Effects of High Water Table and Short-Term Flooding on Growth, Yield, and Seed Quality of Sunflower

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Abstract: Sunflower, a major edible oil crop producing a high-quality and healthful oil for human consumption and also recycled for use as feedstock to produce biodiesel fuel, is recently being cultivated in rotation with rice in the paddy field. The oil of cultivars with a high oleic acid content has higher oxidation stability and better nutritional properties than the standard cultivars, which have a high linoleic acid content. In this study, we evaluated the effects of excess water on plant growth, seed yield, and oil quality. Seed yield, the major yield components, the oleic acid content and the total oil content were negatively affected by a shallow water table. In particular, waterlogging at the establishment stage decreased the growth and seed yield severely. In addition, waterlogging during the flowering and maturation stages tended to decrease the oleic acid content and to increase the linoleic acid content. These results will be useful for improving management practices to increase the seed yield and improve the oil quality of sunflower in rotation with upland paddy rice.

Key words: Crop rotation, Fatty acid, Oleic acid, Rotational paddy field, Sunflower, Water table.

In Japan, sunflower cultivation in rotation with upland paddy rice has started to increase. The oil after use in cooking is recycled as feedstock to produce biodiesel fuel. Soil moisture, soil fertility (Zubriski and Zimmerman, 1974), shade condition and so on have been reported to affect the seed yield (Dedio and Putt, 1980). The oleic acid found in sunflower oil has been proven to inhibit lipogenesis and cholesterologenesis (Francesco et al., 2007). Barradas et al. (1990) reported that consumption of oleic acid tended to decrease the incidence of ischaemic heart disease. Berry and Reivin (1997) reported that oleic acid had antioxidant properties. Such properties can protect cells against stress caused by high oxygen levels (Kinter et al., 1996). Trémolières et al. (1982) reported that a high temperature during maturation increased the amount of oleic acid. Water conditions in the field have been reported to affect growth and oil content (Mahmoud et al., 2007). Garcia-Diaz et al. (2002) reported that oleate desaturase, which is involved in the metabolic transformation of oleic acid into linoleic acid, was regulated by the temperature and availability of oxygen. Oleate desaturase was more active at a low temperature. On the contrary, low oxygen availability inactivated the enzyme. These studies demonstrated that water conditions and the availability of oxygen affect sunflower seed quality. Therefore, it is important to understand the effects of the shallower water table and of waterlogging, water covering the soil surface, both of which are commonly encountered in crop rotation with rice, on the growth and oil quality of sunflower.

Some researchers have studied the effects of short-term waterlogging on sunflower. Waterlogging during the vegetative and floral initiation stages inhibited leaf expansion (Orchard et al., 1986), and waterlogging at anthesis reduced seed yield more than it did at the six-leaf and visible-buds stages (Orchard and Jessop, 1984). Grassini et al. (2007) reported that waterlogging during the grain-filling stage caused adverse physiological responses: leaf area, leaf capacity to fix carbon, water absorption, and grain yield were all decreased. Orchard and So (1985) reported that waterlogging reduced the availability of oxygen and increased ethylene concentrations in the soil, thereby reducing root growth and leading to other physiological effects. Jayasekera et al. (1989) reported that hypoxic flooding of sunflower roots promoted rapid ethanol synthesis in the roots (i.e., anaerobic respiration), and that the ethanol was metabolized by ADH (alcohol...
dehydrogenase) in both the shoots and the roots to avoid its accumulation. Although flooding has been reported to affect the growth of sunflower, the difference in the response to a high water table remains unknown.

We studied the effects of a shallow water table and waterlogging on sunflower growth, yield, and seed quality (oil content and the fatty acid composition) to develop an appropriate method to enhance sunflower growth, yield, and seed quality.

Materials and Methods

1. Experiment I

The effects of contrasting soil moisture conditions on sunflower were examined in the summer of 2005 in two rotational paddy fields (E7 and F7) with different soil moisture conditions (Fig. 1) after paddy rice cultivation at Tsukuba-mirai City, Ibaraki, Japan. In the F7 field, rapeseed, *Brassica napus*, was grown during winter before sunflower, and in the E7 field, oats, *Avena sativa* was grown before sunflower. After sowing of sunflower, seeds of the previous crop germinated spontaneously between the rows. Some allelopathic effects of the rapeseed juveniles have been reported (Yasumoto et al. 2010). All of these seedlings were removed to prevent competition for nutrients and the allelopathic effects. A compound fertilizer was broadcasted prior to planting to provide 8.4 g m⁻² each of N (as (NH₄)₂SO₄), P (as P₂O₅), and K (as K₂O), in both fields. No top dressing was applied.

