TEMPERATURE AND LIGHT EFFECTS ON SEED GERMINATION

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This review discusses what is known and is not known about how temperature and light affect seed germination.

How can we increase the percent germination of difficult to germinate species? Two environmental stimuli which have the greatest potential for increasing seed germination are temperature and light. This review discusses what is known and is not known about how temperature and light affect seed germination.

Although it is somewhat technical, the review below lets you know the 'state of the art' of the environmental physiology of seed germination. Most studies have been done on weed species. However, the concepts which we have learned from them may have application on many bedding plant and perennial species of commercial significance.

Introduction

The breaking of seed dormancy involves a complex sequence of events which may or may not interact to influence germination. The potential for germination arises from both environmental and hormonal stimuli. Two of the most important environmental stimuli which effect seed germination are temperature and light. Although the effects of temperature and light on seed germination have been researched extensively, a full understanding of how these 2 stimuli influence seed germination and dormancy is only now being understood.

What is the ecological significance of developing a system whereby temperature and light influence seed dormancy? The basis for seed dormancy is presumably an environmental adaptation to allow the survival of a species through adverse environmental conditions. Seed dormancy allows the seed to conserve its reserves until environmental conditions are favorable for survival of the seedling. Temperature is perhaps the most limiting factor of the physical environment with respect to species distribution. Competition for light can also limit seedling survival when temperature is not limiting.

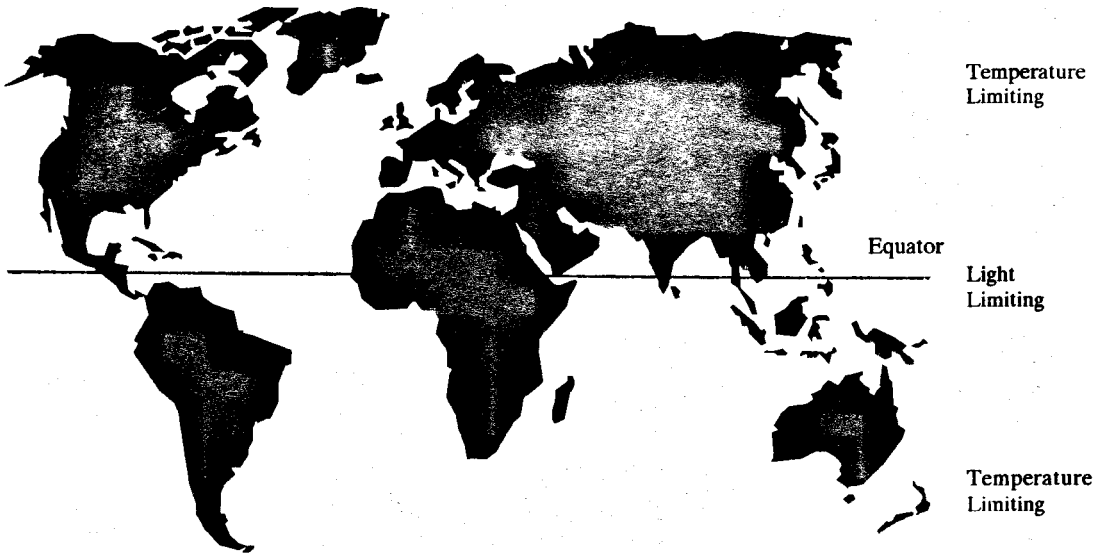

Figure 1. *World map showing temperature limitations on species indigenous to temperate regions and light limitations on species indigenous to tropical regions.*

The greater importance of either temperature or light in the breaking of dormancy is dependent on the most limiting factor for seedling survival in the indigenous environment of the species (Went, 1953). For instance, the germination of a number of temperate species, where cold winters may be the most limiting environmental factor, often require a chilling treatment for successful germination to occur (Toole, 1973) (Figure 1). In contrast, the germination of tropical species, where competition for light may be the most limiting environmental factor, often require an exposure to red light for successful germination (Smith, 1975). It is important to realize, however, that temperature and light often both influence seed dormancy regardless of the place of origin of a species (Smith, 1975). In addition, breaking of seed dormancy and/or germination of all plant species can be inhibited by non-optimal temperature or light conditions regardless of the primary stimulatory mechanism for germination.

