The sweetpotato (*Ipomoea batatas* (L.) Lam., Convolvulaceae) is an edible tuberous root that was originally found in Central America. Its global production volume is around 104,000,000 t (FAO 2014; http://www.fao.org/home/en/), with close to 75% of the amount produced in Asia, and China itself produces around 71,000,000 t, which accounts for 70% of the global production. Large quantities of the crop are also produced in Southeast Asian countries, such as Indonesia and Vietnam, and in African countries, such as Nigeria and Uganda. Therefore, the sweetpotato is a vital source of nutrients for human populations and is especially important for various developing countries in Africa and Southeast Asia.

In Japan, on the other hand, the annual production of sweetpotato is ~86,500 t (FAO 2014), and most of the crop is produced in Kagoshima, Ibaraki, and Chiba (JRTA 2010). The form and characteristics currently desired in Japan are not simply a matter of yield, but also run the gamut from taste, nutritional qualities, and processing. Of the cultivars cultivated for consumption in Japan, intensely sweet cultivars, such as ‘Beniharuka’, are preferred in addition to the long-cultivated ‘Kokei No. 14’, and cultivation also leans toward types that are high in sugar content and superior in flavor (Kai et al. 2010). Furthermore, islands between Tanegashima in Kagoshima prefecture and the Nansei Islands of Okinawa have long been used for growing anthocyanin-containing cultivars, such as the purple-fleshed sweetpotato (JRTA 2010). In recent years, a number of other cultivars have also been grown, in order to facilitate the expansion of uses for sweetpotatoes by producing cultivars that are well suited for the crop’s various functions. For example, purple sweetpotato cultivars, such as ‘Ayamurasaki’ and ‘Akemurasaki’, are used as raw material for producing natural anthocyanin colorants (Sakai et al. 2010, Yamakawa et al. 1997), and other purple sweetpotato cultivars, such as the ‘Purple Sweet Lord’, are used for food (Tamiya et al. 2003). In addition, several cultivars also yield tuberous roots with high levels of β-carotene, and there is currently an expectation that the demand for such functional foods will expand. Furthermore, the ‘J-Red’ cultivar is used for juice (Yamakawa et al. 1998), the ‘Sunny Red’ cultivar is used for powders (Yamakawa et al. 1999), and the ‘Ayakomachi’ cultivar is used in salads and other cooking materials (Kai et al. 2004). In addition, in order to expand demand among regular households, various cultivars are also being grown in response to changes in consumer demand, such as the ‘Quick Sweet’ cultivar, which demonstrates an appealing flavor, even when cooked with a microwave (Katayama et al. 2003).
In addition to meeting consumer demand, another important objective in the domestic breeding of sweetpotato in Japan is to confer disease resistance. Particularly because sweetpotato has a tuberous root, and its underground portion is susceptible to soil-borne diseases. For example, although many Streptomyces spp. are useful, in that they produce antibiotics, some are known to cause common scab on root crops, and the actinobacteria S. ipomoea causes sweetpotato soil rot (Person and Martin 1940). In the case of the latter, when sweetpotato is invaded by bacteria, the underground portion blackens and starts to decay, round black specks appear on the tuberous root, and the plant decomposes (JRTA 2010, Person and Martin 1940). Furthermore, the sweetpotato loses considerable commercial value if there are any black specks. Unfortunately, most domestic cultivars are susceptible to the disease. Thus, the breeding of disease-resistant cultivars is desired. Therefore, when considering both consumer demand and disease resistance, there are various plant breeding objectives in sweetpotato.

The construction of genetic linkage maps is important for gene cloning, quantitative trait locus (QTL) detection, comparative genomic research, and marker-assisted breeding. However, in sweetpotato, linkage map construction has been challenging, owing to the species’ complex genomic architecture: high heterozygosity, general self-incompatibility, and hexaploidy, with a large number of small chromosomes (2n = 6x = 90), as mentioned above. For linkage map construction in such outcrossing heterozygous species, Grattapaglia and Sederoff (1994) developed a two-way pseudo-test cross strategy, in which linkage analysis is conducted for each parent separately, since dominant markers that are heterozygous in one parent and recessive homozygous in the other parent will segregate in the F1 generation, resulting in the development of two parental linkage maps. In hexaploids like sweetpotato, only simplex, duplex, and triplex alleles can produce polymorphisms in the progeny, and alleles at higher doses produce non-polymorphism. Based on the allele dosage (simplex, duplex, or triplex), several variations in segregation ratios are detected, and these ratios are affected by cytological characteristics (autohexaploid, tetradiplod, or allohexaploid) (Table 1).

However, the ploidy type of sweetpotato has been a mystery for many years, and it has not yet been clearly determined. A number of studies have suggested that sweetpotato is allohexaploid (Jones 1965, Magoon et al. 1970, Sinha and Sharma 1992, Ting and Kehr 1953), whereas Shiotani and Kawase (1989) proposed that the genome constitution of sweetpotato should be B1B1B2B2B2B2 based on the frequent occurrence of tetravalents and hexavalents. On the other hand, several relatively recent genetic linkage analyses suggest that sweetpotato is autohexaploid, with some preferential pairing (Cervantes-Flores et al. 2008a, Kriegner et al. 2003, Ukoskit and Thompson 1997, Zhao et al. 2013).

As mentioned above, in outcrossing heterozygous species, such as sweetpotato, a two-way pseudo-test cross strategy has been applied to construct linkage maps, in which dominant markers that are heterozygous in one parent and recessive homozygous (=null) in the other parent are analyzed. During the construction of linkage maps in hexaploids, marker types are classified according to their segregation ratios in the mapping population for three hypothetical cytological types (autohexaploid, tetradiplod, and allohexaploid): (a) simplex markers, which are present as a single copy in one parent and absent in the other parent, segregate in a 1:1 (presence:absence) ratio, regardless of the cytological types; (b) duplex markers, which are present as two copies in one parent and absent in the other parent, segregate in a 4:1 (hexaploidic), 5:1 (tetradsomic), or 3:1 (disomic or tetradsomic) ratio; and (c) triplex markers, which are present as three copies in one parent and absent in the other parent, segregate in a 19:1 (hexaploidic), 11:1 (tetradsomic), or 7:1 (disomic) ratio (Table 1) (Jones 1967), whereas double simplex markers occur as single copies in both parents and segregate in a 3:1 ratio (Certavantes-Flores et al. 2008a, Kriegner et al. 2003).

Because the simple 1:1 segregation ratio is only detected in simplex markers, for any cytological characteristics (autohexaploid, tetradiplod, or allohexaploid), simplex markers are highly useful for linkage analysis, and in linkage map construction, simplex markers are used to build an initial framework map, followed by the insertion of duplex, triplex, and double simplex markers. Thus, obtaining a large number of simplex markers is critical for forming the framework map, which is a basis of the linkage groups, and duplex and triplex markers are used for identifying the corresponding homologous linkage groups in the map. Therefore, the screening and genotyping of polymorphic markers based on the calculation of segregation ratios is apparently more tedious in polyploids than in diploids. However, although genetic and linkage analysis in sweetpotato has lagged far behind that in other plant species, both linkage map construction and QTL mapping in the species have been reported. In this review, we summarize the results of previous genetic studies and describe future perspectives on genetic study in sweetpotato.

| Marker dosage       | Autohexaploid (hexaploidic) | Tetradiplod (tetrasomic, tetradsomic, disomic) | Allohexaploid (disomic) |
|---------------------|-----------------------------|-----------------------------------------------|-------------------------|
| Simplex             | Aaaaaa 1:1                  | Aaaa aa 1:1                                  | Aa aa aa 1:1            |
| Duplex              | AAaaa 4:1                   | AAAA aa 5:1†                                 | AA Aa 3:1               |
|                     |                             | AAAA Aa 3:1‡                                | AA aa 1:0               |
|                     |                             | aaa AA 1:0                                   |                         |
| Triplex             | AAaaa 19:1                  | AA Aa aa 1:0                                 | AA Aa 7:1               |
|                     |                             | AAAa Aa 11:1                                | AA Aa aa 1:0            |
|                     |                             | AAaa AA 1:0                                  |                         |

† Tetrasomic inheritance.
‡ Tetradsomic inheritance.
§ Disomic inheritance.
1. Linkage map construction in sweetpotato

