Effects of Air Supply on the Growth of Tiller Buds in Floating Rice*

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Abstract A few experiments were carried out to analyze the mechanism underlying the inhibition of tiller buds by submergence in deep water of the subtending leaf sheaths in floating rice. The growth of the tiller buds was inhibited by the deep water treatments. Air was supplied, under deep water, to the inner space between the leaf sheaths where the young 4th node or 5th node tiller bud grows (while inhibited by deep water) at the plant age of 5 or 6, respectively. The aeration treatment promoted the growth of the exposed tiller bud and of that immediately below it. A small window was made in the midrib of the basal part of the 5th leaf sheath in order to expose the subtended 5th node tiller bud to water and drown it under shallow water (deep enough to drown the tiller bud) conditions at the plant age of 6. The drowning treatment inhibited the growth of the exposed tiller bud to a similar extent to that of the deep water treatment, in spite of the shallow water conditions. Aeration applied to the tiller bud inhibited by the drowning treatment promoted the growth. On the basis of the results obtained it is suggested that gas exchange between the inner space and atmosphere may be inhibited by the submergence of the tips of leaf sheaths, and that the lack of oxygen required for respiration or accumulation of ethylene may be the cause of the inhibition of growth of the tiller buds. In future further studies will be carried out to analyze the role of ethylene in this function.

Key words aeration, floating rice, growth, leaf sheath, submergence, tiller bud

Introduction

It is well-known that the number of tillers or panicles of rice plants decreases under deep water conditions not only in floating rice17,21 but also in ordinary indica7 and japonica4,21

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rice types. It was previously reported that the development of tiller buds which were growing inside the subtending leaf sheaths when the water depth was increased was severely inhibited by the deep water treatment\textsuperscript{7}. Moreover the growth of the tiller buds was strongly inhibited when the subtending leaf sheaths were entirely submerged in water, whereas the growth was not inhibited when only the tips of the subtending leaf sheaths stood above the water surface\textsuperscript{8}.

The mechanism underlying the inhibition of the growth of the tiller buds caused by submergence of the subtending leaf sheaths has not been clarified yet. It was reported that the level of O\textsubscript{2} in the tissues was markedly reduced as a result of submergence\textsuperscript{16}. The aeration in the inner space between the leaf sheaths may be inhibited under such deep water conditions when the tips of the subtending leaf sheaths are located under the water surface, and inadequate air supply may cause the inhibition of the tiller buds growing inside the leaf sheaths through the lack of oxygen required for the respiration and growth. Therefore experiments were carried out in order to determine whether aeration plays a role in the growth of tiller buds inside the subtending leaf sheaths.

**Materials and Methods**

Three experiments were carried out in 1985 and 1986; Expt. 1 and Expt. 3 in 1985 and Expt. 2 in 1986, at the Agricultural and Forestry Research Center, University of Tsukuba. Kanlang Phnom, a floating rice variety of indica type from Cambodia, was used as the material. The seeds were originally provided by Dr. Tadashi Yamaguchi, Kobe University, and subsequently produced by one of the authors, Kagawa at the University of Tsukuba.

In Expt. 1 and Expt. 2, the seeds were sown in soil amended with 5 g of chemical fertilizer (N, K\textsubscript{2}O, P\textsubscript{2}O\textsubscript{5} 14% each) for Expt. 1 and 10 g for Expt. 2 in 1/2000 a Wagner pots on July 15th in Expt. 1 and July 8th in Expt. 2. Six plants were grown in a pot.

The plants were divided into 3 plots in Expt. 1 and 5 plots in Expt. 2 as follows:

**Expt. 1**

Plot A (shallow water control): Plants cultivated continuously at a water depth of 2 cm. Plot B (deep water control): After the plant age\textsuperscript{*1} of 6 was reached, the water level was raised and maintained at the depth required for submerging the tip of the leaf sheath of the 5th leaf\textsuperscript{*2}.

Plot C (aeration under deep water): After the plant age of 6 was reached, air was supplied into the space between the leaf sheaths of the 5th leaf and 6th leaf, where the 5th node tiller bud\textsuperscript{*3} was growing, through an injector needle connected to an air pump, for the purpose of supplying air to the 5th node tiller bud, under the same deep water conditions as those in Plot B.

**Expt. 2**

Plot A (shallow water control): Plants cultivated continuously at a water depth of 2 cm. Plot B-1 (deep water control-1): After the plant age of 6 was reached, the water level was raised and maintained at the depth required for submerging the leaf sheath of the 5th leaf, then raised and maintained at the depth required for submerging the leaf sheath of the 6th leaf.

