Variation in Growth and Yield Performance of Seventeen Water Chestnut Accessions (Trapa spp.) Collected from Asia and Europe

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Abstract: Water chestnut is an aquatic annual herb, and its fresh, edible fruit is a valuable crop. The huge variation in growth and yield of water chestnuts has not been well documented. In this study, the yield performance of 17 water chestnut lines, eight from China (Trapa acornis L., T. bicornis L., T. bispinosa Roxb., T. quadrispinosa Roxb), one from France (T. natans L.), one from India (T. bispinosa Roxb.), three from Italy (T. natans L.), three from Japanese (T. incisa L., T. japonica Flerov, T. natans L. var. rubeola Makino), and one from Korean (T. japonica Flerov.) were cultivated in Saga City, Japan during the summer, 2005, and the morphological characters of their fruit were analyzed. European lines were early flowering, but had a lower yield due to poor canopy density and lower rosette density. All the Asian lines had a higher rosette density. In spite of the smaller number of fruits per rosette, the Chinese lines had a higher yield than the other lines because the fruit was larger. The yield performance of the Indian line was similar to that of the Chinese lines. The Korean and Japanese lines produced a large number of small fruits per unit land area. Apart from the variation in fruit size, a huge variation in shape including the height, width and the spines were observed. Path analysis revealed that productive rosette number m⁻² and the single fresh fruit weight are two direct yield determinants while number of fruits per rosette has indirect negative influence on yield via productive rosette number and single fruit weight.

Key words: Aquatic plant, Paddy field cropping, Trapa, Water chestnut, Yield.

Water chestnut (Trapa sp.) is a common aquatic herb distributed in various parts of the world. It has been commercially cultivated for the edible fruits in water bodies of low, flat lands or lakes in India, China and Italy (Daniel et al., 1983; Kumar et al., 1985; Mazumdar, 1985). Its storage organ, the cotyledon, contains about 80% starch, 5% protein and significant amounts of vitamins (Tulyathan et al., 2005). In many countries in the torrid and temperate zones, people eat the fruit of the native stock as a grain food and the stem and leaves as vegetables. The fruit is used as a substitute for cereals in the Indian subcontinent. Production of water chestnut should help resolve global food problems to some extent and would help to utilize the increasing water levels due to global warming, at least partly. In Japan, water chestnut is distributed all over the country and locally introduced into paddy fields as an alternative crop (Momoshima and Nakamura, 1979; Arima et al., 1992a, 1999a).

In water chestnut, many physiological (Unni, 1984; Agrawal and Mohan, 1995; Smith, 1995; Groth et al., 1996) and agronomical studies (Kusum and Chandra, 1980; Arima et al., 1990, 1992a, 1992b, 1992c, 1999a) have been conducted. Vegetative growth characteristics and yield performance of several Japanese and Chinese water chestnut lines have been elucidated and the lines forming larger fruits were found to have a higher yield potential (Arima et al., 1999a). Apart from the fruit size, fruit number per unit land area and canopy characters such as rosette number, productivity of individual rosettes are also believed to be important yield determinants. However their relative contributions to final fruit yield have not been reported to date. Since water chestnut is distributed and used in most parts of the world, the analyses of both utilized and non-utilized lines in a single experiment may reveal the important yield components and their interrelationship. Therefore, in this study we examined both the vegetative and reproductive growth characteristics of 17 water chestnuts collected from Italy and France as European lines and from China, India, Japan and Korea as Asian lines, and evaluated fruit morphological characters in detail. The basic information obtained were used to examine the huge diversity of water chestnuts, and thereby to identify important yield components. Subsequent path analysis revealed the direct and indirect influences of yield components on fruit yield. This methodology can be used to characterize different ecotypes and for future breeding programs to
improve the yield.

