Evaluation of mother and daughter root traits in sweet potato germplasm cultivated by direct planting

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ABSTRACT
Direct planting (i.e. the planting of seed roots) in sweet potato results in the formation of two root types – 'mother' and 'daughter' roots. High and stable daughter root yields are necessary to improve the acceptance of direct planting cultivation because mother roots have no commercial value. To establish a basis for the effective breeding, the root traits of 28 sweet potato genotypes cultivated by direct planting were evaluated for mother root weight, daughter root weight (DRW), total root weight (TRW), ratio of DRW to TRW (RDRW), and ratio of mother root enlargement. Significant differences between the genotypes were observed for all five traits (p < 0.01). However, we concluded that RDRW is a reliable indicator for performance under direct planting cultivation because it showed the highest estimated heritability (0.57), and genotypes with high RDRW also indicated notably low values for coefficient of variation.

Introduction
Sweet potato (Ipomoea batatas (L.) Lam.) is generally propagated using stem cuttings. However, stem cutting preparation accounts for over a third of the total labor associated with sweet potato cultivation in Japan (MAFF, 2020). In addition, the current propagation system is yet to be mechanized, thereby maintaining high labor demands and production costs. Thus, an alternative system is strongly needed to reduce production costs of sweet potato cultivation in Japan.

Direct planting systems, such as those used in potato (Solanum tuberosum L.) cultivation, involve the planting of seed roots rather than stem cuttings, can be implemented to reduce labor requirements and production costs (Shikata, 1976). However, this type of planting is not typically used in sweet potatoes because most sweet potato genotypes produce enlarged mother roots, which have no commercial value (George et al. 2011; Kobayashi, 1968). Indeed, direct planting in sweet potato cultivation results in the formation of both 'mother' roots, which develop from the planted seed roots, and 'daughter' roots, which are newly formed after planting; harvested mother roots are generally enlarged, owing to their function as a sink for...
photosynthetic products (Kobayashi, 1972), and are often deformed (Shikata, 1976), reducing their quality and commercial value.

Long-term breeding efforts for the generation of direct planting cultivars (Kobayashi, 1968, 1972; Kusuhara et al., 1972) have improved breeding materials, in regard to resistance against mother root enlargement, and several promising cultivars (e.g. 'Tamaakane') have been released (Sakai et al., 2011). However, few farmers have shifted to direct-planting systems and cultivars because of their inferior yield. Furthermore, George et al. (2014) reported a significant genotype × environment interaction and yield instability in direct-planted sweet potato. Thus, cultivars with higher and more stable daughter root yields are needed to promote direct planting cultivation in Japan.

Efficient breeding programs for developing direct-planting cultivars require a better understanding of sweet potato root traits. Genotypes must be screened over multiple years based on root traits, but the heritability of root traits have rarely been investigated in terms of direct planting (George et al. 2011; Kusuhara et al., 1972). In addition to a shortage of previous reports on this topic, these reports are a mixture of experiments using cut roots as seeds and experiments using whole roots as seeds. A seed root planter for direct planting cultivation in sweet potato was newly developed to reduce high labor demands (Matsuo & Ishii, 2021). This machine was designed to plant whole roots and not cut roots. This is because the practice of cutting roots requires labor and increases the risk of rot before sprouting (Nakazawa, 1973), although cutting increases the number of seed root pieces. Besides, cutting seed roots is known to affect the degree of mother root enlargement (Adachi et al., 2011; Nakazawa, 1973). Therefore, results from experiments using whole roots as seeds become more important when we assume to plant seed roots by this type of a machine. Thus, the aim of the present study was to evaluate genotypic traits of mother and daughter roots, including their heritability, using whole roots as seeds to improve breeding indicators in direct planting cultivation.

