

Effect of Tree Spacing on Vegetative Growth and Reproduction in an Early Growth Stage in Two Cultivars of *Ficus carica* L.

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The nursery stocks of two fig varieties, ‘Masui dauphine’ and ‘Houraishi’ (*Ficus carica* L.), were raised by cutting in a nursery, transplanted with changing tree density to an experiment field on July 8, 2004, and cultivated using straight-line training in the Agricultural Food and Environmental Science Research Center of Osaka Prefecture, Japan. The density grades per 1.0-a land area (100 m²) were 200, 66.7, 40, and 6.06. The growth of the aboveground vegetative parts of each tree was monitored at irregular intervals in 2005 by measuring the length and diameter of three organs, i.e. trunk, primary scaffold limb and fruit-bearing shoots. The linear dimensions of the three organs were transformed into dry weight values of woody organs and leaves, giving individual vegetative weight per tree. The fruit were harvested daily during the fruiting season from August to December 2005. The mean values of individual vegetative weight at different densities were approximated well by the reciprocal equation of the C-D effect (hereafter, the SK model), which was proposed by Shinozaki and Kira ca. 50 years ago. Mean annual fruit production per tree at a given density grade was also covered by the SK model, suggesting the clear effect of density on vegetative growth and fruit production in young fig monocultures. The coefficients of the equation conformed to conventional recognition about the poorer vegetative growth and richer fruit harvest in ‘Masui dauphine’ than in ‘Houraishi’. The observed density dependency of the reproductive allocation (RA) represented the decrease of RA with the increase of density in two cultivars although the predicted density dependency of RA was contradictory to that of the observation of the ‘Masui dauphine’.

Key Words: density, *Ficus carica* L., ‘Houraishi’, ‘Masui dauphine’, reciprocal equation of the C-D effect.

Introduction

The major sources of fig production in Japan are confined to rather limited regions, Aichi, Wakayama, Fukuoka, and Hyogo Prefectures (Sugiura et al., 2004); however, fig cultivation is expected to become more popular in other regions because figs are easier to cultivate and give a quicker return with lower initial financial investment than other fruits (Kabumoto et al., 1996). Recent researches in Japanese fig horticulture appear to focus on the breeding of new cultivars (Awamura et al., 1998; Nogata and Awamura, 2005), fruit quality (Yahata and Awamura, 1996; Yahata and Nogata, 1999, 2000), countermeasures against the Ceratocystis canker and soil sickness with microorganism origins (Hosomi and Kawaradani, 2004; Hosomi and Uchiyama, 1998; Hosomi et al., 2002; Shimizu et al., 2002), and the effect of close planting on the growth

and yield of figs (Mano and Hamada, 2005). All of these studies should contribute to the popularization of fig cultivation through the improvement of fruit production, fruit quality, labor saving practices, and land use efficiency. Our present study deals with the effect of tree density on growth and yield in two common fig varieties, ‘Masui dauphine’ (San Piero *sensu* Condit) and ‘Houraishi’ (conventional Japanese cultivar possibly from China), of *Ficus carica* L., with reference to their land use efficiency in fruit production.

Plant density in terms of the number of plants in a given land area has a profound influence on plant growth (Hirano, 1989; Kira et al., 1953) and its control is one of the basic research subjects in agronomy (Kuroda et al., 1996). In conjunction with plant density, the law of the constant final yield and reciprocal equation of the C-D effect (Shinozaki and Kira, 1956) is ubiquitous with respect to total plant dry weight or yield as the sum of leaves, branches, trunks, roots and crops, including fruit in manmade plant populations with rather short longevity. The crop weight or yield is considered to be

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part of the total plant weight or yield, and its dependency on plant density is expressible by combining the reciprocal equation of the C-D effect (hereafter, the SK model) and allometry rule (Hirano, 1989; Hozumi, 1973; Kuroda et al., 1997; Shinozaki and Kira, 1956). In this study, we describe an outline of research methods for our focal spacing experiment, which was conducted at the Agricultural, Food and Environmental Science Research Center of Osaka Prefecture, Japan (hereafter, ARCO) since 2004, apply the SK model to the data of aboveground vegetative growth and reproduction, and examine the density effects in young fig populations. We also discuss the allometric relation between aboveground vegetative mass and fruit mass, and clarify the dependency of per tree annual fruit production on tree density. The results are expected to supply a rational administrative base in the practice in fig orchards.

Materials and Methods

Fig cultivation

Two common fig varieties, 'Masui dauphine' and 'Houraishi' (*Ficus carica* L.), were adopted for cultivation and their nursery stocks were raised by cutting. One-year-old shoots were cut into small pieces, separately inserted in the rooting medium of a rock wool cube of 10 cm × 10 cm × 10 cm on April 30, 2004 and kept in the shade at ARCO. The average initial length per cutting was 20 cm, 17.83 g in dry weight in 'Masui dauphine' and 13.30 g in 'Houraishi', respectively. The mean specific gravity per cutting was 0.4106 g·cm⁻³ ($n=5$) in 'Masui dauphine' and 0.4004 ($n=10$) in 'Houraishi'. Since the difference between the two specific gravity values was insignificant ($p > 0.05$), the overall mean specific gravity of 0.4038 g·cm⁻³ was adopted and used for the transformation of wood volume into wood dry weight.

Rooted cuttings having new shoots greater than ca. 15 cm in total height were transplanted in rows in the experimental field of ARCO on July 8, 2004. Each planting row was ca. 1.0 m in initial width and 2.5 m in inter-row spacing, which was measured by the distance between the centerlines of a pair of the closest planted rows, and ran from north to south. Fig tree density was regulated by changing the inter-plant spacing or the distance between nursery stocks in a given row.

