J Plant Growth Regul (1997) 16:47–53

Journal of
Plant
Growth
Regulation

Effects of Waterlogging on Nitrogen Accumulation and Alleviation of Waterlogging Damage by Application of Nitrogen Fertilizer and Mixtalol in Winter Rape (*Brassica napus* L.)

W. Zhou,[1,]* D. Zhao,[2] and X. Lin[3]

[1]Department of Agronomy and [2]Central Laboratory, Zhejiang Agricultural University, Hangzhou 310029; and [3]Department of Agronomy, China National Rice Research Institute, Hangzhou 310006, China

Received July 3, 1996; accepted December 26, 1996

Abstract. A study on the physiological and yield effects of waterlogging and the alleviation of waterlogging damage by the application of nitrogen fertilizers and mixtalol in winter rape was conducted in experimental tanks especially designed for controlling soil moisture content. The results showed that waterlogging at the seedling and stem elongation stages causes a significant decrease in nitrogen content and rate of nitrogen accumulation. Leaf chlorophyll content, superoxide dismutase and catalase activities, and root oxidizability (capacity for root oxidation) and root exudate were also reduced by waterlogging. The experiments confirmed that the physiological function of rape plants was retarded during the time of waterlogging at the seedling stage, and its adverse effects remained. Plant height, stem width, and the number of primary branches per plant were decreased significantly by waterlogging at the seedling and stem elongation stages. Pods per plant and seeds per pod were also reduced significantly, giving a 21.3 and 12.5% decrease of seed yield from the control for treatments at the seedling and stem elongation stages, respectively. Foliar sprays of nitrogen fertilizers at the seedling stage or mixtalol at the flowering stage alleviated plant damage caused by waterlogging by retarding chlorophyll and nitrogen degradation, increasing superoxide dismutase and catalase activities and root oxidizability, and improving yield components and seed yield of waterlogged plants. Therefore, besides draining off water, alleviation of waterlogging damage may be controlled by applying nitrogen fertilizer and a suitable plant growth regulator at appropriate growth stages.

Abbreviations: SOD, superoxide dismutase; NBT, nitro blue tetrazolium; CAT, catalase; TTC, red tetrazolium.

*Author for correspondence.

Key Words. *Brassica napus* L.—Waterlogging—Physiological characteristics—Nitrogen fertilizer—Mixtalol

Oilseed rape (*Brassica napus* L.) is the most important source of edible oil in China and is expanding rapidly as a rotation crop following rice (Zhou 1994). Excess moisture or drought during rape growth is an important factor in low yield (Zhou 1994). Low oxygen concentration because of waterlogging affects growth and development, including carbohydrate metabolism and respiratory activity (Pezeshki 1994). Waterlogging is a serious international problem, especially when the water table remains near the soil surface following rape transplant and establishment, and consequently, yield reduction is observed (Cannell and Belford 1980, Yin et al. 1980, Zhou 1994).

The adverse effects of waterlogging on terrestrial plants are complex phenomena and appear to vary with the genotype, pretreatments, the plant developmental stage, and the duration and severity of flooding. Waterlogging affects physiological characteristics and the seed yield of winter rape throughout its life cycle (Zhou and Lin 1995). To date, the following specific responses have been examined: formation of new aerenchymatous roots during and after desubmergence or waterlogging of the soil, and underwater accelerated growth of stems and petioles (Drew et al. 1979a, Justin and Armstrong 1987, Atwell et al 1988, Voesenek and Blom 1989, Laan et al. 1991, Voesenek et al. 1993).

The application of nitrate and other nitrogen fertilizers alleviates waterlogging damage to barley and maize plants (Drew et al. 1979b, Chen 1989). Plant growth regulators are used increasingly to manipulate growth and yield, and synthetic cytokinins have been reported to alleviate waterlogging damage (Nickell 1982, Drew et al. 1979b). Mixtalol (a mixture of long chain aliphatic alcohols varying in chain length from C_{24} to C_{34}) is a recent chemical introduction which has been reported to stimulate plant growth, delay plant senescence, and enhance yield and yield components (Srivastava and Menon 1987, Setia et al. 1989, Zhou and Xi 1993, Zhou et al. 1995). The present experiments were conducted to evaluate the effects of waterlogging on nitrogen accumulation and the alleviation of waterlogging damage by the application of nitrogen fertilizers and mixtalol in winter oilseed rape.

