshihikari. BSL27 showed longer flag leaf and longer panicle length which was 26% larger than Koshihikari for both traits (Uehara et al. 2017). Individual lines carrying a specific trait can be developed as a trait introgression donor line. A new locus *qPE12* for panicle exsertion was fine mapped, delimiting *qPE12* to a 190-kb region using F_2 population of CSSL-C115/9311. C115 carrying introgression segments of Nipponbare showed significantly shortened panicle exsertion, uppermost internode length and plant height. Genetic analysis indicated that shortened panicle exsertion was due to allele from Nipponbare which was recessive and controlled by a single Mendelian factor (Zhao et al. 2018). Physiological responses to salt stress in two rice CSSLs (CSSL8-94 and CSSL8-95) carrying drought tolerance QTL were compared with recurrent parent KDML105 and salt-tolerant Pokkali. Both CSSLs showed better salt tolerance than recurrent parent KDML105. Co-expression network analysis showed that genes Os08g419090, Os08g43230 and Os08g43440 were involved in chlorophyll biosynthetic process and cytochrome P450 might play vital roles in salt stress tolerance (Nounjan et al. 2016, 2018). Elite CSSLs also can be released as an improved variety or as parental lines for hybrid breeding in a shorter duration.

In maize, two test populations were constructed using CSSLs (lx9801 × Chang 72) and two test inbred lines Zheng 58 and Xun 9058 (CSSL × Zheng 58 and CSSL × Xun 9058) to identify heterotic loci (HL) for plant height (PH) and ear height (EH) and kernel traits in maize. Three heterotic loci (hlPH4a, hlPH7c and hlPH1b) for plant height and three (hlEH1d, hlEH6b and hlEH1b) for ear height were identified across four environments and 21 heterotic loci in two environments (Wang et al. 2016, 2018). Mano and Omori (2013) developed flooding-tolerant interspecific introgression lines carrying chromosome segments of teosinte (*Zea nicaraguensis*) in maize (*Zea mays* subsp. mays). IL-18 containing a *Z. nicaraguensis* chromosome segment on the long arm of chromosome 4 showed the greatest tolerance to flooding, suggesting the presence of a major QTL in that region for subsequent high-resolution mapping. Lin et al. 2012 developed a set of 17 cucumber chromosome segment introgression lines (CSILs) from a cross between D8 (powdery mildew (PM) susceptible cultivar) and JIN5-508 (resistant cultivar). Whole-genome resequencing of SSL508-28 carrying PM resistance genes from JIN5-508 helped identify single SNPs and InDels. Between SSL508-28 and D8, a total of 15,682 SNPs and 6262 InDels were identified. qRT-PCR analysis revealed an upregulation of two transcripts, Csa2M435460.1 and Csa5M579560.1, in SSL508-28, which indicated that these two transcripts are candidate genes for resistance to powdery mildew in cucumber (Xu et al. 2016). In another study, whole-genome resequencing of SSL508-28, Jin5-508 and D8 led to the identification of a ~ 6.8 Mb substituted segment predicted to contain 856 genes. RNA-seq analysis was done to study differences in gene expression between SSL508-28 and D8. Eight potential candidate genes that underlie QTL *Pm5.1* were identified based on expression data and annotation (Xu et al. 2017). In cotton, resistance to root-knot nematode and *Fusarium* wilt was studied using CSSLs developed in *G. hirsutum* TM-1 background with chromosome segment substitutions from *G. barbadense* Pima 3-79 or *G. tomentosum* (Ulloa et al. 2016). This study confirmed the presence of QTL based on substitution with the positive or negative allele for resistance, and regions harboring nematode and Fusarium wilt resistance genes were identified.

