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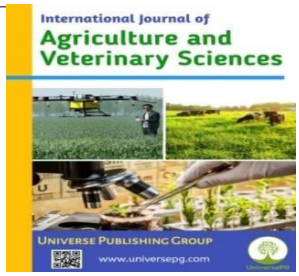

Genomic Insights into the Cultivated Common Buckwheat: A Comprehensive Review on Genetic Diversity, Population Structure, and Marker Technologies

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ABSTRACT

Common buckwheat (*Fagopyrum esculentum*), a pseudo-cereal crop initially grown in Southern China, belongs to the Polygonaceae family. It has been cultivated extensively in Asia, America, and Europe, exhibiting traits like out-crossing and self-incompatibility. This review aims to consolidate studies on buckwheat's genetic diversity and population structure, utilizing a range of morphological and genetic traits for analysis. Genotyping is pivotal for pinpointing and assessing genes that offer agronomic benefits, and for comprehending population structures and allele frequency variations. Linkage models were first established in the 1980s using allozyme and morphological markers. Common buckwheat displays variations in its morphological traits, potentially attributable to its out-crossing behavior, also referred to as self-incompatibility. Allozyme markers were widely employed in population genetic research until the early 2000s. Conversely, RAPD analysis utilizes short 11 bp DNA fragments, amplified by PCR using RAPD primers at low annealing temperatures to facilitate DNA binding. The evolution of PCR technology spurred the development of diverse DNA marker schemes for linkage mapping in the 2000s. Nonetheless, these PCR-based markers failed to cover the entire genome, posing challenges for buckwheat genetic analysis. The emergence of next-generation sequencing has enabled genome-wide assessments across various species, buckwheat included. Recently, approximately 8,885 markers, representing 757 loci, were mapped to eight linkage groups in buckwheat, proving effective for genomic selection aimed at enhancing yield.

Keywords: Genomic insights, Genetic diversity, Morphological markers, RAPD, and Self-incompatibility.

INTRODUCTION:

Common buckwheat (*F. esculentum* Moench) is a pseudo-grain primarily found in southwest China, believed to be its place of origin, distribution, and diversification (Konishi *et al*., 2005). Buckwheat sprouts are rich in antioxidants, particularly rutin, vitexin, and flavonoids, compared to other cereals (Nam *et al*., 2018). These glycosides are present in buckwheat flowers and green leaves (Nešović *et al*., 2021). Buckwheat flowers are valuable sources of nectar and medicinal properties, with the honey produced potentially serving as a supplement to combat pathogens resistant to arsenals (Abedin *et al*., 2020; Islam *et al*., 2016; Sayed *et al*., 2015; Begum *et al*., 2018; Kreft *et al*., 2006; Uddin *et al*., 2023; Abedin *et al*., 2021).

Two methods are commonly used to study buckwheat genetic diversity: morphological markers and genetic markers. In the morphological study, grains from cultivated common buckwheat collected from various regions were examined for seed size, width, thickness, and weight, as well as seed value and the ratio of seed width to length. In the molecular study, allozyme markers were employed to analyze genetic resources from cultivars. Self-incompatibility poses a significant challenge to *F. esculentum* cultivation, hindering pure line production and promoting outcrossing (Matsui and Yasui, 2020). Polymerase chain reaction (PCR) was extensively used for genetic polymorphism analysis of common buckwheat in the 2000s (Balážová *et al*., 2018). Random amplification of polymorphic DNA (RAPD) markers has been used to study the initial cultivation of common buckwheat. Amplified Fragment Length Polymorphism (AFLP) markers have been used to investigate genetic linkages between cultivated populations and the main cultivation of common buckwheat (Konishi *et al*., 2005). RAPD markers are associated with a self-pollinating gene, while AFLP markers are linked to a shattering gene. Simple Sequence Repeat (SSRs), also known as microsatellite markers, is commonly used to study genetic variability across various crop species. Due to their codominant inheritance and high variability, microsatellite markers offer diverse applications. Several recent studies have explored microsatellite markers to assess the genetic diversity of cultivated *F. esculentum*. "Next Generation Sequencing" has been employed for improving and breeding agronomically important buckwheat varieties. DNA microarrays, constructed from gene sequences obtained through NGS, are used for quantitative trait locus (QTL) analysis and genetic selection in common buckwheat cultivation (Yasui, 2020). The primary focus of this review is to summarize studies on the genetic diversity and population structure of buckwheat, utilizing various morphological and genetic traits for analysis.

Morphological Markers

Common buckwheat exhibits variations in its morphological characteristics, possibly due to its outcrossing nature, also known as self-incompatibility. Variations are evident in several traits, including seed size, shape, leaf size, leaf shape, flower color, leaf lobes, and initiation of flowering, plant branching, raceme length, maturity time, and seed coat color (**Table 1**).

Table 1: Lists of morphological and allozyme markers used in common buckwheat genetic diversity and population structure analysis.