I. Effect of Temperature and Light on Seed Germination: Seed of many temperate species require a chilling treatment, after seed are imbibed, before germination can occur (VanDeWoude and Toole, 1980). The effectiveness of a chilling treatment increases linearly as temperature decreases from 18 to 4°C. Stratification is the process of delivering a cool moist treatment to seed to encourage germination (Hartmann and Kester, 1959).

The effectiveness of a chilling treatment in potentiating germination can be greatly modified by light (Toole, 1962; 1973). For instance, the length of a chilling treatment can be greatly reduced in some species by a red light exposure prior to chilling (Brevington and Hoyle, 1981; Toole et al, 1962; Duke et al, 1977).

Irradiation of seed immediately after a chilling treatment can increase the percent germination of some species. Seed of *Pinus strobus* typically require 30 to 90 days of chilling prior to germination. Red light irradiation of seed after only 2 days of chilling increased germination from 9 to 32% (Toole et al, 1955; 1962).

The promotive role of red light prior to or during chilling is reversible with far red light if the far red exposure is given shortly after the exposure to red light (Taylorson and Hendricks, 1969; Cone and Kendrick, 1986). This reversibility of the red light stimulation of germination by far red light suggests phytochrome involvement (Smith, 1975) (Figure 2).

Phytochrome is a pigment in the plant which enables a plant to detect whether it is being shaded by other plants. Phytochrome also allows the plant to determine the length of the photoperiod (and/or nyctoperiod) (Smith, 1975). Phytochrome has 2 forms, P_r and P_{fr}. P_r absorbs red light (660 nm) and then converts to P_{fr}. Conversely, P_{fr} absorbs far red light (720 nm) and converts to P_r. P_r is continually being synthesized and P_{fr} is continually being degraded (Figure 3). The effect of red and far red light on seed dormancy prior to and during chilling suggests that high endogenous P_{fr} levels favor germination (Mancinelli et al, 1967; Takaki et al, 1981).

There are a number of theories as to how red light and temperature may interact to stimulate seed germination. VanDeWoude and Toole (1980) found that temperatures below 18°C greatly increase the sensitivity of *Lactuca sativa* seed to the P_{fr} form of phytochrome. A chilling treatment is associated with the preservation of P_{fr} within the seed through low reversion rate from P_{fr} to P_r (Brevington and Hoyle, 1981). As stated above, high P_{fr} levels are believed to encourage germination.

Hendricks and Taylorson (1976) defined a temperature sensitivity of membrane leakage with probe fluorescence at temperatures above 17°C in seed of *Avena*, *Lactuca*, *Barbarea*, *Autilon*, *Lychnis*, *Daucua*, and *Datura*. They suggested that temperatures above 17°C after imbibition result in membrane lipid dissocia-

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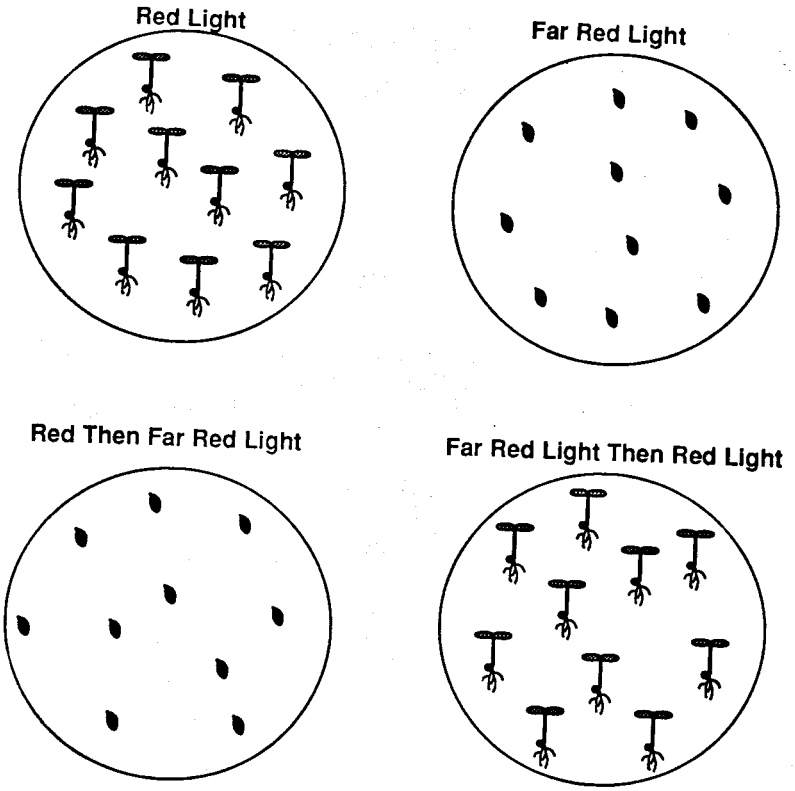