CSSLs for hybrid improvement

The utilization of heterosis has been accepted as a potential way to improve crop yield. CSSL libraries can be employed

in various ways to improve hybrid vigor to evade hybrid weakness and cross-incompatibility, especially when distant parents are involved. For the creation of interspecific or intersubspecific hybrids; instead of directly using wild accessions with desirable traits, CSSLs of the donor parents in the background of cross-compatible parental lines can be employed. Crossing a set of CSSLs as seed parent (A line) with a specific pollen parent (R line) or a tester and identifying the best combinations with highest heterosis is a useful strategy in heterosis breeding programmes. CSSLs can be developed in elite parental backgrounds with new donors for Rf (restorer of fertility) genes and can be studied for floral biology related to outcrossing traits to identify novel Rf gene donors in elite background. It also helps in dissecting the chromosome segments associated with heterosis and heterotic QTL in interspecific and intersubspecific crosses (Yu et al. 2005). Test of dominance is also possible comparing homozygous CSSLs with heterozygous CSSLs (Nadeau et al. 2000). CSSLs are recommended for heterosis analysis to avoid genetic drag arising from incompatible epistasis while using distant hybrids (Semel et al. 2006; Lippman and Zamir 2007; Bian et al. 2010; Xin et al. 2011; Wang et al. 2012a, b). A single segment substitution line with C563-C63 region for long stigma length was identified from Nipponbare/Kasalath. A secondary F_2 population of SSSL14/Nipponbare to fine map *qSTL3* led to detection of three genes, viz. *LOC_Os03g14850*, *LOC_Os03g14860* and *LOC_Os03g14880*, in the locus (Liu et al. 2015) and demonstrated the role of these genes in stigma length. Thus, a new gene-specific InDel marker LQ30 was developed which can be used in MAS to increase stigma length in male sterile lines, to facilitate increased production of hybrid seed. Peng et al. (2017) developed chromosome segment substitution line hybrids (CSSLHs) by crossing Changhui T025 male parent with a set of 37 CSSLs generated from *indica* cv. Habataki/*japonica* cv. Sasanishiki. Four heterosis QTLs *qHppp10*, *qHph1–1*, *qHtgw4–1* and *qHdsp1* for density of spikelets per plant were detected on field evaluation of these CSSLHs for yield-related traits. CSSLs help in differentiating pleiotropy and linkage effect of QTL; if different CSSLs have number of sub-QTL regions, then their phenotypic effect can be resolved by comparing these CSSLs (Alpert and Tanskley 1996; Yamamoto et al. 1998). A set of 146 CSSLs and 244 HCSSLs were produced from an *indica* rice cultivar Dongnanihui 810, with ZhangPu wild rice (*Oryza rufipogon* Griff.) as donor (Yang et al. 2016), and *qPa-6-2* gene for purple apiculus was precisely mapped to an 88 kb region on chromosome 6 using two heterozygous CSSL populations (HCSSLs) derived from this cross without developing secondary F_2 populations. Exploitation of heterotic QTL using chromosome segment substitution lines for yield traits in rice (Tao et al. 2016; Li et al. 2016; Peng et al. 2017) and kernel traits in maize (Wang et al. 2018) was recently reported.

QTL mapping and gene discovery

Many of the complex traits such as yield are often quantitative in nature and controlled by several genes and quantitative trait loci (QTLs). Precise mapping of all the QTL controlling a specific trait and minor QTL with small effect requires very large populations to include all the recombination events and with minimum background effects. There has been a burst of studies on mapping novel genomic regions and QTL hot spots using CSSLs for yield-related traits, quality traits and resistance to biotic and abiotic stresses (Supplementary Table 1). QTLs have been mapped for several other traits such as mature seed culturability (Zhao et al. 2009), germination (Li et al. 2011), mesocotyl elongation (Lee et al. 2012, 2017), high shoot iron concentration (Fukuda et al. 2012), protein content (Zhang et al. 2008; Zheng et al. 2012), chlorophyll content, RuBisCO in flag leafs (Kanbe et al. 2008, 2009), seed dormancy (Marzougui et al. 2012), anther length, apical dehiscence, length of anther (Tazib et al. 2015), root traits (Zhou et al. 2016), hydraulic conductance (Adachi et al. 2010) and heterosis (Tao et al. 2016) based on CSSLs. Most of these studies were conducted using SSR markers and fewer using RFLPs or SNPs.