Morphological markers	Sequences	References
Seed size	-	(Pan and Chen, 2010)
Seed shape	-	
Leaf size	-	
Leaf shape	-	
Flower colours	-	
Leaf lobes	-	
Initiation of flowering	-	
Plant branching	-	
Raceme length	-	
Allozyme markers		(Ohnishi and Ohta, 1987
gwA	-	
gwB	-	
gwC	-	
gwD	-	
gwE	-	
U808	AGAGAGAGAGAGAGAGC	(Zhou *et al*., 2012)
U815	CTCTCTCTCTCTCTCTG	
U818	VDVCTCTCTCTCTCTCT	
U834	AGAGAGAGAGAGAGAGYT	
U840	GAGAGAGAGAGAGAGAYT	
U842	GAGAGAGAGAGAGAGAYG	
U852	TCTCTCTCTCTCTCTCRA	
U857	ACACACACACACACACYG	
U886	VDVCTCTCTCTCTCTCT	
U888	BDBCACACACACACACA	
M01	CACACACACACAR	

M02	CACACACACACARY
M03	CACACACACACARG
M04	GTGTGTGTGTGTYR
M05	GCTGCTGCTGCTY
M06	AGCAGCAGCAGCY
M07	AGCAGCAGCAGCGY
M08	AGCAGCAGCAGCAY

A notable variation is observed in flower morphology: common buckwheat flowers are perfect but incomplete, lacking petals but featuring a calyx composed of pink, white, and pink-white colored sepals measuring 6-7 mm. The tepals are connected by a 2-3 mm long pedicle (Cawoy *et al*., 2009). These flowers produce yellow-colored nectarines attached to stamens, and the petals are bundled dimly at the branch tips with short pedicels appearing at the leaf axils. Common buckwheat employs distylous self-incompatibility (SI) breeding system. Within this system, two distinct flower types exist: long-styled flowers, or "pin flowers," characterized by long styles and short stamens, and short-styled flowers, commonly known as “thrum flowers,” which have short styles and long stamens. Pollen grains from thrum flowers are larger than those from pin flowers.

Intra-morph incompatibility occurs in the style during crosses between thrum plants, where thrum pollen tube growth is inhibited in the upper part of the style, accompanied by hypertrophy at the tips of the pollen tubes. Conversely, when pollinating between pin flowers, pollen grain growth is hindered at the midpoint of the female genital part of the common buckwheat flowers, without any signs of hypertrophy (Matsui and Yasui, 2020). The S locus governs both self-incompatibility (SI) and flower style (long or short). Additionally, thrum plants exhibit heterozygosity at this locus (Ss), while pin flowers are characterized by homozygosity (ss) (Matsui and Yasui, 2020). Notably, the SS genotype is absent in this system (Yasui *et al*., 2012).

Ohnishi and colleagues identified an inactive morphological variant of cultivated common buckwheat through sib-crosses and utilized them as genetic traits. Ohnishi identified 37 morphological markers governed by a single gene and revealed linkage relation-ships among 22 common buckwheat genes (Wang *et al*., 2017). Although morphological traits may be considered outdated, they can still provide valuable insights for the buckwheat improvement.

Allozyme Markers

Codominant or allozyme markers, which are forms of isozymes, have been widely used as reliable indicators of genetic variation among populations of crop species at different levels. Ohnishi and her colleagues identified various allozyme markers that have been instrumental in the development of genetic resources for common buckwheat (Yasui, 2020). In 1987, Ohnishi and Ohta developed an initial linkage map for cultivated common buckwheat, incorporating several allozyme markers (**Table 1**) (Ohnishi and Ohta, 1987). Subsequent studies elucidated the global population structure of cultivated common buckwheat using 64 populations predominantly collected from Asian countries such as China, Japan, Korea, and Nepal (Ohnishi, 1993). Another role of allozyme markers is to aid in tracing the origin of common buckwheat. Ohnishi identified the first natural progenitor species of common buckwheat through allozyme marker analysis (Konishi *et al*., 2006). Additionally, a study utilized 18 allozyme and ISSR markers to assess polymorphisms and establish the genetic structure of the common buckwheat genome (**Table 1**) (Zhou *et al*., 2012).

Table 2: Lists of RAPD and SCAR markers with their respective primer sequences used in common buckwheat genetic diversity and population structure analysis.

Marker’s Name	Primer’s Name	Sequences (5’-3’)	References
RAPD and SCAR	SCoT 12	ACGACATGGCGACCAACG	(Balážová *et al*., 2018)
	SCoT 23	CACCATGGCTACCACCAG	
	SCoT 26	ACCATGGCTACCACCGTC	
	SCoT 28	CCATGGCTACCACCGCCA	
	SCoT 29	CCATGGCTACCACCGGCC	
	SCoT 30	CCATGGCTACCACCGGCG	
	SCoT 36	GCAACAATGGCTACCACC	
	OPA-01	CAGGCCCTTC	(Javornik and Kump, 1993)

OPA-13	CAGCACCCAC	
OPB-01	GTTTCGCTCC	
OPC-05	GATGACCGCC	(Sharma and Jana, 2002)
OPC-13	AAGCCTCGTC	
OPC-14	AGCATGGCTC	
OPD-06	ACCTGAACGG	
OPD-16	AGGGCGTAAG	
OPL-08	AGCAGGTGGA	
OPL-12	GGGCGGTACT	
OPM-02	ACAACGCCTC	
OPM-04	GGCGGTTGTC	
OPM-16	GTAACCAGCC	
OPN-05	ACTGAACGCC	
OPN-10	ACAACTGGGG	
OPN-19	GTCCGTACTG	
OPC-01	TTCGAGCCAG	(Murai and Ohnishi, 1996)
OPC-02	GTGAGGCGTC	
OPC-03	GGGGGTCTTT	
OPC-04	CCGCATCTAC	
OPC-05	GATGACCGCC	
OPC-06	GAACGGACTC	
OPC-07	GTCCCGACCA	
OPC-08	TGGACCGGTG	
OPC-09	CTCACCGTCC	
OPC-10	TGTCTGGGTG	
OPC-11	AAAGCTGCGG	
OPC-12	TGTCATCCCC	
OPC-13	AAGCCTCGTC	
OPC-14	TGCGTGCTTG	
OPC-15	GACGGATCAG	
OPC-16	CACACTCCAG	
OPC-17	TTCCCCCCAG	
OPC-18	TGAGTGGGTG	
OPD-19	CTCCCCACTT	
OPD-20	ACCCGGTCAC	

