Planting density influence yield, plant morphology and physiological characteristics of determinate 'Suzukoma' Tomato

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Abstract

The effect of planting densities on yield, plant morphology, and physiological characteristics in determinate-type cooking 'Suzukoma' tomato were examined [high density (HD), medium density (MD), and low density (LD), corresponding to 792, 396, and 264 plants• a^{-1}]. Although the fruit yield per plant under HD was 0.6 and 0.5-fold lower than that under MD and LD, respectively, the yield per area under HD was 1.2- and 1.5-fold higher than that under MD and LD, respectively, because planting density under HD was 1.5- and 3.0-fold higher than under MD and LD, respectively. There were no differences among planting densities on fruit set ratio, fruit weight, marketable fruit ratio, and soluble solids content. Lateral shoot length at the first cotyledonary node and third to fifth true leaf nodes under HD was shorter than one third of those under LD. Hence, the total numbers of flowers and fruits per plant were the lowest under HD. The extent of reduced photosynthetic rates and SPAD values for the third, fifth, and seventh true leaves under HD were not so larger compared to LD, despite being extremely reduced photosynthesis photon flux density (PPFD) at a low position in the plant community. The causes of decreased lateral shoot length at intermediate nodes under HD compared to LD suggested that the concentrations of isopentenyl adenine riboside (iPR) and trans-zeatin riboside (tZR) in stems, and IAA, iPR, tZR, and trans-zeatin (tZ) in lateral shoots under HD were lower than in those under LD. From these results, it was indicated that yield per area under HD was higher than under LD due to the morhological and physiological change of the plants by light conditions in the plant community.

Key words: Flower number, lateral shoot length, photosynthetic rate, plant growth regulator, *Solanum lycopersicum*

Introduction

In commercial production of processing and cooking tomatoes, it is important for producers to maximize fruit yield per area. Since, most processing and cooking tomato cultivars exhibit a determinate growth habit, the lateral shoots are generally retained to ensure fruit yield (Yanokuchi, 1997).

Studies on planting density effect on yield of processing tomatoes have indicated that cultivation under high planting densities increases total yield per area, decreases the number of fruits per plant, and decreases average fruit size (Reeve *et al.*, 1962; Frost and Kretchman, 1988; Sato *et al.*, 2004). Several studies have attributed the reduced fruit number under high planting density to the development of fewer inflorescences and flowers, and lower fruit set ratio (Reeve *et al.*, 1962; Zahara and Timm, 1973).

During the production of indeterminate tomato cultivars, lateral shoots are not usually retained. When indeterminate cultivars are grown under high planting densities, internode lengths are increased, leaf areas are decreased, and total fruit yield per area is increased (Papadopoulos and Ormrod, 1990, 1991; Logendra *et al.*, 2001; Dong *et al.*, 2008; Kirimi *et al.*, 2011). About plant morphology which would be influenced by planting densities, shoot growth and branching are mainly related to the relationships between IAA and cytokinin (CK) concentrations in plants (Leyser, 2009; Shimizu-Sato *et al.*, 2009; Cleland, 2010).

Although, different planting densities would be expected to influence plant morphology, flower number, and fruit yield in determinate processing and cooking tomato cultivars, there is little information about the effects of planting density on these morphological and physiological characteristics in determinate tomato cultivars.

The new determinate cooking tomato cultivar 'Suzukoma', which was registered (No. 22566) in 2013 at the Ministry of Agriculture, Forestry and Fisheries of Japan, was used in the present study. Planting density for processing and cooking tomato cultivation is generally about 150-250 plants• a^{-1} (Arima and Nakamura, 1969; Takahashi and Hayashi, 1981; Sato *et al.*, 2004; Patanè and Cosentino, 2010). Because 'Suzukoma' is an extremely early-maturing cultivar, a compact vine with joint-less, and resistant to fruit cracking, it is potentially suitable for getting high yields in the soil and solution cultures at high planting density (Abe *et al.*, 2013). Since, this is a purebred cultivar, it is beneficial for growers to have a lower seed cost than other ones in commercial production. Therefore, in recent years the cultivation of this cultivar is gradually increased in Japan. However, it has hardly been investigated that the reason why high planting density (about 400 plants• a^{-1}) compared to the recommended planting density could increase fruit yield in this cultivar. Therefore, the objectives of this study were to evaluate the effects of planting density on fruit yield, plant morphology, flower number, and physiological characteristics.

Materials and methods

Experimental site, plant material, and growing conditions: The cooking tomato cultivar 'Suzukoma' (*Solanum lycopersicum* L.) developed by the National Agriculture and Food Research Organization (NARO) Tohoku Agricultural Research Center,

Morioka, Japan; and ZEN-NOH, Hiratsuka, Japan was used for the present experiment. Seeds were sown in yellowish pumice (diameter 2-5 mm) in plastic containers (34.5 × 27.0 × 7.5 cm) on 21 Apr, 2015. All containers were placed in a greenhouse at Shimane University, Matsue, Japan (35°49' N and 133°07' E). Plants were potted into black plastic pots (diameter 12 cm, 0.6 L) in potting medium containing a 1:1 (v/v) ratio of sandy loam: bark compost on 4 May, 2015. When the sixth true leaf had fully expanded, tomato plants were transplanted into an experimental field with the soil surface covered with black 0.02-mm polyethylene film and with addition of 7.0 kg•a^{-1} of N:P$_2$O$_5$:K$_2$O=16:9:10 fertilizer on 23 May, 2015 at Yatsuka-cho, Matsue, Japan (35°29' N and 133°10' E).