**Materials and methods**

**Experimental site and plant materials**

Field experiments were performed over three years (2019–2021) at the Kyushu-Okinawa Agricultural Research Center, NARO, Miyakonojo, Miyazaki Prefecture, Japan (31°45 N, 131°00 E), using 28 genotypes (Table 1). Five of them (Nos.1–5 in Table 1) were derived from a direct planting breeding program, known to produce mother roots with limited enlargement, and classified as ‘indirect daughter root type’, since the plants produce daughter roots from adventitious sprouts, rather than from the mother root. The other 23 genotypes (Nos.6–28 in Table 1) were cultivars or landraces that were selected without consideration of direct planting suitability and covered a wide range of genetic diversity. The origins in Table 1 are described in accordance with the NARO GenBank database.

**Experimental design**

Direct planting was performed in late March, as described by Sakaigaichi et al. (2021), using whole roots as seeds that had been harvested in the prior fall and kept in a storehouse. Specifically, seed roots weighing 74–176, 40–177, and 52–167 g in 2019, 2020, and 2021, respectively, were planted on March 20, 2019, March 18, 2020, and March 24, 2021. The roots were planted in 0.74 m² plots, each containing three hills, at a density of 4.04 roots m⁻² (interhill space, 33 cm). Because it was difficult to prepare seed roots of 28 genotypes, this experiment was designed such that one replication plot was considered each year. In addition, chemical fertilizer (4 g N m⁻², 6 g P₂O₅ m⁻², and 10 g K₂O m⁻²) was applied as a basal dressing each year, and a black biodegradable film was mulched to warm the soil and inhibit weed growth.

**Harvesting and data processing**

Harvest surveys were conducted on September 3, 2019, August 31, 2020, and August 25, 2021. During each harvest, all storage roots were extracted from the plots using machines and then sorted into mother and daughter roots, without distinguishing between indirect and direct daughter roots. Fresh mother root weight per hill (MRW), fresh daughter root weight per hill (DRW), and total root weight per hill (TRW) were calculated. The ratio of DRW to TRW (RDRW) was also calculated as an index of yield partitioning, with values of 0.00 and 1.00 indicating yields of 100% mother roots and daughter roots, respectively. In addition, ratio of mother root enlargement (RMRE) was evaluated by calculating the ratio of MRW to initial seed root weight.

**Statistical analysis**

Coefficient of variation (CV) values were calculated for each variable in order to compare the degree of variation among genotypes, and analysis of variance
(ANOVA) and estimation of broad-sense heritability were performed according to Katayama et al. (1999). Specifically, ANOVA was performed using genotype as the fixed effect and year as a random effect. Meanwhile, heritability was calculated as follows:

\[ h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_y + \sigma^2_e) \]

where \( \sigma^2_g \), \( g \), \( y \), and \( e \) indicate variance, genotype, year, and error, respectively. Correlation among the variables (MRW, DRW, TRW, RDRW, and RMRE) was evaluated by calculating Pearson’s correlation coefficient (\( r \)). Statistical analyses were performed using the SPSS version 21.0 (IBM, Armonk, NY, USA).

**Results**

Mean MRW ranged from 61 g (‘Tamaakane’) to 833 g (‘Hawaii No. 2’; Table 1), and the MRW CV values ranged from 2% (‘Kyushu No. 199’) to 104% (‘Shiroyutaka’). The mean MRW values of ‘Suzukogane’ and ‘Resisto’ were as low as that of ‘Tamaakane’, and the mean MRW of ‘Koganesengan’ (728 g) was the second highest. Mean DRW ranged from 66 g (‘Hiyake’) to 1364 g (‘Kyushu No. 198’; Table 1), and the DRW CV values ranged from 10% (‘Kyushu No. 199’) to 138% (‘Hakusan Zairai’). The mean DRW values of ‘Suzugakone’, ‘Tamaakane’, and ‘Kyushu No. 199’ were as high as that of ‘Kyushu No. 198’. Mean TRW ranged from 440 g (‘Yen485’) to 1576 g (‘Kyushu No. 198’; Table 1), and the TRW CV values ranged from 2% (‘Beijing 553’) to 61% (‘Yen500’). In general, landraces or old cultivars, such as ‘Yen485’ and ‘Hiyake’, had lower TRWs. RDRW ranged from 0.10 (‘Hakusan Zairai’) to 0.95 (‘Tamaakane’; Table 1), and the RDRW CV values of the direct planting genotypes were very small (Nos.1 to 5). RMRE ranged from 0.53 (‘Tamaakane’) to 7.77 (‘Hakusan Zairai’; Table 1), and as observed for RDRW, the RMRE CV values of the direct planting genotypes were relatively small.