Materials and Methods

1. Plant materials and growth conditions

Seventeen lines of water chestnut eight from China (Trapa acornis L., T. bicornis L., T. bispinosa Roxb., T. quadrispinosa Roxb.), one from France (T. natans L.), one from India (T. bispinosa Roxb.), three from Italy (T. natans L.), three from Japan (T. incisa L., T. japonica Flerov, T. natans L. var. rubrota Makino), and one from Korea (T. japonica Flerov) were used. Plots of 5 m × 30 cm land area and measured leaf area using an automatic area meter with at least three replications. The crop completed the life cycle with the onset of cold in autumn when the leaves turned yellowish and fell off. The fruit also dropped when mature. After the cropping season, the field was drained and the fruit was harvested. The number of fruits m⁻² and the fresh weight of the fruit were examined. The total fresh weight of fruit (yield) was determined as follows.

\[
\text{Yield (g m}^{-2}\text{)} = \frac{\text{Number of productive rosettes (m}^{-2}\text{)} \times \text{Number of fruits per rosette}}{\text{Fresh weight of a fruit (g)}} \tag{Eq-1}
\]

or,

\[
\text{Yield (g m}^{-2}\text{)} = \frac{\text{Number of fruits (m}^{-2}\text{)} \times \text{Fresh weight of a fruit (g)}}{\text{Eq-2}}
\]

At least ten randomly selected fruits were used to examine individual fruit characteristics estimation such as fresh and dry weights of fruit, edible portion percentage, fruit width and height. In order to estimate the edible portion percentage, fruit wall was peeled-off and the edible weight of a single fruit is given as a ratio to its total fresh weight was calculated.

2. Data collection

Two weeks after transplanting, we examined the plants for the number of rosettes m⁻², the number of leaves per rosette and the rosette diameter at two-week intervals. The number of leaves emerged per rosette per week was checked 4 to 6 weeks after transplanting, when the canopy showed exponential growth. The time to the first flower and the time to canopy fall are shown as the days from transplanting. The leaf area and the leaf area index (LAI) were measured at the beginning of flowering. To estimate the LAI, we harvested all the productive leaves from a 30 cm × 30 cm land area and measured leaf area using an automatic area meter with at least three replications. The crop completed the life cycle with the onset of cold in autumn when the leaves turned yellowish and fell off. The fruit also dropped when mature. After the cropping season, the field was drained and the fruit was harvested. The number of fruits m⁻² and the fresh weight of the fruit were examined. The total fresh weight of fruit (yield) was determined as follows.

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3. Statistical analyzes

Data were analyzed using the SAS package (Version 6.1). For the initial analysis, least squares were
obtained and the variations were expressed as standard errors. Further the correlation \( (r^2) \) was checked using Pearson’s correlation coefficient and the significance was expressed at \( \alpha = 0.05 \).

Path analysis was used to partition the relative contribution of yield components to yield via standardized partial-regression coefficients. The correlation coefficients were separated into direct and indirect influences that one variable has on another (Dewey and Lu, 1959). The model in Eq-1 is multiplicative and an additive model for path analysis was generated by logarithm transformation:

\[
\ln (Yield) = \ln (\text{Number of productive rosettes}) + \ln (\text{Number of fruits per rosette}) + \ln (\text{Fresh weight of a fruit}) \quad \text{Eq-3}
\]

The correlations among transformed variables of yield and yield components were assessed from the Pearson product moment correlation statistic from PROC CORR and path coefficients were obtained from standardized regression coefficients from PROC REG in SAS (Dewey and Lu, 1959; Ball et al., 2001). The direct effect of each yield component on yield is the path coefficient from that component to yield. The indirect effect of one component through a second component is the product of the path coefficient from the second component and the correlation between the two components (Dewey and Lu, 1959).

### Results

1. **Time to the first flower**

   Under the experimental conditions, the time to the first flower varied with the line of water chestnut. The European lines flowered the earliest, followed by Japanese, Korean, Chinese and Indian lines in this order (Table 1). The European lines flowered about one month after transplanting, but the Indian line flowered three months after transplanting. Water chestnuts collected from higher latitudes flowered early and a significant negative correlation was observed between the flowering time and the latitude of the collection site (Fig. 1).