Figure 2. *The effects of red and far red light on lettuce seed germination.*

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tion and both ion and amino acid leakage which ultimately results in a loss of seed germination potential.

Short term temperature pulses can also stimulate seed germination in some species.

II. Temperature Fluctuation: Fluctuations in temperature stimulate germination in some species (Aragino, 1981). *Rumex retroflexus* is skotoblastic (germination is inhibited by dark); *Rumex* seed will not germinate at either 20 (68°F) or 30°C (86°F) in the dark. However, germination can be as great as 100% when the temperature is fluctuated, in the dark, between 20 and 30°C diurnally, i.e. in a 24 hour cycle (Toole et al, 1955). *Cucumis anguria* is photoblastic (inhibited by light) but will germinate in the light if temperatures are fluctuated between 15 and 35°C (Felippe, 1980). Seed of *Rumex obtusifolius* which is skotoblastic will germinate in the dark if temperatures fluctuate between 15 (59°F) and 35°C (95°F).

The effect of temperature fluctuations on germination can be negated by exposure of seed to far red light (Felippe, 1980). When temperatures are alternated between 5 and 25°C, far red light will inhibit germination of both *Rumex* and *Cucumis* (Felippe, 1980). Presumably, this is an ecological adaptation to allow germination of *Rumex* during periods of the year when fluctuations in day and night temperature are great and when seedling survival would not be limited by competition from adjacent plants. Shading by adjacent plants increases the proportion of far red light versus red light which shaded plants are exposed to. A high far red:red light ratio allows the plant to perceive that it is being shaded by adjacent plants.

Short term temperature pulses can also stimulate seed germination in some species (Takaki et al, 1981). *Cucumis* seed imbibed at 25°C can be stimulated to germinate by a 2 hour 0°C temperature pulse (Felippe, 1980). Low temperature treatment of *Rumex obtusifolius* also stimulates germination (Takaki et al, 1981). Seed of *Rumex*, *Nicotiana* and *Nigella* can be stimulated to germinate by a short term high temperature pulse (Aragino, 1981). Similarly, *Lactuca* seed was stimulated to germinate by exposure to 33°C for 30 minutes (Hendricks and Taylorson, 1976). Stimulation of germination by a high temperature pulse in *Cucumis* is reversible by an exposure of seed to far red light (Felippe, 1980; Takaki et al, 1981). High temperature pulse stimulation of germination is not reversible by far red light in *Rumex obtusifolius* unless seed is exposed to red light prior to the far red exposure. Presumably, the red light