CSSLs were used in fine mapping and identification of candidate genes for several agronomically important traits in major crops. Secondary F_2 populations derived from crossing recurrent parent with a single segment line helped to precisely dissect specific chromosome segments and study epistatic interactions. QTLs affecting appearance quality (AQ) traits such as grain length, grain width, length to width ratio, percentage of grains with chalkiness and degree of endosperm chalkiness were dissected using two sets of reciprocal introgression lines (Minghui63 × 02428). Two important background-independent QTL (BI-QTL) and stable-expressed QTL (SE-QTL) regions were identified on chromosome 5 for *qPGWC5*, *qDEC5*, *qGW5.1* and *qLWR5* (BISER-I) and 7 for *qGL7*, *qLWR7*, *qPGWC7* and *qDEC7* (BISER-II). The 4.8–5.2 Mb region on chromosome 7 was detected affecting almost all AQ traits across different environments at both genetic backgrounds. Two secondary F_2 populations were developed using two ILs, DQ28 (MH63-ILs) and DQ438 (02428-ILs), and validated for BISER-II (newly reported). Of 59 epistatic QTLs detected, four stable-expressed QTLs were detected in different environments, but no BI-QTL indicating that genetic background has stronger effect on AQ traits than the environmental factors (Qiu et al. 2017).

Sub-CSSL population or advanced intercross lines (AIL) derived from CSSLs can be used for simultaneous identification, mapping and transfer of multiple desirable QTLs for

target traits. This is useful in QTL pyramiding programs as has been done in rice (Singh et al. 2016). This approach has the potential to finely narrow down large QTLs significantly than a conventional backcross due to generation of more recombination events for target region in the population and facilitates identification and positional cloning of the underlying genes (Wang et al. 2003). Yamamoto et al. (2009) reported that CSSL with one or more donor segments can reduce genetic background noise in finding QTL with additive minor effects compared to any primary mapping populations like F_2 or RIL. De novo variations and donor background interactions in the CSSLs may sometimes affect precision of QTL mapping. NILs developed from CSSLs have been used to overcome such drawbacks and used for mapping (Fukuoka et al. 2010; Subudhi et al. 2015). Once the preliminary QTL mapping is over a set of selected CSSLs with segments harboring different QTL, gene for a complex trait can be crossed again with its recurrent parent to fine map the gene, clone it, determine the gene action and the interaction of QTL with its background.

Barley is one of the well-studied crops for QTL identification using CSSL (Matus et al. 2003). Pillen et al. (2003) demonstrated the effect of marker and environment (M × E) interaction for 13 quantitative traits in six environments using 136 BC_2F_2 RCSLs population. A total of 86 putative QTL were identified, of which 29 (34%) QTL from the exotic parent had favorable effect on traits. 64 putative QTL showed significant marker main effect, 27 showed significant M × E) interactions and 5 QTLs showed both effects. An *Hsp* allele associated with a mean increase of 7.7% yield across six environments coincided with the earlier barley QTL known at the same chromosome position. von Korff et al. (2004) demonstrated that pre-ILs can serve to verify QTL through candidate gene analysis of the introgressed segments. Accordingly, the effect of the introgression at a locus known to carry the photoperiod response gene *Ppd-H1* was verified in two genetic backgrounds and in four different environments (von Korff et al. 2004). QTL for seed dormancy (Sato and Takeda 2009), multiple disease resistance (Yun et al. 2006), morphological traits (Gyenis et al. 2007), agronomic and malting traits (von Korff et al. 2005, 2006; Schmalenbach et al. 2009; Schmalenbach and Pillen 2009), powdery mildew (*Blumeria graminis* f. sp. *hordei* L.) and leaf rust (*Puccinia hordei* L.) resistance (Schmalenbach et al. 2008) were also reported using these CSSLs. A subset of four out of 24 RCSLs barley lines (Matus et al. 2003) were used to investigate the differences in stem soluble carbohydrate content under drought in a Mediterranean-type environment (Mendez et al. 2011). Line 89 showed the maximum content of fructans and was considered as most tolerant to terminal drought but showed the lowest grain weight and yield. Similarly, a subset of 80 from the set of these 140 RCSLs were evaluated in microplots for their agronomic characteristics and their contrasting yield response to soil water availability (Pozo et al. 2012). Deeper root system and/or difference in the photosynthetic rates suggest that drought-tolerant RCSLs have higher stress tolerance index (STI) and $\Delta^{13}C$ values (Pozo et al. 2012).