Random Amplified Polymorphic DNA (RAPD) and Amplified Fragment Length Polymorphism (AFLP) Markers

Random Amplified Polymorphic DNA (RAPD) is a crucial marker used for identifying genotypes and varieties across a wide range of plants (Korir *et al*., 2013). RAPD analysis amplifies small DNA fragments of about 11 bp using PCR with RAPD primers at low annealing temperatures, which promote DNA binding. **Tables 2** lists various RAPD and SCAR markers along with their respective primers. While RAPD is a cost-effective method, it may be less effective when using small primers and short annealing temperatures. Balážová *et al*. (2018) employed seven RAPD markers to evaluate 17 buckwheat varieties, identifying 52 genomic segments, of which 38 were polymorphic. Another study utilized three RAPD primers to detect polymorphisms between populations and cultivars, identifying three cultivar-specific RAPD markers. Sharma and Jana (2002) used eight primers to assess genetic diversity identifying 240 fragments of which 63.75% were monomorphic and 37.25% were polymorphic. Murai and Ohnishi (1996) analyzed 42 buckwheat landraces using 32 RAPD primers and found 45.9% polymorphic genes. Sequence Characterized Amplified Regions (SCAR) markers are another approach for common buckwheat development, enhancing the robustness of PCR products. SCAR markers amplify DNA fragments using specific 14-29 bp primers (Bhagyawant, 2016), often designed based on RAPD primer sequences. Both RAPD and SCAR markers have been integrated into buckwheat linkage maps. Despite their simplicity and affordability, RAPD markers can lack repeatability, which led to the development of Amplified Fragment Length Polymorphism (AFLP) technology (Vuylsteke *et al*., 2007). AFLP was designed to address the repeatability issues of RAPD markers and has been used to create genome-wide chromosomal maps for common buckwheat, identifying 222 AFLP genetic markers (Talukdar and Sinjushin, 2015).

Table 3: Lists of AFLP markers with their respective primer sequences used in common buckwheat genetic diversity and population structure analysis.

Marker's Name	Primer's Name	Sequences (5'-3')	References
AFLP	N2F1(T)[a]	GTGTTTGTAGTCGTAATTTCTTC	(Nagano *et al*., 2001)
	N2F2(T)	GTTTCTCCCCCCCTACTC	
	N2F3(T)	GTTCGTTCTAACAACGTCGAATGA	
	N2R1(T)	CTCTTAATGGTTGAAGTAAGCTGC	
	N2R2(T)	GCTGCAACAATCTTGCTTGTTTTGG	
	N2R3(T, 1)	CGCCGCTGTTACCTCTCA	
	N7F1(T)	GAAATCACCCATGGAGTAAGTG	
	N7F2(T)	CACCCATGGAGTAAGTGTTTC	
	N7F3(T)	GGAGACCATGCGCTCTACA	
	N7R1(T)	GCCAAACATCTCGCGTACCAG	
	N7R2(T)	TCGCGTACCAGAGGGTGTGC	
	N7R3(T, 1)	CCTTTGTGAATGAGGTACCCAC	
	AD1(T)	NGTCGASWGANAWGAA	
	AD2(T)	GTNCGASWCANAWGTT	
	AD3(T)	WGTGNAGWANCANAGA	
	N2 – Mse+213(1)	CTCCAAACACCCGTTTAGATAGG	
	N7 – Eco+710(1)	CACGCAACCAGGTGAACCTACC	
	AG	F: GCTTGGAAGAATGGCCTCAAAACAA R: GCAAGGTTCGAATCTGGTTTCTCA	(Yasui *et al*., 2008)
	FLO/LFY	F: GCAACCGCCGCTACATCTCTCAAC R: TGCGTCAATGTCCCAACCTT	
	AG	F: GCTTGGAAGAATGGCCTCAAAACAA R: GCAAGGTTCGAATCTGGTTTCTCA	
	FLO/LFY	F: GCAACCGCCGCTACATCTCTCAAC R: TGCGTCAATGTCCCAACCTT	
	AG	F: GCTTGGAAGAATGGCCTCAAAACAA R: GCAAGGTTCGAATCTGGTTTCTCA	
	FLO/LFY	F: GCAACCGCCGCTACATCTCTCAAC R: TGCGTCAATGTCCCAACCTT	
	AG	F: GCTTGGAAGAATGGCCTCAAAACAA R: GCAAGGTTCGAATCTGGTTTCTCA	
	FLO/LFY	F: GCAACCGCCGCTACATCTCTCAAC R: TGCGTCAATGTCCCAACCTT	
	AG	F: GCTTGGAAGAATGGCCTCAAAACAA R: GCAAGGTTCGAATCTGGTTTCTCA	

Table 4: Lists of SSR markers with their respective primer sequences used in common buckwheat genetic diversity and population structure analysis.