2. **Vegetative growth characteristics**

   Throughout the growth period, a huge variation in morphological characteristics has been observed among the lines. After transplanting, the number of rosettes increased in all the lines, as was reported previously (Arima et al., 1999a). The number of rosettes per unit land area in the maximum canopy was between 5-160 rosettes m\(^{-2}\). Japan-3 was exceptional in producing an extraordinary large number of rosettes throughout the growth period, and produced the maximum canopy of 160 rosettes m\(^{-2}\) (Table 2). None of the Chinese lines produced more than 60 rosettes m\(^{-2}\) and the European lines had less than 11 rosettes m\(^{-2}\) even at the maximum growth stage. Even though a significant variation was observed in the rosette development among different lines, the rate of new leaf emergence in a rosette was the same in all the lines during the vegetative growth phase, which was around 6-7 leaves week\(^{-1}\) rosette\(^{-1}\) (Table 2). A huge variation in the productive rosette density was observed at the time of the first flower. The number of productive rosettes was 4 in Italy-3 and 113 in Japan-3 (Table 2). European lines produced a significantly smaller number of rosettes per unit land area. The diameter of the rosette also depended on the line throughout the growth period. European lines produced larger rosettes than the other lines, and Japan-3 had the smallest rosettes. The diameter of the largest rosette at the time of flowering was 38 cm in Italy-3 and 11 cm in Japan-3. A significant negative correlation \( (r^2 = -0.75) \) was observed between the number of rosettes per unit land area and the average
and they had an LAI of 1–1.5 (Table 2). The lines other and Japanese lines produced a moderate size canopy Indian and Chinese lines, LAI was over 2. The Korean lines, however, maintained green leaves until October and the Indian line until November (Table 1). Once water chestnut reached the flowering stage, achieving vertically oriented canopy architecture. the rosettes leaves over the water surface, instead of that is, the water surface was completely covered with rosette leaves. Once the canopy closure was achieved, new leaves tended to emerge from the water level due to the canopy crowding. In the European lines, however, due to the small number of rosettes per unit land area, enough space was available to spread the rosettes leaves over the water surface, instead of achieving vertically oriented canopy architecture. Once water chestnut reached the flowering stage, rosette production ceased. Therefore, the early-flowering European lines have a shorter duration for new rosette production. Leaves of the European lines turned yellow and fell in mid-September, the life cycle being completed very early. The Chinese, Japanese and Korean lines, however, maintained green leaves until October and the Indian line until November (Table 1).

### 3. Fruit yield

In general, the European lines produced a large number of fruits per rosette averaging 13–19 except for Italy-1 (Table 3). Chinese lines used in this experiment produced a smaller number of fruits per rosette compared with the European lines, China-1 and the China-5 had the smallest number of fruits per rosette. Similarly, the number of fruits per unit land area also varied greatly ranging from 36 to approximately 1500 fruits m$^{-2}$ (Table 3). On the average, the Korean and Japanese lines produced a significantly larger number of fruits m$^{-2}$ (greater than 180), Japan-3 produced over 1500 fruits m$^{-2}$. Italy-1 was an extraordinary line producing a small number of fruits per rosette and per land area. The Indian line was similar to the Chinese lines with respect to the fruit yield per unit land area, but the number of fruits per rosette was larger in the Indian line than in the other Chinese lines. Fruit weight, an agronomically important parameter, was heaviest in China-1 and China-8, fruit weight being over 1200 g m$^{-2}$ (Table 3). The Indian and European lines produced a large number of fruits per rosette, the Korean and Japanese lines produced a large number of fruits m$^{-2}$, the Chinese lines produced a larger fruit mass per unit land area compared to all other lines and it was over 650 g m$^{-2}$. In Italy-1, fruit weight was the lowest (90 g m$^{-2}$), which was due both to the smaller number of rosettes m$^{-2}$ and smaller number of fruits per rosette (Table 3).