Nine cultivars with a high proportion of linoleic acid (linoleic type), eleven cultivars with 40–60 % oleic acid (medium-oleic type), and one with at least 82% oleic acid (high-oleic type) were cultivated in each field (Fig. 2). The seeds were sown on 30 May in field F7 and 31 May in field E7 with a row spacing of 0.6 m and 0.8 m, respectively. The seed spacing was 0.3 m and planting depth was 3 cm in both fields.

The stem length, number of seeds in a flower disk, yield, oil concentration (% of seed weight), oil content, and oleic and linoleic acid contents were measured at maturity. The stem length and number of seeds in a flower disk were measured with 5 plants as replicates. Their yield, oil concentration, oil content, oleic and linoleic acid contents of total fatty acids were measured with 3 replicates. The flowering and maturing times were determined according to the guidelines of the National Institute of Agrobiological Sciences (http://www.gene.affrc.go.jp/manuals-plant_characterization_en.php). The volumetric soil moisture content were measured using a soil moisture probe (Profile Probe PR2, Daiki Rika Kogyo Co. Ltd., Tokyo), with special pipes installed in six randomly selected plots in each field. The soil moisture was measured at depths of 10, 20, 30, 40, 60, and 100 cm twice a week, and averages of the measured values from the six plots were used to represent the overall soil moisture. Five plants were sampled from each 21 cultivars at maturity. The heads were separated from the plants to provide for separate measurements.

We dried the heads and seeds of the five sampled plants were dried using the same method as Izquierdo et al. (2002), in an oven at 60°C for 18 h. The yield in each plot was determined by harvesting all plants in two
The oil content and fatty acids contents of the seeds were determined as follows. Two g of seeds from each sample were crushed using an automated mill and the oil was extracted with n-butyl alcohol. The oil content and fatty acid composition were determined by the method of Caviezel (Pendl et al., 1998), using a gas chromatograph (B-820, Nihon Büch Co. Ltd., Tokyo). The fatty acid contents were calculated as the percentage of the area under the corresponding peak to the total peak area.

2. Experiment II
The effects of different water table depths on sunflower cultivation were examined in 2007 and 2008. The two cultivars Hybrid sunflower (Hybrid), (a linoleic type; Kaneko Seeds Co. Ltd., Maebashi City, Gunma prefecture), and
63M80 (a medium-oleic type; Pioneer Hi-Bred International, Inc., Johnston, Iowa, USA) were selected based on the results of experiment I. They were grown in an artificially inclined field with a concrete frame at the Ibaraki Agriculture Institute, Ryugasaki City, Ibaraki prefecture (Fig. 3a). The field was 830 cm long and 860 cm wide and was inclined about 25%. The lower end faced east. The plot contained 10 rows running perpendicular to the slope that were 120 and 190 cm long, and the actual height differences between rows were 9 cm and 8 cm, in 2007 and 2008, respectively, with a different depth to the water table in each row. The ditch surrounding the inclined plot was constantly filled with water after planting, from 11 July in 2007 and 26 June in 2008, until the end of the experiment (Fig. 3b). The volumetric soil moisture content was measured using the Profile Probe PR2 at depths of 40, 60 and 100 cm from the soil surface. The water content was measured at three locations with different water table depths: 9, 46, and 86 cm in 2007 and 12, 45, and 78 cm in 2008 (Fig. 4).

The two hybrid sunflower varieties: Hybrid. and 63M80 were sown early (7 June in 2007 and 5 June in 2008) and late (26 June in 2007 and 2008) in adjacent plots. The climatic data during the growing season were obtained from the Ibaraki Government’s Ryugasaki Agriculture Institute. The space between rows was 0.95 m in 2007 and 0.90 m in 2008, the space between plants was 0.2 m and the planting depth was about 3 cm in both years. Just before planting, a compound fertilizer was uniformly broadcasted at the same rate as in Experiment I in both years. No top dressing was applied. The same parameters as in experiment I and the flower disk diameter, thousand-kernel weight, leaf nitrogen (N) content and total oil content (mg seed$^{-1}$) were measured. Root growth of the two cultivars at flowering (22 August) was examined by excavating the whole root systems of three plants sown on 26 June in 2008 at two water table depths (3.7 and 20.2 cm). The N content (the SPAD value, an indicator of the leaf greenness) at flowering was also measured using a hand-held optical sensor (SPAD-502, Konica Minolta, Inc., Tokyo, Japan) in five plants per plot at the center of the youngest fully expanded leaf in each plant, and then averaged. The leaf N content was estimated from the SPAD value, which was calibrated using 15 sample leaves. The total N concentration in these leaves measured with an automatic NC analyzer (Sumigraph NC22F, Sumika Chemical Analysis Service, Tokyo, Japan) showed a significant correlation with the value estimated from the SPAD value (Fig. 5). The growth and yield in the inclined plots at maturity were analyzed using three to five plants for each water table depth.