To date, several studies have constructed genetic linkage maps in sweetpotato (Cervantes-Flores et al. 2008a, Chang et al. 2009, Krieger et al. 2003, Li et al. 2010, Monden et al. 2015, Ukoskit and Thompson 1997, Zhao et al. 2013) (Table 2). The first one was reported by Ukoskit and Thompson (1997), who constructed low-density linkage maps using randomly amplified polymorphic DNA (RAPD) markers, with a mapping population of 76 progenies derived from ‘Vardaman’, which exhibits high early root yield, drought tolerance, and susceptibility to root-knot nematode (RKN), and ‘Regal’, which is resistant to disease, RKN, and insects. Ukoskit and Thompson analyzed the segregation ratios of 196 RAPD markers in each parent and then used the markers to construct linkage maps. Of the 196 markers, 76 (74.5%) and 67 (71.3%), 17 (16.7%) and 21 (22.3%), and four (3.9%) and three (3.2%) were simplex, duplex, and triplex markers, in ‘Vardaman’ and ‘Regal’, respectively. In order to develop linkage maps, the linkage relationships of simplex RAPD markers were first analyzed and used to construct a framework map for each parent, and then duplex and triplex markers were inserted into the framework map manually, which increased the mapping efficiency. In linkage maps that only contained simplex markers, 25 and 20 markers were included in the ‘Vardaman’ and ‘Regal’ maps, respectively, and adding duplex and triplex markers increased the total number of mapped markers to 48 and 46. In addition, the authors also reported that the main advantage of using non-simplex markers was the identification of homologous linkage groups, of which three were identified in both maps. This work was the first to report using the pseudo-test cross mapping strategy in sweetpotato, which enabled the construction of genetic linkage maps and demonstrated the high probability that sweetpotato is autohexaploid, not allohexaploid.

Afterward, several researchers reported the construction of genetic linkage maps in sweetpotato using molecular markers, such as amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), and sequence-related amplified polymorphism (SRAP) markers. In particular, the application of AFLP markers enabled researchers to dramatically increase the number of mapped markers and linkage groups. The method used for linkage map construction was basically the same as that reported by Ukoskit and Thompson (1997): simplex markers were first used to construct a framework map, and then the duplex, triplex, and double-simplex markers were inserted, in order to detect homologous groups. Krieger et al. (2003) developed linkage maps using AFLPs in an F1 mapping population that was derived from a cross between ‘Tanzania’ and ‘Bikilamaliya’ and obtained a total of 90 and 80 linkage groups, which included 632 and 435 markers in the ‘Tanzania’ and ‘Bikilamaliya’ maps, respectively, which had total lengths of 3655.6 and 3011.5 cM (Table 2). Meanwhile, Cervantes-Flores et al. (2008a) developed another set of linkage maps using AFLPs and a mapping population that was derived from a cross between ‘Tanzania’ and ‘Beauregard’. In the ‘Tanzania’ map, 86 linkage groups, which included 947 markers, were obtained, and the entire length of the maps was estimated as 5792 cM, with an average between-marker distance of 4.5 cM (Table 2). In the ‘Beauregard’ map, 90 linkage groups, which included 726 markers, were obtained, and the entire length of the maps was 5276 cM, with an average between-marker distance of 4.8 cM (Table 2). In addition, these studies also supported the conclusion that sweetpotato is autohexaploid, not allohexaploid; however, some preferential pairing between certain chromosomes was reported, as well.

Moreover, the genetic linkage map in sweetpotato with

| Types of markers | Total number of markers | Total length (cM) | Average length of markers (cM) | Parent cultivar | Populations | Software | Paper |
|------------------|------------------------|------------------|------------------------------|----------------|-------------|----------|-------|
| RAPD             | 48                     | 474.6            | 9.9                          | Vardaman       | 76 progenies derived from Vardaman × Regal | MAPMAKER 3.0 | Ukoskit and Thompson (1997) |
|                  | 46                     | 489.1            | 10.6                         | Regal          |             |          |       |
| AFLP             | 632                    | 3655.6           | 5.8                          | Tanzania       | 94 progenies derived from Tanzania × Bikilamaliya | JoinMap 3.0 | Krieger et al. (2003) |
|                  | 435                    | 3011.5           | 6.9                          | Bikilamaliya   |             |          |       |
| AFLP             | 726                    | 5276             | 4.8                          | Beauregard     | 240 progenies derived from Tanzania × Beauregard | JoinMap 3.0 and MAPMAKER/EXP 3.0 | Cervantes-Flores et al. (2008) |
|                  | 947                    | 5792             | 4.5                          | Tanzania       |             |          |       |
| ISSR             | 37                     | 479.8            | 12.9                         | Nancy Hall     | 119 progenies derived from NH × TN27 | MAPMAKER 3.0 | Chang et al. (2009) |
|                  | 47                     | 853.5            | 17.7                         | Tainung 27     |             |          |       |
| SRAP             | 473                    | 5802.46          | 10.2                         | Luoxushu 8     | 240 progenies derived from Luoxushu 8 × Zhengshu 20 | JoinMap 3.0 | Li et al. (2010) |
|                  | 328                    | 3967.9           | 12.0                         | Zhengshu 20    |             |          |       |
| AFLP, SSR        | 2077                   | 8184.5           | 3.9                          | Xushu 18       | 202 progenies derived from Xushu 18 × Xushu 781 | JoinMap 3.0 | Zhao et al. (2013) |
|                  | 1954                   | 8151.7           | 4.2                          | Xushu 781      |             |          |       |
| Retrotransposon-based | 124                   | 931.5           | 11.6                         | Purple Sweet Lord | 98 progenies derived from PSL × 90IDN-47 | JoinMap 4.1 | Monden et al. (2015) |
|                  | 122                    | 734.3            | 9.8                          | 90IDN-47       |             |          |       |

Table 2. Summary of linkage maps constructed in sweetpotato.
the highest marker density was constructed by Zhao et al. (2013), using AFLP and SSR markers in an F1 mapping population of ‘Xushu 18’ and ‘Xu 781’. In the ‘Xushu 18’ map, 90 linkage groups were obtained, which included 2077 markers, and the total length of the maps was 8184.5 cM, with an average between-marker distance of 3.9 cM (Table 2). Meanwhile, in the ‘Xu 781’ map, 90 linkage groups were obtained, which included 1954 markers, and the total length of the maps was 8151.7 cM, with an average between-marker distance of 4.2 cM (Table 2). This was the first study to establish 90 complete linkage maps, a number which corresponds to the species’ actual chromosome number, and remains the only study to have accomplished this to date. However, the AFLP markers in Zhao et al.’s linkage map exhibited a clustered distribution, and in several linkage groups, such as XUSHU18(02.09), XUSHU18(10.51), XU781(01.03), and XU781(05.28), many markers were clustered. This clustering could have resulted from a biological basis, thus, reflecting the suppressed or reduced genetic recombination in heterochromatic regions around the centromeres and telomeric regions (Tanksley et al. 1992), but other authors have suggested that AFLP markers generated using EcoRI and MseI tend to exhibit uneven distributions as a result of the frequency of EcoRI-recognized A/T-rich regions in pericentromeric heterochromatin (Isidore et al. 2003, Truco et al. 2007).

In addition, the genotyping and screening of polymorphic classical DNA markers, such as AFLPs and SSRs, can be tedious and time-consuming, although this depends on the relatedness of the parental cultivars and the types of markers used. For example, Zhao et al. (2013) reported that a total of 2893 AFLP primer combinations were screened using parental cultivars and a small subset of progeny, but only 304 (10.5%) produced good quality polymorphic and segregating bands. Meanwhile, in the case of SSR markers, only 68 of 173 SSR primer pairs (39.3%) exhibited polymorphic bands of acceptable quality and were used to develop SSR markers in the entire mapping population.