Experimental design and treatments: The experimental plants were planted in double rows 160 cm wide, with spacing between rows of 30 cm, at three planting densities: high density (HD; 15 cm between plants), medium density (MD; 30 cm between plants), or low density (LD; 45 cm between plants), corresponding to 792, 396, or 264 plants•a^{-1}, respectively. The main stem was trained using a stake during the cultivation period. Uniform alleys (60 cm) were allowed between the plantings for all densities. Three replicates of sixteen plants per treatment were transplanted. The eight innermost plants in each replicate were investigated, and the eight outermost plants in each replicate were not included.

Measurements of plant growth, fruit yield, soluble solids content (SSC): Main stem length, plant height, diameter of stem between fourth and fifth nodes, and length of lateral shoot at all nodes were measured at 1, 3, and 7 weeks after transplanting (WAT). The length, width, and thickness of the third, fifth, and seventh true leaves were measured at 7 WAT. The first flowering date of the terminal flower trusses was noted and number of flowers was counted. After harvesting fully ripe fruits twice per week from 11 July to 11 Aug, 2015, individual fruit weight, number of total fruits, and number of marketable fruits (*i.e.* discounting malformed or cracked fruits, or those with blossom-end rot or sunburn) were recorded. SSC were evaluated by a digital refractometer (APAL-1, As One Corp., Osaka, Japan) with hand-squeezed fresh juice samples from 30 fruits per treatment.

Measurements of photosynthetic photon flux densities (PPFD), SPAD values, and photosynthetic rate: PPFD (400-700 nm) were measured at leaf canopy heights of the third true leaf (lower position), fifth true leaf (intermediate position), and seventh true leaf (upper position) using a spectroradiometer (MS-720, Eko Instruments, Tokyo) on 29 June, 2015. The SPAD values and photosynthetic rate of the tip leaflet of leaves at the same positions as those evaluated for dimensions were measured at 7 WAT using a chlorophyll meter (SPAD-502; Konica Minolta Inc., Tokyo). After that, photosynthetic rates were measured with a portable photosynthesis system (LC pro+; ADC, Hoddesdon, UK) with a 1656 µmol•m^{-2}•s^{-1} PPF, under growth chamber temperature of 32.1°C ± 0.5°C and ambient CO$_2$ concentration of 370 ± 5 µmol•mol^{-1}.

Quantification of auxin and CKs: Tomato seedlings were transplanted on 18 May, 2015 into black plastic pots (diameter 15 cm, 1.9 L) containing the same potting medium and fertilizer as for the field experiment and placed in a greenhouse at Shimane University. The stems and lateral shoots of the fourth and fifth

nodes of plants grown in the same arranged pots as field cultivation under the HD or LD treatments were excised on 6 June, 2015. Stem and lateral shoot length showed that the effect of HD treatment on stem elongation and reduction of lateral shoot growth was same in the field experiment and greenhouse. Therefore, the auxin and CKs contents were analyzed using greenhouse-grown samples. Excised stems and lateral shoots were immediately frozen in liquid nitrogen and stored at -80 °C until analysis.