Fruit characteristics are also important quality and quantity parameters apart from the bulk yield. Each fruit normally carries either two or four spines or splinters in the exodermis depending on the line. The spines are either very sharp or blunt depending on the species (Fig. 2). Except for China-1, 2, 3 and

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### Table 2. Vegetative growth characteristics of different water chestnuts lines.

| Line      | Number of maximum rosettes (m$^{-2}$) | Number of productive rosettes (m$^{-2}$) | Rosette diameter (cm) | Number of leaves per rosette | LAI | Leaf emergence rate (leaves per rosette week$^{-1}$) |
|-----------|--------------------------------------|------------------------------------------|-----------------------|-----------------------------|-----|-----------------------------------------------------|
| China-1   | 49±3.1                               | 36±1.2                                   | 21.8±0.4              | 23±0.5                      | 2.32±0.06 | 7.0±0.3                                           |
| China-2   | 30±3.2                               | 29±2.1                                   | 23.7±2.0              | 23±0.5                      | 2.06±0.07 | 7.5±0.4                                           |
| China-3   | 39±2.6                               | 27±0.9                                   | 24.7±1.8              | 23±0.4                      | 2.07±0.19 | 7.3±0.3                                           |
| China-4   | 36±2.7                               | 31±0.6                                   | 20.3±1.4              | 21±0.6                      | 2.12±0.02 | 7.2±0.4                                           |
| China-5   | 55±2.8                               | 38±2.8                                   | 16.7±0.8              | 25±0.3                      | 2.20±0.06 | 7.2±0.5                                           |
| China-6   | 51±3.4                               | 35±2.2                                   | 13.9±0.9              | 24±0.7                      | 2.22±0.09 | 6.8±0.3                                           |
| China-7   | 45±5.0                               | 37±1.9                                   | 14.7±1.0              | 22±1.1                      | 2.62±0.23 | 7.1±0.2                                           |
| China-8   | 29±4.3                               | 28±2.9                                   | 27.5±1.6              | 24±0.5                      | 2.14±0.03 | 7.5±0.3                                           |
| Korea     | 24±3.2                               | 19±1.4                                   | 27.7±1.5              | 23±0.8                      | 2.07±0.04 | 7.3±0.3                                           |
| France    | 9±0.8                                | 6±0.7                                    | 32.4±1.0              | 30±1.5                      | 0.43±0.09 | 6.9±0.3                                           |
| Italy-1   | 10±1.4                               | 9±1.4                                    | 24.3±0.7              | 34±2.1                      | 0.19±0.05 | 7.0±0.4                                           |
| Italy-2   | 9±1.1                                | 7±1.7                                    | 28.9±1.4              | 31±1.7                      | 0.24±0.01 | 7.2±0.2                                           |
| Italy-3   | 5±0.5                                | 4±0.8                                    | 38.3±2.5              | 40±1.0                      | 0.21±0.02 | 7.0±0.5                                           |
| Japan-1   | 33±2.8                               | 31±1.4                                   | 27.7±1.0              | 25±0.3                      | 1.37±0.08 | 6.9±0.3                                           |
| Japan-2   | 62±5.6                               | 62±2.3                                   | 19.2±0.9              | 21±0.8                      | 1.56±0.11 | 7.0±0.4                                           |
| Japan-3   | 161±16.3                             | 115±12.5                                 | 11.3±0.7              | 18±0.4                      | 1.15±0.08 | 6.5±0.4                                           |
| Korea     | 78±8.3                               | 75±11.7                                  | 15.3±0.4              | 22±0.8                      | 1.42±0.21 | 7.3±0.2                                           |

Maximum rosette number m$^{-2}$ was determined from a series of observations at two-week intervals. Leaf emergence rate in the vegetative phase, and all other estimates were made at the beginning of flowering. The values represent the mean ± S.E.; n=3 for the first two columns and n=10 for all other values.
4, all other lines had sharp spines (Table 4). All eight Chinese lines and the Indian line had significantly larger fruit in terms of fresh fruit weight, dry fruit weight, fruit height and fruit width compared with the European, Korean and Japanese lines. Japan-3 had the smallest fruits. Fresh weight of a single fruit varied from 0.21 to 20 g and dry weight from 0.14 to 7.42 g. China-1 and China-7 had the heaviest fresh and dry weights, respectively (Table 4). Fruit height varied from 9 to 34 mm and width from 4 to 26 mm. Edible portion were over 50% in fresh weight basis in all the lines and was as high as 86% in Japan-3.