The heads and seeds of three to five plants were dried by the same method as in Experiment I and the sampled roots were washed using a colander. The roots and other samples were dried at 60°C until the weight became constant (for about 48 hr) in a forced-air circulation oven by the same method as reported by Izquierdo et al. (2002), to obtain the dry weights. The oil and fatty acids contents of the seeds were measured using the same method as in Experiment I.

3. Experiment III

The effects of waterlogging on sunflower at different developmental stages were examined by a pot experiment in 2009. The pots were 50 cm long, 65 cm wide, and 45 cm deep, and the same hybrid varieties as in Experiment II (i.e., Hybrid. and 63M80) were used. Before planting, a compound fertilizer was applied at the same rate as in Experiment I, with no top dressing. Waterlogging treatments were imposed at different developmental stages, establishment, flower bud initiation, flowering, and maturity, and the control pots were drained according to the usual practice (Fig. 6). Because the flowering time was delayed by waterlogging at the stage of establishment, the seeds of the plants for this treatment were sown on 2 June, while the others on 9 June 2009, to roughly adjust the flowering times in all experimental blocks. The duration of the waterlogging was the same as in the experiments.
Fig. 3. (a) The artificially inclined plot used in Experiment II. (b) The plants on the left were sown early (left; 7 June in 2007 and 5 June in 2008) and those on the right were sown late (right; 26 June in both years).

Fig. 6. The four developmental stages at which waterlogging was imposed: (a) establishment, (b) flower bud initiation, (c) flowering, and (d) maturity.

reported by Wample and Davis (1983), namely 4 days in each treatment. The following parameters were measured: plant height, stem length, disk diameter, stem thickness, leaf number, total N, root dry weight and total dry weight. Yield, and seed quality (thousand-kernel-weight, oil concentration and content, fatty acid composition) were analyzed at physiological maturity (i.e., 40 days after flowering) using three to five plants as replications per cultivar.

The heads and seeds of three to five plants were dried by the same method as in Experiment 1 and the sampled roots were carefully washed using a colander. The roots
and other samples were dried using the same method as reported by Izquierdo et al. (2002), at 60°C until constant weight (for about 48 hr) in a forced-air circulation oven, to determine the dry weights.

The oil and fatty acids contents in the seeds were determined using the same method as in Experiment 1.

4. Statistical analysis

All data were expressed as mean values and standard deviations, and analyzed by a one-way analysis of variance (ANOVA), with Tukey’s multiple-range test, when the ANOVA revealed a significant difference at P<0.05. Pearson’s correlation coefficients among the parameters were also calculated. All statistical analyses were performed with version 11.0 of the Japanese SPSS software (SPSS Inc., Chicago, USA).

Results

1. Experiment I

(1) Soil moisture conditions in the two fields

Fig. 1 shows the soil moisture at different depths during this experiment from early July to the beginning of October (Fig. 1). This period covered the growth stages from flowering to maturation, although the duration of these stages varied with the variety and field (Fig. 2). During this period, soil water content was generally higher in F7 than in E7. The largest difference between the two fields was observed at a depth of 20 cm (Fig. 1).

(2) Effects of soil water content on the development, growth, yield, and seed quality

The flowering dates did not vary greatly with the field or
Fig. 9. Soil water contents in the inclined plot. The water table depths were: 2007: ○, 86 cm; ×, 46 cm; and ■, 9 cm. 2008: ○, 78 cm; ×, 45 cm; and ■, 12 cm.

Fig. 10. The temperature conditions and ripening periods in the inclined plot. Hybrid (linoleic type), ●; and 63M80 (medium oleic type), ■, sown on 7 June in 2007. Hybrid (linoleic type), ○; and 63M80 (medium oleic type), □, sown on 26 June in 2007. Hybrid (linoleic type), ●; and 63M80 (medium oleic type), ■, sown on 5 June in 2008. Hybrid (linoleic type), ○; and 63M80 (medium oleic type), □, sown on 26 June in 2008.
cultivar (Fig. 2). However, the maturity dates of some cultivars varied with the field. Under wetter conditions (F7), the cultivars 6150, 62A91, and 62H81 matured earlier, whereas the cultivars North Queen, Hybrid, 63M80, and Hysun 424 matured later (Fig. 2). Figure 7 shows the air temperature in E7 and F7; the mean temperature of many fields with medium oleic cultivars was lower and the cumulative temperature was higher in F7 than in E7.