ANOVA indicated that genotypic differences among all five variables were significant (\( p < 0.01; \) Table 2) and that year had a significant effect on MRW, RDRW, and RMRE (\( p < 0.01 \)). Heritability was the highest for RDRW (0.57), followed by DRW (0.51), TRW (0.43), and RMRE (0.40), and was the lowest for MRW (0.33). In addition, MRW was significantly correlated with DRW, RDRW, and...
between daughter and mother roots was described ($h^2 = 0.4–0.6$); however, this result was obtained using cut roots as seeds. Kusuhara et al. (1972) indicated that a heritability of appearance of indirect root type was higher than that of other root types. Their report is helpful to discuss cross combination, but the heritability shown in this study is also worth screening clones in ongoing breeding programs. Consequently, we believe that the estimated heritability of root traits related using whole roots in this study is more useful in direct planting programs than that reported in previous studies.

This study indicates that RDRW (0.57) had a relatively higher heritability than DRW (0.51) for direct planting cultivation (Table 2). Interestingly, the genotypes with high RDRW also indicated notably low RDRW CV values (Figure 1). Furthermore, this trend was clearer for RDRW than for DRW (Figure 1). This result is novel considering previous reports (George et al. 2011; Kusuhara et al., 1972). This low variation in RDRW is especially valuable considering the typical year-to-year fluctuations observed during preliminary yield trials, which often involve small plot sizes. Thus, RDRW could significantly accelerate the early stages of direct planting breeding programs by providing a means of accurate genotype screening.

In addition to improving RDRW, breeding programs must also focus on increasing yield potential. For example, some genotypes (e.g. ‘Kyukie 366’; Table 1) may be associated with high RDRW but unimpressive DRW. However, focusing on the partitioning of photosynthetic products among the mother and daughter roots is likely to encourage the crossing of genotypes that are already deemed suitable for direct planting, and such inbreeding is likely to have a significant effect on overall yield (Yoshida, 1986). Therefore, broadening the genetic basis of breeding material is key to increasing yield under direct planting. Interestingly, the lack of correlation between TRW, which is related to yield potential, and RMRE (Table 3) suggests that high-yield direct planting cultivars can be developed, regardless of mother root enlargement, and that breeding programs should consider crossing high yield genotypes (e.g. ‘Shiroyutaka’; Table 1) with genotypes suitable for direct planting, such as those with high RDRW.

### Table 2. Analysis of variance and heritability of yield traits in 28 sweet potato genotypes cultivated by direct planting.

| Sources of variation | Degree of freedom | MRW | DRW | TRW | RDRW | RMRE |
|----------------------|-------------------|-----|-----|-----|------|------|
| Genotype (g)         | 2                 | 27  | 146,748 ** | 370,373** | 291,231** | 0.174** | 11.3** |
| Year (y)             | 2                 | 2   | 281,403 ** | 21,063 | 181,116 | 0.179** | 20.8** |
| Error (e)            | 54                | 54  | 53,984 | 91,326 | 87,455 | 0.031 | 3.4 |
| Heritability ($h^2$) |                   | 0.33 | 0.51 | 0.43 | 0.57 | 0.40 |

DRW, daughter root weight per hill; MRW, mother root weight per hill; RDRW, ratio of daughter root weight per hill to total root weight per hill; RMRE, ratio of mother root enlargement (i.e. ratio of MRW to seed root weight per hill); TRW, total root weight per hill; **, significant difference at $p < 0.01$. $MS_g = \sigma^2_e + 3 \sigma^2_g, MS_y = \sigma^2_e + 28 \sigma^2_y, MS_e = \sigma^2_y$ Heritability ($h^2$) = $\sigma^2_e/(\sigma^2_g + \sigma^2_y + \sigma^2_e)$