Marker's Name	Primer's Name	Sequences (5'-3')	References	Marker's Name	Sequences (5'-3')	Marker's Name	Sequences (5'-3')
EST	M13	F: GTAAAACGACGGCCAGT R: AAACAGCTATGACCATGTTCA	(Hara *et al*., 2011)	Fest_F0077_2	F: TTCGGGAGAAATCACAAATACG R: TCGAAAGGATTGTTTGCAGTTG	Fest_F0076_9a	F: TTCTGTTAGTTAAAATGAAAATACA R: ATAGCAACGGACACAAATAA
	FeCOL3	F: TCAAGACTCAGCTGGTGAACG R: GGACGGATCAGAAAACTCGTC		Fest_F0081_7	F: CATTACAACACACGCATCGG R: AGCAAGGCAAGCTCTTCTGG	Fest_L0426_12	F: ATCGATTTCGAGGGGTTTTG R: TATTGAGGAGGCCCATTCTG
	FeCCA1	F: TCGAGCCAAGCAGTTACTACG R: CCACAAGAGGAACGGTCAAC		Fest_F0083_8	F: CATGCGCAAACTCCCTTTC R: CGTACCACGATCAATTTACAGATCA	Fest_L0432_1	F: CAAAGCAGGCAGAGAAAGCA R: GCAGATGCAAAATCAACTTCCC
	FeELF3b	F: TTGGGAGTTCTGGGGATGAG R: TGCCTTGCTCTTTTCCTGGT		Fest_F0087_2	F: 5'-CAGACCTCAAATGTTCCACCAG R: 5'-GAAGAGGCAAAGGAGGCAAG	Fest_L0480_1	F: TGCTGCAACTCACGAGATTAAC R: TGGATGCCAGTTCAAAGGTC
	Fest_F0005b	F: CAAGCCAACAAGCTGGAGAA R: AATGGGAGAATGCTTAGTTGCTTAC		Fest_F0100_15a	F: TCCAATCGCGTTGACAGAA R: GAAAATGCCGTCCCACAAG	Fest_L0490_2	F: GAGCAGCGGGTTGTCTTCT R: TAGCGTCTCCAAACTGTCCG
	Fest_F0035	F: CAGCTAAGGCAGACGGTTGA R: TCATTGCCAGATCTCATTGGA		Fest_F0102_1a	F: GGGCAGACTCGGTGCTATTC R: GGTGAAGGGATTGTGGCTGT	Fest_L0494_6	F: TCCACAATCTCTCCTTCCTCC R: AGCACCAACAAACGCAAAAC
	Fest_F0049	F: GTGAAATTATGTTTTCTTTTAGAGG R: TTCTTGTCTATGAGCACTGAAA		Fest_F0139_3	F: ATTCTGGTGTTCACTGCTCTTA R: GAGGCCATTGATCGTGATTC	Fest_L0506_1	F: CGTCGTCATTCTCGCTCTCC R: GCATTCATCATTGGGGCTGT
	Fest_F0052a	F: GGACGGACATTGGCTGATTAC R: TGACCAACCACACACAAAACAC		Fest_L0030_1	F: AAAGAAGGAAAAGGCTCCCC R: GATGCAACTATCCATGCCCC	Fest_L0542_3a	F: GCGAATTCGGTTTCACAAAA R: TACCCTCGCCGACTACAACA
	Fest_F0056a	F: AAGGATCACAAGAAACCGGAA R: CAAGCCAAGTATCCATGACAAAC		Fest_L0041_2	F: GTCCACAGGAGGAAAGGCAC R: CGTGAAACACCAAATTACGACC	Fest_L0543_1	F: TTGATTCCTGGGCAACAGAG R: ACTTGACAGCAATGCAAAACG
	Fest_F0057	F: TCTTTGTTGTGTCCAAGATTGCTG R: CCAAATCGTAATCATAAGCGTTCC		Fest_L0046_2	F: CATGTTCTCAAGCAGCACAAAA R: GGATACAGGGTTGGTGGAGG	Fest_L0556_6	F: CCCTAATAACCCCGAAACCC R: AAAGCCTTCTCAGCAGTGTCC
	Fest_F0078	F: AAAACCCCTCTTTTCTCCCC R: TGGCCTTGATTCCACCTTCT		Fest_L0064_2	F: CGGAGAATGGCTTCCAAGAG R: GAGAAGTGGCATCTGGCTGG	Fest_L0578_2	F: GGCCCGTCAAAACCAAAA R: CCCTGAACCTCAATTGCGAC
	Fest_F0090	F: CAGCAGTTCATGCATCTGGTAA R: CGATGATGATGATGGTGGAGA		Fest_L0101_1	F: GGCATCCATGTTTAGCTCTGG R: ACCTCAAGGGCACGGTTCT	Fest_L0606_4	F: TGACAAGATGAAGGAGCTGGA R: AGCAGGAGAGCCTGTTGATTT
	Fest_F0095	F: ATTACTGCCACCTCATCAGACC R: AGATCGCTCAGTATCGTGCC		Fest_L0124_7	F: CCACCTGGTCCTTCGTCTTC R: GAAACGCCACCAACCATACC	Fest_L0609_1a	F: TGCCTCTAACTTGTTCCAATTCC R: TCGTCGACATCATCTTCCGT
	Fest_F0110	F: GAGGAGGAACAAGACGCACA R: TCAAGCCAGTGACATACCACAA		Fest_L0130_2	F: CTGAACCAACACAAACGATCAA R: TGGTTTGGAACAAGGAAGTCG	Fest_L0706_2	F: TGCCTCTAACTTGTTCCAATTCC R: ACAGAAACCCAATCAATCCACC
	Fest_F0117	F: GAGTCCTTTTCCAAGCCCATC R: TGGAGAGGTCAATTCCAGCC		Fest_L0136_5	F: AAGCAGCACCTTCACAGCAA R: CGAAGAAGCTGGGGTCGTAG	Fest_L0712_10	F: TAACAACCCGCTCTCTTCCC R: ATCCATGACACGTCTCGCTC
	Fest_F0119b	F: GGGAGGATTCATTTCTACAGCA R: CCAATGTCAGCAGCTTAAGAGAG		Fest_L0169_3	F: AACCTCGCATTTTCAGTCCC R: ACAGCAATACTCCGGGCTTC	Fest_F0032_2	F: ACGCATTCAAATTCAATGCA R: GAAGAAGCTGGCGAAGAAGA
	Fest_F0129	F: TGGACGAGCTTTCATAGACG R: TCTTCTGAAACATAAATCACAAATG		Fest_L0186_3	F: CCACACACACCAAAAGCACC R: CACAGAACTAGGACGACTCCTGAA	Fest_F0034_1	F: TACTTGATCCAAATCCTTAATATTAGGA R: CGGGATTCTTTGGTGGTTT
	Fest_F0129	F: CACATACCAACCAGAACTCAATACA R: GCCCGAGTATCGTTTGCTCTC		Fest_L0211_5b	F: GGGAATCGGAGTTGGTTACTCTC R: CTGGTGGCTTTGGATGGTTT	Fest_F0043_1	F: TACCGGCTTCCCATTGTCAA R: 5'-TTCCGGAAAGAGGAATCACC
	Fest_L0080	F: CTTCAGTTTTCCAGTTCCTTCCA R: CAGCGCAATGTTTCCCTTC		Fest_L0219_2	F: GCTTGTAGATGGGGTGTTGG R: CGTTTCGGCAGAGTTTCATC	Fest_F0050_3	F: GTGTCCTCGAAAAGTCCACC R: GCCCTTAGGGAGATCAGGAA
	Fest_L0080	F: GAAAGAGTTCAAACAAGAGC R: AACACCACTCTTCAAAGTTC		Fest_L0266_5	F: TCTCTCATCCCAAAACCCAA R: TAATCCAACGGCTCAAACCA	Fest_F0075_2	F: AGAAGTGAGGATGACTTTAA R: ATTTCCCATTGGCTTTTT
	Fest_F0031_1	F: CAAAGCACGTCCAAACAACA R: GGATAATGGCGGTGTCAAAA		Fest_L0292_1	F: ACCCGTCCCAGTCAAAGAAA R: AAAGTCATAAACCCTGATGCCC	Fest_F0079_1	F: TCGATTTTTACCTTCACCCGCCATGGTCAA R: CAGTTTAACGGCAAACATACCCTTTT
	Fest_F0053_2	F: GCGTTATTTCCCGACTGATG R: GATGCACATAGACATGGCTGG		Fest_L0377_4	F: CGTTTTCATGGTGTCGTTCC R: CGGAGAAACGGGTAAGGTGT		