Figure 8 shows the relationships in the growth, yield, oil content, and oil quality between the two fields. The stem lengths at flowering were shorter in F7 (wetter conditions) than in E7 in all cultivars. However, the relationship between F7 and E7 in the number of seeds per flower disk varied with the cultivar. For example, this number in Hybrid (a linoleic type) was higher and that in 63M91 was lower than in F7. The yield in F7 was generally lower than that in E7. The oil content and oleic acid content were slightly lower in F7, but the linoleic acid content was slightly higher in F7. However, the differences in oil content and fatty acid composition between the two fields were smaller than the differences in the number of seeds in a flower disk and in the seed yield.

2. Experiment II

Effects of water table depth on growth, yield, and quality

Figure 9 shows the soil water content at three locations with different water table depths in the inclined plot. The largest difference in soil moisture conditions among the three sampling depths (40, 60, and 100 cm) was found in the treatments with water table depths of 40 and 45 cm in 2007 and 2008, respectively. At about 10 cm above the water table, the soil water content was always high, regardless of the depth.

Figure 10 shows the ripening periods in the different treatments. The ripening period varied with the cultivar and water table depth. The period tended to be shorter under the shallow water table conditions as a result of later flowering and earlier maturation. Except for the late-sowing treatment in 2008, the trends were similar in both years (Fig. 11). Due to the difference in the ripening periods, there were some differences in the cumulative temperature among the treatments and cultivars (Fig. 10). The cumulative temperatures for the plants with 0- and 9.2-cm water table depths in 2007 and 3.7-cm depth in the early-sowing block in 2008, were lower, because the ripening period was shorter, even though there were no large differences in the mean temperature (Fig. 10).

The effects of water table depths on sunflower morphology, yield, and oil quality are shown in Figures 12 and 13 and Tables 1 and 2. In both years, stem length and flower disk diameter (which is known to be affected by seed growth and the number of seeds per disk (Knödies 1978)), seed yield, number of seeds per disk and total leaf N tended to be decreased at water table depths of less than 30 cm (Fig. 12, Tables 1 and 2). The effects of water table depth on the growth of sunflower roots clearly differed with the variety. It was clear that even with the water table depth of 3.7 cm, the roots of Hybrid grew vigorously near the ground surface compared with those of 63M80 (Fig. 13).

Tables 1 and 2 summarize the yield, oil content, and fatty acid composition (oleic and linoleic acids) at different water table depths. In the plot with a water table depth shallower than about 30 cm, oil accumulation in the seeds was significantly reduced in both years. The accumulation of oil in a seed tended to be great in the early-sowing group in both years (Tables 1 and 2, Fig. 14). The decreases in the oil concentration, oil content, and oleic acid content with a shallower water table were somewhat clearer in the early-sowing group (Tables 1 and 2). Except for the oleic acid content on the depths of water table were 0 cm in 2007 and 3.7 cm in 2008 for Hybrid, and 3.7 cm depth in 2008 for 63M80 in the late-sowing group the results were similar in both years.

3. Experiment III

Effects of waterlogging at different growth stages on the growth and quality of sunflower

Table 3 summarizes the effects of waterlogging at different growth stages on sunflower growth in the pot experiment. In 63M80, the total dry weight was decreased significantly by waterlogging at all growth stages, whereas in Hybrid, it was only decreased significantly by waterlogging at the establishment stage. The root growth varied with the cultivar. In 63M80, most waterlogging treatments significantly decreased the root dry weight, but in Hybrid, in the root dry weight was not significantly decreased by any treatment. In addition, more adventitious roots appeared after flooding in Hybrid, than in 63M80. Fig. 15 shows typical photos of adventitious root formation after 1 week of waterlogging at the stage of flower bud initiation.