Materials and Methods

Plant Culture

The winter season experiments were conducted at Zhejiang Agricultural University, Hangzhou (30°10′N, 120°12′E). Concrete containers (400 × 100 × 120 cm) with drainage holes 15 cm apart in the side were constructed in the field 50 cm apart. Fitted frames covered with plastic film prevented the entry of rain, when necessary. The containers were filled with a silt loam soil containing 0.18% total nitrogen, 2.11% organic matter, 52 mg/liter readily available phosphorus, and 127 mg/liter readily available potassium. Fertilizers, at the equivalent of 200 kg of N/ha, 60 kg of P_2O_5/ha, and 110 kg of K_2O/ha, were mixed thoroughly in the soil of each container.

Oilseed rape (*B. napus*) cv. 601 was sown on 7 October in a separate seedbed of silt loam soil. Fifty seedlings were transplanted on 21 November (at the five-leaf stage) into each container. Plants were subjected to waterlogging to the soil surface for 30 days at various stages of growth in a randomized block design using three replicates: (1) the seedling stage (from 2 December to 1 January); (2) the stem elongation stage (from 18 February to 20 March); (3) the flowering stage (from 18 March to 17 April); and (4) the pod formation stage (from 18 April to 18 May). In the control treatment (CK), the solid moisture was kept at 80% of field capacity during the whole growth period.

A 2,000-mg/liter suspension of mixtalol (a mixture of tetracosanol, hexacosanol, octacosanol, triacontanol, doctriacontanol, and tetratriacontanol in varying concentrations) was formulated and provided by the Seed Regulator Laboratory of Zhejiang Agricultural University. In exact duplicate experiments during the next season, 1% urea solution and 4 mg/liter mixtalol were applied as foliar sprays at the rate of 400 mL of formulated solution per container (750 liters of formulated solution/ha), to rape plants waterlogged for 5 days at the seedling and flowering stages, respectively (with three replicates), to evaluate the remediation of plant damage caused by waterlogging. Conventional methods of cultivation were followed during the growing period. All plants were harvested on 22 May.

Measurement Techniques

Ten plants taken from the central rows of each plot were used for physiological analyses and morphological measurements during plant growth. Plant nitrogen content was measured by the H_2SO_4–H_2O_2 digestion method (Lin et al. 1993). Leaf chlorophyll content was determined by the acetone/ethanol mixture assay method (Chen 1984). Leaf superoxide dismutase (SOD) activity was analyzed by the method of Zhu et al. (1990). Leaf tissue (500 mg) was homogenized at 4°C in 5 mL of 50 mM phosphate buffer (pH 7.0) containing 1% insoluble polyvinylpyrrolidone with a mortar and pestle. The homogenate was centrifuged at 15,000 ×*g* for 10 min, and the supernatant obtained was used as the enzyme extract. SOD activity was assayed essentially as described by Dhindsa et al. (1981) by measuring the ability to inhibit the photochemical reduction of nitro blue tetrazolium (NBT). The 4-mL reaction mixture contained 50 mM phosphate buffer (pH 7.8), 77.12 μM NBT, 0.1 mM EDTA, 13.37 mM methionine, 0–10 μL of enzyme extract, and 100 μL of 80.2 μM riboflavin (riboflavin was added last). Leaf catalase (CAT) activity was analyzed by the hydrogen peroxide reduction method (Zhou and Lin 1995). Leaf extracts were treated with 5 mL of 0.1 N H_2O_2 and kept at 20°C for 5 min. Then 1 mL of 20% KI solution was added with 3 drops of 10% $(NH_4)_6Mo_7O_{24}$ solution and 5 drops of 1% starch solution. 0.02 N $Na_2S_2O_3$ was used to titrate the reaction solution until the disappearance of blue color. CAT activity was assayed by determining the rate of reduction of hydrogen peroxide during a given period.