Table 3 provides a collection of AFLP markers with their respective primers. Nagano *et al*. (2001) used 500 polymorphic loci from hybrid genes, obtained from crosses between common buckwheat and wild buckwheat (F2 progeny), to identify a marker (N7) with length polymorphisms across parent lines. Yasui *et al*. (2008) utilized AFLP libraries to identify markers associated with the dwarf E locus and to study gene cloning processes. AFLP genome analysis has significantly advanced buckwheat genetics and crop development research by enabling high-accuracy genotype analysis.

Simple Sequence Repeat (SSR) and Expressed Sequence Tag (EST) Markers

Simple sequence repeats (SSR) markers, also known as microsatellite markers, consist of tandem repeats of short nucleotide sequences and are widely distributed throughout the genomes of eukaryotic organisms. Due to their co-dominant nature, multifactorial inheritance, and high mutability, SSR markers are valuable tools for studying broad genetic variations within and between populations. They offer an extensive range of applications because of their co-dominant mode of inheritance. Several studies have utilized SSR markers to characterize genetic resources, establish genetic relationships, and investigate population structures of various crops. The uses of SSR markers are detailed in **Table 4**.

Table 5: Lists of EST markers with their respective primer sequences used in common buckwheat genetic diversity and population structure analysis.

Marker's Name	Primer's Name	Sequences (5'-3')	References	Primer's Name	Sequences (5'-3')	References	Primer's Name	Sequences (5'-3')	References
SSR	GB-FE-001	F: TGAAACCCAACCATCAGG R: CGACAGTGGCTGGAGAAC	(Ma *et al*., 2009)	Fem 1407	F: GTGATGATAGTTGCCTCTG R: CTTGGCTTAGACCTCTCGTA		NTCP9	F: CTTCCAAGCTAACGATGC R: CTGTCCTATCCATTAGACAATG	
	GB-FE-012	F: ACTGCACCCCAGAGGATT R: GCTGTATCCATGCCCGTA		Fem 1582	F: TCTGGAGAAGCTAAACCCAC R: CCGCAGTTTGTAGGGAGGGA		RC3	F: TAGGCATAATTCCCAACCCA R: CTTATCCATTTGGAGCATAGGG	
	GB-FE-014	F: AGGAGCAGAGGTGGTGGT R: CGGAGCCTCTGCAACC		Fes 1816	F: ACCGGAAGTGAGTTGATAA R: GCAACTCGTAGAGTCCCACA		RC6	F: GAATTTTAGAACTTTGAATTTTTTACCC R: AAGCGTACCGAAGACTCGAA	
	GB-FE-035*	F: TGCAATGACTTGGAGGAGA R: ACCACCATTCAACAAGCG		Fes 2507	F: AGGCAAGATTTCAGTTAGG R: CTTGTGCGTTATTTGAGTC		TaSE3	F: CACCGATCGATCAACAAGTCAAAA R: CATCATCATCGGTTCTTGGA	(Fujita *et al*., 2009)
	GB-FE-043	F: TTCAGCACCTGGATGGAC R: TGTCCCCAATGTGAAAGG		Fes 3164	F: CATTGGCTAAAGGTACAGGA R: CAACACATGCTATTAGACGG		TaSE6	F: CCTAAGAGAGCTTGCGTTCGTCAT R: CACAAAGAAAGAAGACCCCTCATTG	
	GB-FE-054*	F: TGTTGGACTTCCTAGACCTG R: CATGAAAAGGGGATGCAA		Fes 3664	F: ACTCGGTCAAAGTGTTCTTCGT R: GAGGTCTTAATCTGTTGCATCC		TaSE37	F: ATCCGCTACGGAAGAAATACCACA R: GTTGCTGGCCTGCCATGTTTA	