Five fig tree spacing grades were used, as given in the first column of Table 1. The area per tree in the third column is the product of inter-plant spacing in the second column and inter-row spacing of 2.5 m. Fig tree density in the fourth column is equivalent to the reciprocal value of area per tree. The number of plots represents the replication of cultivation experiments at respective spacing grades. The shortage of available nursery stock, land area and labor limits the replication in 'Houraishi' cultivation. Border trees were planted at the terminal ends of planting rows. The details of the spatial arrangement of planting rows, plots with different densities, and border trees are not described here, since the focal experimental field at ARCO is uniform in micro topography, soil etc.

After planting in the field, the fig trees were managed by customary straight-line training (Kabumoto et al., 1996), where the height of the trunk was 40 cm, and the expected length of the primary scaffold limb (hereafter limb) was equivalent to the given inter-plant spacing in a planting row (Table 1). Limb direction along a row coincided with that of the row. The spacing of a single fruit-bearing shoot (hereafter, shoot) was 20 cm for all limbs. Hence, the expected number of shoots per tree in each spacing grade is given by dividing the inter-plant spacing per row in Table 1 by 20 cm. Shoots were allowed to grow in a natural form without pinching. Fruit was thinned on a limited number of nodes, if several fruit formed at one node. Watering, fertilization, disbudding, pest control, defense against bird and mammal damage in the growing season, and shoot pruning in winter etc. followed the normal schedule for fig orchard management. In watering and fertilization, water and fertilizer pellets were sprinkled on the entire surface of the respective rows, as uniformly as possible.

Monitoring vegetative growth

Fig tree growth was monitored after planting on June 8, 2004. The enumeration of fruit production was initiated in 2005, since the shoots were insufficient in many plots in 2004. In the plots with the largest inter-plant spacing (Table 1), the limbs were still under construction in August 2006; therefore, this study analyzes the growth and fruit production data during ca. 12 months from April 21, 2005 to March 2, 2006,

Table 1. Plant spacing and other related characteristics in plots.

| Spacing grade | Inter plant spacing per planting row [m/row] | Area per tree [m ²] | Density [1/a] | Number of plots | | Number of trees per plot [1/plot] |
|---------------|--|---------------------------------|---------------|-----------------|------|-----------------------------------|
| | | | | M.* | H.** | |
| 1 | 0.2 | 0.5 | 200.0 | 8 | 2 | 6 |
| 2 | 0.6 | 1.5 | 66.67 | 8 | 2 | 5 |
| 3 | 1.0 | 2.5 | 40.00 | 8 | 2 | 4 |
| 4 | 6.6 | 16.5 | 6.061 | 8 | 2 | 1 |
| 5 | 20.0 | 50 | 2.000 | 8 | 2 | 1 |

Asterisks, * and **, stand for 'Masui dauphine' and 'Houraishi', respectively.

excluding data from cultivation plots with the largest inter-plant spacing. The outline of growth monitoring and phenological events in these 12 months is briefly given below.

Growth was monitored monthly, although the monitoring dates differed among months: April 21, June 3, July 7, August 18, September 20, and October 19 in 2005, and February 21, 2006. The trees shed their leaves after October 2005 and had no leaves on February 21, 2006. The shoots borne in 2005 were pruned on March 2, 2006. The monitored items concerned the sizes of different aboveground vegetative parts; i.e., 1) trunk diameter 20 cm aboveground, 2) limb diameter and limb length, 3) shoot base diameter, 4) diameter at the top of a shoot, and 5) shoot length. In the measurement of limbs, a focal limb was separated into northern and southern segmental parts, for each of which the limb length and diameters at limb terminals were measured. These five itemized variables were measured for all trunks, limbs and shoots in ‘Houraishi’ trees. In ‘Masui dauphine’ trees, 1st, 2nd, and 3rd variables were measured for all trees, while the 4th and 5th variables of shoots were measured for selected sample trees. Twelve, ten, eight and two ‘Masui dauphine’ trees were sampled from the plots of the 1st, 2nd, 3rd, and 4th spacing grade, respectively (Table 1). Hence, the total number of samples was 32 trees, although it increased from 94 to 98 shoots due to the growth of limbs.

Fruit management and harvest

The fruit was thinned on several nodes, as already described, but the quantity was small in dry weight because there were few thinned fruit and they were removed at the earliest opportunity. Abortion was not detected in fruit of visible size, since fungal diseases such as rhizopus rot were controlled by germicides, as soon as possible. Fruit loss by frugivores was also suppressed by using nets, fences and chemicals for fruit defense, the details of which are described later. Thus, the loss of fruit before harvest was minimized. The mature or ripe fruit were successively harvested during the fruiting season from August to December 2005. The harvested fruit were individually measured by fresh weight within a day after harvest. Twenty pieces of fruit were sampled monthly, and their fresh and dry weights were measured to calculate a conversion factor from fresh to dry weight.

Immature or unripe green fruit were left on the leafless bare shoots in December 2005. This situation was part of our shoot and fruit management, in which shoots and fruit were allowed to grow naturally without pinching. Immature fruit were also harvested on December 16, 19, and 21, 2005 and weighed by the same procedures as for mature fruit measurement. Thus, the fruit were mature and immature in this study.

Conversion of linear dimensions to dry weight dimensions

The dry weight of different aboveground vegetative parts was calculated by using the linear dimensions, which were observed in the aforementioned growth monitoring. Trunk diameter was transformed into dry weight by assuming a columnar trunk form and by using a trunk length of 40 cm and wood specific gravity of $0.4038 \text{ g}\cdot\text{cm}^{-3}$ for both varieties.

The limb diameters at two terminals and limb length in a northern segmental limb of a focal limb were converted into dry weight by assuming a trapezoid conic shape of the segmental limb and by using the specific gravity. The dry weight of a southern segmental limb was similarly calculated. The limb dry weight per tree was calculated by summing up two weight values of segmental limbs.

The dry weight of a given shoot was calculated by the same principle as for limb weight computation, if the shoot length and diameter at shoot terminals were measured. For ‘Masui dauphine’ shoots measured by the shoot base diameter alone, the shoot dry weight was computed by the following allometric equations,

$$1/H = 1/(aD^b) + 1/c \quad (1)$$

$$w(fs) = 0.2803(D^2H)^{0.9331} \quad (2)$$

where H is shoot length in cm, D is the shoot base diameter in cm, $w(fs)$ is shoot dry weight in g, and the symbols, a , b , and c , in Eq. (1) stand for empirical coefficients specific to cultivars and time. The coefficients of 0.2803 and 0.9331 in Eq. (2) are common to the two cultivars and different shoot growth stages in different months. Eq. (2) was obtained by combining all the $w(fs)$ values computed for ‘Masui dauphine’ and ‘Houraishi’ shoots by using the observed shoot diameters and length, as already described. The coefficient of determination of the $\log w(fs)$ vs. $\log D^2H$ relation was greater than 0.999 ($n=1132$, $p<0.001$). The coefficients of a , b , and c in Eq. (1) were calculated monthly for ‘Masui dauphine’ trees, as listed in Table 2. If H is unknown, H is estimable by substituting the observed shoot base diameter and coefficients in Table 2 into Eq. (2). The shoot dry mass per tree was calculated by

Table 2. Coefficients of Eq. (1) for shoot base diameter vs. shoot length relations.

| Year | Month | a [cm cm ^{-b}] | b [Dimensionless] | c [cm] | r^2 |
|------|-------|-------------------------------|------------------------|-------------|-------|
| 2005 | Jun. | 26.08 | 2.018 | ∞ | 0.832 |
| 2005 | Jul. | 97.38 | 2.103 | 228.9 | 0.738 |
| 2005 | Aug. | 99.25 | 2.287 | 294.0 | 0.662 |
| 2005 | Sep. | 43.97 | 3.653 | 281.6 | 0.708 |
| 2005 | Oct. | 92.01 | 2.107 | 360.2 | 0.710 |
| 2006 | Feb. | 37.05 | 3.415 | 311.6 | 0.783 |

The r^2 represents the coefficient of determination between calculated and observed values.

summing the $w(fs)$ values of respective shoots belonging to a tree.

The dry weight of leaves per shoot or $w(fs/l)$ and shoot length H were observed in August and September 2004 and 2005 by selecting various shoots with different sizes. Leaf loss due to leaf senescence or accidents was not detected in the selected shoots. The two observed variables led to the following allometric equations for estimating $w(fs/l)$ on a dry weight basis of g from H in cm ,

$$w(fs/l) = 0.2802H^{1.055} \quad (3)$$

$$w(fs/l) = 0.4089H^{1.124} \quad (4)$$

where Eqs. (3) and (4) were used for ‘Masui dauphine’ and ‘Houraishi’ trees, respectively, and their coefficients of determination in log-transformed quantities were 0.993 ($n=40$) and 0.998 ($n=47$) in Eq. (3) and Eq. (4), respectively. Leaf dry mass per tree stood for the sum of $w(fs/l)$ values belonging to a focal tree. Leaves rarely sprouting from a limb were ignored, since their number per tree was small. The quantity of disbudded small sprouts in trunks, limbs and shoots was also ignored because we practiced frequent disbudding and tried to keep plant mass loss to a minimum in disbudding. The root weight was incalculable because root sampling was impossible due to the scarcity of planted fig trees of ‘Houraishi’ and the field management plan of ‘Masui dauphine’ in ARCO.

The least squares method was adopted for the determination of regression equations with linear or non-linear coefficients by using a computer software package (DeltaGraph ver. 4.5, Japan Poladigital, Japan) on a Macintosh platform.

Results

Mean standing crop per tree in vegetative organs

The sum of dry weight of aboveground vegetative organs, such as trunks, limbs, shoots and leaves, in an individual fig tree was tentatively designated the vegetative mass per tree or individual vegetative weight in this study, although the rare leaves on limbs and roots were excluded from weight computation. This quantity of aboveground fig organs is determinable for each tree grown at a given plot of given plant density and its mean value is calculable with respect to plant density, as shown in Table 3. In the table, the mean individual vegetative weight value on the growth monitoring date of February 21, 2006 represents the weight of leafless trees. The values on April 21, 2005 and March 2, 2006 represent the mass of trunks and limbs, respectively, since shoots were pruned. The other values in different months stand for the mass of trees with green leaves. All these values give the transient mean standing crop per tree in aboveground vegetative organs in a strict sense and decrease with an increase of tree density, suggesting a

Table 3. Per tree mean dry weight of total aboveground vegetative organs (g/tree), annual fruit production (g/year/tree) and aboveground net production (g/year/tree) at different plant densities.

| Cultivars | Date | Plant density [1/a] | | | |
|------------------|----------------|---------------------|--------|--------|--------|
| | | 200 | 66.7 | 40.0 | 6.06 |
| ‘Masui dauphine’ | Apr. 21, 2005 | 48.6 | 83.0 | 100.3 | 174.0 |
| | Jun. 3, 2005 | 51.7 | 136.2 | 180.4 | 293.3 |
| | Jul. 7, 2005 | 225.9 | 553.3 | 785.8 | 1574.3 |
| | Aug. 18, 2005 | 384.8 | 794.2 | 1253.2 | 2460.9 |
| | Sep. 20, 2005 | 591.7 | 1145.3 | 1935.8 | 4670.5 |
| | Oct. 19, 2005 | 622.3 | 1203.3 | 2012.7 | 5301.5 |
| | Feb. 21, 2006 | 605.7 | 1103.3 | 1825.6 | 5027.2 |
| | Mar. 2, 2006 | 116.8 | 322.7 | 532.4 | 2427.8 |
| | Mature fruit | 286 | 708 | 1349 | 3237 |
| | Immature fruit | 32 | 80 | 150 | 467 |
| | Net production | 891.7 | 1908.3 | 3411.4 | 8831.6 |
| ‘Houraishi’ | Apr. 21, 2005 | 64.7 | 89.4 | 122.1 | 122.3 |
| | Jun. 3, 2005 | 97.1 | 194.6 | 269.3 | 245.1 |
| | Jul. 7, 2005 | 504.9 | 961.4 | 1451.6 | 1855.7 |
| | Aug. 18, 2005 | 801.4 | 1580.9 | 2408.8 | 3530.8 |
| | Sep. 20, 2005 | 979.8 | 2056.5 | 3110.1 | 5427.2 |
| | Oct. 19, 2005 | 1099.8 | 2318.5 | 3647.7 | 6541.8 |
| | Feb. 21, 2006 | 905.8 | 1731.2 | 2766.2 | 6015.4 |
| | Mar. 2, 2006 | 207.5 | 518.5 | 849.9 | 3178.2 |
| | Mature fruit | 187 | 446 | 806 | 1561 |
| | Immature fruit | 15 | 56 | 110 | 328 |
| | Net production | 1237.1 | 2731.1 | 4441.6 | 8308.5 |

density effect in individual vegetative weight.

