The co-operation of leaf orientation, photorespiration and thermal dissipation alleviate photoinhibition in young leaves of soybean plants


Abstract: Chloroplast pigments, gas exchange, chlorophyll a fluorescence kinetics and leaf orientation were extensively studied in soybean leaves from emergency to full expansion. During the development of soybean leaves, chlorophyll content, the ratio of Chl a/Chl b and photosynthesis increased, indicating a gradual development of photosynthetic apparatus during leaf expansion. During daily courses, not only fully expanded leaves, but also young leaves were not seriously photoinhibited by strong irradiance under field condition. However, serious photoinhibition occurred in young leaves when vertically exposed to 1 200 μmol/(m²•s) irradiance, and the photoinhibition was alleviated with leaf expansion. It can be referred that there might be some regulative mechanisms behind these controversial phenomena. Under 1 200 μmol/(m²•s) irradiance, photorespiration (P′) in young leaves measured by gas exchange were obviously low, whereas the ratio of photorespiration/mass photosynthesis (P′/Pm) were distinctly enhanced, demonstrating that photorespiration might play a mild role against photoinhibition in young leaves. When leaves were placed in a horizontal position and vertically subjected to 1 200 μmol/(m²•s) irradiance, the actual photosystem II (PSII) efficiency (ΦPSII) in young leaves were drastically down regulated, whereas, non-photochemical quenching (NPQ) were increased significantly. The significant down-regulation of ΦPSII in young leaves under high irradiance was relieved gradually with leaf expanding, and NPQ declined during this process. Compared with the fully expanded leaves...
young leaves, containing higher xanthophyll pool, exhibited a much higher level of zeaxanthin (Z) + antheraxanthin (A) to Chl when exposure to high irradiance. Remarkably, during the development of leaf, the petiole angle gradually increased over time. In addition, the midrib angle decreased with the increasing of irradiance during the diurnal courses in young leaves, whereas, in mature leaves no distinct changes was observed. These data indicated that the leaf orientation might reduce the irradiance reaching surface of young leaves under natural condition. Thus, we deduced that the co-operation of leaf angle, photorespiration and thermal dissipation depending on xanthophyll cycle under natural condition might alleviate the photoinhibition in young leaves.

Key words: photosynthesis; chlorophyll a fluorescence; photoinhibition; xanthophyll cycle; photorespiration; leaf orientation.

...
叶角的测定
选取受光良好的叶片
进行叶柄倾角的测定。
方法参考张守仁和高荣孚等
叶柄倾角为叶柄与着生位置铅垂线间夹角。
悬挂角为叶中脉垂直运动离开水平面的角度。
在清朗无风的天气使用直尺和量角器测量以上角度。

叶绿体色素的测定
参考的方法。
选择合适的叶片用直径
打孔器打取叶圆片。
混匀。
随意抽取其中
片以
丙酮
于暗
处浸提。
其间每隔
左右取出振荡片刻。
使色素均匀分布于丙酮溶液中。
用日本岛津公司生产的
分光光度计分别在
及
测定。
计算出叶绿素
及类胡萝卜素
的含量。

叶黄素组分的测定
大豆叶片经充分暗适应后
平展置于
强光下分别处理
随后迅速用液氮冷冻。
环氧玉米黄质
紫黄质
玉米黄质
等组分用高效液相色谱
按
和
方法测定。
叶片剪碎后用
丙酮于暗处研磨提取。
下
离心。
上清液用
微孔滤膜过滤后。
每次取
进样。
色谱柱为
流动相流量为
梯度洗脱程序为
液洗脱
接着
的线性梯度洗脱。
再
换成
液。
流动相
液为乙睛
甲醇
缓冲液
液为甲醇
正己烷
检
测波长。
色素含量根据色素峰面积及
和
的转换系数计算。
以上每个实验至少重复
次。

结果分析
叶片展开过程中叶绿素含量的变化
从表
中可以看出。
在刚伸出叶片
近完全展开叶
和完全展开叶
中单位叶面积的叶绿素总量
分别为
和
大豆幼叶的叶绿素含量显然比完全展开叶片低。
不同展开时期
的增加量明显高于
所以
比值依次增加
分别为
和
表
大豆叶片展开过程中叶绿体色素含量的变化
表
大豆叶片展开过程中叶绿体色素含量

<table>
<thead>
<tr>
<th></th>
<th>Chl a</th>
<th>Chl b</th>
<th>Car</th>
<th>Chl (a+b)</th>
<th>Chl a/Chl b</th>
<th>Car/Chl (a+b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>33% A</td>
<td>63.57±8.4</td>
<td>28.86±1.8</td>
<td>19.92±1.1</td>
<td>92.43</td>
<td>2.20</td>
<td>0.22</td>
</tr>
<tr>
<td>78% A</td>
<td>125.40±9.6</td>
<td>40.99±2.4</td>
<td>37.80±1.3</td>
<td>166.39</td>
<td>3.06</td>
<td>0.23</td>
</tr>
<tr>
<td>100% A</td>
<td>190.49±9.1</td>
<td>53.11±2.6</td>
<td>51.31±1.4</td>
<td>243.60</td>
<td>3.59</td>
<td>0.21</td>
</tr>
</tbody>
</table>

* ± SE Values are means ± SE. n=51(1) 33% A, 78% A, 100% A, Full expanded leaves area. 100% A, Almost fully expanded leaves area.