	GB-FE-055*	F: CTGCTTGGATCCCATTGA R: AGCCTCTCGATCCCTCTG		GB-FE-001	F: TGAAACCCAACCATCAGG R: CGACAGTGGCTGGAGAAC	(Song *et al*., 2011)	TaSE63	F: CGTGTGCTCTCGCAGTTTCATAGT R: CCTCGCCTTCTAATTAAGCTCCGT	
	GB-FE-080	F: CGAGGTGGGCAGTAGAGA R: GAGGAGGACGAGGAGGTG		GB-FE-012	F:ACTGCACCCCAGAGGATA R: GCTGTATCCATGCCCGTA		TaSE92	F: TCGCCGTACCCTACCATACCATAC R: AGCGGTTACAGTACGTCCATGTTG	
	GB-FE-169	F: CAACCCTATGCAGCGTTC R: GAGGGGAAGCTGCTTGTT		GB-FE-014	F:AGGAGCAGAGGTGGTGGT R: CGGAGCCTCTGCAACC		TaSE96	F: TGGGACAAGTCCCTAGGTAAGACG R: GTAGTCCGCCCAGCCTCTACTTTT	
	GB-FE-191	F: AATCAATGACCAGCACGC R: CTGATGGAGGATGCCAAA		GB-FE-035	F:TGCAATGACTTGGAGGAGA R: ACCACCATTCAACAAGCG		TaSE117	F: CCACATAAAAATGCTGGACGCATA R: GGGAGAAGCTCCAGAAGGAATCTC	
	(cag)17	F: GAACCAACAACATCAGTTTCAGC R: GTTTCGAGGTTAGTAGCTGGGAT	(Chauhan *et al*., 2010)	GB-FE-043	F:TTCAGCACCTGGATGGAC R: TGTCCCCAATGTGAAAGG		TaSE123	F: TGTAGGAGTAGGAATCAGGGCTGC R: GACCACCAGATCTTGGAGCAAACT	
	(ga)28	F: AATTTCTGGATGGAGTAGTGCCT R: ATGGACAATGATGGAGTGTAACC		GB-FE-054	F:TGTTGGACTTCCTAGACCTG R: CATGAAAAGGGGATGCAA		TaSE149	F: TCAAGTTCTTGCCATTCTCTTCCC R: TATGGCCCTTGCTGTAGCTTCACT	
	(ca)4(ac)3a(ac)17	F: CCTCTTCTCTCTTCCCTTGCTAC R: GTGAAACAAAGAGACTGAGCCAT		GB-FE-055	F:CTGCTTGGATCCCATTGA R: AGCCTCTCGATCCCTCTG		TaSE151	F: TGGTCACGTTTACAGGTTCAATGG R: TCTTATCAACCCACACGCCTTAAA	
	(tc)20	F: GCTCTTAGGCAGTTGGGTCC R: TCTCTCTCTCCCTTTCTCCTCTC		GB-FE-001	F: TGAAACCCAACCATCAGG R: CGACAGTGGCTGGAGAAC				
	(ct)17	F: CAGCTCCAATTCCTTTCTTCTTC R: GCTTCATATCTCTCTCCTCCCTC		GB-FE-012	F:ACTGCACCCCAGAGGATA R: GCTGTATCCATGCCCGTA				
	(tac)14	F: CCTTCCTTACTCACCCTTTGTCT R: CAATAAGTGAGAGTTGCGTCTCC		GB-FE-014	F:AGGAGCAGAGGTGGTGGT R: CGGAGCCTCTGCAACC				
	(ga)55	F: CCTAGTCTAGACGATCGCGG R: AGGAAATGAGGAGAGTGGTTAGG		GB-FE-035	F:TGCAATGACTTGGAGGAGA R: ACCACCATTCAACAAGCG				
	(cca)15	F: CTACCACCACTCCACCACTCTC R: GACCTCGGAGAAGAAGACGTAG		GB-FE-043	F:TTCAGCACCTGGATGGAC R: TGTCCCCAATGTGAAAGG				
	(tc)21	F: AACCCTCTCAGTATCAGCAGTTG R: AACTTCTGCAGTTGCTACCAAAG		GB-FE-080	F:CGAGGTGGGCAGTAGAGA R: GAGGAGGACGAGGAGGTG				
	(ag)38	F: CATATCCTCCGTGTCCATAGTGT R: AGTATGTCAAGCAACCCAATCAC		GB-FE-169	F:CAACCCTATGCAGCGTTC R: GAGGGGAAGCTGCTTGTT				
	(gaa)7	F: CAAATTGAGAAAGACGGAGAGG R: GAAGATCCGACTCAACTTCTTCA		GB-FE-191	F:AGTAATCAATGACCAGCACGC R: CTGATGGAGGATGCCAAA				
	(gaaag)7	F: TCTGACGAAGAAAGAGAGATGCT R: AAGTCTTAGCCAACTAGATCCCG		CCMP02	F: GATCCCGGACGTAATCCTG R: ATCGTACCGAGGGTTCGAAT	(Tang *et al*., 2014)			
	(caa)5	F: ACTCAGGATGTAACAGGGTTGAG R: GATGTTAGGTGATCTTGTGGGAA		CCMP07	F: CAACATATACCACTGTCAAG R: ACATCATTATTGTATACTCTTTC				
	Fem 1322	F: AAGCATTCATTCATTCATTC R: GAGTTTGTTGTGTTTGGAGG	(Joshi *et al*., 2007)	CSU05	F: TGTTCGATAGCAAGTTGATTG R: GAGTTAGTTGAACTTATCACTC				