Plot B-2 (deep water control-2): After the plant age of 6 was reached, water level was raised and maintained at the depth required for submerging the leaf sheath of the 6th leaf. Plot C-1 (aeration under deep water conditions-1): Air was supplied into the space between the leaf sheaths of the 4th leaf and 5th leaf, where the 4th node tiller bud was growing, for the purpose of supplying air to the 4th node tiller bud, by the same procedure as that described for Plot C of Expt. 1, under the

\textsuperscript{*1}: The plant age was expressed by the number of leaves whose leaf blade had completely emerged out from the leaf sheath of the leaf immediately below it.

\textsuperscript{*2}: The leaf with vestigial leaf blade and next to the coleoptile was referred to as the 1st leaf. Leaves were numbered in ascending order. Tip (collar part) of the leaf sheath was submerged, which is described simply as "submerge the leaf sheath" in this paper for convenience. As for the submergence treatment, see the previous paper\textsuperscript{8}.

\textsuperscript{*3}: The tiller or tiller bud which developed at the axil of the 5th, 6th,...leaf was referred to as the 5th, 6th,...node tiller or tiller bud.
same deep water conditions as those in Plot B-1 after the plant age of 5 was reached.

Plot C-2 (aeration under deep water conditions-2): Air was supplied into the space between the leaf sheaths of the 5th leaf and 6th leaf, where the 5th node tiller bud growing, under the same deep water conditions as those in Plot B-2 after the plant age of 6 was reached.

The air was supplied near the tip of the tiller bud in avoiding to hurt the bud in the aeration treatments (Plot C in Expt. 1 and Plots C-1 and C-2 in Expt. 2). The aeration procedure is illustrated in Fig. 1.

The plants were harvested when the plants of Plot A reached the plant age of 8 in both experiments.

In Expt. 3, the seeds were sown in 2 rows, 5 cm apart from each other, with a spacing of 4 cm in a row in soil placed in plastic boxes 40 cmx31 cmx12 cm (depth) on August 12th. The soil in the box was amended with 35 g of chemical fertilizer (N, K₂O, P₂O₅ 14% each). Twenty plants were grown in a box. The plants were grown at a water depth of 2 cm before use for the experiments.

The plants were divided into the following 4 plots:

Plot A (shallow water control): Plants cultivated continuously at a water depth of 2 cm.

Plot B (deep water control): After the plant age of 6 was reached, the water level was raised and maintained at the depth required for submerging the leaf sheath of the 5th leaf.

Plot C (exposure to water under shallow water conditions): A small window (10 mm lengthx2 to 3 mm width) was made in the midrib of the basal part of the 5th leaf sheath, which was subtending the 5th node tiller bud, in order to expose the tiller bud to water and drown it, under a shallow water depth of about 2 to 3 cm. The treatment was carried out at the plant age of 6.

Plot D (exposure and aeration under shallow water conditions): Air was supplied to the 5th node tiller bud which was exposed to water in the same manner as in Plot C. Air was supplied to the tiller buds by making small holes just below the tiller buds on a vinyl pipe laid on the ground surface, with the aid of an air pump. The treatment was initiated at the plant age of 6.

The 3rd leaves and 3rd node tiller buds of the plants of Plots C and D were removed for convenience of the treatments. The 3rd leaves and the subtended tiller buds of the plants of Plots A and B were also removed in order to make the experimental conditions more uniform.

The exposure and aeration treatments are illustrated in Fig. 2.

The plants were harvested 5 days after the initiation of the treatments.

Results

I. Expt. 1 (Table 1)

The growth of the tiller buds at the 4th and 5th nodes was inhibited by the deep water treatment (Plot B), especially the growth of the 5th node was completely inhibited. Aeration applied to the 5th node tiller bud (Plot C) promoted the growth of the tiller buds at the 5th node and 4th node, especially that of the latter which was longer than the tiller buds in the
Table 1  Effects of air supply into the space between the leaf sheaths on the growth$^{1)}$ of tillers (or tiller buds) and leaf sheaths under deep water conditions  Expt. 1 (1985)

<table>
<thead>
<tr>
<th>Plant age</th>
<th>Plot</th>
<th>Tiller at node$^{2)}$</th>
<th>Leaf sheath of leaf $^{6)}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>6$^{3)}$</td>
<td>A</td>
<td>109±3.0</td>
<td>0.34±0.01</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>336±42.6</td>
<td>2.24±0.16</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>259±47.6</td>
<td>3.55±0.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td>464±12.7</td>
<td>1.93±0.13</td>
</tr>
<tr>
<td>8$^{4)}$</td>
<td></td>
<td>1.35±0.07</td>
<td>1.47±0.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>137±2.4</td>
<td>154±2.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.9±0.8</td>
<td>163±16.7</td>
</tr>
</tbody>
</table>

Note  $^{1)}$Length (mm), mean±s.e.  $^{2)}$Nodal position was numbered in ascending order. The leaf which developed next to the coleoptile and lacked a leaf blade was referred to as the 1st leaf.  $^{3)}$Treatments were started.  $^{4)}$Plants were harvested when the plants in Plot A reached the plant age of about 8.