Root oxidizability (capacity for root oxidation) was measured by the red tetrazolium (TTC) reduction method (Shen et al. 1991). The roots were washed free of soil, and then 1.0 g of roots from each treatment was placed in a 25-mL test tube and sealed with a rubber stopper. The tubes were treated with 5 mL of 0.4% TTC solution and 5 mL of 1/15 M phosphate buffer (pH 7.0). After incubation for 3 h at 37°C, the tubes were treated with 2 mL of 2 N H_2SO_4. Then roots were ground with ethyl acetate (total of 10 mL) to extract red triphenylformazane, and the extract was read at 485 nm. Root exudate was determined by gravimetric analysis (Ding and Shen 1985).

Plant height, stem width, branching position (distance between the cotyledon node and lowest primary branch), number of primary branches, pods per plant, seeds per pod, and seed weight were recorded from ten random plants of each treatment, at harvest. Seed yield was obtained as the aggregate of all plants. Data from the three replications were pooled, and statistical inferences were made based on Duncan's New Multiple Range Test between the control and various treatment means.

Results

Effect of Waterlogging on Nitrogen Accumulation

The nitrogen concentration in various rape organs was obviously reduced after plants were subjected to waterlogging for 30 days at different stages of growth (Table 1). The most significant effect of waterlogging was observed on the leaves of each treatment, which contained 35.05, 26.39, and 25.88% less nitrogen than the controls for per plant, and 7.73, 6.70, and 3.33% less than the controls for the nitrogen concentration (in dry weight %), respectively. Stem nitrogen contents both in dry weight % and per plant were also reduced significantly 13.94 and 28.37%, respectively, relative to the controls with waterlogging at the stem elongation stage. The nitrogen contents of stem and flower were not affected markedly by waterlogging at the flowering stage.

During prolonged waterlogging, old roots senesced and died gradually, and short fleshy lateral roots developed at the soil line. Consequently, the root nitrogen concentrations (in dry weight %) were not affected much by waterlogging, but the root nitrogen content per plant was reduced significantly, 18.85, 12.98, and 16.32% relative to the controls with waterlogging at seedling,

Table 1. Changes in nitrogen contents of various rape organs after waterlogging at different growth stages for 30 days.

Treatment	Seedling		Stem elongation			Flowering			
	Leaf	Root	Leaf	Stem	Root	Leaf	Stem	Flower and pod	Root
CK									
DW%[a]	4.01	2.06	3.88	2.08	1.29	4.21	1.05	3.96	1.10
mg/pl[b]	305.6	26.0	535.5	208.0	57.8	395.7	198.1	268.1	71.1
Waterlog.									
DW%	3.70*[c]	2.13	3.62*	1.79*	1.34	4.07	1.02	4.05	1.05
mg/pl	198.5**	21.1*	394.2**	149.0**	50.3*	293.3**	188.6	280.1	59.5*
+CK%									
DW%	−7.73	3.40	−6.70	−13.94	3.88	−3.33	−2.88	2.27	−4.55
mg/pl	−35.05	−18.85	−26.39	−28.37	−12.98	−25.88	−4.80	4.48	−16.32

[a] Nitrogen content in dry weight %.
[b] Nitrogen content per plant (mg/plant).
[c] * and **, significant at the 0.05 and 0.01 level of probability, respectively.

stem elongation, and flowering stages, respectively (Table 1).

The rate of nitrogen accumulation was reduced significantly after plants were subjected to waterlogging for 30 days at various stages of growth (Fig. 1). The waterlogged plants treated at the seedling, stem elongation, and flowering stages had low rates of nitrogen accumulation, which were decreased significantly, 42.3, 41.8, and 29.4%, respectively, relative to the controls. Waterlogging at the seedling stage not only affected the nitrogen accumulation of plants at seedling stage itself (reduced 42.3%), but it also affected the rate of nitrogen accumulation at the stem elongation and flowering stages (reduced 37.5 and 50.0%, respectively). Waterlogging at the stem elongation stage affected the rate of nitrogen accumulation of plants at the stem elongation stage itself (reduced 41.8%); but as plants reached the flowering stage (when the soil moisture was suitable, and the growth conditions of plants were gradually improved), the adverse effect of waterlogging on rates of nitrogen accumulation was alleviated, and only a 6.7% decrease of the rate of nitrogen accumulation was observed at the flowering stage, suggesting that the plants gradually recovered.