In recent years, efficient and genome-wide genotyping has been achieved in dramatically less time by using next-generation sequencing (NGS) technologies (Goodwin et al. 2016, Heard et al. 2010, Nielsen et al. 2011), and NGS-based genetic linkage analyses have been pursued in many crop species (Baird et al. 2008, Baxter et al. 2011, Bielenberg et al. 2015, Chutimanitsakun et al. 2011, Gardner et al. 2014, Guajardo et al. 2015, Ipek et al. 2016, Ma et al. 2012, Poland et al. 2012, Pootakham et al. 2015, Russell et al. 2014, Shirasawa et al. 2016a, Spindel et al. 2013, Verma et al. 2015, Wang et al. 2012, Ward et al. 2013, Wu et al. 2014, Xiao et al. 2015). However, few studies have used NGS-based approaches for the genetic analysis of sweetpotato.

In one NGS-based study in sweetpotato, Monden et al. (2015) analyzed comprehensive retrotransposon insertion polymorphisms and developed genetic linkage maps. Because a large number of retrotransposon insertions are distributed throughout the genomes of eukaryotes and because such insertions are genetically inherited, retrotransposon insertion polymorphisms can be used to develop molecular markers (Kalander 2011, Kalander et al. 2011, Kumar and Hirochika 2001, Poczai et al. 2013, Schulman et al. 2004). For example, in cultivated strains, Rtsp-1, which is one of the active retrotransposon families in sweetpotato, exhibits high rates of insertion polymorphisms (Monden et al. 2014, Tahara et al. 2004), which indicates that the insertion sites are highly likely to be useful for linkage map construction. Accordingly, the authors performed high-throughput Illumina NGS of Rtsp-1 insertion sites in a number of cultivars and found that the presence or absence of insertion sites could be used as the basis for efficient genotyping. However, in this case, the number of developed markers was relatively small, and the coverage was also low since the method relied on the copy number of a targeted retrotransposon family (~250 in this case). Thus, further research is needed to increase the number of mapped markers by analyzing insertion sites in other retrotransposon families with high copy numbers or by introducing different types of molecular markers. An advantage of the research was that NGS technology allowed the authors to reduce the time and labor required for genotyping, and, interestingly, the retrotransposon-based markers also indicated an extremely high proportion of simplex markers (~90%) (Monden et al. 2015), which demonstrates the utility of retrotransposon-based markers for linkage map construction in polyploid species. Therefore, more research focused on higher-density linkage map construction is needed for precise QTL detection, marker-assisted selection, and breeding.

### 2. QTL analysis in sweetpotato

Several QTL mapping analyses have been conducted using the constructed linkage maps (Cervantes-Flores et al. 2008a, Zhao et al. 2013) for identifying agronomically important genes or genomic regions, and so far, such analyses have targeted economically important traits, such as nematode resistance, starch content, dry-matter content, β-carotene content, and root yield. The first QTL analysis in sweetpotato was conducted by Cervantes-Flores et al. (2008b) in order to identify target genes or chromosomal regions associated with RKN resistance, by using a mapping population of ‘Tanzania’ and ‘Beauregard’. In sweetpotato, RKN is known for causing significant reductions in yield and for damaging tuberous roots, and the characteristic symptoms of RKN damage are round to spindle-shaped swellings (galls) on fibrous roots and cracks on fleshy tuberous roots (Lawrence et al. 1986, Nakayama et al. 2012). Although nematicides provide a fairly effective means of controlling RKN, they are expensive and highly neurotoxic. Thus, it is preferable to develop resistant cultivars as more economical and sustainable strategy. Although the resistance of sweetpotato to RKN is not well understood, previous studies have suggested that several genes may be involved and that
resistance to different RKN species should be conferred by different genes (Cervantes-Flores et al. 2002a, 2002b, Sano et al. 2002). In the study of Cervantes-Flores et al. (2008b), an F1 mapping population was developed from ‘Tanzania’ and ‘Beauregard’ parental cultivars, owing to previous reports of high levels of resistance in ‘Tanzania’ to multiple RKN species and the high susceptibility of ‘Beauregard’ (Cervantes-Flores et al. 2002a, 2002b). Genetic maps constructed by Cervantes-Flores et al. (2008a) were used for QTL mapping, and RKN resistance was assessed as the number of egg masses observed on the roots. The frequency distribution of resistance in the mapping population (n = 240) was highly skewed, with most of the progeny exhibiting moderate to high levels of resistance, which suggested that RKN resistance was a quantitative trait that was likely controlled by a few major genes. The subsequent QTL analysis identified nine chromosome regions that were associated with RKN resistance, seven of which (rkn1 to rkn7) were observed in ‘Tanzania’ and two of which (rkn8 and rkn9) were observed in ‘Beauregard’ (Table 3). All the QTLs observed in ‘Tanzania’ and their interactions explained ~40% of the variation in egg masses; however, no single major QTL explained more than 15% of the variation. One the other hand, the study also identified three unmapped duplex markers that were highly associated with RKN resistance, accounting for as much as 45% of the variation in egg masses. Therefore, the three unmapped markers might be associated with a locus or loci with major effects (data not shown); however, further research was needed to validate their QTLs, through the inclusion of additional markers. One the other hand, another study conducted QTL mapping analysis for targeting the southern root-knot nematode (SRKN) resistance, and identified genomic regions with a large effect on resistance, and successfully developed sequence-specific PCR markers associated with QTL(s) for resistance to multiple races of SRKN in sweetpotato (Nakayama et al. 2012).

Subsequently, other QTL analyses have been conducted to identify genes and/or chromosomal regions that control economically important traits, such as root yield, dry-matter content, and starch content. For example, Cervantes-Flores et al. (2011) conducted QTL mapping analysis for dry-matter, starch, and β-carotene content using a mapping population of 240 plants that were derived from a cross between two parental cultivars with significantly different traits, namely ‘Tanzania’, which is a white cream-colored African landrace that has a high dry-matter content (>30%), and ‘Beauregard’, which is an American orange-fleshed cultivar with a low dry-matter content. The authors found that the distribution of dry-matter and starch content in the mapping population was continuous, whereas that of β-carotene content was highly skewed, and transgressive segregations were also observed in all three traits, which suggested that the traits were quantitative. In addition, 13, 12, and eight QTLs were identified for dry-matter, starch, and β-carotene content, respectively (Table 3), and among the three traits, dry-matter and starch content were highly correlated (r > 0.8), whereas β-carotene content was negatively correlated with both starch (r = –0.6) and dry-matter (r = –0.3) content. Therefore, it is reasonable to assume that most of the QTL regions that significantly affected starch content also affected dry-matter content.

Zhao et al. (2013) developed the first map that included 90 complete sweetpotato linkage groups, and subsequent analyses conducted by Xiao-xia et al. (2014) and Li et al. (2014) were able to identify QTLs and co-localizing markers for agronomically important traits, such as dry-matter (Zhao et al. 2013), starch content (Xiao-xia et al. 2014), and yield (Li et al. 2014). In these three studies, QTL mapping was conducted using the linkage map based on AFLP and SSR markers, to obtain a mapping population of 202 plants that were derived from a cross between ‘Xushu 18’, which is the most widely grown cultivar in China and has high yield and moderate starch and dry-matter content, and ‘Xu 781’, which has low yield and high starch and dry-matter content. The analysis identified 27, eight, and nine QTLs for dry-matter content, starch content, and root yield (Table 3), and both dry-matter and starch content were distributed normally, whereas root yield was abnormally distributed, as reported by Brondani et al. (2002) in rice. However, transgressive segregation was observed in all three traits, which indicates that the three traits are quantitative, and as expected, a number of QTLs were detected for all three traits. For dry-matter content, 27 QTLs (DMN-1 to DMM-22 and DMN-1 to DMN-5) were identified, in which DMM-11 QTL accounted for the largest amount of phenotypic variation in ‘Xu 781’ (45.1%) and was co-localized with a single SSR marker (C55-5s) on map XU781(06.36). For starch content, eight QTLs (DMF-1 to DMF-6, DMMN-1, and DMMN-2) were identified, in which DMF-4 accounted for the largest amount of phenotypic variation in ‘Xu 781’ (38.8%) and was co-localized with the E36M63-10ds marker on map XU781(07.40). For root yield, a total of 45 QTLs were detected, using phenotypic data from two different locations and three time points, and nine of the QTLs were identified at the same genomic regions in at least two different environments and identified as stable. In particular, the YIEF-2 QTL in ‘Xushu 18’ explained the largest amount of phenotypic variation (59.3%) and was co-localized with the E53M30-12d marker on map XUSHU18(03.16). In addition, the parental cultivars also differ in their resistance to root rot, stem nematodes, and sweetpotato feathery mottle virus (SPFMV), which suggests that similar QTL analyses could be used to identify chromosome regions that affect these traits, as well.