### 4. Yield components and their contribution to yield

The model we used (Eq.3) with three independent yield components explained most of the variation in yield with adjusted $R^2$ value over 0.95 (Table 5). Regression analysis revealed the adequacy of the fitted model (Prob. > 0.0001; data not shown). Yield was significantly correlated with all three yield components, where number of fruits per rosette correlated negatively while productive rosette number m$^{-2}$ and fresh single fruit weight showed a positive correlation (Table 5). Productive rosette number m$^{-2}$ and fresh single fruit weight had higher direct effects, 1.2416 and 1.2654 respectively, and had minor negative indirect effects via other variables (Table 5). Even though the direct effect of the number of fruits per rosette was positive, large negative indirect effects of number of fruits per rosette on yield via productive rosette number m$^{-2}$ and fresh single fruit weight were observed (Table 5), reflecting the inverse relationship between the number of fruits per rosette and the yield.

### Discussion

In this study, we analyzed the fruit yield performance of 17 water chestnut lines collected from southern Europe and Asia in detail, along with several important vegetative growth characteristics. Rosette number is an important yield component since the rosette bears the fruit. New rosettes are produced from the lateral buds on the stem. However, once the water chestnut reaches the flowering stage, new rosette development stops and growth habit becomes determinate (Arima et al., 1992b, c, 1999a, b). Previously, we reported that vigorous vegetative growth in the early stages is indispensable to enhance the number of rosettes per land area (Arima et al., 1992a, b). Furthermore, the flower bud formation of water chestnut was found to be under the control of day length (Arima et al., 1993). Accordingly, European lines originating in high latitudes flowered very early and produced a smaller number of rosettes per unit land area and completed the life cycle very early. On the other hand, the Indian line, which originated in low latitude, required more than three months until flowering and around eight months to complete its life cycle. However, it should be emphasized that the growth durations and yield performances in their natural habitats might be slightly different from those at the experimental site due to the different environmental conditions.

Even though the European lines produced a smaller number of rosettes per unit land area, they tend to produce a large number of fruits per rosette. However, the number of fruits m$^{-2}$ was still smaller in the European lines. The Japanese and the Korean

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### Table 3. Canopy yield characteristic shown by yield components.

| Line       | Number of fruits per rosette | Number of fruits (m$^2$) | Total fruit weight (g m$^{-2}$) |
|------------|------------------------------|--------------------------|---------------------------------|
| China-1    | 1.8 ± 0.1                    | 63.8 ± 1.7               | 1223.6 ± 22.7                   |
| China-2    | 2.8 ± 0.4                    | 79.0 ± 4.8               | 969.0 ± 22.9                    |
| China-3    | 2.9 ± 0.3                    | 80.0 ± 5.8               | 736.0 ± 51.9                    |
| China-4    | 3.0 ± 0.2                    | 93.7 ± 4.0               | 869.0 ± 17.9                    |
| China-5    | 1.7 ± 0.2                    | 65.0 ± 2.8               | 827.0 ± 52.1                    |
| China-6    | 3.2 ± 0.1                    | 112.0 ± 4.2              | 676.0 ± 19.3                    |
| China-7    | 2.5 ± 0.2                    | 90.3 ± 1.9               | 982.7 ± 49.7                    |
| China-8    | 3.4 ± 0.7                    | 91.5 ± 9.8               | 1228.5 ± 32.6                   |
| India      | 3.9 ± 0.6                    | 71.0 ± 7.2               | 903.7 ± 101.7                   |
| France     | 16.0 ± 2.2                   | 99.3 ± 9.3               | 316.7 ± 34.0                    |
| Italy-1    | 4.4 ± 0.4                    | 36.7 ± 3.3               | 92.7 ± 3.1                      |
| Italy-2    | 13.5 ± 4.6                   | 84.7 ± 13.2              | 304.3 ± 49.5                    |
| Italy-3    | 19.0 ± 4.1                   | 71.0 ± 8.8               | 134.0 ± 3.1                     |
| Japan-1    | 6.1 ± 0.4                    | 186.7 ± 3.6              | 965.0 ± 11.7                    |
| Japan-2    | 3.0 ± 0.3                    | 187.3 ± 13.2             | 549.0 ± 21.3                    |
| Japan-3    | 13.6 ± 3.3                   | 1527.0 ± 163.5           | 309.0 ± 72.2                    |
| Korea      | 3.8 ± 0.5                    | 353.7 ± 16.4             | 613.3 ± 30.4                    |