Fig. 2  Diagram to illustrate the procedure applied to expose the 5th node tiller bud to water, and supply air to the exposed tiller bud, under the shallow water conditions required for submerging the tiller bud only

2. Expt. 2 (Table 2)

The growth of the tiller buds at the 3rd node and above it or the 4th node and above it was inhibited by the deep water treatment in Plot B-1 or B-2, respectively, although some of the differences were not significant. Aeration applied to the 4th node tiller buds (Plot C-1) or to the 5th node tiller buds (Plot C-2) promoted the growth of the tiller buds at the 3rd node and 4th node or those at the 4th node and 5th node, respectively. The growth of the tiller buds at the 3rd node or 4th node was remarkably promoted by the aeration treatment applied to the tiller buds at the 4th node (Plot C-1) or at the 5th node (C-2), respectively. The 3rd node tillers, in case of aeration applied to the 4th node tiller buds, and the 4th node tillers, in case of aeration applied to the 5th node tiller buds were longer than those in the shallow water control (Table 2). The elongation of the leaf sheaths of the 6th leaf and above it was promoted by the deep water treatment in Plot B-1 or Plot B-2 (no data for the leaf length of the 5th leaf and below it). The aeration treatment in Plot C-1 and Plot C-2 inhibited the elongation of the corresponding leaf sheaths.

3. Expt. 3 (Table 3)

The deep water treatment applied to the tip of the 5th leaf sheath after the plant age of 6 was reached inhibited the growth of the tiller buds at the 4th to 6th nodes (Plot B). The inhibition was most severe for the 5th node tiller buds. Exposure of the 5th node tiller buds to water by opening a small window in the midrib of the basal part of the 5th leaf sheath (Plot C) severely inhibited the growth of the buds to a similar extent to that of the deep shallow water control.

The elongation of the leaf sheaths of the 6th and 7th leaves was promoted by the deep water treatment in Plot B. The elongation of the leaf sheaths of the 6th and 7th leaves was inhibited by the aeration treatment in Plot C, and the leaf sheath of the 7th leaf was significantly shorter than that in the shallow water control (Plot A).
Table 2  Effects of air supply into the space between the leaf sheaths on the growth\(^1\) of tillers (or tiller buds) and leaf sheaths under deep water conditions. Expt. 2 (1986)

1) Length of tillers or tiller buds (mm) mean±s.e.

<table>
<thead>
<tr>
<th>Plant age</th>
<th>Plot</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>5(^b)</td>
<td>A</td>
<td>38±4.0</td>
<td>2.4±0.36</td>
<td>0.3±0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>69±6.2</td>
<td>2.2±0.10</td>
<td>0.4±0.01</td>
</tr>
<tr>
<td>7(^c)</td>
<td>A</td>
<td>287±32.7</td>
<td>264±10.3</td>
<td>127±8.3</td>
<td>7.1±1.44</td>
</tr>
<tr>
<td></td>
<td>B-1</td>
<td>64±9.5</td>
<td>5±0.8</td>
<td>22±1.4</td>
<td>5.2±0.68</td>
</tr>
<tr>
<td></td>
<td>C-1</td>
<td>578±8.8</td>
<td>26±6.5</td>
<td>49±15.0</td>
<td>4.5±1.33</td>
</tr>
<tr>
<td>8(^d)</td>
<td>A</td>
<td>342±12.0</td>
<td>252±8.3</td>
<td>80±11.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>B-2</td>
<td>324±6.7</td>
<td>10±1.3</td>
<td>75±14.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C-2</td>
<td>565±32.5</td>
<td>25±8.8</td>
<td>13±1.0</td>
<td></td>
</tr>
</tbody>
</table>

2) Length of leaf sheaths (mm) mean±s.e.