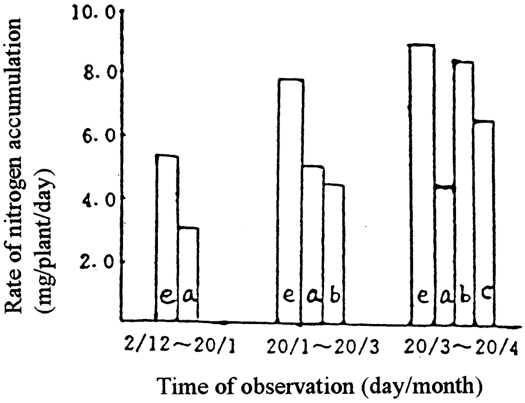

Fig. 1. Effect of waterlogging on the rate of nitrogen accumulation (mg/plant/day) of rape plants. *e, a, b,* and *c* represent the control, treatments of waterlogging at the seedling, stem elongation, and flowering stage, respectively.

Effect of Waterlogging on Yield Components

Plant height and stem width were decreased significantly by waterlogging at the seedling and stem elongation stages (Table 2). Plants waterlogged at the seedling stage had a lower branching position and fewer primary branches than the control. Terminal raceme length was reduced significantly by waterlogging at the stem elongation stage. No obvious differences in stem width, branching position, and primary branch and terminal raceme length were found between the controls and plants that were waterlogged at flowering or pod formation stages.

Table 2 also shows that pods per plant and seeds per pod were reduced by waterlogging. The greatest effect resulted from treatments at the seedling and stem elongation stages. For those two treatments, pods per plant were decreased 28.2 and 22.3%, and seeds per pod were decreased 8.2 and 13.9%, respectively, from the controls. No significant difference in seed weight was observed between any treatment and the control. The seed yield of waterlogged plants at seedling and stem elongation reached only 1,037.1 and 1,152.9 kg/ha, respectively,

Table 2. Effect of waterlogging at different growth stages on yield components and yield of rape plants measured at harvest.

Treatment[a]	Plant height (cm)	Stem width (cm)	Branching position[b] (cm)	Primary branch (no.)	Terminal raceme length (cm)	Pods/plant (no.)	Seeds/pod (no.)	Seed weight (mg)	Seed yield (kg/ha)
CK	178.1	1.92	64.5	7.0	63.8	446.2	12.2	2.71	1,317.9
WS	155.4*[c]	1.38**	51.2*	6.2*	61.9	320.3**	11.2*	2.54	1,037.1**
WE	155.5*	1.65*	64.4	6.5*	54.3*	346.8**	10.5*	2.69	1,152.9*
WF	162.9*	1.80	65.9	6.7	62.7	417.7	11.5	2.76	1,293.2
WP	168.8	1.81	61.1	6.9	63.7	397.0*	11.4	2.71	1,250.3

[a] Treatments of WS, WE, WF, and WP represent waterlogging at seedling, stem elongation, flowering, and pod formation stages, respectively.
[b] Distance between the cotyledon node and lowest primary branch.
[c] * and **, significant at the 0.05 and 0.01 level of probability, respectively.

Table 3. Effect of nitrogen fertilizer (N) on leaf chlorophyll and nitrogen contents and leaf SOD and CAT activities of rape plants waterlogged for 5 days at the seedling stage (measured 15 days after N treatment).

Item	Treatment	Leaf position[a] 6	7	8	9
Chlorophyll (mg/g FW)	CK	0.31[b]aA	0.43aA	0.65aA	0.72aA
	Waterlog.	0.19cB	0.28cC	0.52cB	0.61cB
	Waterlog. + N	0.23bB	0.35bB	0.58bAB	0.66bAB
Nitrogen (DW%)[c]	CK	3.05aA	3.26aA	3.52aA	3.68aA
	Waterlog.	2.36cB	2.60cB	2.83cB	2.89cB
	Waterlog. + N	2.80bAB	2.84bAB	3.05bAB	3.20bAB
SOD activity (unit/g FW/min)	CK	10.30aA	13.54aA	18.27aA	20.65aA
	Waterlog.	5.27cC	9.08cB	14.30cB	18.51bA
	Waterlog. + N	6.42bB	10.52bB	16.02bAB	19.30bA
CAT activity (H_2O_2 mg/g FW/min)	CK	7.03aA	7.52aA	8.40aA	9.34aA
	Waterlog.	3.98cC	5.81cB	6.73cB	8.04bA
	Waterlog. + N	4.80bB	6.30bAB	7.19bAB	8.51bA

[a] All leaves are labeled, and the first emerged leaf is designated 1.
[b] Within columns, means followed by the same capital and small letters are not significantly different at the 0.01 and 0.05 level of probability, respectively.
[c] Nitrogen content in dry weight %.