The growth of sunflower (plant height, stem length, disk diameter, stem thickness, leaf number, root dry weight, and N accumulation) was severely suppressed by waterlogging at the establishment stage in both varieties (Table 5). The leaf N contents were significantly lower in the plants that were waterlogged at the stages of establishment, flower bud initiation, and flowering (Table 3). Table 4 summarizes the effects of waterlogging on the seed and oil yields and the fatty acids compositions. The seed yield, thousand-kernel weight and oil accumulation tended to be decreased by waterlogging at the establishment stage. Especially in 63M80, the oil accumulation was suppressed significantly by waterlogging at the establishment stage. In Hybrid, even though the mean and cumulative temperatures did not vary greatly, the fatty acid composition tended to vary with the waterlogging time. In 63M80, waterlogging at flower bud initiation and maturing significantly decreased the oleic acid content (Table 4).
Fig. 11. Ripening periods in the inclined field.
(a) In 2007: ●, Start of flowering; ▲, End of flowering; →, Maturity.
(b) In 2008: ●, Start of flowering; ▲, End of flowering; →, Maturity.
Fig. 12. Effects of water table depth on growth (stem length and flower disk diameter) in the inclined plot.

(a) Hybrid (linoleic type), ●; and 63M80 (medium oleic type), ■; sown on 7 June in 2007.
Hybrid (linoleic type), ○; and 63M80 (medium oleic type), □; sown on 26 June in 2007.
** and *, significant difference between the two sowing dates at the 1% and 5% levels, respectively; ns, not significant.

(b) Hybrid (linoleic type), ●; and 63M80 (medium oleic type), ■; sown on 5 June in 2008.
Hybrid (linoleic type), ○; 63M80 (medium oleic type), □; sown on 26 June in 2008.
** and *, significant difference between the two sowing dates at the 1% and 5% levels, respectively; ns, not significant.
Fig. 13. Root growth of sunflower grown at water table depths of 3.7 cm (left) and 20.2 cm (right). (a) Hybrid (linoleic type). (b) 63M80 (medium oleic type).

Fig. 14. Oil accumulation in sunflower grown in the inclined plot. ns, not significant. ** and *, significant difference between the two sowing dates at the 1% and 5% levels, respectively. Symbols are same as those in Figs. 10, 12.

Fig. 15. Differences in the growth of adventitious roots after 1 week of waterlogging at the flower bud initiation stage in (a) Hybrid (linoleic type) and (b) 63M80 (medium oleic type).
flower disk and decreased yields than in E7. In many
reduced stem elongation in F7, as well as fewer seeds per
sunflower. In the present study, many cultivars showed
been few studies on the effects of high soil moisture on
and the oil content of the grains. However, there have
reported that water deficiency reduced seed and oil yield
180 cm, but this difference was not considered to affect the
examined in two fields, F7 and E7 with different soil
yield, and seed quality in 21 sunflower cultivars were
lected in 2007.

| Sowing date | Cultivar | Water table depth (cm) | Seed yield (g plant⁻¹) | Number of seeds per flower disk | Thousand-kernel weight (q) | Leaf nitrogen content (%) | Oil concentration (%) | Oil content (mg seed⁻¹) | Fatty acid composition |
|-------------|----------|------------------------|------------------------|-------------------------------|---------------------------|--------------------------|----------------------|-------------------------|------------------------|
| Early Sowing | Hybrid. | 86.0 | 101.2 a | 1307 a | 74.0 a | 5.5 a | 40.1 bc | 29.7 a | 53.9 a | 36.8 c |
| (7 June) (linoleic) | 57.2 | 41.1 b | 914 a | 47.8 b | 4.2 bc | 44.0 a | 21.0 b | 41.0 b | 46.9 b |
| 28.4 | 61.5 b | 1077 a | 52.0 b | 4.6 b | 45.7 a | 23.7 b | 40.3 bc | 47.7 ab |
| 9.2 | 51.7 b | 814 ab | 50.8 b | 4.6 b | 41.9 b | 21.3 b | 36.0 c | 52.0 a |
| 0.0 | 2.7 c | 176 b | 28.3 c | 3.7 c | 34.9 c | 9.9 c | 43.5 ab | 41.4 c |
| Late Sowing | Hybrid. | 86.0 | 104.9 a | 1279 a | 82.0 a | 3.7 a | 41.1 b | 35.7 a | 77.6 a | 14.2 c |
| (20 June) (linoleic) | 57.2 | 60.9 b | 995 a | 61.3 b | 4.0 b | 45.1 ab | 27.7 b | 71.8 ab | 19.0 bc |
| 28.4 | 58.6 b | 1066 a | 63.8 b | 3.9 bc | 47.6 a | 30.4 a | 67.2 bc | 29.3 ab |
| 9.2 | 28.0 c | 500 b | 56.0 c | 3.3 bc | 42.2 b | 23.6 c | 65.2 c | 25.8 a |
| 0.0 | 6.6 c | 297 b | 22.4 d | 2.5 c | 26.0 c | 5.8 d | 58.3 d | 25.7 a |