<table>
<thead>
<tr>
<th>Plant age</th>
<th>Plot</th>
<th>6</th>
<th>Leaf sheath of leaf(^1)</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>5(^b)</td>
<td>A</td>
<td>3.7±1.86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>158±3.7</td>
<td>5.5±1.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7(^c)</td>
<td>A</td>
<td>177±2.7</td>
<td>179±2.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B-1</td>
<td>251±3.8</td>
<td>271±2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>C-1</td>
<td>176±16.4</td>
<td>261±3.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8(^d)</td>
<td>A</td>
<td>173±3.1</td>
<td>183±2.2</td>
<td>170±3.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>B-2</td>
<td>213±3.0</td>
<td>297±2.0</td>
<td>330±2.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C-2</td>
<td>185±3.4</td>
<td>260±11.8</td>
<td>289±5.6</td>
<td></td>
</tr>
</tbody>
</table>

Note \(^1\)See the note\(^2\) in Table 1. \(^2\)At the beginning of the treatments in B-1 and C-1. \(^3\)At the beginning of the treatments in B-2 and C-2. \(^4\)Seven days after the start of the treatments in B-1 and C-1. The plant age of the plants in Plot A was about 7. \(^5\)Eight days after the start of the treatments in B-2 and C-2. The plant age of the plants in Plot A was about 8.

Table 3  Effects of exposure of the 5th node tiller bud to water and supply of air to the tiller bud on the growth of tiller buds under submerged conditions (2 to 3 cm depth) Expt. 3 (1985)

<table>
<thead>
<tr>
<th>Days after treatments</th>
<th>Plot</th>
<th>Plastochron index(^2)</th>
<th>Length (mm) of tiller buds at node(^1)</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0(^b)</td>
<td>A</td>
<td>8.45±0.016</td>
<td>93±4.1</td>
<td>1.41±0.07</td>
<td>0.35±0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>10.05±0.027</td>
<td>334±12.1</td>
<td>12.90±3.45</td>
<td>2.92±0.36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>10.00±0.035</td>
<td>123±9.6</td>
<td>1.47±0.07</td>
<td>1.31±0.07</td>
<td></td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>10.23±0.047</td>
<td>353±13.1</td>
<td>2.34±0.24</td>
<td>1.97±0.20</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>10.27±0.022</td>
<td>311±13.2</td>
<td>3.08±0.23</td>
<td>6.77±1.49</td>
<td></td>
</tr>
</tbody>
</table>

Note \(^1\)See the note\(^2\) in Table 1. \(^2\)Reference length 10 mm. \(^3\)Plant age expressed by the number of emerged leaves was 6.

water control, in spite of the shallow water conditions. Since the aeration applied to the tiller buds exposed to water promoted the growth of the buds slightly but significantly, and promoted remarkably the growth of the tiller bud immediately at the upper node, the tiller buds were longer than those in the shallow water control.
Discussion

1. Elongation of leaf sheaths

The elongation of the leaf sheaths of the 6th leaf and above it was promoted by the deep water treatment which was started at the plant age of 6 in Expt. 1 and Expt. 2. It had been already reported that the elongation of the leaf sheaths and leaf blades was promoted by the deep water treatment\(^7\).\(^8\).\(^10\).\(^13\).\(^21\). The leaf sheaths whose elongation was promoted by the deep water treatments were those which had not completed the elongation yet at the start of the treatment, though the leaf sheath of the 6th leaf was at the last stage of elongation. The results showing that the elongation of the leaf sheaths at the growing stage is promoted by the deep water treatment are in agreement with the findings previously reported\(^7\).\(^8\).\(^10\).\(^21\).

The aeration treatments applied to the space between the leaf sheaths of the 4th and 5th leaves (Plot C-1 in Expt. 2) or between those of the 5th and 6th leaves (Plot C in Expt. 1 and Plot C-2 in Expt. 2) inhibited the elongation of the leaf sheaths which was promoted by the deep water treatments. Based on the above results it appears that the aeration treatment actually supplied air to the space between the leaf sheaths.

The leaf sheaths of the 6th and 7th leaves in Plot C-1 of Expt. 2 or those of the 7th and 8th leaves in Plot C of Expt. 1 and Plot C-2 of Expt. 2, in which air was not supplied directly through the injector needle to the space between the leaf sheaths, were also affected by the aeration treatment and the results suggest that air may have been supplied to the spaces between the inner young leaf sheaths due to the air pressure (Fig. 3).

2. Growth of tiller buds

The growth of the tiller buds at the 3rd node and above it or the 4th node and above it was inhibited by the deep water treatment applied at the plant age of 5 or 6, respectively, in the 3 experiments. The tiller buds which displayed growth inhibition were those which were growing inside the subtending leaf sheaths when the deep water treatments were initiated\(^7\), which confirmed the observations previously reported\(^7\).\(^8\).