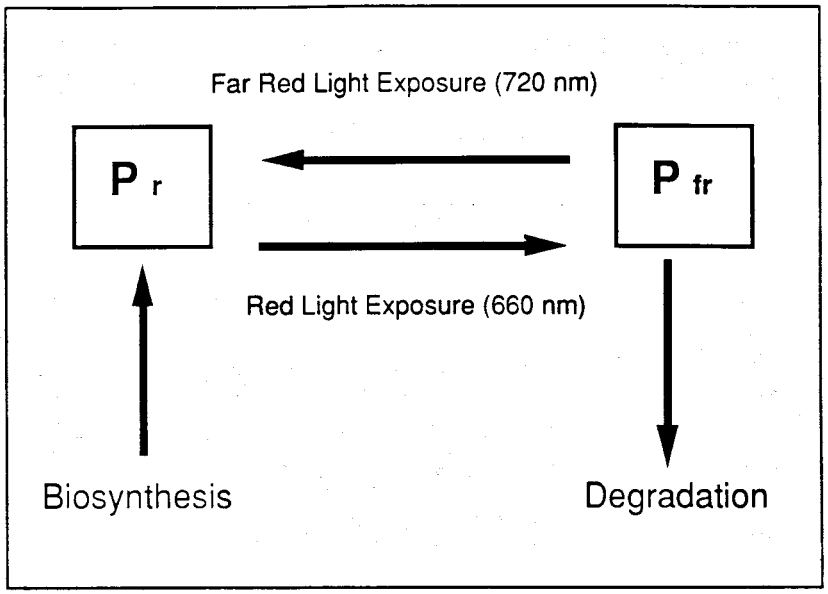

Figure 3. *Effect of red and far red light on phytochrome (P) form.*

exposure is necessary to completely cycle the phytochrome pool (Takaki et al, 1981). Takaki et al (1981) suggested that high temperature pulses may increase the available P_{fr} to above a threshold level in the seed through an increase in phytochrome synthesis.

The effectiveness of a high temperature pulse in stimulating seed germination of some species is greatly enhanced by an exposure to red light (Toole, 1973; Taylorson and Hendricks, 1972). However, red light enhancement of a high temperature pulse is only effective in stimulating enhancement of seed germination if the red light exposure occurs after or during an exposure of the seed to temperatures below 32°C (Taylorson and Hendricks, 1979). For example, exposure of *Amaranthus retroflexus* seed to red light while seed maintained at 40°C (104°F) resulted in only 2% germination (Taylorson ahd Hendricks, 1969). However, germination at 40°C was greatly enhanced if the exposure to red light at 40°C was followed by a 10 minute exposure to 32°C (90°F) then returned to 40°C. In fact, a 64 minute exposure to 15°C (59°F) before moving seed back to 40°C increased *Amaranthus* germination to 80%. Based on these results Taylorson and Hendricks (1979) suggested that phytochrome must interact with a reaction center which is stable at temperatures at or below 32°C in order to elicit a response, i.e. germination.

III. Interaction Between Light, Temperature and Hormones: The hormonal content of seed changes as the length of time which seed are stratified increases. Abscisic acid (ABA) content decreases as the length of a chilling period increases in *Fraxinus americana*, *Juglans regia* and *Corylus avellana* (Wareing and Saunders, 1971). Higher concentrations of abscissic acid are associated with an inhibition of germination.

In contrast to ABA, gibberellin content increases as the length of the stratification time increases in *Corylus*. Gibberellins are associated with the promotion of germination. In fact, application of gibberellic acid (GA_{4+7}) has been shown to overcome the stratification requirement of a number of species (Taylorson and Hedricks, 1976; Felippe, 1980). Gibberellins can also overcome inhibition of germination of *Cucumis*, skotoblastic, in light (Felippe, 1980).

Light also influences seed hormone content. Felippe et al (1980) showed that seed gibberellin content increased after an exposure to red light and/or high temperatures. Cytokinin content of seed has also been shown to increase in seed following an exposure of seed to light (Wareing and Saunders, 1971). Exogenous applications of cytokinin stimulate germination of a number of light sensitive species (Felippe, 1980).

Interestingly, The effectiveness of cytokinins and gibberellins on stimulating *Cucumis* germination is greatly enhanced

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by an exposure of seeds to red light (Felippe, 1980). Such a synergism was not observed in *Chenopodium album* (Karssen, 1968).

IV. Perception of Light and Temperature: Perception of light quality (or color) is achieved through alterations in the phytochrome chromophore between the P_{fr} state and the P_r state (Smith, 1975). This alteration in the chromophore is believed to result in an interaction with the plasma membrane within a cell to elicit a response (Mackenzie et al., 1975; Marme, 1977). More recent studies have suggested that phytochrome is not associated with the plasma membrane, but instead suggest that phytochrome is distributed throughout the cytosol (Saunders et al., 1983). After irradiation (exposure) with red light, phytochrome is sequestered into dense structures within the cytosol (Speth et al., 1986). Interestingly, these structures disappear within 1-4 hours after they are formed. Speth et al. (1986) have suggested that P_{fr} induces aggregation of some unknown protein receptor which ultimately leads to a germination response.