In addition to applications in breeding programs, the availability of CSSLs makes gene discovery easier and it is worth developing CSSLs to promote basic studies in any crop. Causal genes for a trait can be identified using a CSSL with contrasting trait than its recurrent parent, or two contrasting CSSLs. Fine mapping of QTL regions and identification of candidate genes were reported using CSSLs. Candidate genes *LOC_Os05g01710* for bacterial leaf streak resistance at *qBlsr5a* (Xie et al. 2014), *LOC_Os10g32124*, *LOC_Os10g32190* for brown rice rate (Ren et al. 2016) and *Os01g62920* gene for seed shattering at $qSH1^{JCQ}$ locus (Cheng et al. 2016) were reported. Liu et al. (2012) reported anthocyanin regulatory C1 protein as a predicted candidate region for purple coloration at gene *Pa-6* locus. The spreading panicle (*Spr3*) locus was fine mapped using large F_2 population derived from SG-64 (CSSL carrying a segment of *spr3* from *O. glaberrima* × Wuyujing-7), and candidate genes were predicted from sequence analysis. It was concluded that *Spr3* is an unknown genetic factor in controlling the outspreading of the primary branches in rice inflorescence (Luo et al. 2008). CSSLs harboring a region for a particular trait were used to develop secondary mapping population for fine mapping/prediction of genes. Zhou et al. (2009) used an F_2 population from the cross of C-51(a CSSL harboring *qPGWC-7*)/9311 to fine map *qPGWC-7* to a 44 kb region, containing 13 predicted genes. Four resistance genes predicted for watery lesions at *qWL6* on WBPH infestation were identified using CJ06/TN1 doubled haploid CSSLs (Yang et al. 2014). Comparative transcriptome analysis of DC90 (chilling-tolerant CSSL) and 9311 performed under early chilling stress resulted in identification of 659 DEGs in DC90 which might have contributed to enhanced chilling stress. They reported that DC90 has an introgression segment on the short arm of chromosome 12 which results in transcriptomic reprogramming in early chilling stress (Wang et al. 2017). CSSL (SL18) which contains a segment of Kasalath on chromosome 5 in the genetic background of Nipponbare was crossed to a *spl7* mutant line (KL210) to develop F_2 population for fine mapping and cloning spotted leaf gene *Sp17* (Yamanouchi et al. 2002). Genetic analysis of CSSL58 (carrying a segment from *O. rufipogon*)/TeQing population led to the identification of recessive gene *spd6* (small panicle and dwarfness) on the short arm of chromosome 6 (Shan et al. 2009). Chromosome regions affecting traits (CRATs) were identified for yield traits using two sets of CSSLs between Koshihikari and Nipponbare. By combining the SNP database of the parents and positional cloning,

the CRATs were narrowed down to six genes associated with plant height and stem diameter (Ujiie and Ishimaru 2014).