Table 4. Effect of nitrogen fertilizer (N) on root oxidizability and root exudate of rape plants waterlogged for 5 days at the seedling stage (measured 15 days after N treatment).

Treatment	Root oxidizability (TTC mg/g FW/h)	Root exudate (g FW/plant/h)
CK	0.560[a]aA	0.260aA
Waterlog.	0.489bA	0.217cB
Waterlog. + N	0.531aA	0.238bAB

[a] Within columns, means followed by the same capital and small letters are not significantly different at the 0.01 and 0.05 level of probability, respectively.

significant decreases relative to the control of 21.3 and 12.5%.

Effect of Nitrogen Fertilizer on Waterlogging Damage

Leaf chlorophyll and nitrogen contents and SOD and CAT activities were reduced significantly after plants were exposed to waterlogging at the seedling stage, but a foliar spray of nitrogen fertilizer alleviated the plant damage caused by waterlogging (Table 3). The nitrogen fertilizer-treated plants had higher leaf chlorophyll and nitrogen contents and higher SOD and CAT activities than the waterlogged plants, although the values were still lower than the control. The most significant effect of nitrogen fertilizer was observed on the lowest leaf (leaf 6) and gave readings of 21.1, 18.7, 21.8, and 20.6% higher than the waterlogging treatment for leaf chlorophyll and nitrogen contents and SOD and CAT activities, respectively.

The root oxidizability and root exudate of waterlogged plants increased with the application of nitrogen fertilizers (Table 4). The nitrogen fertilizer-treated plants had high root oxidizability and root exudate, which were increased significantly, 8.6 and 9.7%, respectively, relative to the waterlogging treatment.

The yield components and seed yield of waterlogged plants also improved with the foliar application of nitrogen fertilizers (Table 5). Plant height, stem width, and

Table 5. Effect of nitrogen fertilizer (N) on yield components and yield of rape plants waterlogged for 5 days at seedling stage (measured at harvest).

Treatment	Plant height (cm)	Stem width (cm)	Branching position[a] (cm)	Primary branch (no.)	Pods/plant (no.)	Seeds/pod (no.)	Seed weight (mg)	Seed yield (kg/ha)
CK	176.2[b]aA	1.85aA	62.8aA	7.3aA	428.7aA	15.0aA	3.05aA	1,345.8aA
Waterlog.	146.9cA	1.47cB	54.7bA	6.2bA	375.2bA	13.2bA	2.85aA	1,217.4bA
Waterlog. + N	158.3bA	1.60bAB	59.1abA	6.7aA	406.8aA	14.1abA	2.87aA	1,312.6aA

[a] Distance between the cotyledon node and lowest primary branch.
[b] Within columns, means followed by the same capital and small letters are not significantly different at the 0.01 and 0.05 level of probability, respectively.

primary branches were increased significantly by nitrogen application at the seedling stage. The nitrogen-treated plants had more pods per plant and higher seed yields, which were increased significantly, 8.4 and 7.8%, respectively, relative to the waterlogging treatment.

Effect of Mixtalol on Waterlogging Damage

Leaf chlorophyll and nitrogen contents and SOD and CAT activities were obviously reduced after plants were subjected to waterlogging at the flowering stage, and foliar sprays of mixtalol retarded the degradation of chlorophyll and nitrogen and the reduction of SOD and CAT activities (Table 6). The mixtalol-treated plants had higher leaf chlorophyll and nitrogen contents and SOD and CAT activities than the waterlogging-treated plants, and their average values (from four leaves) were increased 16.1, 5.0, 7.3, and 11.1%, respectively. A better effect of mixtalol was obtained on the lower leaves (leaf 16); and their leaf chlorophyll, nitrogen content, and SOD and CAT activities were increased significantly, 28.2, 6.9, 10.4, and 16.6%, respectively, relative to the waterlogging treatment.