How is temperature perceived? This is a difficult question since it inherently suggests the presence of a receptor. In one respect, the entire seed responds to temperature since the rate of every metabolic reaction is affected. There is, however, some evidence to suggest that there may be temperature receptors. The effects of temperature on phytochrome reversion and degradation are well known (Smith, 1975). Therefore, one may suggest that phytochrome is a temperature receptor as total phytochrome and the ratio of P_{fr} to P_r are altered by temperature. In addition, the phytochrome-receptor complex or the receptor itself may play a role in temperature sensing in plants.

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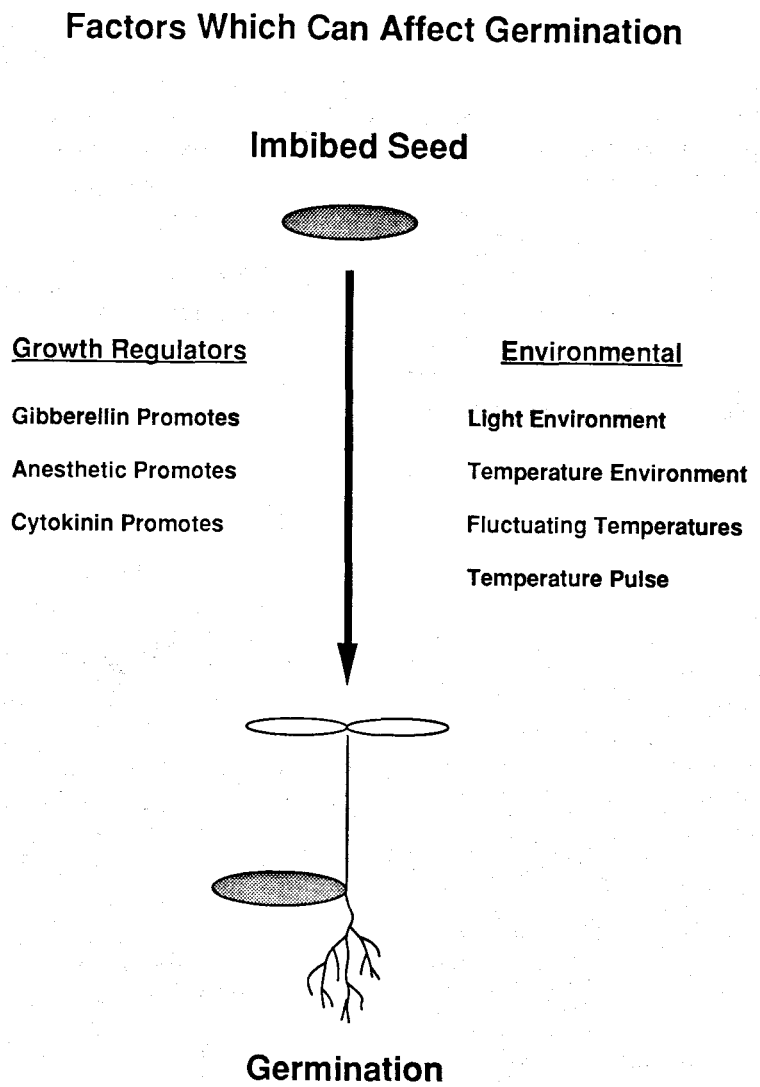

Figure 4.

Most seed can not germinate at temperatures above 30°C (86°F) (Hendricks and Taylorson, 1979). This loss of germination potential at high temperatures has been attributed to membrane leakage and alterations in membrane organization within the seed (Hendricks

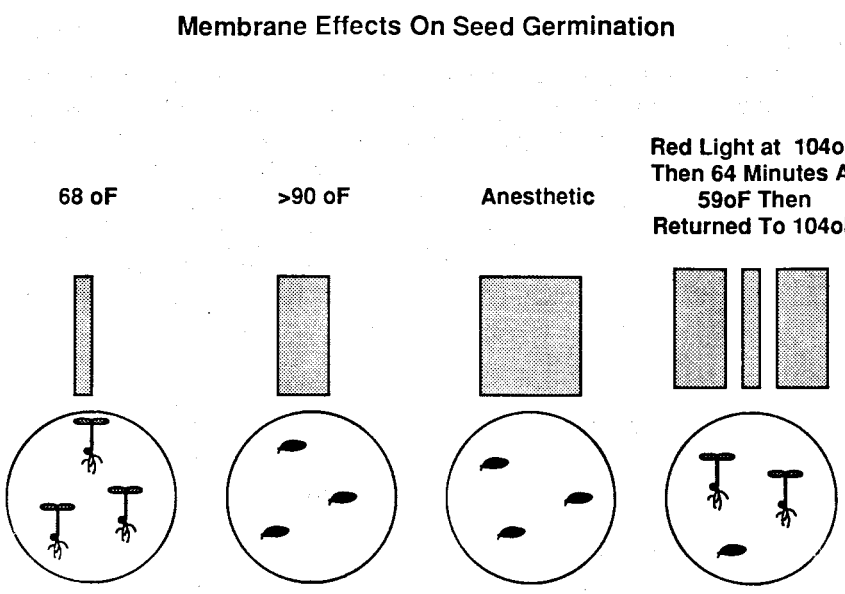

Figure 5.

and Taylorson, 1979). Many seed leak endogenous sugars and amino acids at temperatures above 30°C (Aragino, 1981; Hendricks and Taylorson, 1976; Hendricks and Taylorson, 1979). Seed which do not show membrane leakage at temperatures above 30°C such as *Amaranthus albus* and *Amaranthus theophrasti* germinate successfully at temperatures above 30°C (Hendricks and Taylorson, 1978). The dramatic increase in seed germination at temperatures below 30°C suggest that membrane lipids may have to be intact for successful germination to occur (Aragino, 1981). Temperatures above 32°C (90°F) disrupt membrane organization and may limit germination (Taylorson and Hendricks, 1979). Therefore, temperatures may also be sensed by a gradient in membrane organization (Figure 5).

The importance of the plasma membrane in potentiating seed germination is unequivocal. Disruption of the plasma membrane with high concentrations of anesthetic virtually eliminates stimulation of germination by chilling or red light (Hendricks and Taylorson, 1979). Interestingly, low concentrations of anesthetic can stimulate dark germination of *Panicum dichotomiflorum* seed, which normally require light for germination (Taylorson and Hendricks, 1979).

V. Potential Ways Which Temperature Effects Seed Germination:

Most seed cannot germinate at temperatures above 30°C (86°F).

Either temperature or light can often stimulate seed germination. This suggests that temperature and light affect seed germination through 2 different parallel mechanisms, rather than in sequence, which interact to potentiate germination. However, the numerous interactions between temperature and light suggest that although the initial perception of temperature and light by a seed may be different, the transduction pathway, which ultimately results in germination, is similar. The question arises then as to where the interaction between temperature and light occurs and where do the transduction pathways coincide.

The effects of temperature and light on seed germination are often synergistic.

The initial effects of either light or short term temperature pulses on seed germination does not require protein synthesis (Taylorson and Hendricks, 1972). Therefore, the initial response of a seed to either temperature or light is physical and not metabolic in nature. In other words, the primary effect of temperature or light does not involve the transduction pathway in itself but rather some physical phenomenon which initiates a biochemical response.

Perhaps a receptor is associated with the cellular membrane. Initiation of a response may require dissociation of the receptor from the membrane surface. High temperatures may limit the effectiveness of the receptor by not allowing membrane dissociation. In contrast, short term temperature pulses may encourage receptor separation from the membrane surface.

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Alternatively, a receptor may be present in the cytosol at all times. Stimulation of germination may require an intact membrane in which the receptor-phytochrome complex must bind with stimulate a biochemical response. In contrast, phytochrome could modify the receptor to allow binding to the membrane.

How could temperature alterations and/or pulses alter the receptor? Perhaps the receptor is also temperature sensitive in the same way as the membrane. Short term pulses may alter the receptor to allow an interaction with the membrane.

There are synergistic relationships between growth regulators and either temperature or light.

There are synergistic relationships between growth regulators and either temperature or light. The synergism of either cytokinin or gibberellin and light in stimulating germination indicates that light and plant growth regulators are not acting sequentially to stimulate germination. Instead, the effect of growth regulators and light or temperature on germination are initially independent. Presumably this is due to a separation of processes involved in hormone synthesis versus physical temperature and/or light perception. Therefore, the effects of light, temperature and hormones on the breaking of seed dormancy and germination must result from a variety of parallel but mutually interacting mechanisms. It is probable that some physical mechanism is involved which may combined with hormonal responses to induce a synergism.