A significantly salt-tolerant line CSSL16 (KDML105/DH212) than KDMLK105 was subjected to a co-expression network analysis. A candidate locus, *PsbS1*, with increased expression under salt stress was identified which is likely to contribute to tolerance (Chutimanukul et al. 2018). A CSSL harboring protein content (PC) QTL, *qPC-1* region, was fine mapped to a 41-kb region, and it was found that Habataki *qPC-1* allele controls PC by reducing glutelin content (Yang et al. 2015). A NIL carrying chromosome segments containing OsSPS1, a gene encoding sucrose phosphate synthase (SPS), from Kasalath in the genetic background Koshihikari increased spikelet number per panicle by 38–47% which was higher than Koshihikari (Hashida et al. 2013). To understand the genetic basis of brown spots induced by heat stress on mature leaves in rice, the causal gene, *BROWN-SPOTTED LEAF 1* (*BSPL1*), on chromosome 5 was mapped using progeny derived from CSSL-SL518 and Koshihikari and it was speculated that spot formation caused by *BSPL1* was suppressed by one or more Nona Bokra genes (Fukuda et al. 2014). Furuta et al. (2015) evaluated three sets of CSSLs derived from crossing *O. nivara*, *O. rufipogon* and *O. glaberrima* in an *O. sativa* cultivar cv. Koshihikari background for awn elongation and loss of awns in cultivars during domestication process. They demonstrated that *O. sativa* is awnless due to two dysfunctional genes Regulator of Awn Elongation 1 (*RAE1)* and *RAE2*, while mutation(s) in *RAE3* caused the phenotype in *O. glaberrima* (Acc IRGC104038). Evaluation of *O. nivara* CSSLs and *O. rufipogon* CSSLs illustrated that *RAE1* and *RAE2* can also induce the formation of long awns independently. In tomato, genes were cloned and identified for fruit color (Ronen et al. 2000), fruit weight QTL *fw2.2* (Frary et al. 2000) and sugar yield QTL *Brix9-2-5* (Fridman et al. 2004) using introgression lines. Furthermore, candidate genes for the control of quantitative traits were identified using *Solanum pennellii* IL population (Baxter et al. 2005; Rousseaux et al. 2005; Schauer et al. 2006; Bermudez et al. 2008; Di Matteo et al. 2010; Chitwood et al. 2013; Perez-Fons et al. 2014). Bermudez et al. (2008) identified 127 candidate genes using tomato introgression lines, and among these, 85 genes were cloned and partially sequenced, 37 of these candidates were confirmed for allelic variation at the amino acid level and 56 gene-metabolite co-locations were recovered by correlation of parallel transcript and metabolite profiling. Recently, Ruggieri et al. (2015) identified 12 candidate genes potentially involved in ascorbic acid (AsA) accumulation using introgression lines and one among these was differentially expressed between the two *Solanum* species. The introgression lines used from QTL to gene provide a valuable new resource which could be employed for both genetic studies and breeding.

Conclusion and future perspective

CSSLs accelerate the whole-genome large-scale gene discovery and development of superior varieties along with advantages of broadening the genetic base of staple and commercial crops through introgressions from distant genotypes. The strategy to develop CSSLs must be based on the major purpose of its utilization as either gene discovery or crop improvement. A strategy which alternates, backcrossing and selfing, before each marker-assisted selection to minimize segregation and obtain a maximum number of homozygous segments can help in developing CSSLs with narrow homozygous marker-defined regions with maximum donor introgressions. The significantly different lines can be further explored for fine mapping and gene discovery. The power of statistical significance of phenotyping and QTL detection from CSSLs is higher as phenotypic variance is mainly from a single or a few segments without any interaction effects and additionally the possibility of a better comparison with background genotype. CSSLs also allow distinguishing additive from epistasis effect as well as pleiotropy from linkage. Advanced intercross lines generated between two CSSLs having significant trait/QTL can accelerate fine mapping and gene discovery. Direct application of CSSL development in agriculture includes improved cultivars from phenotypically significant CSSLs which can be evaluated under multi-location trials for varietal release. Prebreeding and developing CSSLs can easily be a component in breeding programmes, and as the value of introgressions becomes obvious, it will have long-term impact on exploration, collection and use of plant genetic resources and in crop improvement. It is expected that the development and availability of a genomic resource such as CSSLs in crops will spawn a lot of studies with basic and applied value, improve the understanding of introgression and adaptive variation and contribute to improvement of major crops to meet global demands to cope with climate change.

Author Contribution statement NS and DB planned the structure of manuscript. DB, SM, MS wrote the draft and prepared tables. DB prepared illustrations. All authors contributed to the final draft.

Acknowledgements Authors acknowledge ICAR National Professor Project (F. No. Edn/27/4/NP/2012-HRD) Indian Council for Agricultural Research, Government of India, for financial support. Authors are grateful to Dr. D.S. Brar for critically reviewing an earlier version of the manuscript and constant encouragement. We thank Director, ICAR-IIRR, for support.

Compliance with ethical standards

Conflict of interest Authors declare that there is no conflict of interest.

Ethical standard The authors declare that the experiments comply with the current laws of the country in which they were performed and are in compliance with ethical standards.

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