Discussion
In this study, the effects of high soil moisture on growth, yield, and seed quality in 21 sunflower cultivars were examined in two fields, F7 and E7 with different soil moisture content. The space between rows was 0.6 m and 0.8 m for F7 and E7 respectively. Diepenbrock et al. (2001) reported that the achene yield increased with the increase in row spacing. In this study, the row spacing was 60 cm or 80 cm, but this difference was not considered to affect the yield significantly. Nel et al. (2001) reported that water deficiency reduced sunflower seed yield. Afkari (2010) reported that water deficiency reduced seed and oil yield and the oil content of the grains. However, there have been few studies on the effects of high soil moisture on sunflower. In the present study, many cultivars showed reduced stem elongation in F7, as well as fewer seeds per flower disk and decreased yields than in E7. In many medium-oleic cultivars, the ripening period tended to be longer in F7 than in E7 due to delay of maturing time. The mean air temperature tended to be lower and cumulative temperature tended to be higher in F7.

Nagao and Yamazaki (1984) and Sobrino et al. (2003) reported that the oleic acid to linoleic acid ratio increased with increasing temperature during the grain filling stage. In addition, seeds from plants grown at a low temperature had higher activities of microsomal oleoyl phosphatidylcholine desaturase that increase the contents of unsaturated lipids (Garces et al., 1992). Sarmiento et al. (1998) reported that oleate desaturase was activated at low temperature then the 18:2 composition increased in all lipids, and at high temperature the oleate desaturase was repressed then the fatty acid become enriched in 18:1. Izquierdo et al. (2006) reported that the increase in the minimum night temperature during the grain-filling stage up to 22.6°C linearly increased the oleic acid content. Flagella et al.
Yasumoto et al. — Effects of High Water Table and Short-term Flooding on Sunflower (2002) reported that the oleic acid to linoleic acid ratio was decreased by early-sowing (lower mean temperature) and by irrigation (i.e., higher soil moisture). In this study, we found that the oil content and oleic acid content tended to decrease in many cultivars in wet fields. In linoleic-type cultivars, except for 62A91, however, linoleic acid contents tended higher and oleic acid contents tended to be lower in F7 (Figs. 7, 8). From these results, it was thought that the growth, yield, and seed quality of sunflower were affected by both temperature and soil moisture conditions. Under higher soil moisture conditions, the growth, yield, oil content and the oleic acid content tended to decrease. However, since the number of seeds in a disk and yield were higher in F7 than in E7 (Fig. 8), Hybrid. may have some mechanism to tolerate the high soil water content. In medium-oleic-type cultivars, 63M02 and 63M91, the number of seeds in a disk was decreased more severely by the wet condition than in linoleic-type cultivars. Except for Hysun 450, the yield of medium-oleic-type cultivars was higher in F7 than in E7, and the decrease of yields on wet field was more serious than in linoleic-type cultivars.

In Experiment II, the effects of different water table depths of the growth, yield, and seed quality of sunflower were examined. Except for 63M80 in 2008, the ripening period tended to be shorter in the plot with a shallower water table (Fig. 10). Though there was little difference in mean temperature, the cumulative temperature tended to be lower in the plots with a shallower water table. The cumulative temperature was somewhat lower and the maturation was somewhat earlier in the linoleic-type cultivar (Hybrid) than in the medium-oleic cultivar (63M80) (Figs. 10, 11).

There were some growth and yield differences between the two years (Tables 1 and 2, Fig. 11). One possible explanation is the difference in the climatic conditions between the two years (i.e., the mean and cumulative temperature and cumulative temperature).
temperatures were higher in 2008; Fig. 10). The differences in growth, seed yield and oil contents between the two years were clearer when the water table was shallower than about 30 cm (Tables 1 and 2, Figs. 12 and 14).

Means within a column labeled with different letters differ significantly between growth stages at the time of waterlogging (P < 0.05, Tukey’s multiple-comparison test, n = 3).