The values represent the mean ± S.E.; n = 10 for the first and third column and n = 3 for the second column.
lines produced more than three fruits per rosette, and significantly larger number of rosettes m⁻², thus producing a significantly larger number of fruits m⁻². Even though the Chinese lines produced a moderate number of rosettes per unit land area and a small number of fruits per rosette, the fruit weight per unit land area in the Chinese lines was significantly heavier than that in either the European or other Asian lines. These results show that fruit yield per land area greatly depends on the individual fruit weight, the number of fruits per rosette and the number of rosettes per land area.

Path analysis was performed to obtain further insight into relationships among the yield and identified yield components. As it is given by path coefficients water chestnut yield is directly influenced by the productive rosette number m⁻² and the single fresh fruit weight. The same positive relationship was given by the positive correlation coefficient as well. Even though number of fruits per rosette had a positive contribution on yield directly, strong indirect negative influences via productive rosette number m⁻² and the single fresh fruit weight was observed. Therefore, the negative correlation of yield and fruits per rosette was due to indirect effects. Thus, productive rosette number m⁻² and the single fresh fruit weight are important yield determinants of water chestnut than number of fruits per rosette. Further the model that we tested can be used in yield estimations and also gives information for future breeding programs.

These yield components can vary with the cultivation condition and also with the genetic background. The number of fruits per rosette is determined by the number of flowers per rosette, flower bud distribution pattern on the stem and the length of the effective flowering period. The effective flowering duration for water chestnut is defined as the duration from the first flower to fruit maturation. Even if flowering occurred later on, a large number of mature fruits cannot be produced due to the lower temperature in autumn. The effective flowering duration in the European lines and the Indian line was longer than that in many other lines used in this experiment, and was over three months. European lines were early flowering and had an effective flowering duration that was long enough. The Indian lines flowered later, but maintained active growth even until late November, and had a long effective flowering duration. The longer effective flowering duration in the European and Indian lines resulted in a larger number of fruits per rosette. The small-fruited lines, such as Japan-3 and Japan-1 produced many fruits per rosette and this was particularly due to their different flower bud distribution pattern on the stem compared with the large-fruited Indian and Chinese lines. This flower bud distribution pattern should be investigated in detail.

The higher yield in the Chinese lines was due to the
the largest number of fruit over 1,500 fruits m$^{-2}$.

In this case, the lines having blunt spines, from China -1, China -2, China -3 and China -4 would be better options to be used in crop improvement and breeding. In this study, huge morphological and physiological variations were observed in water chestnuts originating from different locations. However, in a given line the vegetative and reproductive characteristics were highly correlated and conserved. Among the lines used in this experiment, the Chinese lines and the Indian line had larger fruit and higher yield than the other lines.

The values represent the mean±S.E.; $n=10$. (B) Blunt, (S) Sharp.

(a). The length from the flower scar to the base of a fruit; (b), Excluding the spine; (c), Based on the dry weight.

| Line   | Number of spines (fruit$^{-1}$) | Fresh fruit weight (g) | Fruit dry weight (g) | Fruit height$^a$ (mm) | Fruit width$^a$ (mm) | Edible portion$^a$ (%) |
|--------|---------------------------------|------------------------|----------------------|-----------------------|----------------------|------------------------|
| China-1| 2(B)                            | 20.6±1.0               | 5.1±1.2              | 33.5±1.0              | 26.1±1.0              | 57.6±0.3               |
| China-2| 4(B)                            | 14.7±0.9               | 5.3±0.3              | 27.3±1.0              | 21.5±0.4              | 59.7±0.2               |
| China-3| 0(B)                            | 9.8±0.9                | 2.5±0.4              | 23.1±0.6              | 19.0±0.8              | 70.2±0.2               |
| China-4| 4(B)                            | 10.6±0.6               | 3.9±0.4              | 25.8±0.4              | 20.5±0.7              | 70.6±0.3               |
| China-5| 2(S)                            | 14.9±0.8               | 5.4±0.3              | 28.3±0.3              | 18.4±0.4              | 61.8±0.2               |
| China-6| 2(S)                            | 6.7±0.4                | 2.7±0.2              | 20.6±0.6              | 16.5±0.4              | 73.5±0.3               |
| China-7| 4(S)                            | 10.9±0.7               | 3.0±0.3              | 25.6±0.8              | 19.9±0.6              | 67.4±0.3               |
| China-8| 4(S)                            | 18.1±0.8               | 7.4±0.4              | 30.1±0.9              | 26.0±0.7              | 57.2±0.2               |
| Korea  | 2(S)                            | 16.3±1.4               | 5.3±0.3              | 33.8±1.1              | 26.5±1.1              | 59.2±0.3               |
| France | 4(S)                            | 5.1±0.4                | 2.3±0.2              | 26.8±0.5              | 19.1±1.2              | 57.4±0.2               |
| Italy-1| 4(S)                            | 2.5±0.2                | 1.4±0.1              | 20.5±0.6              | 13.1±0.5              | 66.8±0.3               |
| Italy-2| 4(S)                            | 4.4±0.5                | 2.1±0.2              | 23.6±1.1              | 16.4±0.8              | 52.1±0.2               |
| Italy-3| 2(S)                            | 4.0±0.2                | 2.0±0.1              | 21.1±0.5              | 14.3±0.3              | 58.2±0.3               |
| Japan-1| 4(S)                            | 4.9±0.3                | 2.9±0.2              | 20.0±0.3              | 17.1±0.5              | 52.7±0.2               |
| Japan-2| 2(S)                            | 1.8±0.2                | 1.1±0.1              | 17.0±0.5              | 9.8±0.4               | 78.2±0.3               |
| Japan-3| 2(S)                            | 0.2±0.0                | 0.1±0.0              | 9.4±0.3               | 3.9±0.2               | 85.9±0.3               |
| Korea  | 2(S)                            | 1.9±0.1                | 1.2±0.1              | 17.3±0.3              | 9.5±0.2               | 52.3±0.3               |

Table 4. Growth and morphological characteristics of a single mature fruit.

Table 5. Direct (underlined) and indirect effects of productive rosette number m$^{-2}$, fruits per rosette and fresh single fruit weight on yield of water chestnut.

| Component              | Productive rosette number Adj. n | Fruits per rosette | Fresh fruit weight | Correlation with yield | $R^2$(Adj) | n |
|------------------------|----------------------------------|--------------------|-------------------|-----------------------|-----------|---|
| Productive rosette number | *1,2416"**†                | -0.3720            | -0.3012            | 0.5681 *              | 0.96      | 17 |
| Fruits per rosette    | -0.6630                         | 0.6967"**          | -0.7094           | -0.6759 "**           |           |   |
| Fresh fruit weight    | -0.2965                         | -0.3906            | 1.2654"***         | 0.5791 "*             |           |   |

* ** and ***: 5.1 and 0.1 % level significance, respectively.
† The direct and indirect effects of a particular component are within a row. For example, the direct effect of productive rosette number m$^{-2}$ on yield was 1.2416, the indirect effect of productive rosette number m$^{-2}$ on yield via number of fruits per rosette was -0.3720. Variables were transformed to the natural logarithm.
Also, we identified the yield components, which have the agronomical, biotechnological and economical importance. Thus, the results presented here would be useful for subsequent crop management and improvement.

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* In Japanese with English abstract.
** In Japanese.