The aeration treatments applied to the tiller buds under deep water conditions promoted the growth of the exposed tiller buds. In addition, the growth of the 3rd node and 4th node tiller buds or that of the 4th node and 5th node tiller buds was promoted by the aeration applied to the 4th node tiller buds or to the 5th node tiller buds, respectively; that is, the growth of the tiller buds immediately below the tiller buds subjected to aeration as well as that of the exposed tiller buds was promoted by aeration. It is thus likely that part of the air supplied may have penetrated into other spaces, where the tiller buds grow, between the leaf sheaths in the plants, as mentioned in the case of the elongation of the leaf sheaths.

It was observed that the growth of the tiller buds immediately below the exposed tiller buds was promoted more strongly than that of the tiller buds subjected to aeration. This phenomenon may be ascribed to the fact that the former tiller buds were growing faster than the latter ones based on the exponential growth characteristics\(^6\).

The growth of the tiller buds exposed to water under shallow water conditions (Plot C, Expt. 3) was almost entirely inhibited to a similar extent to that of the deep water control. Translocation of nutrients from the subtending leaf may have been partially inhibited by the small window made at the basal part of the leaf sheath. However, it is unlikely that the
nutrient supply was associated with the inhibition of the tiller buds, since the removal of the 3rd leaf at the plant age of 4 or the removal of the 4th leaf at the plant age of 5 inhibited the growth of the 3rd node or 4th node tiller buds only to a small extent\(^5\). The aeration applied to the tiller buds exposed to water promoted the growth significantly, though the growth was less vigorous than that of the materials in the shallow water control.

Raskin and Kende reported that the level of O\(_2\) in the tissues of deep water rice was markedly reduced as a result of submergence\(^5\). They reported in addition that continuous air layers trapped between the leaf blades and the surrounding water constitute the major path of aeration in partially flooded deep water rice\(^5\). It was shown in the present study that (1) the growth of the tiller buds was promoted by the aeration treatment under deep water conditions, (2) the growth of the tiller buds was severely inhibited when the buds were exposed to water until they drowned, and (3) that the growth inhibition by drowning was partially alleviated by air supply. It was reported, in addition, in the preceding paper that the growth of the tiller buds was inhibited by submergence only when the tip part of the subtending leaf sheaths was located under the water surface\(^5\). Based on these observations, it is suggested that gas is exchanged between the inner space where a tiller bud grows, and the outer atmosphere at the tip part of the subtending leaf sheath when the tip part stands above the water surface, and that the gas exchange is inhibited by complete submergence of the subtending leaf sheath possibly by water pressure or some other factors. However it remains to be determined whether the air supply through the air layer between the leaf and surrounding water\(^5\) is inhibited by complete submergence of the leaf sheath. It appears likely that the lack of air, probably oxygen, plays a role, at least in part, in the inhibition of the growth of the tiller buds by deep water that submerges entirely the subtending leaf sheaths.

It is obvious that oxygen is required for respiration and growth. Yamada et al. reported that under a reduced oxygen tension, aerobic respiration was impaired and at the same time that anaerobic respiration was promoted resulting in the increase in the consumption of hexoses associated with the decrease in the production of energy\(^19,20\). Oxygen supply coupled with calcium peroxide increased the number of tillers\(^14\). The inhibition of the tiller buds by the submergence of the subtending leaf sheaths may be caused by the lack of oxygen required for respiration.

It was reported that the level of oxygen in the tissues was markedly reduced as a result of submergence, and the low O\(_2\) concentration stimulated ethylene synthesis\(^16\). It was also reported that the ethylene-producing capacity of young seedlings of floating rice was increased during submergence\(^9\), and that the ethylene concentration in the aerenchyma of the leaf sheaths was increased by submergence of the leaf sheaths\(^12\). Ethylene, which plays an important role in the elongation of internodes\(^11,16,18\) and leaf sheaths as well as leaf blades\(^9\) under deep water conditions, was reported to inhibit the growth of the lateral buds in pea\(^2,3\) and bean plants\(^22\). These facts, in addition to the results currently obtained, may suggest that the gas exchange between the inner space of rice plants and the atmosphere above the water surface is blocked by the submergence of the leaf sheaths, and that the ethylene concentration inside the plants increases through either the promotion of ethylene synthesis and/or accumulation of ethylene. Further considerations on the role of ethylene in the inhibition of the growth of tiller buds by submergence of the subtending leaf sheaths require additional experiments.

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