For analysis of indole-3-acetic acid (IAA) and CKs in stems and lateral shoots, 0.2-0.4 g fresh weigh of tissue was collected, homogenized in liquid nitrogen, and extracted in 2.5 mL 80 % (v/v) aqueous acetonitrile containing 1 % (v/v) acetic acid. As internal standards, [^{2}H$_5$] indole-3-acetic acid (IAA), [^{2}H$_6$] N^6-(Δ^2-isopentenyl) adenine (iP), [^{2}H$_5$] *trans*-zeatin (tZ), [^{2}H$_3$] dihydrozeatin (DZ), [^{2}H$_6$] iP riboside (iPR), [^{2}H$_5$] tZ riboside (tZR), and [^{2}H$_3$] DZ riboside (DZR) (OlChemim, Olomouc, Czech Republic) were added to the extraction solvent in advance. After extraction for 1 h at room temperature, solids were removed by centrifugation and re-extracted for 20 min in 2.5 mL of the same extraction solution. The extract was evaporated to water phase and then purified following Katsumata *et al.* (2011). In brief, after evaporation to water phase, extracts were applied to an Oasis HLB column (Waters, Milford, MA, USA), and then the column was eluted with 80 % (v/v) aqueous acetonitrile containing 1 % (v/v) acetic acid. The eluate was evaporated to water phase and applied to an Oasis MCX column (Waters). The column was eluted sequentially with 0.35 M aqueous NH$_4$OH to obtain the neutral/acidic fraction, and then 0.35 M NH$_4$OH in 60 % (v/v) aqueous acetonitrile to obtain the basic fraction. The basic fraction containing CK nucleobases, CK nucleosides, and CK glucosides was evaporated to dryness. The neutral/acidic fraction was evaporated to water phase and applied to an Oasis WAX column (Waters). The column was washed with 80 % (v/v) aqueous acetonitrile, and then eluted with 80 % (v/v) aqueous acetonitrile containing 1 % (v/v) acetic acid to obtain the acidic fraction. The acidic fraction containing IAA was evaporated to dryness. The dried acidic and basic fractions were dissolved in 3 % aqueous acetonitrile containing 0.01 % acetic acid and subsequently analyzed on a liquid chromatography-quadrupole tandem mass spectrometry system (LC/MS/MS, Acquity UPLC/ MS/MS System, Waters, USA). IAA was separated using an ODS column (BEH C18, 1.7 µm, 2.1 mm × 100 mm, Waters) at a flow rate of 0.2 mL·min^{-1} with gradients of solvent A (distilled water containing 0.01 % acetic acid) and B (acetonitrile containing 0.05 % acetic acid), according to the following profile: 0 min with 97 % A + 3 % B, 20 min with 50 % A + 50 % B, and 25 min with 100 % B. CKs were separated with the same gradient but the following eluent profile: 0 min with 97 % A + 3 % B, 20 min with 75 % A + 25 % B, and 32 min with 100 % B. The column temperature was 40 °C. Quantification was performed in selected ion recording mode. The capillary voltage was 2.5 kV, cone voltage was 18-39 V, and collision energy was −16 to −24 V, depending on the molecular species. Data were analyzed using Mass Lynx software (Waters). IAA, iP, tZ, DZ, iPR, tZR, and DZR were quantified by the internal standard method using the corresponding deuterated IAA and CKs. Quantification of IAA and CKs was conducted in three independent technical replicates. CKs of these six types in tomatoes were measured in accordance with a previous report (Matsuo *et al.*, 2012).
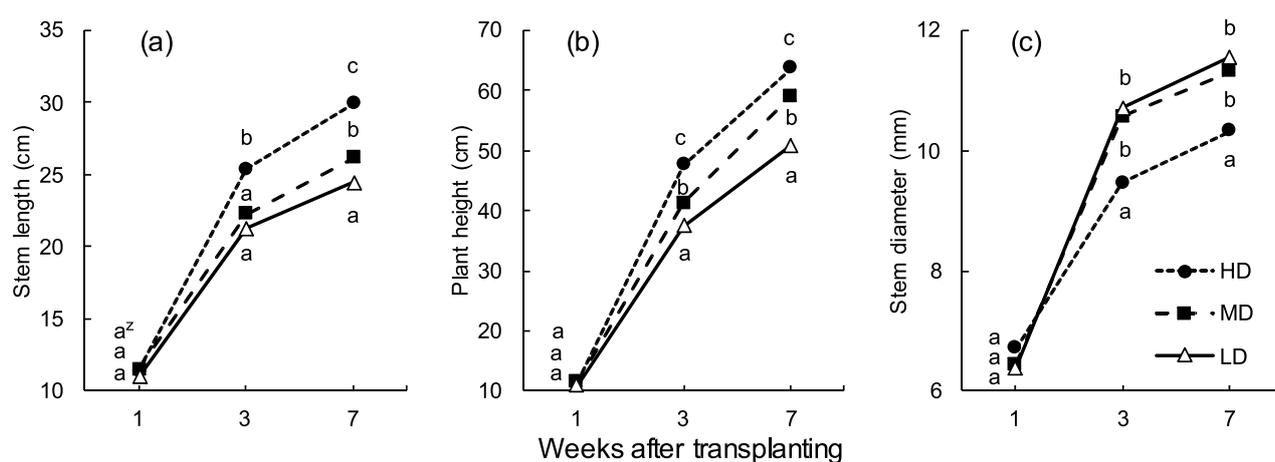
Fig. 1. Effect of planting at high (HD, 792 plant•a⁻¹), medium (MD, 396 plant•a⁻¹), or low (LD, 264 plant•a⁻¹) density on stem length (a), plant height (b), and stem diameter (c) at 1, 3, and 7 weeks after transplanting in the determinate 'Suzukoma' tomato. Vertical bars indicate the SE of the treatment means. Means with different letters are significantly different according to Tukey's test at $P < 0.05$ ($n = 8$).

Statistical analysis: Data were analyzed using Student's *t*-test in SPSS version 19.0.0 (SPSS, Chicago, IL, USA) and the mean separations were performed using Tukey's multiple range test at $P < 0.05$.