The mixtalol-treated plants had high root exudate, which was increased significantly, 7.6% relative to the waterlogging treatment; its root oxidizability was increased insignificantly, 5.5% relative to the waterlogging control (Table 7). The results indicated that exogenous plant growth substances could improve the growth of waterlogged plants; but even with the application of chemical substances, it was impossible for plants to recover completely from waterlogging damage.

Discussion

The present experiments indicate that the physiological reactions to waterlogging were associated with decreases in leaf nitrogen and chlorophyll contents, SOD and CAT activities, root oxidizability, and root exudate. In addition, waterlogging at the seedling and stem elongation stages resulted in significant accumulation of leaf malondialdehyde and ethylene production and reduction of the leaf photosynthetic rate in rape plants (Zhou and Lin 1995). Dong et al. (1983) and Lin et al. (1984) reported that plant senescence was associated with the degradation of chlorophyll, the accumulation of malondialdehyde, and ethylene production, the decrease of SOD and CAT activities, and root oxidizability. Therefore, premature senescence in rape plants resulted from exposure to waterlogging, and the plants became seriously damaged. Waterlogging also breaks down the balance of endogenous hormones. Gibberellic acid and cytokinin content decrease significantly while abscisic acid and ethylene contents increase significantly when plants are subjected to waterlogging (Reid and Crozier 1971, Hiron and Wright 1973, Bradford and Yang 1980, Jackson et al. 1987, Brailsford et al. 1993, Voesenek et al. 1993). The inhibition of physiological function of plants caused by waterlogging leads to decreases in plant growth and photosynthesis and consequently, to smaller seed yield (Zhou and Lin 1995).

The seedling stage of rape plants was most susceptible to waterlogging, followed by the stem elongation and pod formation stages. In contrast, plants waterlogged at the flowering stage could withstand prolonged waterlogging. Waterlogging is the major physiological constraint during the seedling stage, and there is a significant correlation between seed yield and growth during this stage (Macdonald and Gordon 1978, Yin and Zhang 1982, Hu 1983, Zhou 1994). The present experiments confirmed that the physiological function of rape plants was retarded during the time of waterlogging at seedling stage, and its adverse effects remained afterward, resulting in a highly significant decrease of yield (Zhou and Lin 1995). The ability of rape to withstand prolonged waterlogging at flowering is due partly to the fact that the water requirement during this stage is the greatest (Zhou 1994).

The present experiments indicated that foliar spraying of nitrogen fertilizers at the seedling stage could alleviate the plant damage caused by waterlogging and could increase the leaf chlorophyll and nitrogen contents, SOD and CAT activities, root oxidizability, and root exudates. The yield components and seed yield of waterlogged plants also improved with the foliar application of nitrogen fertilizers. Plant growth regulators are increasingly used to manipulate growth and yield. Synthetic cytoki-

Table 6. Effect of mixtalol (MTL) on leaf chlorophyll and nitrogen contents and leaf SOD and CAT activities of rape plants waterlogged for 5 days at the flowering stage (measured 15 days after MTL treatment).

		Leaf position[a]			
Item	Treatment	16	17	18	19
Chlorophyll (mg/g FW)	CK	0.66[b]aA	0.75aA	0.87aA	1.04aA
	Waterlog.	0.39cC	0.53cB	0.72bB	0.85bB
	Waterlog. + MTL	0.50bB	0.66bA	0.83aAB	0.90bAB
Nitrogen (DW%)[c]	CK	3.80aA	3.95aA	4.08aA	4.16aA
	Waterlog.	3.31cA	3.51bA	3.76bA	3.90bA
	Waterlog. + MTL	3.54bA	3.70bA	3.91abA	4.05abA
SOD activity (unit/g FW/min)	CK	19.65aA	21.14aA	22.80aA	24.52aA
	Waterlog.	13.62cB	16.02cB	18.83cB	21.31bA
	Waterlog. + MTL	15.04bB	17.32bB	20.12bAB	22.40bA
CAT activity (H_2O_2 mg/g FW/min)	CK	10.32aA	11.18aA	12.38aA	12.85aA
	Waterlog.	6.97cB	8.27cB	9.60cB	11.06cA
	Waterlog. + MTL	8.13bB	9.42bB	10.52bAB	11.82bA

[a] All leaves are labeled, and the first emerged leaf is designated 1.
[b] Within columns, means followed by the same capital and small letters are not significantly different at the 0.01 and 0.05 level of probability, respectively.
[c] Nitrogen content in dry weight %.