Per tree mean annual quantity in fruit production and net production

The fruit was separated into mature and immature fruit, as already described. The daily records of harvested fruit mass were combined by discriminating the respective density grades. Therefore, the data of mature and immature fruit in Table 3 show the annual mean quantity per tree grown at specified density and suggest the increase of mean annual fruit productivity per tree with the decrease of density. By combining these data of fruit production and the aforementioned individual vegetative weight, we tried to estimate the mean annual net production per tree per year in aboveground organs (p_n), although litterfall was not directly measured in this study. We considered four hypothetical conditions with respect to litterfall, annual leaf and shoot production, disbudded quantity of vegetative organs and annual plant mass increase in the computation of p_n , as described below.

Concerning litterfall, flower litterfall appeared to be suppressed due to the syconium structure of the inflorescence (Kabumoto et al., 1995) and was ignored in this study. Fruit abortion did not occur, as already described. Trunks, limbs, and shoots survived throughout growth monitoring. Branch litterfall was not found in our fig cultivation, since succulent shoots without secondary branches were adopted for fruit-bearing shoots. Bark litterfall did not occur, since falling bark is generally suppressed in woody organs of focal figs; thus, we did not need to take account of the litterfall of flowers, fruit, stems, limbs, shoots, branches and bark in the computation of p_n . Hence, the first assumptive condition was related with grazing loss by frugivores and herbivores, such as raccoon dogs, birds, longicorn beetles and thrips etc, some of which commonly occur in fig orchards (Kabumoto et al., 1996). Fruit grazing by raccoon dogs was prevented by establishing a zinc plate fence around the experimental field. Both fruit grazing by birds (gray starlings) and wood grazing by longicorn beetles were prevented, since the field was totally covered by a fine net as a windbreak. Attacks from small insects, such as thrips and spider mites, were controlled with insecticide spray, as soon as they were found around the fruit, young leaves, and shoot tops; therefore, we assumed that grazing loss by frugivores and herbivores was negligible, even if it occurred. Leaf litterfall is included in the annual production of leaves, as described below.

The second condition concerned annual leaf production and shoot production, two of which were considered to be included in the individual vegetative weight on October 19, 2005 (Table 3), when the living leaf biomass per tree culminated. Since we calculated the leaf weight per shoot by substituting the shoot base diameters and shoot length in October into the allometric equations of

Eqs. (3) and (4), which were obtained from healthy sample shoots without a trace of defoliation in August and September, the per tree leaf mass in October approximated the annual leaf production. A similar explanation is applicable for the estimation of annual shoot production per tree.

The third assumption was related with the quantity of disbudded small sprouts. The weight of disbudded sprouts was not measured; however, we considered that plant mass loss due to disbudding was kept to a minimum and could be ignored, since we often repeated disbudding, as already described. The fourth assumption was related with the calculation of the annual plant mass increase in stems and limbs, which we considered to be included in the difference between individual vegetative weight in October and April 2005. The root dynamics was not measured and was inevitably ignored in this study.

If the above considerations for hypothetical data handling are acceptable in the computation of p_n , we can obtain a minimum estimate for the mean p_n per tree per year at a given density, by summing up the three quantities, the mass of aboveground vegetative organs on October 19, 2005, mature and immature fruit mass, respectively, and by subtracting the initial plant mass on April 21, 2005 in Table 3. The estimated p_n in Table 3 decreased with the increase of fig tree density, suggesting an effect of density on p_n .

SK model applied to the standing crop of vegetative mass and annual fruit production

The SK model proposed by Shinozaki and Kira (1956) is written in the mathematical form as,

$$1/w = A\rho + B \quad (5)$$

where w is mean individual plant weight on a dry weight basis, ρ is plant density, and A and B are coefficients specific to plant species (or cultivars) and time. In this study, w is the aforementioned mean individual vegetative weight in grams and excludes root weight, and ρ is fig tree density per 1.0-a (100 m²). The model can express the ρ vs. w relations observed on different dates and in different months, as shown in Figure 1 and Table 4. The correlation coefficients between observed values and calculated values of Eq. (5) are significant ($p < 0.05$), excluding the earlier growth stages in April and June in 'Houraishi' (r^2 in Table 4).

Variable w was expressible well by Eq. (5) even in leafless and shootless seasons, such as April 2005 and February and March 2006, although model fitness to the observed data was believed to be higher in total plant weight than in partial plant weight (Shinozaki and Kira, 1956). With respect to aboveground vegetative mass per tree, coefficients A and B of Eq. (5) were always greater in 'Masui dauphine' than in 'Houraishi' and clearly represented the poor vegetative growth of 'Masui dauphine' (Table 4).

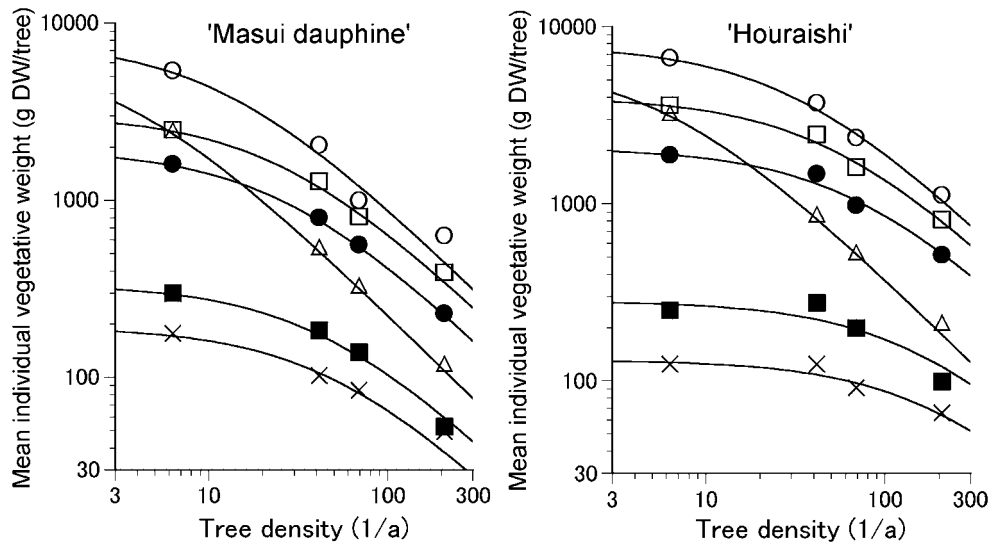


Fig. 1. SK model or the reciprocal equation of the C-D effect applied to mean individual vegetative weight in 'Masui dauphine' (left) and 'Houraishi' (right) populations cultivated at different tree densities per 1.0-a (100 m²). The crosses, closed squares, closed circles, clear squares, clear circles and triangles stand for different growth-monitoring dates, April 21, June 3, July 7, August 18, October 19 in 2005 and March 2, 2006, respectively. Curves represent calculated values of Eq. (5) characterized by coefficients in Table 4. Growth data on September 20, 2005 and February 21, 2006 are omitted here because their calculated trajectories were so close to that of October 19, 2005.

Table 4. Coefficients of the SK model applied to vegetative growth and fruit production.

| Time | 'Masui dauphine' | | | 'Houraishi' | | |
|----------------|--|--|-------|--|--|-------|
| | $A \times 10^{-6}$ [a/g]* or [a·year/g]** | $B \times 10^{-3}$ [1/g]* or [year/g]** | r^2 | $A \times 10^{-6}$ [a/g]* or [a·year/g]** | $B \times 10^{-3}$ [1/g]* or [year/g]** | r^2 |
| Apr. 21, 2005 | 102.5 | 5.205 | 0.984 | 38.47 | 7.6510 | 0.884 |
| Jun. 3, 2005 | 67.13 | 2.985 | 0.997 | 23.02 | 3.559 | 0.812 |
| Jul. 7, 2005 | 19.10 | 0.5191 | 0.999 | 6.889 | 0.4871 | 0.970 |
| Aug. 18, 2005 | 12.46 | 0.3303 | 0.996 | 4.893 | 0.2511 | 0.987 |
| Sep. 20, 2005 | 9.44 | 0.1568 | 0.996 | 4.461 | 0.1567 | 0.996 |
| Oct. 19, 2005 | 9.417 | 0.1315 | 0.997 | 4.016 | 0.1280 | 0.995 |
| Feb. 21, 2006 | 10.46 | 0.1356 | 0.997 | 6.011 | 0.1298 | 0.996 |
| Mar. 2, 2006 | 43.49 | 0.1483 | 0.999 | 25.66 | 0.1591 | 0.999 |
| Mature fruit | 14.73 | 0.2189 | 0.994 | 21.41 | 0.5077 | 0.990 |
| Immature fruit | 145.5 | 1.258 | 0.998 | 203.4 | 1.812 | 0.996 |

* Dimension the standing crop of vegetative organs.

** Dimension annual fruit production.

The r^2 represents the coefficient of determination between observed and calculated values of Eq. (5) or Eq. (6).

The SK model paraphrases the reciprocal equation of the C-D effect proposed by Shinozaki and Kira (1956).

Model robustness is also true in the relationship between ρ and mean annual mature (or immature) fruit production per tree, as represented in Figure 2 and Table 4, confirming a well known agronomic fact about the richer fruit harvest in 'Masui dauphine' than in 'Houraishi', implying a limited type of allometric relation between different fig tree organs on a mean tree size basis, as described below.

Allometric relation between fruit mass and vegetative mass on a mean value basis

Denoting the mean annual mature-fruit production per tree and mean individual vegetative weight by symbols, $w(f)$ and w , respectively, we considered an allometric

relation between $w(f)$ and w . Since the variable $w(f)$ is also expressible by Eq. (5), we rewrote the coefficients of the ρ vs. $w(f)$ relation of Eq. (5) in the form,

$$1/w(f) = A(f)\rho + B(f) \quad (6)$$

where $A(f)$ in a unit of (a·year/g) and $B(f)$ in (year/g) are specific to cultivars and time. Symbol f in the parentheses of $A(f)$ and $B(f)$ represents an abbreviated expression of fruit. By eliminating variable ρ from Eqs. (5) and (6), we get

$$1/w(f) = P/w + Q \quad (7)$$

$$P = A(f)/A \text{ and } Q = B(f) - A(f)B/A \quad (8)$$

Since the sets of coefficients, (A and B) and ($A(f)$ and

$B(f)$), are explicitly given in Table 4, the new coefficients, P and Q , are easily calculable as listed in Table 5, where coefficient Q is negative in many months. The coefficient of determination (r^2) between observed $w(f)$ and calculated $w(f)$ of Eq. (7), which is characterized by the coefficients in Table 5, is rather high, excluding the growth data in ‘Houraishi’ in April and June 2005 (Table 5).

With respect to immature fruit, the coefficients of P and Q in Eq. (7) were also calculated by using A , B ,

$A(f)$, and $B(f)$ values (A and B in Table 4). The calculated P and Q are given in Table 5, together with the coefficients of determination between observed $w(f)$ and calculated $w(f)$ of Eq. (7). The fitness of Eq. (7) to the observed w vs. $w(f)$ relations for immature fruit was also high, excluding the growth data in ‘Houraishi’ in April and June 2005 (r^2 in Table 5). Thus, the allometric relation of Eq. (7) supported the applicability of the SK model to the fruit production data, although we should carefully discriminate the notations of coefficients, such as A and $A(f)$ etc., in Eqs. (5) and (6).

Discussion

Excessive immature fruit in ‘Houraishi’

In our experimental straight-line training for fig cultivation, the elongation of a succulent shoot continued even in October and accumulated numerous nodes as the bases for leaf and fruit buds along the shoot; however, prolonged shoot elongation resulted in a mismatch between the timing for fruit bud sprouting and the time necessary for fruit maturity, and led to immature fruit due to the shortage of time or temperature. In conventional fig cultivation by practical straight-line training, immature fruit is seldom produced because shoots are pinched and not allowed to elongate freely. Hence, our data on immature fruit are rather difficult to obtain in practical fig cultivation and are suitable for evaluating the potential for fruit productivity in focal varieties.

The density dependency of mature and immature fruit production was formulated by the SK model, which is rewritten in the form of Eq. (6) for the description of mature fruit production $w(f)$. To discriminate the immature fruit mass from the mature fruit mass, we introduced a new symbol, $w(f')$, for the mean annual

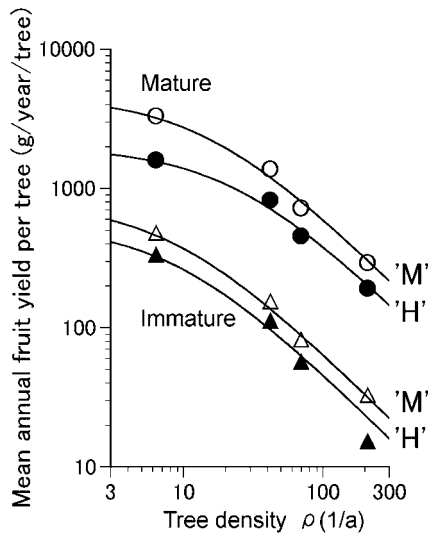


Fig. 2. SK model applied to the mean annual fruit yield per tree in ‘Masui dauphine’ (clear symbols) and ‘Houraishi’ (closed symbols). The circles and triangles, respectively, represent the observed mature and immature fruit yields at different densities. Curves give calculated ρ vs. w relations in the form of Eq. (5). Symbols ‘M’ and ‘H’ stand for the abbreviated expressions of ‘Masui dauphine’ and ‘Houraishi’, respectively.

Table 5. Calculated coefficients and coefficients of determination of Eq. (7).

| Fruit condition | Time | ‘Masui dauphine’ | | | ‘Houraishi’ | | |
|-----------------|---------------|------------------|--------------------|---------|-------------|--------------------|---------|
| | | P | $Q \times 10^{-3}$ | r^2 | P | $Q \times 10^{-3}$ | r^2 |
| Mature fruit | Apr. 21, 2005 | 0.1437 | −0.5291 | 0.979* | 0.5565 | −3.7504 | 0.735 |
| | Jun. 3, 2005 | 0.2194 | −0.4361 | 0.995** | 0.9301 | −2.8024 | 0.374 |
| | Jul. 7, 2005 | 0.7712 | −0.1814 | 0.995** | 3.1079 | −1.0061 | 0.992** |
| | Aug. 18, 2005 | 1.182 | −0.1716 | 0.998** | 4.3756 | −0.5910 | 0.999** |
| | Sep. 20, 2005 | 1.560 | −0.0258 | 0.997** | 4.7994 | −0.2444 | 0.997** |
| | Oct. 19, 2005 | 1.564 | 0.01321 | 0.996** | 5.3312 | −0.1747 | 0.998** |
| | Feb. 21, 2006 | 1.408 | 0.02795 | 0.994** | 3.5618 | 0.0454 | 0.993** |
| | Mar. 2, 2006 | 0.3387 | 0.1687 | 0.995** | 0.8344 | 0.3750 | 0.991** |
| Immature fruit | Apr. 21, 2005 | 1.420 | −6.131 | 0.989** | 5.2872 | −38.641 | 0.599 |
| | Jun. 3, 2005 | 2.167 | −5.212 | 0.998** | 8.8358 | −29.635 | 0.124 |
| | Jul. 7, 2005 | 7.618 | −2.696 | 0.998** | 29.5253 | −12.57 | 0.990** |
| | Aug. 18, 2005 | 11.68 | −2.599 | 0.999** | 41.5696 | −8.6261 | 0.999** |
| | Sep. 20, 2005 | 15.41 | −1.159 | 0.999** | 45.5952 | −5.3328 | 0.998** |
| | Oct. 19, 2005 | 15.45 | −0.7738 | 0.999** | 50.6474 | −4.6709 | 0.999** |
| | Feb. 21, 2006 | 13.91 | −0.6282 | 0.998** | 33.8380 | −2.5802 | 0.996** |
| | Mar. 2, 2006 | 3.346 | 0.7618 | 0.998** | 7.9267 | 0.55086 | 0.996** |

Asterisks, * and **, represent significance levels of r , $p < 0.05$, and $p < 0.01$, respectively. Dimensions of P and Q are year and year/g, respectively.