Results

Effects of planting density on fruit yield, number, and SSC: Yield, fruit weight, fruit number, fruit set ratio, marketable fruit ratio, and SSC under each treatment are shown in Table 1. Fruit yield per plant was the lowest under HD (1.3 kg•plant⁻¹) compared to MD (2.1 kg•plant⁻¹) and LD (2.6 kg•plant⁻¹); however, fruit yield per area was about 1.3 or 1.5-fold greater under HD (1036 kg•a⁻¹) than under MD or LD, respectively. Fruit number per plant was significantly reduced under HD (35.1 fruits•plant⁻¹) compared to MD or LD, whereas per area was significantly increased under HD (27770 fruits•a⁻¹) compared to MD or LD, respectively. Fruit weights, fruit set ratios, marketable fruit ratios, and SSC did not differ significantly among planting densities.

Effects of planting density on first flowering date and number of flowers: The numbers of days from sowing to the

first flowering and the numbers of flowers for each treatment are shown in Table 2. The number of days from sowing to first flowering was significantly delayed by 1.4 days under HD relative to LD. The number of flowers between the sixth true leaf and the terminal flower truss did not differ among planting densities. However, the numbers of flowers between the cotyledons and the second true leaf, and those between the third and fifth true leaves, were significantly lower under HD compared to LD. Further, the total number of flowers per plant in HD was significantly lower than in the other planting densities, at 150.8 flowers•plant⁻¹, and the number of flowers truss per plant and flowers per truss under HD were the lowest among all planting densities, at 27.1 flower trusses•plant⁻¹ and 5.6 flowers•plant⁻¹, respectively.

Effect of planting density on the plant growth: Stem length, plant height, and stem diameter at 1, 3, and 7 WAT are shown in Fig. 1. Stem length and plant height were significantly greater under HD than those in LD at 3 and 7 WAT. Stem diameter at 3 and 7 WAT were significantly lower under HD compared to other planting densities.

Lateral shoot length of each node at 1, 3, and 7 WAT are shown

Table 1. Effects of at high (HD, 792 plant•a⁻¹), medium (MD, 396 plant•a⁻¹), or low (LD, 264 plant•a⁻¹) planting density on fruit yield, mean fruit weight, fruit number, fruit set ratio, marketable fruit ratio, and soluble solids content (SSC) in the determinate 'Suzukoma' tomato.

Plant density	Fruit yield		Fruit weight (g)	Fruit number		Fruit set ratio (%)	Marketable fruit ratio (%)	SSC (ºBrix)
	(kg/plant)	(kg/a)		(Number/plant)	(Number/a)			
HD	1.3aᶻ	1036b	37.0a	35.1a	27770b	23.9a	93.4a	5.4a
MD	2.1b	822a	39.5a	52.4b	20741a	26.7a	94.3a	5.3a
LD	2.6c	690a	37.2a	69.9c	18464a	23.6a	93.7a	5.4a

ᶻ Means with different letters within each column are significantly different according to Tukey's test at $P \leq 0.05$ ($n = 30$ in SSC, $n = 8$ all others)

Table 2. Effects of planting at high (HD, 792 plant•a⁻¹), medium (MD, 396 plant•a⁻¹), or low (LD, 264 plant•a⁻¹) density on the number of days to first flowering, number of flowers, and number of flower trusses in the determinate 'Suzukoma' tomato.

Plant density	Days from sowing to 1st flowering (day)	Number of flowers (Number/plant)			Total number of flowers (no./plant)	Number of flower trusses (no./plant)	Number of flowers (no./truss)
		Cotyledons to 2nd true leaf	3rd to 5th true leaf	6th to terminal flower truss			
HD	49.6bᶻ	41.0a	23.8a	85.9a	150.8a	27.1a	5.6a
MD	49.1ab	64.3a	48.6b	94.3a	207.1b	33.9b	6.1a
LD	48.2a	116.9b	92.4c	98.2a	307.6c	41.1c	7.5b