Because of the complex structure of the sweetpotato genome, genetic linkage analysis of sweetpotato has been more difficult than that of other crop species, and although several studies have performed linkage and QTL mapping in sweetpotato, the number of such studies is quite smaller than that in other crop species. In addition, the lack of a whole genome sequence or gene annotation in sweetpotato...
| Trait                      | Cultivar      | Name of QTL | Linkage group | Closest marker | LOD (Additive) effect | $R^2$ (%) | Paper                     |
|----------------------------|---------------|-------------|---------------|---------------|-----------------------|-----------|--------------------------|
| Root-knot nematode resistance | Tanzania     | rkn1        | T0.5.26       | E42M6022      | –                     | 0.16      | 4.0                      |
|                            |               | rkn2        | T0.7.38       | E35M4414      | –                     | 0.18      | 3.7                      |
|                            |               | rkn3        | T0.7.41       | E38M4512      | –                     | 0.30      | 9.1                      |
|                            |               | rkn4        | T0.8.46       | E36M3411      | –                     | 0.21      | 5.4                      |
|                            |               | rkn5        | T0.1.01       | E32M4920      | –                     | 0.16      | 3.7                      |
|                            |               | rkn6        | T0.7.37       | E46M3201      | –                     | 0.20      | 4.4                      |
|                            |               | rkn7        | T0.7.39       | E32M3722      | –                     | 0.32      | 11.5                     |
|                            | Beauregard    | rkn8        | B0.4.24       | E40M6008      | –                     | 0.20      | 4.5                      |
|                            |               | rkn9        | B0.7.39       | E42M3525      | –                     | 0.17      | 2.2                      |
| Top weight                 | Nancy Hall    | TW          | NH Group 9    | ISSR 807-7    | 4.9                   | 198.72    | 20.5                     |
|                            |               | TW1         | TN27 Group 11 | ISSR 857-2    | 5.2                   | 114.27    | 16.0                     |
|                            |               | TW2         | TN27 Group 11 | ISSR 824-3    | 5.8                   | 140.44    | 20.2                     |
|                            |               | TW3         | TN27 Group 12 | ISSR 857-5    | 6.0                   | 127.68    | 24.7                     |
|                            | Tainung 27    | RW1         | NH Group 8    | ISSR 822-4    | 3.2                   | 121.24    | 25.1                     |
|                            |               | RW2         | NH Group 9    | ISSR 807-7    | 3.4                   | 109.38    | 29.5                     |
|                            | Nancy Hall    | SC1         | NH Group 1    | ISSR 809-3    | 5.8                   | 2.80      | 20.5                     |
|                            |               | SC2         | NH Group 3    | ISSR 826-4    | 4.1                   | 2.41      | 14.2                     |
|                            |               | SC3         | NH Group 4    | ISSR 827-6    | 4.3                   | 1.83      | 15.9                     |
|                            | Tainung 27    | SC1         | TN27 Group 1  | ISSR 819-6    | 2.9                   | 1.92      | 20.4                     |
|                            |               | SC2         | TN27 Group 2  | ISSR 811-5    | 5.0                   | 1.18      | 28.3                     |
|                            |               | SC3         | TN27 Group 11 | ISSR 857-2    | 4.2                   | 1.71      | 22.8                     |
| Root weight               | Nancy Hall    | FC1         | NH Group 1    | ISSR 809-7    | 2.7                   | 1.54      | 10.7                     |
|                            |               | FC2         | NH Group 2    | ISSR 811-1    | 5.9                   | 1.98      | 27.8                     |
|                            |               | FC3         | NH Group 6    | ISSR 809-14   | 2.5                   | 2.54      | 14.1                     |
|                            |               | FC4         | NH Group 7    | ISSR 825-16   | 2.5                   | 2.09      | 20.4                     |
|                            | Tainung 27    | FC1         | TN27 Group 3  | ISSR 810-4    | 3.9                   | 1.62      | 29.9                     |
|                            |               | FC2         | TN27 Group 12 | ISSR 857-6    | 3.8                   | 1.01      | 22.8                     |
| Root skin color           | Nancy Hall    | RS1         | NH Group 2    | ISSR 811-2    | 9.1                   | 1.51      | 20.0                     |
|                            |               | RS2         | NH Group 3    | ISSR 826-2    | 9.4                   | 1.80      | 26.1                     |
|                            |               | RS3         | NH Group 6    | ISSR 825-15   | 8.9                   | 2.31      | 29.8                     |
| Root shape                | Nancy Hall    | RN           | NH Group 9    | ISSR 823-7    | 2.7                   | 10.62     | 14.8                     |
| Dry-matter content        | Beauregard    | dm1          | B0.1.03       | E42M3421      | –                     | negative  | –                        |
|                            |               | dm2          | B0.4.23       | E43M5403      | –                     | negative  | –                        |
|                            |               | dm3          | B0.5.26       | E35M4511      | –                     | positive  | –                        |
|                            |               | dm4          | B0.7.40       | E32M3202      | –                     | positive  | –                        |
|                            |               | dm5          | B1.1.61       | E40M4010      | –                     | positive  | –                        |
|                            |               | dm6          | B1.1.62       | E36M5103      | –                     | negative  | –                        |
|                            |               | dm7          | B1.2.00       | E34M4906      | –                     | negative  | –                        |
|                            |               | dm8          | B0.8.09       | E35M4086      | –                     | positive  | –                        |
|                            | Tanzania      | dm9          | T0.1.05       | E35M5603      | –                     | positive  | –                        |
|                            |               | dm10         | T0.2.97       | E43M5242      | –                     | negative  | –                        |
| Starch content            | Nancy Hall    | sta1         | B0.1.03       | E42M3421      | –                     | negative  | –                        |
|                            |               | sta2         | B0.4.23       | E43M5403      | –                     | negative  | –                        |
|                            |               | sta3         | B0.7.39       | E42M3525      | –                     | positive  | –                        |
|                            |               | sta4         | B0.7.40       | E32M3202      | –                     | positive  | –                        |
|                            |               | sta5         | B1.1.61       | E40M4010      | –                     | positive  | –                        |
|                            |               | sta6         | B1.1.62       | E36M5103      | –                     | negative  | –                        |
|                            |               | sta7         | B1.2.00       | E34M4906      | –                     | negative  | –                        |
|                            | Tanzania      | sta8         | T0.1.04       | E35M4203      | –                     | positive  | –                        |
|                            |               | sta9         | T0.2.97       | E43M5242      | –                     | negative  | –                        |
| β-Carotene content        | Nancy Hall    | caro1        | B0.4.23       | E43M5403      | –                     | positive  | –                        |
|                            |               | caro2        | B0.8.48       | E38M3725      | –                     | negative  | –                        |
|                            |               | caro3        | B1.1.62       | E36M5103      | –                     | positive  | –                        |
|                            |               | caro4        | B1.2.00       | E40M4002      | –                     | negative  | –                        |
|                            | Tanzania      | caro5        | T1.3.74       | E45M3611      | –                     | positive  | –                        |
|                            |               | caro6        | T1.3.76       | E40M3105      | –                     | positive  | –                        |
|                            |               | caro7        | T78           | E46M3901      | –                     | positive  | –                        |
|                            |               | caro8        | T82           | E36M4015      | –                     | negative  | –                        |
has hindered the validation of mapped regions and then isolation of target genes. Therefore, further research, especially to establish a genome sequence and gene annotation, is needed to validate QTL mapping results and to assist in marker-assisted sweetpotato breeding programs.