immature fruit mass per year per tree and rewrote the ρ vs. $w(f')$ relation in the form,

$$1/w(f') = A(f')\rho + B(f'), \quad (9)$$

where $A(f')$ and $B(f')$ are given in Table 4. By eliminating ρ from Eqs. (6) and (9), we get

$$1/w(f') = (A(f')/A(f))/w(f) + B' - (A(f')/A(f))B \quad (10)$$

Substituting the coefficient values in Table 4 into Eq. (10), we get

$$w(f') = 1/(9.878/w(f) - 9.043 \times 10^{-5}), \quad w(f) < 1.092 \times 10^5 \quad (11)$$

$$w(f') = 1/(9.500/w(f) - 3.011 \times 10^{-3}), \quad w(f) < 3.155 \times 10^3 \quad (12)$$

where Eqs. (11) and (12) are available for 'Masui dauphine' and 'Houraishi', respectively. The coefficient of determination between observed and calculated values was 0.999 ($p < 0.01$) in the two equations. The deduction of Eq. (12) from Eq. (11) gives the difference of $w(f')$ between focal varieties, is always negative within the definitional range of $w(f) < 3155$ and suggests more excessive $w(f')$ in 'Houraishi' than in 'Masui dauphine'. Therefore, the poorer fruit harvest in 'Houraishi' in this study is also explainable by the extravagant $w(f')$ in the $w(f)$ vs. $w(f')$ relation, although alternative explanations for $w(f')$ might focus either on the optimum temperature or suitable land.

Density dependency of mean annual net production per tree

The mean annual net production per tree (p_n) was tentatively represented by the sum of four plant mass values, a) aboveground vegetative organ mass on October 19, 2005, b) annual mature fruit mass, c) annual immature fruit mass, and d) negative value of initial plant mass on April 21, 2005, as already described. Since the four element variables of p_n , respectively, can be expressed by the SK model with the coefficients in Table 4, the dependency of p_n on density ρ is also expressible as the composite function of four SK models. The calculated ρ vs. p_n trajectory of the composite function either for 'Masui dauphine' or 'Houraishi' appears to be similar to that of a single SK model (Fig. 3), although the SK model can not be superposed in mathematics. In fact, the following two approximate expressions with respect to p_n and ρ , $1/p_n = 5.754 \times 10^{-6}\rho + 7.825 \times 10^{-5}$ for 'Masui dauphine' and $1/p_n = 3.524 \times 10^{-6}\rho + 9.841 \times 10^{-5}$ for 'Houraishi', respectively, could predict the observed p_n in the accuracy to $\pm 1.0\%$ in relative errors within the range of ρ (1/a, 200/a).

The predicted ρ vs. p_n trajectories for two cultivars cross each other at $\rho = 9.2/a$ (Fig. 3). The p_n of 'Masui dauphine' is smaller than that of 'Houraishi', when $\rho > 9.2/a$, but greater than that of 'Houraishi' in the other extent of ρ . This alternative pattern of the cultivar's

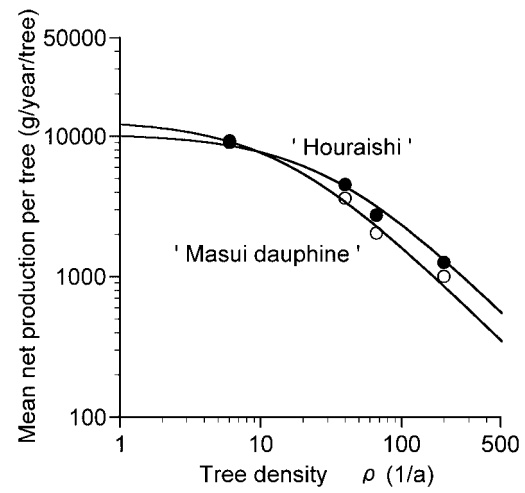


Fig. 3. Change of mean annual net production per tree with respect to tree density. Clear and closed circles stand for observed values in 'Masui dauphine' and 'Houraishi', respectively. Curves give calculated trajectories of net production to tree density.

preponderance in ρ vs. p_n trajectories was not observable in ρ vs. w (vegetative mass) and ρ vs. $w(f)$ (fruit mass) relations; however, these detailed differences between cultivars were lower than our expectation and appeared to represent the similarity between cultivars. If cultivar similarity is true in p_n , their contrasting traits in both vegetative growth and fruit productivity should be explained by reproductive allocation.

Reproductive allocation

The reproductive allocation (RA) of plants in a given population with a given density is a measure of the reproductive efforts in focal plants and can be defined by the ratio of fruit production to net production (p_n) (Silvertown, 1987). Since mature and immature fruit were separately measured in this study, we calculated RA for two quantities, the sum of mature and immature fruit (total fruit), and mature fruit, respectively, and examined the change of RA with respect to ρ by using the fruit mass and p_n data (Table 3 and Fig. 4).

The observed RAs for the total fruit and mature fruit, respectively, in 'Masui dauphine' were in an approximate range between 0.30 and 0.45, although RAs for total fruit were always greater than those for mature fruit. Furthermore, RA peaked at $\rho = 40/a$, although its peak might have been coincidental. On the other hand, RAs for total fruit and mature fruit, respectively, in 'Houraishi' were in a range between 0.15 and 0.25, and decreased with an increase of ρ . Thus, the difference of RAs between two cultivars was very clear and well explained the suppressed vegetative growth and dominant fruit productivity in 'Masui dauphine', and vice versa in 'Houraishi' (Fig. 4).

In order to identify the response of RA to ρ , RA values for total fruit and mature fruit were calculated for 'Masui dauphine' and 'Houraishi', respectively, by using Eqs.

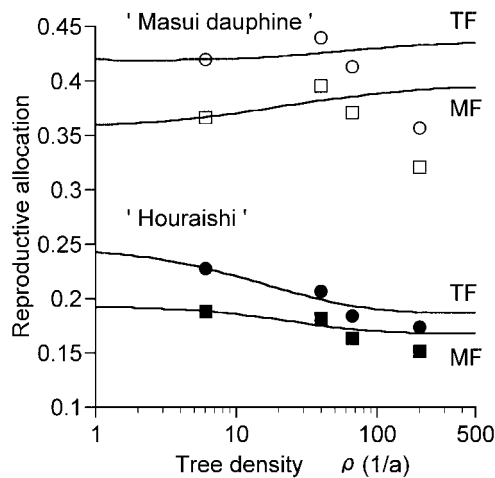


Fig. 4. Per tree mean annual reproductive allocations in two cultivars. Circles and squares represent observed values for total fruit and mature fruit, respectively, while clear and closed symbols show 'Masui dauphine' and 'Houraishi', respectively. Curves give predicted relationships between reproductive allocations and tree density. Symbols 'TF' and 'MF' stand for total fruit and mature fruit, respectively.