### Table 3. Correlation among root traits of 28 sweet potato genotypes cultivated by direct planting.

|          | MRW | DRW | TRW | RDRW | RMRE |
|----------|-----|-----|-----|------|------|
| MRW      | -   | -0.484** | -0.767** | 0.948** |
| DRW      | -   | 0.784** | 0.856** | -0.602** |
| TRW      | -   | 0.421* | -0.006 | |
| RDRW     | -   | -     | -0.861** | |
| RMRE     | -   | -     | -     | -     |

The results of the present study support previous reports, and thus indicate the reliability of our findings. For example, the present study determined that ‘Tamaakane’ sweet potato is suitable for direct planting, in terms of RDRW and RMRE (Table 1), as reported previously (Sakai et al., 2011), and ‘Koganonagan’ sweet potato, which is known to yield enlarged mother roots under direct planting (Adachi et al., 2012), yielded the second-largest MRW (Table 2).

As shown in Table 2, heritability was higher in RDRW (0.57) and DRW (0.51), but lower in RMRE (0.40) and MRW (0.33). These results suggest that breeding indicators based on daughter root traits, such as RDRW and DRW, are more reliable than those based on mother root traits, such as RMRE and MRW, in direct planting of sweet potato. The heritability of traits related to conventional transplanting has been investigated (Jones, 1977; Katayama et al., 1999; Yoshida, 1985) and subsequently used as indicators in breeding programs; however, few studies have evaluated the heritability of root traits in direct planting cultivation (Geroge et al. 2011; Kusuhara et al., 1972). In the review of Geroge et al. 2011, a heritability of partitioning in yield

Discussion

The results of the present study correspond to previous reports, and thus indicate the reliability of our findings. For example, the present study determined that ‘Tamaakane’ sweet potato is suitable for direct planting, in terms of RDRW and RMRE (Table 1), as reported previously (Sakai et al., 2011), and ‘Koganonagan’ sweet potato, which is known to yield enlarged mother roots under direct planting (Adachi et al., 2012), yielded the second-largest MRW (Table 2).

RMRE (Table 3). DRW was significantly correlated with TRW, RDRW, and RMRE, whereas TRW was significantly correlated with RDRW, and RDRW was significantly correlated with RMRE. However, no correlations were observed between either MRW and TRW ($r = 0.164, p = 0.405$) or TRW and RMRE ($r = -0.006, p = 0.975$).
In addition to daughter root yield, breeding programs must also focus on and improve other agronomic traits, such as disease resistance and root starch content. For example, the breeding of cultivars resistant to foot rot disease (*Diaporthe destruens* (Harter) Hirooka, Minosh., & Rossman) is an urgent issue, owing to its severe economic impact and recent discovery in the south Kyushu region of Japan (Kobayashi, 2019). The newly released cultivar ‘Konaishin’, which was developed for starch use and high yield, exhibits relatively high resistance to foot rot disease (Kobayashi, 2020) and, thus, represents a valuable breeding resource. Even though the suitability of ‘Konaishin’ sweet potato for direct planting is yet to be investigated, we believe that the findings of the present study would provide a basis for rapidly evaluating and introducing promising germplasm, such as ‘Konaishin’, as breeding materials, even without any prior knowledge of performance under direct planting.

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**Disclosure statement**

No potential conflict of interest was reported by the author(s).

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**Figure 1.** Relationship between daughter root traits and their variations. Black and white symbols (Nos. 1–5 and 6–28, respectively) indicate the genotypes derived from the direct planting breeding program and from other sources. CV, coefficient of variation; DRW, daughter root weight per hill; RDRW, ratio of daughter root weight per hill to total root weight per hill.
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