Table 7. Effect of mixtalol (MTL) on root oxidizability and root exudate of rape plants waterlogged for 5 days at the flowering stage (measured 15 days after MTL treatment).

Treatment	Root oxidizability (TTC mg/g FW/h)	Root exudate (g FW/plant/h)
CK	0.295[a]aA	0.148aA
Waterlog.	0.272bA	0.118cB
Waterlog. + MTL	0.287abA	0.127bAB

[a] Within columns, means followed by the same capital and small letters are not significantly different at the 0.01 and 0.05 level of probability, respectively.

nins, cycocel, glutathione, and active oxygen scavengers (such as 8-hydroxyquinoline and ascorbate) have been reported to alleviate plant damage caused by waterlogging (Drew et al. 1979b, Liu 1992, Yan et al. 1993, Li et al. 1991). Foliar sprays of mixtalol at flowering are found to stimulate plant growth, delay plant senescence, and increase seed yield (Zhou and Xi 1993, Zhou et al. 1995). Ni et al. (1995) reported that foliar sprays of mixtalol to submerged rice plants could increase photosynthesis and flooding tolerance. The present experiments indicated that foliar sprays of mixtalol at flowering could attenuate the effects of waterlogging, retard the degradation of chlorophyll and nitrogen and the reduction of SOD and CAT activities, and improve the growth condition of waterlogged rape plants. Therefore, besides draining off water, alleviation of waterlogging damage may be accomplished by applying nitrogen fertilizers and suitable plant growth substances at appropriate stages of growth.

Acknowledgment. This project was supported by the Science Commission of Zhejiang Province, China.

References

Atwell BJ, Drew MC, Jackson MB (1988) The influence of oxygen deficiency on ethylene synthesis, 1-aminocyclopropane-1-carboxylic acid levels, and aerenchyma formation in roots of *Zea mays.* Plant Physiol 72:15–22

Bradford KJ, Yang SF (1980) Xylem transport of 1-aminocyclopropane-1-carboxylic acid, an ethylene precursor, in waterlogged tomato plants. Plant Physiol 65:322–326

Brailsford RW, Voesenek LACJ, Blom CWPM, Smith AR, Hall MA, Jackson MB (1993) Enhanced ethylene production by primary roots of *Zea mays* L. in response to subambient partial pressures of oxygen. Plant Cell Environ 16:1071–1080

Cannell RQ, Belford RK (1980) Effects of waterlogging at different stages of development on the growth and yield of winter oilseed rape (*Brassica napus* L.). J Sci Food Agric 31:963–965

Chen FM (1984) Determining the chlorophyll contents of plant leaves by acetone/ethanol mixture assay. Forestry Sci Commun 2:4–8

Chen GP (1989) Alleviation of waterlogging damage to maize plants by the application of nitrogen fertilizers. Acta Agric North China 4:26–31

Dhindsa RS, Plumb-Dhindsa P, Thorpe TA (1981) Leaf senescence: Correlated with increased levels of membrane permeability and lipid peroxidation, and decreased levels of superoxide dismutase and catalase. J Exp Bot 126:93–101

Ding J, Shen ZD (1985) Cytokinins in root exudate of cotton plants. Acta Phytophysiol Sinica 11:249–259

Dong JG, Yu ZW, Yu SW (1983) Effect of increased ethylene production during different periods on the resistance of wheat plants to waterlogging. Acta Phytophysiol Sinica 9:383–389

Drew MC, Jackson MB, Giffard SC (1979a) Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. Planta 147:83–88

Drew MC, Sisworo EJ, Saker LR (1979b) Alleviation of waterlogging damage to young barley plants by application of nitrate and a synthetic cytokinin, and comparison between the effects of waterlogging, nitrogen deficiency, and root excision. New Phytol 82:315–329

Hiron RWP, Wright STC (1973) The role of endogenous abscisic acid in the response of plants to stress. J Exp Bot 24:769–781

Hu QS (1983) The causes of poor seedlings and their preventing practice. Oil Crops China 5:41–42