3. Future research

Recently, NGS technologies have been applied to whole genome sequencing, genome-wide genetic analysis, and high-density linkage map construction, and in sweetpotato, Hirakawa et al. (2015) reported the de novo whole-genome sequencing of Ipomoea trifida (H. B. K.) G. Don., which is considered to be the closest diploid ancestor of the hexaploid cultivated sweetpotato. In *I. trifida*, several ploidy levels from diploid (2n = 2x = 30) to hexaploid (2n = 6x = 90) exist (Kobayashi 1983), and it is considered a wild relative of the hexaploid sweetpotato, *I. batatas*, because the two species can hybridize (Komaki and Katayama 1999, Orjeda et al. 1991, Shiotani and Kawase 1989). In addition, since several molecular and cytogenetic studies have confirmed that the two species are closely related (Huang and Sun 2000, Jarret and Austin 1994, Komaki et al. 1998, Roullier et al. 2013, Srisuwan et al. 2006), the whole genome sequence information of this species is expected to dramatically promote genomic and genetic studies in *I. batatas*.

Higher density linkage maps will also be constructed by applying NGS-based genotyping methods, such as restriction site-associated DNA sequencing (RAD-seq), double digest RAD-seq (ddRAD-seq), and genotyping-by-sequencing (GBS), all of which facilitate the rapid discovery of thousands of single nucleotide polymorphisms (SNPs) in large sequences.

Table 3. (continued)

| Trait       | Cultivar   | Name of QTL | Linkage group | Closest marker | LOD (Additive) effect | R² (%) Paper |
|-------------|------------|-------------|---------------|----------------|-----------------------|--------------|
| Dry-matter content | Xu 781     | DMM_1       | XU781 (02.08) | E10M2-10s      | 4.7 positive         | 16.1         |
|             |            | DMM_2       | XU781 (02.08) | E45M58-14s     | 4.0 positive         | 16.3         |
|             |            | DMM_3       | XU781(03.13)  | E53M27-4s      | 3.0 positive         | 11.1         |
|             |            | DMM_4       | XU781(03.16)  | E51M8-14s      | 3.4 positive         | 17.7         |
|             |            | DMM_5       | XU781(04.19)  | E53M24-19s     | 2.8 positive         | 13.0         |
|             |            | DMM_6       | XU781(04.21)  | E53M41-14s     | 2.5 positive         | 9.8          |
|             |            | DMM_7       | XU781(05.25)  | E26M1-6s       | 2.6 negative         | 12.4         |
|             |            | DMM_8       | XU781(05.26)  | E7M51-6s       | 3.4 positive         | 12.8         |
|             |            | DMM_9       | XU781(06.31)  | E42M64-4s      | 4.3 positive         | 21.6         |
|             |            | DMM_10      | XU781(06.34)  | E51M28-6d      | 3.4 positive         | 10.7         |
|             |            | DMM_11      | XU781(06.36)  | C55-5s         | 4.4 positive         | 45.1         |
|             |            | DMM_12      | XU781(07.37)  | E4M24-26s      | 2.8 positive         | 9.6          |
|             |            | DMM_13      | XU781(07.40)  | E27M62-2d / E36M63-10ds | 5.3 positive   | 29.5         |
|             |            | DMM_14      | XU781(08.44)  | E53M7-3s       | 3.7 positive         | 13.4         |
|             |            | DMM_15      | XU781(09.50)  | E15M57-4d /C60-1s | 3.4 positive   | 20.7         |
|             |            | DMM_16      | XU781(09.50)  | C55-11s        | 3.7 negative         | 13.2         |
|             |            | DMM_17      | XU781(09.51)  | E40M11-8s      | 3.4 positive         | 13.0         |
|             |            | DMM_18      | XU781(11.57)  | E53M16-24s     | 3.1 positive         | 11.2         |
|             |            | DMM_19      | XU781(00.73)  | E60M5-16d      | 2.8 positive         | 9.7          |
|             |            | DMM_20      | XU781(00.74)  | E1M34-7s       | 4.2 positive         | 15.2         |
|             |            | DMM_21      | XU781(00.79)  | C20-2s         | 2.9 positive         | 9.3          |
|             |            | DMM_22      | XU781(00.80)  | E51M28-6d / C24-4d | 3.5 positive   | 31.2         |
|              | Xushu 18   | DMF_1       | XU781(02.09)  | E41M59-2s      | 2.8 positive         | 16.7         |
| Starch content |            | DMF_2       | XU781(03.13)  | E7M9-4ds       | 2.7 negative         | 12.1         |
|              | Xushu 18   | DMF_3       | XU781(06.35)  | E53M16-14ds    | 2.6 negative         | 9.0          |
|              |            | DMF_4       | XU781(06.35)  | E12M59-12d     | 3.0 negative         | 25.3         |
|              |            | DMF_5       | XU781(13.61)  | E52M13-10d     | 2.9 negative         | 10.5         |
|              |            | DMFN_1      | XU781(01.05)  | E31M19-21s     | 5.0 positive         | 20.5         |
|              |            | DMFN_2      | XU781(02.07)  | E51M28-6d      | 4.1 positive         | 14.4         |
|              |            | DMFN_3      | XU781(03.15)  | E17M5-18d      | 2.6 positive         | 10.6         |
|              |            | DMFN_4      | XU781(07.40)  | E36M63-10ds    | 7.2 positive         | 38.8         |
|              |            | DMFN_5      | XU781(08.45)  | E50M49-3d      | 4.6 positive         | 14.0         |
|              |            | DMFN_6      | XU781(10.54)  | C61-2d         | 2.5 positive         | 9.1          |
|              | Xushu 18   | DMMN_1      | XU781(05.27)  | E1M31-17ds     | 3.0 negative         | 16.1         |
|              |            | DMMN_2      | XU781(06.31)  | E50M12-8s      | 2.5 negative         | 14.3         |
| Storage root yield | Xushu 18   | YIEM_1      | XU781(04.20)  | E50M49-4d      | 10.1 negative        | 41.8         |
|              |            | YIEM_2      | XU781(07.38)  | IB_S10_9d      | 9.5 negative         | 37.0         |
|              |            | YIEM_3      | XU781(07.41)  | E54M5-4d       | 11.1 positive        | 51.2         |
|              |            | YIEM_4      | XU781(07.42)  | E21M8-23d      | 10.8 negative        | 46.8         |
|              |            | YIEM_5      | XU781(12.61)  | IB_S10_4d      | 3.9 negative         | 44.1         |
|              | Xushu 18   | YIEF_1      | XU781(01.01)  | E24M1-7d       | 5.3 negative         | 36.3         |
|              |            | YIEF_2      | XU781(03.16)  | E53M30-12d     | 4.6 positive         | 59.3         |
|              |            | YIEF_3      | XU781(11.55)  | E27-8s         | 9.1 positive         | 42.9         |
|              |            | YIEF_4      | XU781(13.62)  | E63M3-10d      | 5.4 positive         | 44.0         |

'–': no information in the paper.
populations by sequencing only the target DNA regions that flank specific restriction enzyme sites (Baird et al. 2008, Elshire et al. 2011, Miller et al. 2007, Peterson et al. 2012, Van Tassell et al. 2008). To date, these methods have already yielded a number of high-density, SNP-based linkage maps, even in non-model species (Baird et al. 2008, Baxter et al. 2011, Bielenberg et al. 2015, Chutimanitsakun et al. 2011, Gardner et al. 2014, Guajardo et al. 2015, İpek et al. 2016, Ma et al. 2012, Poland et al. 2012, Pootakham et al. 2015, Russell et al. 2014, Shirasawa et al. 2016a, Spindel et al. 2013, Verma et al. 2015, Wang et al. 2012, Ward et al. 2013, Wu et al. 2014, Xiao et al. 2015), and in sweetpotato, genotyping and linkage map construction with RAD-seq is already underway (Shirasawa et al. 2016b).

It is generally expected that higher density linkage maps will facilitate rapid and precise QTL detection, as well as the development of molecular markers associated with agronomically important traits, such as disease resistance, root yield, and nutrient content. On the other hand, novel NGS-based methods, such as genome-wide association study, genomic selection, MutMap, and QTL-seq, have also been established and widely applied in several plant species (Abe et al. 2012, Das et al. 2015, Fekih et al. 2013, Huang et al. 2010, Illa-Berenguer et al. 2015, Lu et al. 2014, Singh et al. 2016, Spindel et al. 2015, Takagi et al. 2013a, 2013b, Tian et al. 2011, Wang et al. 2014), without the need to construct linkage maps. However, although these methods are extremely powerful for accelerating plant breeding programs, the application of such methods in sweetpotato are limited by several barriers related to its complex genome structure, heterozygosity, huge genome size, and polyploidy. In addition, the collection and maintenance of large mapping populations are time and labor intensive in sweetpotato, owing to crop’s size, cultivation form, and space requirements, thus further limiting the application of genetic studies. Therefore, researchers from different disciplines will need to collaborate, in order to decipher the crop’s complex genetic architecture, to facilitate genetic studies, and to develop marker-assisted breeding programs, by identifying genes and genomic regions that are involved in agronomically important traits.