(5), (6), and (9). Since the equations are all written according to the algebraic functions of ρ , focal ρ vs. RA relations are easily obtained and are represented in Figure 4, where calculated RA increases slightly in 'Masui dauphine', but consistently decreases in 'Houraishi' with an increase of ρ , although the gradient of the change of RA to that of ρ in 'Houraishi' is not steep also. The correlation coefficient between observed and calculated values of RA was insignificant in 'Masui dauphine' ($r = 0.448$, $n = 8$, $p > 0.05$), but significant in 'Houraishi' ($r = 0.935$, $n = 8$, $p < 0.01$). The discrepancy between observed and predicted RA values in 'Masui dauphine' was difficult to explain but implied the impact of excluded root mass on RA because roots support aboveground organs. In 12-year-old orange trees grown at different densities, the approximate percentage ratios of root mass to total tree mass were in the range of 20% and 30%, and decreased with the increase of density (Ono, 1989); therefore, roots might reconcile the discrepancy of RA in 'Masui dauphine'.

Absence of the particular density maximizing mature fruit yield per unit land area

Mature fruit yield in a unit land area or $y(f)$ is given by multiplying $w(f)$ by tree density ρ and is written in the following form of Eq. (13), when Eq. (6) holds,

$$1/y(f) = 1/(w(f) \times \rho) = A(f) + B(f)/\rho \quad (13)$$

where the reciprocal of coefficient $A(f)$ represents a possible $y(f)$ value at $\rho = 8$ and is recognizable as an index of land use efficiency (Hozumi, 1973). The quantity of $1/A(f)$ is 67.9 kg/a/year and 46.7 kg/a/year in 'Masui dauphine' and 'Houraishi', respectively, again confirming a well-known agronomic fact about larger

fruit mass yield in 'Masui dauphine' than in 'Houraishi' (Table 4).

Apart from the observed difference of $y(f)$ between cultivars, Eq. (13) suggests a monotonous increase of $y(f)$ with an increase of ρ and represents no particular density or $\rho(\text{opt})$ at which $y(f)$ peaks. The lack of $\rho(\text{opt})$ appeared to be true in other comparable data from fig monocultures, which were established by Mano and Hamada (2005). Although the details are not described here, $\rho(\text{opt})$ was indiscernible even three years after planting in their data.

In general, a crop or fruit production per unit land area in plant populations, which are cultivated at different densities, does not follow Eq. (13) but follows another ρ vs. $y(f)$ curve having the maximum point in $y(f)$, as already confirmed in some vegetables (Shinozaki and Kira, 1956), soy beans (Hozumi, 1973), oranges (Hirano, 1989) and apples (Kuroda et al., 1997). This is true in other plant organs, such as branches and leaves, if the focal organ mass per plant is approximated by a power function of the total individual plant mass (w) and if w follows the SK model (Hozumi, 1973). In addition to the result by Mano and Hamada (2005), our result was also completely different from the preceding studies (Kuroda et al., 1997) because the mature and immature fruit mass per tree, and the leafless and shootless individual vegetative weight in winter could be expressed by the SK model. To compromise the contradictions between the results in preceding studies and our results, we introduced an allometric relation written in the form of Eq. (7) with negative or positive coefficients of Eq. (8).

The allometric relation with a functional form of Eq. (7) is popular in forest trees (Ogawa and Kira, 1977). It represents a w vs. $w(f)$ relation having a ceiling point in the dependent variable of $w(f)$, when coefficient Q is positive. When $Q < 0$, it represents a concaved w vs. $w(f)$ relation, which does not have the ceiling point in $w(f)$ but in w as an independent variable. This type of allometric relation with negative Q was not reported in preceding studies of forest trees (Ogawa and Kira, 1977) and its applicability was first confirmed in this study, since fruit productivity has seldom been studied on an individual tree basis in forestry. Switching from a positive to a negative in Q is interesting and should be studied in the future. The proposed Eq. (7) gives a new approach to the repeated use of the SK model or Y-D curve (ρ vs. yield relation) (Shinozaki and Kira, 1956) in different partial organs, although the comparison of various allometric relations is omitted here.

Implication for tree planting and thinning operations in orchards

The maximization of fruit yield is an ideal in orchard management. If the particular tree density or $\rho(\text{opt})$ at which the yield is maximized, is found, the $\rho(\text{opt})$ should offer a guideline for tree thinning operations in orchards. In fact, Kuroda et al. (1997) found the $\rho(\text{opt})$ in apple

orchards and predicted the fruit yield by using a proposed tree thinning plan resting on $\rho(\text{opt})$, which was observed for trees aged ≥ 6 -year-old and sharply decreased with respect to the tree stand age. The extent of $\rho(\text{opt})$ differed between rootstocks on which a focal apple cultivar was grafted, and was in the range of ca. 90/a for young fruited trees and ca. 3/a for aged trees. Unfortunately, we could not identify $\rho(\text{opt})$ in our study of two-year-old figs.

If the absence of $\rho(\text{opt})$ is true even in fig trees older than three years old (Mano and Hamada, 2005), it should be a conspicuous feature of figs because the reverse is also considered to be true. It follows that different planting densities have no bad influence on the harvested quantity of fig fruit if the orchards are fully covered by leaves. The close planting scheme, which was first proposed by Mano and Hamada (2005) for the earlier establishment of fig orchards, includes no contradiction of our results. In commercial fig fruit production, growers need not worry about tree thinning as in apple orchards and can adopt any convenient density that may change from time to time. Thus, an answer to the question about the presence or absence of $\rho(\text{opt})$ becomes an important future research subject in fig horticulture.

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