ᶻ Means with different letters within each column are significantly different according to Tukey's test at $P \leq 0.05$ ($n = 8$).
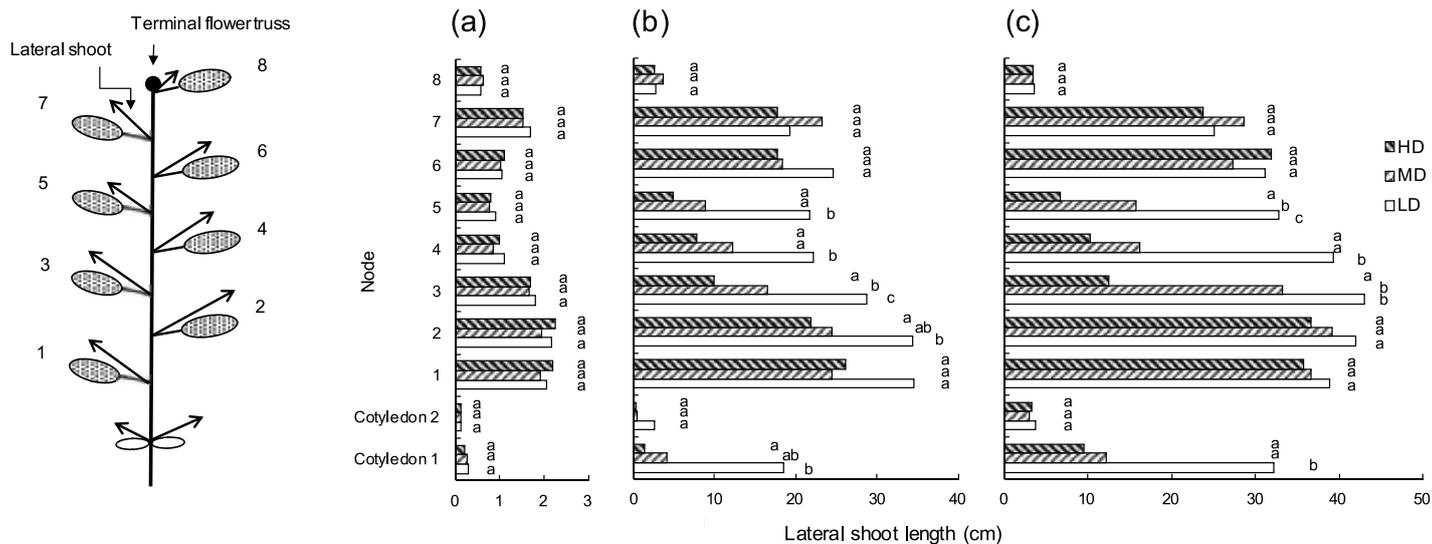
Fig. 2. Effect of planting at high (HD, 792 plant•a⁻¹), medium (MD, 396 plant•a⁻¹), or low (LD, 264 plant•a⁻¹) density on lateral shoot lengths in the determinate 'Suzukoma' tomato at 1 (a), 3 (b), and 7 (c) weeks after transplanting. Means with different letters are significantly different according to Tukey's test at $P < 0.05$ ($n = 8$).
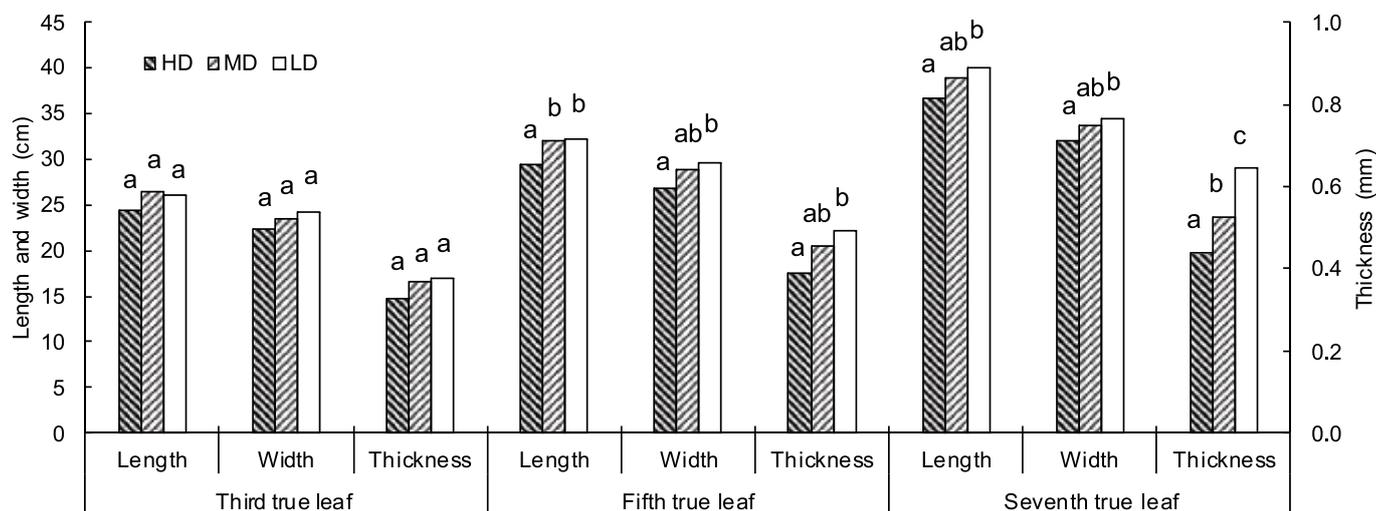

Fig. 3. Effect of planting at high (HD, 792 plant•a⁻¹), medium (MD, 396 plant•a⁻¹), or low (LD, 264 plant•a⁻¹) density on length, width, and thickness of the third, fifth, and seventh true leaves in the determinate 'Suzukoma' tomato. Means with different letters are significantly different according to Tukey's test at $P < 0.05$ ($n = 8$).