In 2011, Hara *et al*. developed SSR genetic tools for buckwheat's genome, revealing significant genetic heterogeneity among common buckwheat cultivars. Microsatellite markers have also been employed to understand the limited gene flow characteristics of common buckwheat (Konishi *et al.,* 2006). In 2009, Ma *et al.* constructed 136 microsatellite markers primarily used to assess genetic diversity in Korean buck-wheat. The applications of these EST markers are listed in **Table 5**. To enhance common buckwheat cultivation in 2011, Hara et al. developed 170 sets of PCR primers based on EST sequences. They successfully identified linkage relationships among 63 co-dominant markers by analyzing restriction endonuclease site polymorphisms and length polymorphisms of PCR products. Bashir *et al*. (2021) analyzed genetic polymorphisms in 52 buckwheat landraces using 7 SSR markers, revealing substantial genetic variations within populations. Overall, the development and utilization of microsatellite

and the EST markers have significantly advanced techniques in population genetics studies and breeding research of buckwheat.

NGS-Based DNA Array and Genotyping by Sequencing (GBS)

The previously mentioned molecular markers were unable to unravel the genetic mystery of self-incompatibility in common buckwheat. In 2010, Next-Generation Sequencing (NGS) was first introduced to genetics and crop development research in common buckwheat. The lists of NGS microarray and Genotyping-by-Sequencing (GBS) markers are provided in **Table 6**.

Table 6: Lists of NGS and Microarray markers with their respective primer sequences used in common buckwheat genetic diversity and population structure analysis.

Marker's	Primer's	Sequences (5'-3')	References
DNA microarray	PstI	F: CACGATGGATCCAGTG R: CTGGATCCATCGTGCA	(Yabe *et al*., 2014)
	IGS (petN, psbI)	CACTAATCTAATAGATAGTATGGTAGAAAGA	
	IGS (rbcL, accD)	ATTCGGCTCAATCTTTTTACTAA	
	IGS (psbT, psbN)	GTTGAAGTAATGAGCCTCCCAATAT	
	Intron (rpl16)	TAAGAATTCAAATAAATCTCAAAATATA	
	IGS (trnH, psbA)	AAATTAAAGGAGCAATACCAA	
	TR1	TATTGTATTATACT	(Cho *et al*., 2015)
	TR2	CATTGTTCAACTCTTTGACAACACCAAAAAAC	
	TR3	AAAGATAAATAAA	
	TR4	ATAATATAATAATAAACAT	
	TR5	ATTTTAAATTTGAGGCGT	
	TR6	TTTATTTTGTTTGTGT	
	TR7	AATTAAGTTAAGAT	
	TR8	ATATACTATATAGA	
	TR9	ATAGAATTCGAATAA	
	TR10	TGTCCTAGAACGAATAC	
	TR11	TATATACTAAATAGAA	
	TR12	TTGACATTTTCATTG	
	TR13	ACCAAACATATGCGGATCCAATC	
	TR14	AAATTCGTCTATGATGAACTGCAT	
	TR15	ACAAAGTACTTCAATTCTGAC	
	TR16	AAACGAAAGAAGAATACTTGC	
	TR17	TTTGACCTATGGTTTTTTTTTCTT	
	TR18	GTGATTGGATCCGCATATGTTTG	
	TR19	CAATGAAAATATCAA	

To enhance the common buckwheat breeding program, Yabe *et al*. (2014) developed microarray probes (50-75 bp length) using NGS based on specific genomic sequences of common buckwheat. In 2016, draft genome sequences of common buckwheat were published, along with the establishment of the Buckwheat Genome Database (BGDB) (Yasui *et al*., 2016). Matsui and Yasui, (2020) demonstrated that BGDB has isolated several agriculturally significant genes. Furthermore, GBS analysis has been conducted using the entire genome as a reference to identify genetic sequences unique to buckwheat crops with thrum flowers, particularly the S-allele-linked region of the S locus (Yasui *et al*., 2016). A significant achievement in GBS analysis was made in 2019; Mizuno and Yasui, (2019) identified 255,517 SNP locations in 46 cultivated common buckwheat genotypes. This analysis revealed significant genetic diversity, with common buckwheat separating into two genetic diversity groups: Asian and European species, showing minimal differentiation between them, consistent with previous research. The Buckwheat genome assembly was then applied to buckwheat landraces worldwide using GBS technology (Yasui *et al*., 2016). GBS employs genomic DNA seq-uences amplified by restriction enzymes and has become popular for identifying a large number of SNPs (Mizuno and Yasui, 2019). Another study successfully detected the S-allele using GBS markers, which consisted of 333 scaffolds covering 5.4 Mb (Yasui *et al*., 2012). Yasui *et al*. (2012) demonstrated that this region contains sequences where GBS readings were found in short-styled plants but absent in long-styled plants and it harbors two genes (SS and ss). Understanding the DNA organization in the S locus can serve as a powerful tool for elucidating genetic interactions in common buckwheat landraces (Mizuno and Yasui, 2019). In conclusion, Next-Generation Sequencing (NGS) and GBS techniques have significantly advanced genetic research and improved breeding efforts in common buckwheat.

Table 7: Analysis of the key findings linked to the formation of genetic marker schemes for cultivated common buckwheat.

Marker's name	Key findings	References
Morphological and allozyme markers	In 1987, 15 morphological and 6 allozyme markers were applied to construct the first linkages design of cultivated common buckwheat.	(Ohnishi and Ohta, 1987)
RAPD	In 1998, Agronomically significant self-compatible gene (Ho) was mapped.	(Aii *et al*., 1998)
AFLP	In 2006, Gene-wide markers were used to generate the chromosome patterns of common buckwheat.	(Konishi *et al*., 2006)
Microsatellite markers	As common buckwheat, SSR markers with 54 loci were created in 2006s.	(Konishi *et al*., 2006)
NGS and GBS markers	In 2014, A high-frequency linkages design was constructed using DNA arrays.	(Yabe *et al*., 2014)
NGS	In 2016, The draft genome database was developed, and numerous agronomically valuable genes were discovered using the genome table.	(Yasui *et al*., 2016)
GBS	In 2019, Established 255,518 SNP locations in 46 grown cultured common buckwheat flowers by using GBS analysis, revealing their significant genetic diversity	(Mizuno and Yasui, 2019)

Population Structure

In this study, we summarized research on various morphological and genetic markers used to assess the genetic and morphological diversity of cultivated common buckwheat landraces (**Table 7**). This information aims to guide the conservation and utilization of buckwheat genomic resources. Genomic resources are vital for developing improved plant varieties with beneficial traits, which can enhance crop management and human nutrition. Preserving the genetic resources of buckwheat is essential, given the decreasing agricultural land. As the cultivated area for buckwheat continues to decline, there is an urgent need to conserve its genetic assets. Drought and desertification, resulting from extensive deforestation, pose global threats. Additionally, many small-scale farmers cannot afford the high-cost inputs required for cultivating high-yielding grain crops like wheat and rice. Consequently, farmers are showing interest in cultivating rainfed crops like buckwheat, which can thrive in low rainfall and low fertility conditions where other local crops struggle. Buckwheat offers an affordable option for resource-poor farmers, requiring less investment while providing a reliable harvest. Furthermore, buckwheat has medicinal properties, making it a valuable crop for these farmers.

CONCLUSION:

This study aimed to review the genetic resources and population structure of buckwheat landraces using a variety of morphological and genetic markers. Initially, allozyme and morphological markers were employed as primary tools for studying the genetic resources of cultivated common buckwheat. As research progressed, RAPD and SCAR markers became pivotal in tracing the origins of common buckwheat. In 2004, AFLP was first used to construct chromosome maps for common buckwheat, contributing to the development of cultivated common buckwheat with 54 loci containing microsatellite markers. DNA array technology plays a vital role in the characterization of cultivated buckwheat's genetic resources.

The advent of NGS technology facilitated the development of BGDB, a genome database housing numerous distinct, agronomically validated genomes. Using GBS, 255,517 SNP sequences were identified in 46 cultivated buckwheat plants, suggesting the potential for gene transfer within the cultivated buckwheat genome. Genetic resources and population structure insights are essential for crop development in buckwheat. Evaluating germplasm plays a crucial role in plant germplasm management programs. The information on genetic diversity obtained from this study can aid in assessing additional germplasm collections and furthering genetic research on cultivated common buckwheat species. This, in turn, can help expand the genetic diversity of current buckwheat cultivars.

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The authors declare there is no conflict of interest.

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