Jackson MB, Waters I, Setter T, Greenway H (1987) Injury to rice plants caused by complete submergence: A contribution by ethylene (ethene). J. Exp Bot 38:1826–1838

Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol 106:465–495

Laan P, Clement JMAM, Blom CWPM (1991) Growth and development of *Rumex* roots as affected by hypoxic and anoxic conditions. Plant Soil 136:145–151

Li JK, Wang ZL, Wang ZX (1991) Effects of active oxygen scavengers on activities of protective enzymes in waterlogged corn plants. Jiangsu J Agric Sci 7:23–28

Lin XQ, Shen HC, Ji YQ, Zhou WJ (1993) Studies on some physiological effects of waterlogging in rape. Acta Agric Univ Zhejiang 19:19–23

Lin ZF, Li SS, Lin GZ, Sun GC, Guo JY (1984) Superoxide dismutase activity and lipid peroxidation in relation to senescence of rice leaves. Acta Bot Sinica 26:605–615

Liu YL (1992) In: Water stress physiology of plants. Agriculture Press, Beijing, pp 144–187

Macdonald IR, Gordon DC (1978) An inhibiting effect of excess moisture on the early development of *Sinapis alba* seedling. Plant Cell Environ 4:313–316

Ni JJ, Yu YL, Duan XM, Fang DY (1995) A study on effects of mixtalol on reducing waterlogging damage in early rice. Acta Agric Univ Zhejiang 21:55–60

Nickell LG (1982) In: Plant growth regulators: Agricultural uses. Springer Verlag, Berlin, pp 1–3

Pezeshki SR (1994) Plant response to flooding. In: Wilkinson R (ed) Plant-environment interaction. Marcel Dekker, New York, pp 289–321

Reid DM, Crozier A (1971) Effects of waterlogging on the gibberellin content and growth of tomato plants. J Exp Bot 22:39–48

Setia RC, Richa, Setia N, Ahuja KL, Malik CP (1989) Effect of mixtalol on growth, yield, and yield components of Indian mustard. Plant Growth Regul 8:185–192

Shen HC, Zhou WJ, Xi HF, Ye QF (1991) A preliminary study of physiological and yield effects of paclobutrazol on *Brassica napus.* Acta Agric Univ Zhejiang 17:423–426

Srivastava HC, Menon KKG (1987) Mixtalol: A new growth regulator for increasing crop productivity. In: Srivastava HC, Bhaskaran S, Menon KKG (eds) Crop productivity. Oxford, New Delhi, pp 43–55

Voesenek LACJ, Banga M, Thier RH, Mudde CM, Harren FJM, Barendse GWM, Blom CWPM (1993) Submergence-induced ethylene synthesis, entrapment, and growth in two plant species with contrasting flooding resistances. Plant Physiol 103:783–791

Voesenek LACJ, Blom CWPM (1989) Growth responses of *Rumex* species in relation to submergence and ethylene. Plant Cell Environ 12:433–439

Yan B, Wang ZL, Liu XZ, Dai QJ (1993) The change of glutathione and its function in corn leaves under waterlogging stress. Plant Physiol Commun 29:416–419

Yin JC, Zhang Y (1982) The relation between the seedling growth and yield formation in oilseed rape. Shanghai Agric Sci Tech 8:9–13

Yin JC, Zhang Y, Wan ZL (1980) A preliminary study of waterlogging tolerance in oilseed rape. Shanghai Agric Sci Tech 6:5–7

Zhou WJ (1994) Oilseed rape cultivation. In: Ding YS (ed) Cultivation of crops. Shanghai Science and Technology Press, Shanghai, pp 357–380

Zhou WJ, Lin XQ (1995) Effects of waterlogging at different growth stages on physiological characteristics and seed yield of winter rape. Field Crops Res 44:103–110

Zhou WJ, Tao SL, Zhao DS (1995) Physiological regulation of mixtalol in rape senescence and its yield effects. J Plant Growth Regul 14:37–40

Zhou WJ, Xi HF (1993) Effects of mixtalol and paclobutrazol on photosynthesis and yield of rape (*Brassica napus*). J Plant Growth Regul 12:157–161

Zhu GR, Zhong HW, Zhang AQ (1990) Plant physiology experiment. Peking University Press, Beijing, pp 242–245