Fig. 4. Effect of planting at high (HD, 792 plant•a⁻¹), medium (MD, 396 plant•a⁻¹), or low (LD, 264 plant•a⁻¹) density on photosynthetic photon flux density (PPFD) (a), soil & plant analyzer development (SPAD) values (b), and photosynthetic rates (c) at the third, fifth, and seventh nodes in the determinate 'Suzukoma' tomato. Means with different letters are significantly different according to Tukey's test at $P < 0.05$ ($n = 8$).
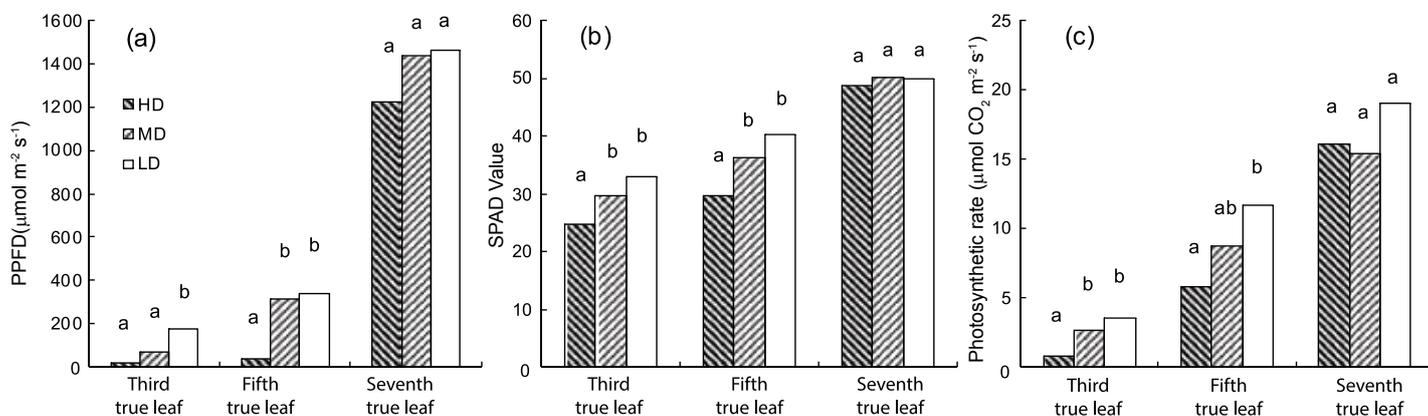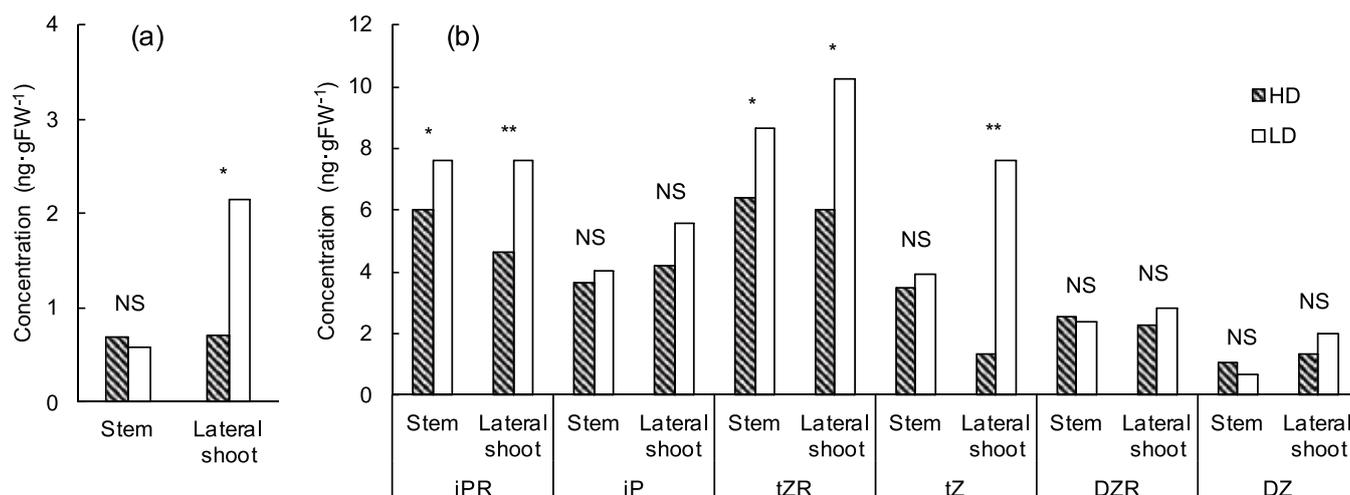
Fig. 5. Effects of planting at high (HD, 792 plant•a⁻¹) and low (LD, 264 plant•a⁻¹) densities on concentration of IAA (a) and CK (b) in the fourth or fifth nodes during greenhouse cultivation of the determinate 'Suzukoma' tomato. Vertical bars indicate the SE of the treatment means. NS, *, ** indicate non-significantly or significantly different at $P < 0.05$ or 0.01, respectively ($n = 3$).

in Fig. 2. At 1 WAT, the lateral shoot length did not differ among planting densities. At 3 WAT, although the lateral shoot length at the first (cotyledonary) node and those at the second to fifth nodes was significantly shorter in HD than those in LD, lateral shoot length at the remaining nodes did not differ among planting densities. At 7 WAT, although the lateral shoot length at the first cotyledonary node and those at the third to fifth nodes were significantly shorter in HD than one third of those in LD, lateral shoot length of other nodes did not differ among planting densities. The length, width, and thickness of the third true leaf did not differ among planting densities (Fig. 3). However, mean values of each of these parameters were lower for the fifth and seventh true leaves under HD compared to LD.

Effect of planting density on photosynthetic photon flux densities (PPFD), SPAD values, and photosynthetic rate: SPAD values and photosynthetic rates of true leaves at the third, fifth, and seventh nodes as well as PPFDs at three positions in the leaf canopy are shown in Fig. 4. Although PPFD values in the upper leaf canopy did not differ among planting densities, those at lower and intermediate leaf canopy positions under HD were the lowest and the values are 10 and 11 % of LD, respectively. SPAD values and photosynthetic rates of the seventh true leaf did not differ among planting densities; however, those of the third and fifth true leaves showed a reduction under HD compared to LD at 75 and 74 % of LD, respectively. Photosynthetic rates of the third and fifth true leaves were lower under HD than LD at 22 and 49 % of LD, respectively.

Effect of planting density on auxin and CKs content: The IAA and CKs concentration in stem and lateral shoots are shown in Fig. 5. Although IAA concentrations in stems did not differ between planting densities, the concentration of IAA in lateral shoots was significantly lower under HD than under LD. The concentrations of iPR and tZR in stems were significantly lower under HD than under LD. The concentrations of iPR, tZR, and tZ in lateral shoots were also significantly lower under HD than under LD. There were no differences in the concentrations of iP, DZ and DZR in stems and lateral shoot between planting densities.

Discussion

In 'Suzukoma' tomato, fruit yield per plant was about 0.6 and 0.5-fold lower under HD (1.3 kg•plant⁻¹) than under MD and LD, respectively; however, fruit yield per area under HD (1036 kg•plant⁻¹) was about 1.3 and 1.5-fold higher than under MD and LD, respectively (Table 1). The fruit yield per unit area is decided by flower number per plant × fruit set ratio × fruit weight × marketable fruit ratio × planting density. In this experiment, because there was no difference among plant densities in the fruit set ratio, fruit weight, and marketable fruit ratio in 'Suzukoma' tomato (Table 1), the yield per area would be decided by flower number and planting density. The flower number under HD (150.8 flower•plant⁻¹) was significantly 0.7- and 0.5-fold lower than those under MD and LD, respectively (Table 2). However, the fruit yield per area under HD was 1.2- and 1.5-fold higher than that under MD and LD, respectively, because planting density under HD was 1.5- and 3.0-fold higher than under MD and LD, respectively. Similarly, the same tendency about the relationship between planting density and fruit yield per plant or area has been observed in other processing and cooking tomato cultivars (Moore *et al.*, 1958; Reeve *et al.*, 1962; Frost and Kretchman, 1988; Sato *et al.*, 2004).

Although planting density is suitable for about 400 plants•a⁻¹ (MD in this experiment) in 'Suzukoma' (Abe *et al.*, 2013), HD was about 3 to 5-fold higher as compared to other planting densities in the processing and cooking tomatoes (Arima and Nakamura, 1969; Takahashi and Hayashi, 1981; Sato *et al.*, 2004; Patanè and Cosentino, 2010). According to previous reports (Ohta and Ikeda, 2015), the shorter lateral shoot length in 'Suzukoma' at maximum 30-40 cm, compared to those in the other processing and cooking cultivars at maximum 50-60 cm, may make it more suitable for high planting density. Although in 'Suzukoma', the higher yield per area in planting distance at 15 cm was obtained in about a half of maximum lateral shoot length, it was necessary in the other processing and cooking cultivars, at least 40-45 cm, more than three quarters of maximum lateral shoot length to obtain higher yield. Thus, such high planting density for higher yield per area could be expected from cultivating this cultivar.

A possible reason that the total number of flowers per plant was significantly lower under HD was the relatively shorter length (about 10 cm less) of the lateral shoots without flowering at the first cotyledonary node and third to fifth node, and the reduced total number of flower by decreased number of flower trusses per plant and flowers per truss under HD compared to MD or LD (Table 2), as in the previous report (Frost and Kretchman, 1988). Reeve *et al.* (1962) reported that the fruit set ratio (56 %) under high planting density was lower than that under low planting density (61 %). Although fruit set ratio (24-27 %) for 'Suzukoma' was low, and did not differ significantly among planting densities (Table 2), the reason is that the extent of fruit load per plant might be high by too many flower number to the plant size of this cultivar.