图
不同展开程度大豆叶片的光合及光呼吸的变化
由图
观察到在叶片展开过程中光饱和光合速率依次增加。
刚伸出叶片最低。
近完全展开叶居中。
完全展开叶最高。
以上结果揭示大豆叶片从伸出到展开过程中伴随光合机构的完善。
光饱和光合速率发生了明显变化。
尽管刚伸出叶片的净光呼吸速率低。
但光呼吸速率与总光合速率之比
高。
随着叶片的展开
逐渐下降。
图
说明，幼叶通过光呼吸消耗的能量相对较多。
此后，随着大豆叶片的展开以这种方式耗散的激发能比例减少。

图
不同展开程度叶片的光抑制差异
经充分暗适应后。
刚伸出叶片
近完全展开叶和完全展开叶
的最大光化学效率
分别为
三者差别较小。
自然状态下
种叶片的
在午间都略有降低。
但下降幅度很小。
图
提示
种叶片都没有发
展期 姜闯道 等。
Fig. 2 Changes of net photorespiration ($P_r$) and the ratio of photorespiration to mass photosynthesis ($P_r/P_n$) during development of soybean leaves

Measurements were made under 1200 μmol/(m²·s) irradiance

Fig. 3 Diurnal variation of the maximal efficiency of PS II photochemistry ($F_{v}/F_{m}$) in different expanding soybean leaves under natural condition

All measurements were made in attached leaves in situ

Table 2 Changes of xanthophylls cycle pigments in different expanding soybean leaves exposed to 1200 μmol/(m²·s) irradiance for different time

<table>
<thead>
<tr>
<th>Xanthophylls (mmol/mol)</th>
<th>Exposure time</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 h</td>
</tr>
<tr>
<td>33% A $(V+A+Z)/Chl$</td>
<td>164±7.6</td>
</tr>
<tr>
<td>(A+Z)/Chl</td>
<td>9±2.7</td>
</tr>
<tr>
<td>78% A $(V+A+Z)/Chl$</td>
<td>138±6.8</td>
</tr>
<tr>
<td>(A+Z)/Chl</td>
<td>9±3.1</td>
</tr>
<tr>
<td>100% A $(V+A+Z)/Chl$</td>
<td>102±6.7</td>
</tr>
<tr>
<td>(A+Z)/Chl</td>
<td>9±2.9</td>
</tr>
</tbody>
</table>

All measurements were made in attached leaves placed in a horizontal position vertically subjected to irradiance
叶片展开过程中的叶角变化及其自然条件下对叶表光强的影响

图(表明刚伸出叶片)

近完全展开叶和完全展开叶的叶柄倾角分别约为 $*+\), - +$ 和 $*-.+/$. 揭示大豆叶片从伸出到展开过程中逐渐由直立状态转变为水平状态。

不同展开程度叶片的悬挂角在一天之中也随光强发生变化。如图所示，刚伸出叶片和近完全展开叶的悬挂角变化幅度较大，完全展开叶变化很小。图-#$/揭示幼叶随入射光强的变化发生明显的运动。

叶柄夹角和悬挂角的变化都可能会影响叶片的叶表光强和光能截获。

自然条件下，使用光合测定系统的光量子探头在叶片原位测量其光强。观察到一天之中刚伸出叶片

近完全展开叶和完全展开叶实际叶表最大光强分别为 $33\%\ A/564789\ A$ 和 $33\%\ A/564789\ A$ 左右。

图$\#\ A$，很显然，随着叶片的展开辐射到叶表的最大光强增加。

图$\*\ A$将不同展开程度的大豆叶片平展垂直暴露于强光下时非光化学猝灭的变化。

图$\#\ A$，实际光化学效率的变化。

### 讨论

叶片展开过程中的光破坏防御机制，尽管大豆幼叶叶绿素含量低，捕获激发能少，但由于其光合机构不完善，光饱和光合速率低，所以捕获的激发能不能完全用于碳同化，也会发生激发能过剩。依赖叶黄素循环的热耗散。

图$(\#\ A)$

期：姜闯道等。

光呼吸和热耗散协同作用减轻大豆幼叶光抑制。
(2) a/b a c a d e a fg

(3)

References:


