LECTURE 5: PHOTOMORPHOGENESIS

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LECTURE OUTCOME

After the completion of this lecture and mastering the lecture materials, students should be able to

1. explain photomorphogenesis including skotomorphogenesis
2. describe the development of ecophysiology as a scientific discipline
3. explain the role of genetic and environmental factors in ecophysiology
4. explain stress response, acclimation response, and adaptation
5. explain some phenomena of ecophysiology
1. INTRODUCTION

1. Light and Plant Life
   1. One of the most dramatic changes in plant growth and development occurs during the transition from life in the dark, just after germination, to life in a light environment when the seedling emerges from soil.
   2. Development in darkness is referred to as skotomorphogenesis, whereas development in the light is referred to as photomorphogenesis.
   3. Photomorphogenesis is the regulatory effect of light on plant form, involving growth, development, and differentiation of cells, tissues, and organs.
4. Morphogenic influences of light on plant form are quite different from light effects that nourish the plant through photosynthesis, since the former usually occur at much lower energy levels than are necessary for photosynthesis.

5. Light serves as a trigger in photomorphogenesis, frequently resulting in energy expenditure orders of magnitude larger than the amount required to induce a given response.

6. After germination, it is extremely important for plants to be able to maintain the skotomorphogenic development before reaching the light to preserve and protect both the shoot apical meristem and cotyledons or primary leaves.

2. Definition

1. Photomorphogenesis is the process by which plant development is controlled by light

2. Photomorphogenesis is any change in form or function of an organism occurring in response to changes in the light environment.

3. Photomorphogenesis is often defined as light-regulated plant development, but there are also changes in morphology and/or cell structure and function, which occur as transient acclimatizations to a changing environment, which are also light regulated.
2. PHOTORECEPTORS

1. Photomorphogenic processes determine the nature and direction of a plant's growth and thus play a key role in its ecological adaptations to various environmental changes.

2. In many plants, photomorphogenesis is the default developmental pathway after germination as characterized by an etiolated appearance of seedlings with a fast-growing hypocotyl or epicotyl, presence of an apical hook, and small and closed cotyledons or primary leaves.

3. The profound effect of light on plant development is initiated by the action of photoreceptor molecules and their attendant signal transduction pathways.

4. Photoreceptors are pigments that absorb light, and initiate cellular response. Absorption spectra of photoreceptors match their action spectra.

5. There are two light-sensing systems involved in the response of plants to light, the red light sensitive or phytochrome system, and the blue light sensitive system.
6. Phytochrome responses:
   Important plant responses regulated by the phytochrome system include
   a) *photoperiodic induction of flowering*,
   b) *chloroplast development* (not including *chlorophyll synthesis*),
   c) *leaf senescence* and
   d) *leaf abscission*.

7. Blue light responses:
   Many plant responses are regulated by blue light, including
   a) *phototropism*,
   b) *stomatal opening* and
   c) *chlorophyll synthesis*.

   The last step of chlorophyll synthesis requires high levels of blue light.
   The other blue light responses are triggered by lower levels of blue light.
3. SEED GEMINATION

- The seeds germinate better in red light and fail in far-red light compared to control seeds in kept in darkness
  1. Lettuce seeds kept in the dark germinate at low frequency
  2. Seeds kept in the dark but briefly exposed, after imbibing water, to red light results in considerable germination
  3. Seeds kept in the dark but briefly exposed, after imbibing water, to far-red light results in virtually no germination.
  4. Seeds kept in the dark but briefly exposed, after imbibing water, to red light and then briefly exposed to far-red light results in virtually no germination.
What is your conclusion?

<table>
<thead>
<tr>
<th>Irradiations</th>
<th>Germination (%)</th>
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</thead>
<tbody>
<tr>
<td>R</td>
<td>88</td>
</tr>
<tr>
<td>R, Fr</td>
<td>22</td>
</tr>
<tr>
<td>R, Fr, R</td>
<td>84</td>
</tr>
<tr>
<td>R, Fr, R, Fr</td>
<td>18</td>
</tr>
<tr>
<td>R, Fr, R, Fr, R</td>
<td>72</td>
</tr>
<tr>
<td>R, Fr, R, Fr, R, Fr</td>
<td>22</td>
</tr>
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</table>
4. PHYTOCHROME

1. Phytochrome Forms

1. Phytochrome has two different chemical structures that are inter-convertible.

2. The forms are named by the color of light that they absorb maximally:
   - Pr is a **blue form** that absorbs very strongly red light (660 nm)
   - Pfr is a **blue-green form** that absorbs very strongly far-red light (730 nm)
   - Both Pr and Pfr have some absorption in the blue-end of the spectrum

3. What is strange about these pigments is that when they DO absorb these photons, they change chemically into the OTHER form

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**Phytochrome**

Phytochrome is a Pigment with Two interconvertible forms
The two forms elicit different responses

no response or inhibition → Pr → Pfr response

red light 670 nm

730 nm far-red light

darkness

Be sure you understand the difference between red and far-red light and the two different forms of phytochrome!

Pfr Pfr

Be sure you understand which form of phytochrome is present when red or far-red light is on!
2. Chemical Structure

1. The difference in absorption between Pr and Pfr have to do with differences in the chemical structures of these two forms.

2. Chlorophyll and phytochrome both have evolved from a tetrapyrrole ring system also found in the phycobilin pigments of bacteria.

3. The chromophore is bound to a protein, just as in the case of chlorophyll. The protein has a mass of 165 kilodaltons.

4. What is interesting is how the chemical structure of phytochrome is altered to its complementary form when struck by photons of the correct energy level (wavelength!).
The structure of the linear tetrapyrrole is shown below. It is attached to the phytochrome protein through a sulfur linkage.

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**Photoconversion of Phytochrome chromophore**

In red light, the phytochrome is in Pfr (trans) form.

In far-red light, the phytochrome is in Pr (cis) form.
3. Biosynthesis of phytochrome

1. Phytochrome is produced in different parts of the cell and assembled from those parts:

   - Phytochrome protein is synthesized on 80S ribosomes
   - Phytochrome chromophore is synthesized in the plastid
   - Protein and chromophore are assembled in the cytosol

2. The phytochrome binding protein is coded in nuclear genes, transcribed in the nucleus and translated on cytosolic ribosomes

3. The phytochrome chromophore, the part responsible for its color, is produced in the plastid. The phytochrome binding protein and chromophore are assembled in the cytosol.

4. However, phytochrome has been found to be associated with plastids in terms of final destination

5. The regulation of the "central dogma" for phytochrome is shown below. Obviously there are feedback mechanisms so that phytochrome levels are kept to essential and not excessive levels.
The phytochrome protein includes a kinase domain that, after exposure to red light (i.e. when the chromophore is in Pfr form), allows the protein to phosphorylate itself.

This way the autophosphorylation of phytochrome protein activates it. It may not proceed to somewhere else in the cell to activate other proteins that need to be phosphorylated to become activated. This is the beginning of the response part of our phytochrome mediated physiology.

5. PHYTOCHROME RESPONSES

1. Phytochrome Concentration
   1. The homeostatic regulation of amount of phytochrome can be observed by measuring its level throughout the plant.
   2. The plant maintains higher levels of phytochrome at its growing points where phytochrome plays important roles in growth responses to light.
   3. Many of the genes for photosynthesis related proteins are regulated by phytochrome.
   4. The active phytochrome moves into the nucleus, joins to the dimer of the PIF 3 transcription factors bound to the G-box promoter of the myb genes.
5. The pre-initiation complex (PIC) binds to the TATA box and the myb genes are transcribed and translated.

![Diagram showing concentration of phytochrome within a plant with different stages of growth and concentration levels.]

6. The myb proteins (CCA1 and LHY) are activated and, as transcription factors, bind to the promoter regions of light-stimulated genes...such as LHCB.

![Diagram illustrating the impact of phytochrome on gene expression, highlighting the mRNA for myb and iihcb in the nucleus and cytosol.]
2. Phytochrome responses in seed germination in *Arabidopsis*.

1. After a seed germinates, the hypocotyl lifts the cotyledons above the soil in some species (epigeous).
2. This growth is rapid until the plant penetrates the soil and is exposed to light.
3. This rapid water-uptake growth of a seedling is called etiolated growth. The seedling has evolved to include a mechanism to ensure that it rapidly penetrates soil before it runs out of stored nutrients in the seeds.
4. Once in the light, the growth of the hypocotyl is inhibited for strong stocky normal growth of the shoot system.

From the diagram, can you tell which color of light (R or FR) is inhibiting hypocotyl growth? So which form of phytochrome (Pr or Pfr) appears to be active in this case?
2. The growth rate of plants is dependent on their genotype and the environment

**Phenotype = Genotype x Environment**

<table>
<thead>
<tr>
<th></th>
<th>PFD $\mu$mol m$^{-2}$ s$^{-1}$</th>
<th>R/FR ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td>1900</td>
<td>1.19</td>
</tr>
<tr>
<td>Sunset</td>
<td>26.5</td>
<td>0.96</td>
</tr>
<tr>
<td>Under Canopy</td>
<td>17.7</td>
<td>0.13</td>
</tr>
<tr>
<td>5mm deep in Soil</td>
<td>8.6</td>
<td>0.88</td>
</tr>
</tbody>
</table>

- **Sun plants:**
  1. have higher light compensation points and
  2. require greater photon flux density to grow and reproduce.

- **Shade plants:**
  1. have lower light compensation points and
  2. require lower photon flux density to grow and reproduce.
3. Plants respond to light at different flux densities by phytochrome

1. Phytochrome initiates different responses by the plant at different photon flux densities in terms of the environmental signal perceived.

2. These are classified as:
   - **VLFR** (Very Low Fluence Responses)
   - **LFR** (Low Fluence Responses), and
   - **HIR** (High Irradiance Responses)

3. Thus phytochrome can elicit correct behavior for the lighting conditions found in the plant's environment.

<table>
<thead>
<tr>
<th>Type</th>
<th>reversible?</th>
<th>Active wavelengths</th>
<th>Protein Form</th>
</tr>
</thead>
<tbody>
<tr>
<td>VLFR</td>
<td>NO</td>
<td>R</td>
<td>phyA</td>
</tr>
<tr>
<td>LFR</td>
<td>YES</td>
<td>R/FR</td>
<td>phyB</td>
</tr>
<tr>
<td>HIR</td>
<td>NO</td>
<td>Etiolated: FR, B</td>
<td>phyA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Greened: R</td>
<td>phyB</td>
</tr>
</tbody>
</table>

— **VLFR** (Very Low Fluence Responses)
— **LFR** (Low Fluence Responses), and
— **HIR** (High Irradiance Responses)
4. Hypocotyl elongation in lettuce observed above, is inhibited by the Pr form of phytochrome A under far-red light.

5. In *Sinapis alba* this same inhibition of hypocotyl elongation is a response to the Pfr form of phytochrome B under red light.

6. The difference between phytochrome A and B has to do with which genes are used to make the phytochrome binding protein.

7. The inhibition of hypocotyl elongation in *Sinapis alba* is an HIR response.
4. Mechanism

CELL WALL

1. Reception

CYTOPLASM

2. Transduction

3. Response

Relay proteins and
second messengers

Activation of cellular
responses

Hormone or
environmental
stimulus

Plasma membrane

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1. The phototropin 1 (phot1) blue-light receptor and the NPH3 protein with which it interacts are both required for phototropism. However, the initial phase of hypocotyl growth inhibition triggered by phot1 does not require NPH3.

2. The transient rise in cytoplasmic calcium concentration trigged by blue light acting through phot1 is not causally related to phototropism but is to the first phase of growth inhibition.

3. The cry1, cry2, and phytochrome A (phyA) photoreceptors are each equally necessary for the activation of anion channels at the plasma membrane of hypocotyl cells within seconds, and the phase of growth inhibition that follows approximately 30 minutes later. The similar behavior of mutants lacking these receptors in this time period is consistent with them working together as a complex, what we refer to as the ‘cry-phy-pie’
4. The anion channels activated by blue light are also calcium sensitive, providing a means for interaction between the phot1 and cry1 signaling pathways.

5. Ultimately, these signal transducing steps cause a decrease in the rate of hypocotyl (stem) cell expansion.

6. Changes in gibberellin and auxin, two growth regulating hormones, appear to be the proximate causes of the cell expansion changes.

Counteracting these growth-suppressing processes is a light-dependent process that "pushes" growth.

7. The ultimate rate of hypocotyl elongation is the resultant of these two opposing influences. The phyB photoreceptor appears to contribute to this push.

Other Mechanism

a) Chromatin-based mechanisms. Evidence emerged that Chromatin-based mechanisms contribute to photomorphogenesis.

b) DELLAs (a family of nuclear growth-restraining proteins that mediate the effect of the phytohormone gibberellin [GA] on growth)