**Literature Cited**

Abe, A., S. Kosugi, K. Yoshida, S. Natsume, H. Takagi, H. Kanzaki, H. Matsumura, K. Yoshida, C. Mitsuoka, M. Tamiru et al. (2012) Genome sequencing reveals agronomically important loci in rice using MutMap. Nat. Biotechnol. 30: 174–178.

Baird, N.A., P.D. Etter, T.S. Atwood, M.C. Currey, A.L. Shiver, Z.A. Lewis, E.U. Selker, W.A. Cresko and E.A. Johnson (2008) Rapid SNP discovery and genetic mapping using sequenced RAD markers. PLoS ONE 3: e3376.

Baxter, S.W., J.W. Davey, J.S. Johnson, A.M. Shelton, D.G. Heckel, C.D. Jiggins and M.L. Blaxter (2011) Linkage mapping and comparative genomics using next-generation RAD sequencing of a non-model organism. PLoS ONE 6: e19315.

Bielenberg, D.G., B. Rauh, S. Fan, K. Gasic, A.G. Abbott, G.L. Reighard, W.R. Okie and C.E. Wells (2015) Genotyping by sequencing for SNP-based linkage map construction and QTL analysis of chilling requirement and bloom date in peach (Prunus persica (L.) Batsch). PLoS ONE 10: e0139406.

Brondani, C., P.H.N. Rangel, R.P.V. Brondani and M.E. Ferreira (2002) QTL mapping and introgression of yield-related traits from Oryza glumaepatula to cultivated rice (Oryza sativa) using microsatellite markers. Theor. Appl. Genet. 104: 1192–1203.

Cervantes-Flores, J.C., G.C. Yencho and E.L. Davis (2002a) Efficient evaluation of resistance to three root-knot nematode species in selected sweetpotato cultivars. Hort. Sci. 37: 390–392.

Cervantes-Flores, J.C., G.C. Yencho and E.L. Davis (2002b) Host reactions of sweetpotato genotypes to root-knot nematodes and variation in virulence of Meloidogyne incognita populations. Hort. Sci. 37: 1112–1116.

Cervantes-Flores, J.C., G.C. Yencho, A. Kriegner, K.V. Pecota, M.A. Faulk, R.O.M. Mwang and B.R. Sosinski (2008a) Development of a genetic linkage map and identification of homologous linkage groups in sweetpotato using multiple-dose AFLP markers. Mol. Breed. 21: 511–532.

Cervantes-Flores, J.C., G.C. Yencho, K.V. Pecota and B. Sosinski (2008b) Detection of quantitative trait loci and inheritance of root-knot nematode resistance in sweetpotato. J. Am. Soc. Hortic. Sci. 133: 844–851.

Cervantes-Flores, J.C., B. Sosinski, K.V. Pecota, R.O.M. Mwang and G.L. Catignani, V.D. Truong, R.H. Watkins, M.R. Ulmer and G.C. Yencho (2011) Identification of quantitative trait loci for dry-matter, starch, and β-carotene content in sweetpotato. Mol. Breed. 28: 201–216.

Chang, K.Y., H.F. Lo, Y.C. Lai, P.J. Yao, K.H. Lin and S.Y. Hwang (2009) Identification of quantitative trait loci associated with yield-related traits in sweet potato (Ipomoea batatas). Bot. Stud. 50: 43–55.

Chutimanitsakun, Y., R.W. Nipper, A. Cuesta-Marcos, L. Cistue, A. Corey, T. Filichkina, E.A. Johnson and P.M. Hayes (2011) Construction and application for QTL analysis of a restriction site associated DNA (RAD) linkage map in barley. BMC Genomics 12: 4.

Das, S., H.D. Upadhyaya, D. Bajaj, A. Kujur, S. Badoni, Laxmi, V. Kumar, S. Tripathi, C.L. Laxmi and Gowda, S. Sharma et al. (2015) Deploying QTL-seq for rapid delineation of a potential candidate gene underlying major trait-associated QTL in chickpea (Cicer arietinum L.). DNA Res. 22: 193–203.

Elshire, R.J., J.C. Glaubitz, Q. Sun, J.A. Poland, K. Kawamoto, E.S. Buckler and S.E. Mitchell (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS ONE 6: e19379.

Fekih, R., H. Takagi, M. Tamiru, A. Abe, S. Natsume, H. Yaegashi, S. Sharma, S. Sharma, H. Kanzaki, H. Matsumura et al. (2013) MutMap+: genetic mapping and mutant identification without crossing in rice. PLoS ONE 8: e68529.

Gardner, K.M., P.J. Brown, T.F. Cooke, S. Cann, F. Costa, C. Bustamante, R. Velasco, M. Troggio and S. Myers (2014) Fast and cost-effective genetic mapping in apple using next-generation sequencing. G3 (Bethesda) 4: 1681–1687.

Goodwin, S., J.D. McPherson and W.R. McCombie (2016) Coming of age: ten years of next-generation sequencing technologies. Nat. Rev. Genet. 17: 333–351.

Grattapaglia, D. and R. Sederoff (1994) Genetic linkage maps of Eucalyptus grandis and Eucalyptus urophylla using a pseudo-testcross: mapping strategy and RAPD markers. Genetics 137: 1121–1137.

Guajardo, V., S. Solis, B. Sagredo, F. Gainza, C. Munoz, K. Gasic and
Genetic linkage analysis in sweetpotato

P Hinrichsen (2015) Construction of high density sweet cherry (Prunus avium L.) linkage maps using microsatellite markers and SNPs detected by genotyping-by-sequencing (GBS). PLoS ONE 10: e0127750.

Heard, E., S. Tishkoff, J.A. Todd, M. Vidal, G.P. Wagner, J. Wang, D. Weigel and R. Young (2010) Ten years of genetics and genomes: what have we achieved and where are we heading? Nat. Rev. Genet. 11: 723–733.

Hirakawa, H., Y. Okada, H. Tabuchi, K. Shirasawa, A. Watanabe, H. Tsuruoka, C. Minami, S. Nakayama, S. Sasamoto, M. Kohara et al. (2015) Survey of genome sequences in a wild sweet potato, Ipomoea trifida (H. B. K.) G. Don. DNA Res. 22: 171–179.

Huang, J.C. and M. Sun (2000) Genetic diversity and relationships of sweetpotato and its wild relatives in Ipomoea series Batatas (Convolvulaceae) as revealed by inter-simple sequence repeat (ISSR) and restriction analysis of chloroplast DNA. Theor. Appl. Genet. 100: 1050–1060.

Huang, X., X. Wei, T. Sang, Q. Zhao, Q. Feng, Y. Zhao, C. Li, C. Zhu, T. Lu, Z. Zhang et al. (2010) Genome-wide association studies of 14 agronomic traits in rice landraces. Nat. Genet. 42: 961–967.

Ilia-Berenguer, E., J.V. Houten, Z. Huang and E. van der Knaap (2015) Rapid and reliable identification of tomato fruit weight and locale number loci by QT-loci. Theor. Appl. Genet. 128: 1329–1342.

Ipek, A., K. Yilmaz, P. Sikici, N.A. Tangu, A.T. Oz, M. Bayraktar, M. Ipek and H. Gullen (2016) SNP discovery by GBS in olive and the construction of a high-density genetic linkage map. Biochem. Genet. 54: 313–325.

Isidore, E., H. van Os, S. Andrzejewski, J. Bakker, I. Barrena, G.J. Bryan, B. Caromel, H. van Eek, B. Ghareeb, W. de Jong et al. (2003) Toward a marker-dense meiotic map of the potato genome: lessons from linkage group I. Genetics 165: 2107–2116.

Japan Root and Tuber Crops Development Association Inc. Foundation (2010) Encyclopedia of sweetpotato.

Jarret, R.L. and D.F. Austin (1994) Genetic diversity and systematic relationship in sweetpotato (Ipomoea batatas (L.) Lam.) and related species as revealed by RAPD analysis. Genet. Resour. Crop Evol. 41: 165–173.

Jones, A. (1965) Cytological observations and fertility measurements of sweet potato (Ipomoea batatas (L.) Lam.). Proc. Am. Soc. Hort. Sci. 86: 527–537.

Jones, A. (1967) Theoretical segregation ratios of qualitatively inherited characters for hexaploid sweetpotato (Ipomoea batatas L.). Technical Bulletin No. 1368. U. S. Department of Agriculture, Economic Research Service, Washington, pp. 1–6.

Kai, Y., K. Katayama, T. Sakai and M. Yoshinaga (2004) Ayakomachi: a new sweetpotato cultivar for cooling material and table use. Sweetpotato Research Front 17: 4.

Kai, Y., K. Katayama, T. Sakai and M. Yoshinaga (2010) Beniharuka: a new sweetpotato cultivar for table use. Sweetpotato Research Front 23: 2.

Kalander, R. (2011) The use of retrotransposon-based molecular markers to analyze genetic diversity. Ratar. Povrt. 48: 261–274.

Kalander, R., A.J. Flavell, T.H.N. Ellis, T. Sjakste, C. Moisy and A.H. Schulman (2011) Analysis of plant diversity with retrotransposon-based molecular markers. Heredity (Edinh) 106: 520–530.

Katayama, K., S. Tamiya, T. Kuranouchi, K. Komaki and N. Nakatani (2003) New Sweetpotato cultivar “Quick Sweet”. Bull. Natl. Inst. Crop Sci. 3: 35–52.

Kobayashi, M. (1983) The Ipomoea trifida complex closely related to sweet potato. In: Shideler, S.F. and H. Rincón (eds.) Proceedings of the 6th Symposium of the International Society of Tropical Root Crops. International Potato Center, Lima, pp. 561–568.

Komaki, K., H.N. Regmi, K. Katayama and S. Tamiya (1998) Morphological and RAPD pattern variations in sweetpotato and its closely related species. Breed. Sci. 48: 281–286.

Komaki, K. and K. Katayama (1999) Root thickness of diploid Ipomoea trifida (H. B. K.) G. Don and performance of progeny derived from the cross with sweetpotato. Breed. Sci. 49: 123–129.

Krieger, A., J.C. Cervantes, K. Burg, R.O.M. Mwanga and D. Zhang (2003) A genetic linkage map of sweetpotato [Ipomoea batatas (L.) Lam.] based on AFLP markers. Mol. Breed. 11: 169–185.

Kumar, A. and H. Hirochika (2001) Applications of retrotransposons as genetic tools in plant biology. Trends Plant Sci. 6: 127–134.

Lawrence, G.W., C.A. Clark and V.L. Wright (1986) Influence of Meloidogyne incognita on resistant and susceptible sweet potato cultivars. J. Nematol. 18: 59–65.

Li, A.X., Q.C. Liu, Q.M. Zhang, L.M. Zhang, H. Zhai and S.Z. Liu (2010) Construction of molecular linkage maps using SRAP markers in sweetpotato. Acta Agron. Sin. 36: 1286–1295.

Li, H., N. Zhao, X. Yu, Y. Liu, H. Zhai, S. He, Q. Li, D. Ma and Q. Liu (2014) Identification of QTLs for storage root yield in sweetpotato. Sci. Hortic. 170: 182–188.

Lu, H., T. Lin, J. Klein, S. Wang, J. Qi, Q. Zhou, J. Sun, Z. Zhang, Y. Weng and S. Huang (2014) QT-loci seq identifies an early flowering QTL located near Flowering Locus T in cucumber. Theor. Appl. Genet. 127: 1491–1499.

Ma, X.F., E. Jensen, N. Alexandrov, M. Troukhan, L. Zhang, S. Thomas-Jones, K. Farrar, J. Clifton-Brown, I. Domnison, T. Swaller et al. (2012) High resolution genetic mapping by genome sequencing reveals genome duplication and tetraploid genetic structure of the diploid Miscanthus sinensis. PLoS ONE 7: e33821.

Magooni, M.L., R. Krishnan and K. Vijaya Bai (1970) Cytological evidence on the origin of sweet potato. Theor. Appl. Genet. 40: 360–366.

Miller, M.R., J.P. Dunham, A. Amores, W.A. Cresko and E.A. Johnson (2007) Rapid and cost-effective polymorphism identification and genotyping using restriction site associated RNA (RAD) markers. Genome Res. 17: 240–248.

Monden, Y., A. Yamamoto, A. Shindo and M. Tahara (2014) Efficient DNA fingerprinting based on the targeted sequencing of active retrotransposon insertion sites using a bench-top high-throughput sequencing platform. DNA Res. 21: 491–498.

Monden, Y., T. Hara, Y. Okada, O. Jahan, A. Kobayashi, H. Tabuchi, S. Onaga and M. Tahara (2015) Construction of a linkage map based on retrotransposon insertion polymorphisms in sweetpotato via high-throughput sequencing. Breed. Sci. 65: 145–153.

Nakayama, H., M. Tanaka, Y. Takahata, K. Matsu, H. Iwahori, Z. Sano and M. Yoshinaga (2012) Development of AFLP-derived SCAR markers associated with resistance to two races of southern root-knot nematode in sweetpotato. Euphytica 188: 175–185.

Nelsen, R., J.S. Paul, A. Albrectsen and Y.S. Song (2011) Genotype and SNP calling from next-generation sequencing data. Nat. Rev. Genet. 12: 443–451.

Orjeda, G., R. Freyre and M. Iwanaga (1991) Use of Ipomoea trifida germplasm for sweet potato improvement. 3. Development of 4x interspecific hybrids between Ipomoea batatas (L.) Lam. (2n = 6x = 90) and I. trifida (H. B. K.) G. Don. (2n = 2x = 30) as storage-root initiators for wild species. Theor. Appl. Genet. 83: 159–163.

Person, L.H. and W.J. Martin (1940) Soil rot of sweet potatoes in Louisiana. Phytopathology 30: 913–926.
(2012) Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. PLoS ONE 7: e37135.

Poczaí, P., I. Varga, M. Laos, A. Cseh, N. Bell, J.P. Valkonen and J.Hyvönén (2013) Advances in plant gene-targeted and functional markers: a review. Plant Methods 9: 6.

Poland, J.A., P.J. Brown, M.E. Sorrells and J.L. Jannink (2012) Development of high-density genetic maps for barley and wheat using a novel two-enzyme genotyping-by-sequencing approach. PLoS ONE 7: e32253.

Pootakham, W., P. Ruang-Aree Natee, N. Jomchai, C. Sonthired, D. Sangsraukru, Y. Yoocha, K. Theerawattanaskul, K. Nirapathpongpoorn, P. Romruensukhrom, S. Tragoornung et al. (2015) Construction of a high-density integrated genetic linkage map of rubber tree (Hevea brasiliensis) using genotyping-by-sequencing (GBS). Front. Plant Sci. 6: 367.

Roullier, C., A. Duputié, P. Wennekes, L. Benoit, V.M. Fernández Bringas, G. Rossel, D. Tay, D. McKey and V. Lebot (2013) Disentangling the origins of cultivated sweet potato (Ipomoea batatas (L.) Lam.). PLoS ONE 8: e62707.

Russell, J., C. Hackett, P. Hedley, H. Liu, L. Milne, M. Bayer, D. Marshall, L. Jorgensen, S. Gordon and R. Brennan (2014) The use of genotyping by sequencing in blackcurrant (Ribes nigrum): developing high-resolution linkage maps in species without reference genome sequences. Mol. Breed. 33: 835–849.

Sakai, T., T. Kumagai, Y. Kai, K. Ishiguro, O. Yamakawa, K. Katayama, Y. Nakazawa and M. Yoshinaga (2010) “Akemurasaki”: a new sweetpotato cultivar. Bull. NARO Kyushu Okinawa Agric. Res. Cent. 53: 1–24.

Sano, Z.I., H. Iwahori, Y. Tateishi and Y. Kai (2002) Differences in the genome sequences of LTR retrotransposons as molecular markers in plants. Methods Mol. Biol. 260: 145–173.

Shiotani, I. V. and T. Kawase (1989) Genomic structure of the sweet potato (Ipomoea batatas (L.) Lam.). J. Hered. 44: 207–211.

Shirasa, K., H. Hirakawa and S. Isobe (2016a) Analytical workflow of double-digest restriction site-associated DNA sequencing based on empirical and optimization in tomato. DNA Res. 23: 145–153.

Shirasa, K., M. Tanaka, Y. Takahata, D. Ma, Q. Cao, Q. Liu, H. Zhai, S.S. Kwak, J.C. Jeong, U.H. Yoon (2016b) A high-density SNP genetic map in autoploid sweetpotato (2n=6x=90). Abst. The 130th Meeting of the Japanese Society of Breeding. pp. 47.

Singh, V.K., A.W. Khan, D. Jaganathan, M. Thudi, M. Roorkiwal, H. Takagi, V. Garg, V. Kumar, A. Chitikineni, P.M. Gaur et al. (2016) QTL-seq for rapid identification of candidate genes for 100-seed weight and root/total plant dry weight ratio under rainfed conditions in chickpea. Plant Biotechnol. J. 14: 2110–2119.

Sinha, S. and S.N. Sharma (1992) Taxonomic significance of karyomorphology in Ipomoea spp. Cytologia 57: 289–293.

Spindel, J., M. Wright, C. Chen, J. Cobb, J. Gage, S. Harrington, M. Lorieux, N. Ahmadi and S. McCouch (2013) Bridging the genotyping gap: using genotyping by sequencing (GBS) to add high-density SNP markers and new value to traditional bi-parental mapping and breeding populations. Theor. Appl. Genet. 126: 2699–2716.

Spindel, J., H. Begum, D. Akdemir, P. Virk, B. Collard, E. Redona, G. Atlin, J.L. Jannink and S.R. McCouch (2015) Genomic selection and association mapping in rice (Oryza sativa): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines. PLoS Genet. 11: e1004982.

Srisuwan, S., D. Sihachakr and S. Siljak-Yakovlev (2006) The origin and evolution of sweet potato (Ipomoea batatas Lam.) and its wild relatives through the cytogenetic approaches. Plant Sci. 171: 424–433.

Takahara, M., T. Aoki, S. Suzuki, H. Yamashita, M. Tanaka, S. Matsunaga and S. Kokumai (2004) Isolation of an active element from a high-copy-number family of retrotransposons in the sweetpotato genome. Mol. Genet. Genomics 272: 116–127.

Takagi, H., A. Abe, K. Yoshida, S. Kosugi, S. Natsume, C. Mitsuoka, A. Uemura, H. Utsushi, M. Tamiru, S. Takuno et al. (2013a) QTL-seq: rapid mapping of quantitative trait loci in rice by whole genome resequencing of DNA from two bulked populations. Plant J. 74: 174–183.

Takagi, H., A. Uemura, H. Yaegashi, M. Tamiru, A. Abe, C. Mitsuoka, H. Utsushi, S. Natsume, H. Kanzaki, H. Matsuura et al. (2013b) MutMap-Gap: whole-genome resequencing of mutant F2 progeny bulk combined with de novo assembly of gap regions identifies the rice blast resistance gene. New Phytol. 200: 276–283.

Tamiya, S., M. Nakatani, K. Komaki, K. Katayama and T. Kuranouchi (2003) New sweet potato cultivar “Purple Sweet Lord”. Bull. Natl. Inst. Crop Sci. 4: 29–32.

Tanksley, S.D., M.W. Granal, J.P. Prince, M.C. de Vicente, M.W. Bonierbale, P. Broun, T. Moulton, J.J. Giovannoni, S. Grandillo, G.B. Martin et al. (1992) High density molecular linkage maps of the tomato and potato genomes. Genetics 132: 1141–1160.

Tian, F., P.J. Bradbury, P.J. Brown, H. Hung, Q. Sun, S. Flint-Garcia, T.R. Rocheford, M.D. McMullen, J.B. Holland and E.S. Buckler (2011) Genome-wide association study of leaf architecture in the maize nested association mapping population. Nat. Genet. 43: 6–11.

Ting, Y.C. and A.E. Kehr (1953) Meiotic studies in the sweetpotato (Ipomoea batatas Lam.). J. Hered. 44: 207–211.

Truco, M.J., R. Antonise, D. Lavelle, O. Ochoa, A. Kozik, H. Witsenboer, S.B. Fort, M.J.W. Jeuken, R.V. Kesseli, P. Lindhout et al. (2007) A high-density, integrated genetic linkage map of lettuce (Lactuca spp.). Theor. Appl. Genet. 115: 735–746.

Ukoskit, K. and P.G. Thompson (1997) Autopolyploidy versus allopolyploidy and low-density randomly amplified polymorphic DNA linkage maps of sweetpotato. J. Am. Soc. Hortic. Sci. 122: 822–828.

Van Tassell, C.P., T.P.L. Smith, L.K. Matukumalli, J.F. Taylor, R.D. Schnabel, C.T. Lawley, C.D. Haudenschild, S.S. Moore, W.C. Warren and T.S. Sonstegard (2008) SNP discovery and allele frequency estimation by deep sequencing of reduced representation libraries. Nat. Methods 5: 247–252.

Verma, S., S. Gupta, N. Bandihiwati, T. Kumar, C. Bhardwaj and S. Bhatia (2015) High-density linkage map construction and mapping of seed trait QTLs in chickpea (Cicer arietinum L.) using genotyping-by-sequencing (GBS). Sci. Rep. 5: 17512.

Wang, Y., M.F. Mette, T. Miedaner, M. Gottwald, P. Wilde, J.C. Reif and Y. Zhao (2014) The accuracy of prediction of genomic selection in elite hybrid rice populations surpasses the accuracy of marker-assisted selection and in equally augmented by multiple field
evaluation locations and test years. BMC Genomics 15: 556.

Ward, J., J. Bhangoo, F. Fernández-Fernández, P. Moore, J.D. Swanson, R. Viola, R. Velasco, N. Bassil, C.A. Weber and D.J. Sargent (2013) Saturated linkage map construction in Rubus idaeus using genotyping by sequencing and genome-independent imputation. BMC Genomics 14: 2.

Wu, J., L.T. Li, M. Li, M.A. Khan, X.G. Li, H. Chen, H. Yin and S.L. Zhang (2014) High-density genetic linkage map construction and identification of fruit-related QTLs in pear using SNP and SSR markers. J. Exp. Bot. 65: 5771–5781.

Xiao, B., Y. Tan, N. Long, X. Chen, Z. Tong, Y. Dong and Y. Li (2015) SNP-based genetic linkage map of tobacco (Nicotiana tabacum L.) using next-generation RAD sequencing. J. Biol. Res. 22: 11.

Xiao-xia, Y., Z. Ning, L. Hui, J. Qin, Z. Hong, H. Shao-Zhen, L. Qiang and L. Qing-Chang (2014) Identification of QTLs for starch content in sweetpotato (Ipomoea batatas (L.) Lam.). J. Integr. Agric. 13: 310–315.

Yamakawa, O., M. Yoshinaga, M. Hidaka, T. Kumagai and K. Komaki (1997) “Ayamurasaki”, a new sweetpotato [Ipomoea batatas] cultivar. Bull. Kyushu Agr. Expt. Sta. 31: 1–22.

Yamakawa, O., M. Yoshinaga, T. Kumagai, M. Hidaka, K. Komaki, H. Kukimura and K. Ishiguro (1998) “J-Red”: A new sweetpotato cultivar. Bull. Kyushu Agr. Expt. Sta. 33: 49–72.

Yamakawa, O., T. Kumagai, M. Yoshinaga, K. Ishiguro, M. Hidaka, K. Komaki and H. Kukimura (1999) Sunny Red: new sweet potato cultivar for powder. Bull. Kyushu Natl. Agric. Exp. Sta. 35: 19–40.

Zhao, N., X. Yu, Q. Jie, H. Li, H. Hu, H. Zhai, S. He and Q. Liu (2013) A genetic linkage map based on AFLP and SSR markers and mapping of QTL for dry-matter content in sweetpotato. Mol. Breed. 32: 807–820.