Several researchers (Frost and Kretchman, 1988; Papadopoulos and Ormrod, 1988; Makoi *et al.*, 2010) reported that plants in high planting density would intercept more light than those in low planting density. In this experiment, although PPFD at low and intermediate leaf canopy positions decreased extremely under HD compared to LD by mutual shading of leaves (Fig. 4a), SPAD values under HD did not decrease the same as PPFD compared to those under LD (Fig. 4b). Since, the photosynthetic rate has positive correlation with nitrogen content shown as SPAD values (Evans, 1989), photosynthetic rates in the fifth and seventh true leaves were not reduced so much under HD compared to those under LD (Fig. 4c). And in tomato plants, the uppermost layer of leaves has been reported to assimilate a disproportionate 66 % of the net CO_2 fixed by the canopy (Acock *et al.*, 1978). This greater contribution of uppermost leaves of the canopy to photosynthesis is reported for several crops (Long *et al.*, 2006), rice (Song *et al.*, 2013), soybean (Miyaji, 1984), and tomato (Sarlikioti *et al.*, 2011). In determinate 'Okitsu F_1 Yozu' tomato, photosynthates produced in the upper canopy leaves were translocated to fruits at the third to fifth nodes below the leaves (Yoshioka and Takahashi, 1984). And in determinate 'Yozu' tomato, the photosynthates produced in the true leaves of lateral shoot are translocated to the fruits of lateral shoots (Shishido and Hori, 1991). Therefore, it is speculated that the extent of decreased photosynthetic rates under HD might not influence so much to fruit weight, fruit set ratio, marketable fruit ratio, and SSC compared to those under the other planting densities.

The lateral shoots at third to fifth intermediate nodes did not elongate under HD as under LD (Fig. 2), this result is similar to those for carnation (Kageyama *et al.*, 1985) and mulberry (Kikuchi, 1980). Since lateral shoot growths were regulated by auxin and CK concentration (Tucker, 1976; Jiang *et al.*, 2012), their concentrations in stems and lateral shoots were analyzed for clarifying the causes of the difference of lateral shoots growth. In stems IAA concentrations did not change depending on planting densities (Fig. 5), whereas iPR and tZR concentrations in the stem under LD increased as compared to those of HD because CKs regulates development of the vascular cambium and radial stem growth (Werner and Schmülling, 2009). However, in the lateral shoots IAA and iP, iPR, and tZR concentrations were significantly greater under LD than under HD. It seems that the lateral shoots under LD would have elongated due to a high concentration of IAA leading to cell elongation (Cleland, 2010) and of CK leading to cell division (Roef and Onckelen, 2010).

When the amount of photosynthate decreases due to a decrease in light intensity, the flow rates of photosynthate to the vegetative organs decrease compared to the fruits (Yoshioka *et al.*, 1977). It is necessary to investigate the relation between the commutation of photosynthate and physiological factors such as changes in metabolism of plant growth regulators. Patrick and Steains (1987) reported that IAA promotes translocation of photosynthate. Auxin (4-chlorophenoxyacetic acid) has the effect of increasing the sink strength, and it is recognized that it gives a change in the balance of source and sink (Shishido and Hori, 1989). Not only when the tomato fruit is used as a sink, but also when the shoot apex having growth activity is taken as sink, it has been accepted that auxin promotes the photosynthate or sugar commutation (Lepp and Peel, 1971; Sagar *et al.*, 2013). Furthermore, the plant growth promoter like auxin is considered to promote the commutation of assimilation products by being influenced by related enzyme activity (Morris, 1982; Patrick, 1982). Therefore, it is thought that the auxin (Cleland, 2010) and CKs (Roef and Onckelen, 2010) increase the growth activity, and the inflow of assimilation products increases accompanying these plant growth regulators.

In this study, stem length and plant height might have increased (Fig. 1a, b), stem diameter might have decreased (Fig. 1c), and leaf size of the fifth and seventh true leaves might have decreased under HD compared to LD due to the same shade avoidance syndrome reaction (SAS) as in the previous studies (Hayashi, 1999; Dong *et al.*, 2008; Roux *et al.*, 2010) under control of the light receptor phytochrome. Since mutual shielding by leaves and lateral shoots under HD increases compared to LD at lower leaf canopy positions in the plant community, the red: far-red ratio decreases, and thereby, stem extension occurs in response to the higher proportion of far-red light (Tao *et al.*, 2008; Roux *et al.*, 2010). The difference of plant growth by light environmental conditions suggested that photomorphogenesis seems to be regulated by some plant growth regulators (*e.g.* auxin, gibberellin, and brassinosteroid) and related genes.

In conclusion, fruit yield per plant decreased, while fruit yield per area increased when 'Suzukoma' was cultivated under high planting density compared to the recommended planting density. Its planting density was higher than other processing and cooking tomatoes because of short lateral shoots lengths. This study clarified that the possible factors under high planting density were decreased number of flowers due to short lateral shoot length influenced by auxin and CKs, and were not so large the extent of the deduction of SPAD values and photosynthetic rates, despite the considerable reduction of PPFD values in low and intermediate canopy positions compared under low planting density. Therefore, the cultivation of this cultivar under high planting density is possible, and it is suggested high yields per area could be obtained because plant morphology was appropriately manipulated.

Acknowledgments

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