Table 3. Effects of waterlogging at different growth stages on the growth of sunflower.

| Development stage of waterlogging | Days from sowing date to end of flowering | Plant height (cm) | Stem length (cm) | Disk diameter (cm) | Stem thickness (cm) | Leaf number | Leaf nitrogen content (%) | Root dry weight (g plant⁻¹) | Total dry weight (g plant⁻¹) |
|----------------------------------|------------------------------------------|------------------|-----------------|-------------------|-------------------|------------|------------------------|---------------------------|---------------------------|
| Hybrid. Establishment            | 69.9 a                                   | 132.1 c          | 126.7 c         | 12.9 c            | 1.4               | 26.8 b     | 1.5 b                  | 6.5                       | 82.7 b                    |
| Flower bud initiation           | 66.8 b                                   | 141.6 b          | 153.5 b         | 14.4 ab           | 1.5               | 26.8 b     | 1.6 b                  | 7.6                       | 100.4 ab                  |
| Flowering                       | 65.3 c                                   | 146.4 ab         | 141.1 ab        | 13.9 bc           | 1.5               | 29.1 a     | 1.6 b                  | 7.3                       | 111.8 ab                  |
| Maturing                        | 65.8 c                                   | 152.9 a          | 146.9 a         | 15.6 a            | 1.5               | 28.8 a     | 3.2 a                  | 8.0                       | 130.1 a                   |
| Cont.                            | 66.2 bc                                  | 153.0 a          | 147.6 a         | 15.2 ab           | 1.5               | 29.7 a     | 2.8 a                  | 8.8                       | 130.0 a                   |
| 63M80 Establishment             | 68.8 a                                   | 128.4 c          | 122.0 c         | 13.6 b            | 1.5 b             | 26.1 d     | 0.5 d                  | 7.4 b                      | 69.7 b                    |
| Flower bud initiation           | 65.6 b                                   | 137.0 b          | 130.0 b         | 15.1 a            | 1.5 a             | 29.0 c     | 1.5 c                  | 10.6 a                     | 99.4 b                    |
| Flowering                       | 65.1 bc                                  | 149.6 a          | 142.7 a         | 15.6 a            | 1.6 a             | 27.4bd     | 2.0 b                  | 8.5 b                      | 95.1 b                    |
| Maturing                        | 65.8 bc                                  | 150.0 a          | 143.0 a         | 14.7 ab           | 1.5 ab            | 29.0 bc    | 2.6 a                  | 6.9 b                      | 81.5 b                    |
| Cont.                            | 64.9 c                                   | 145.0 ab         | 140.0 a         | 16.0 a            | 1.5 a             | 33.0 a     | 2.7 a                  | 16.3 a                     | 148.6 a                   |

Means within a column labeled with different letters differ significantly between growth stages at the time of waterlogging (P < 0.05, Tukey’s multiple-comparison test, n = 3).

In Experiment III, we studied the effects of waterlogging during some stages of sunflower development on the growth, yield, and seed quality. The waterlogging at the establishment stage especially suppressed sunflower growth and decreased the yield seriously. In Japan, water management is important not only during cultivation in rotation with rice paddy fields but also during general cultivation which can be either during the rainy season or typhoon season.

The oil concentration and fatty acid composition in seed were affected by waterlogging from flowering to maturity. The oleic acid content tended to decrease with an increasing water table depth, and the response was similar in 2007 and 2008 except for 63M80 in 2008 (Tables 1 and 2). Because the roots of sunflower can penetrate to a depth of 150 to 270 cm (Weaver, 1926), the water table depth in the present study is quite shallow. In soybean, Shimada et al. (1995) found that fluctuation of the water table depth reduced the yield and 100-seed weight. In the present study, the water table depth remained constant. Lack of variation might have affected the magnitude of the suppression of growth and the decrease of yield and oil content when the water table depth was shallow (from 30 to 50 cm).

Our results suggest that oil accumulation in the seed was greatest at a water table depth of 30 to 50 cm. This suggests that farmers must carefully consider the soil moisture content if they want to obtain high yield and high seed quality in sunflower. The fatty acid composition was also affected by the water table depth. We observed a significant decrease in the oleic acid content and a significant increase in the linoleic acid content with a rising (shallow) water table. There have been some previous reports about the relationship between the fatty acid composition and environmental conditions. For example, Rolletschek et al. (2007) reported about fatty acid composition in developing sunflower seeds, the effect of environmental temperature and the key enzyme involved in fatty acid desaturation. The key enzyme was oleyl-phosphatidyl choline desaturase which is responsible for the desaturation of oleic acid into linoleic acid.

They reported that temperature rise clearly reduced the internal oxygen concentration and specifically limited the oleyl-phosphatidyl choline desaturase activity. In the present study, the low oxygen concentration in the flooded soils may have affected the fatty acid composition by means of these mechanisms.

In Experiment III, we studied the effects of waterlogging during some stages of sunflower development on the growth, yield, and seed quality. The waterlogging at the establishment stage especially suppressed sunflower growth and decreased the yield seriously. In Japan, water management is important not only during cultivation in rotation with rice paddy fields but also during general cultivation which can be either during the rainy season or typhoon season.

The oil concentration and fatty acid composition in seed were affected by waterlogging from flowering to maturity. The oleic acid content tended to be decreased by waterlogging, especially during the period between flowering and maturity. Especially in Hybrid, the oil concentration and oleic acid content were significantly decreased by the waterlogging at maturing time, even though mean and cumulative temperatures were not different or somewhat higher than in other blocks (Table 4).

In the present study, waterlogging during early development (i.e., at the establishment stage) affected growth and yield more seriously than at other stages. Orchard and Jessop (1984) reported that sunflower seed yield was most affected by waterlogging during the anthesis stage. Behera and Behera (1993) reported that biomass production and pigment, protein, and nucleic acid contents of sunflower were lower in plants subjected to...
early waterlogging. Singh et al. (2002) also reported that the detrimental effects of water stagnation on sunflower were greater at the six- to eight-leaf stage (50 days after sowing) than at the flowering stage (80 days after sowing).

Steffens et al. (2005) reported that the oxygen deficiency in waterlogged soil inhibited ATP synthesis, leading to decreased nutrient uptake. In the present study, we examined the response of root growth to waterlogging. We found clear differences with the variety (Table 3, Fig. 13). Though the root dry weight of Hybrid was generally lighter than that of 63M80, Hybrid produced more adventitious roots developed to prevent injury to the shoot and to promote shoot recovery from flooding. Kramer (1951) reported that adventitious roots contribute to plant survival during flooding.

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### Table 4. Effects of waterlogging treatment on the harvest quality of seeds ripening for 40 days after flowering time.

| Cultivar | Development stage at the time of waterlogging | Seed yield (g plant$^{-1}$) | Thousand-kernel weight (g) | Oil concentration (%) | Oil content (mg seed$^{-1}$) | Fatty acid composition | Mean air temperature ($^\circ$C) | Accumulated temperature ($^\circ$C) |
|----------|---------------------------------------------|-----------------------------|---------------------------|-----------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Hybrid.  | Establishment                                | 19 c                        | 31.7 b                    | 52.9 ab               | 16.7                        | 26.5 ab                    | 23.3                        | 933.6                       |
| Flower bud initiation | 21 c                        | 30.6 b                     | 54.5 a                    | 16.6                 | 22.6 b                     | 57.6 ab                    | 22.6                        | 905.4                       |
| Flowering | 23 bc                        | 35.7 ab                    | 49.5 b                    | 17.6                 | 25.9 ab                    | 53.3 b                     | 23.2                        | 882.2                       |
| Maturing | 35 a                         | 35.9 ab                    | 48.3 b                    | 17.5                 | 18.6 c                     | 62.8 a                     | 22.7                        | 930.2                       |
| Cont.    | 30 ab                        | 40.2 a                     | 50.2 ab                   | 20.4                 | 31.3 a                     | 50.5 b                     | 22.6                        | 905.4                       |

| Cultivar | Development stage at the time of waterlogging | Seed yield (g plant$^{-1}$) | Thousand-kernel weight (g) | Oil concentration (%) | Oil content (mg seed$^{-1}$) | Fatty acid composition | Mean air temperature ($^\circ$C) | Accumulated temperature ($^\circ$C) |
|----------|---------------------------------------------|-----------------------------|---------------------------|-----------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| 63M80    | Establishment                                | 14 b                        | 34.5 b                    | 52.2                  | 18.0 b                     | 63.8                        | 22.5                        | 933.6                       |
| Flower bud initiation | 36 a                        | 42.8 ab                    | 53.0                      | 22.7 ab               | 66.7                        | 20.6                        | 22.7                        | 930.2                       |
| Flowering | 24 ab                        | 49.3 a                     | 53.6                      | 26.4 a                | 51.4                        | 34.5                        | 22.9                        | 983.1                       |
| Maturing | 26 ab                        | 45.4 a                     | 52.6                      | 23.9 a                | 63.4                        | 22.9                        | 22.6                        | 905.4                       |
| Cont.    | 30 ab                        | 46.8 a                     | 53.4                      | 25.0 a                | 65.2                        | 21.2                        | 23.2                        | 882.2                       |

Means within a column labeled with different letters differ significantly between growth stages at the time of waterlogging (P<0.05, Tukey's multiple-comparison test, n=3).
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