We are currently experimenting with some of the before mentioned interactions to increase the percent germination and decrease the time for germination on difficult to germinate perennial species. I encourage all of you to experiment with any ideas you may get from this review. If you have any successes, be sure to let me know!

LITERATURE CITED

Aragino, M. 1981. Response of macrophytes to temperature. Encyl. of plant physiology, Vol 12a, Ed. A. Pirson and M.H. Zimmerman. pp. 339-371.

Brevington, J.M. and M.C. Hoyle. 1981. Phytochrome action during prechilling induced germination of *Betula papyfera* Marsh. Plant Physiol. 67:705-710.

Cone, J.W. and R.E. Kendrick. 1986. Photocontrol of seed germination. In: Photomorphogenesis in plants. Ed. R.E. Kendrick and G.H.M. Kronenberg. Marinus Nijoff Pub., Dordecht, The Netherlands. pp. 443-465.

Duke, S.O., G.H. Egley and B.J. Reger. 1977. Model for variable light sensitivity in imbibed dark-dormant seeds. Plant Physiol. 59:244-249.

Felippe, G.M. 1980. Germination of light-sensitive seeds of *Cucumis anguria* and *Rumex obtusifolius*: Effects of temperature. New Phytol. 84:439-448.

Hartmann, H.T and D.E. Kester 1959. Plant Propagation: Principles and Practices. Prentice-Hall, Inc. Englewood Cliffs, New Jersey.

Hendricks, S.B. and R.B. Taylorson. 1976. Variation in germination and amino acid leakage of seeds with temperature related to membrane phase change. Plant Physiol. 58:7-11.

Hendricks, S.B. and R.B. Taylorson. 1979. Dependence of thermal responses of seeds on membrane transitions. Proc. Natl. Acad. Sci. USA 76:778-781.

Karssen, C.M. 1968. The light promoted germination of seeds of *Chenopodium album* L. (II). Effects of (RS)-abscisic acid, Acta Bot. Neerl. 17:293-306.

Mackenzie, J.M., R.A Coleman, W.R. Briggs and L.H. Pratt. 1975. Reversible redistribution of phytochrome within the cell upon conversion to its physiologically active form. Proc. Natl. Acad. Sci. USA 72:799-803.

Mancenelli, A.L., Z. Yaniv and P. Smith. 1967. Phytochrome and seed germination I. Temperature dependence and relative P_{fr} levels in the germination of dark-germinating tomato seed. Plant Physiol. 42:333-337.

Marme, D. 1977. Phytochrome: membranes as possible sites of primary action. Ann. Rev. Plant Physiol. 28:173-198.

McLemore, B.F. 1964. Light during stratification hastens dark-germination of loblolly pine seed. Forest Sci. 10:348-349.

Saunders, M.J., M.M. Cordonnier, B.A. Palevitz and L.H. Pratt. 1983. Immunofluorescence visualization of phytochrome in *Pisum sativum* L. epicotyls using monoclonal antibodies. Planta 159:545-553.

Smith, H. 1975. Phytochrome and Phytomorphogenesis. McGraw-Hill. New York. pp. 121-128.

Speth, V., V. Otto and E. Schafer. 1986. Intracellular localization of phytochrome in oat coleoptiles by electron microscopy. Planta 168:299-304.

Takaki, M., R.E. Kendrick and S.M.C. Dietrich. 1981. Interaction of light and temperature on the germination of *Rumex obtusifolium* L. Planta 152:209-214.

Taylorson, R.B. and S.B. Hendricks. 1969. Action of Phytochrome during prechilling of *Amaranthus retroflexus* L. seeds. Plant Physiol. 44:821-825.

Taylorson, R.B. and S.B. Hendricks. 1972. Interaction of light and a temperature shift on seed germination. Plant Physiol. 49:127-130.

Taylorson, R.B. and S.B. Hendricks. 1973. Phytochrome transformation and action in seeds of *Rumex crispus* L. during secondary dormancy. Plant Physiol. 52:475-479.

Taylorson, R.B. and S.B. Hendricks. 1976. Interactions of phytochrome and exogenous gibberellic acid on germination of *Lamium amplexicaule* L. seeds. Planta 132:65-70.

Taylorson, R.B. and S.B. Hendricks. 1979. Overcoming dormancy in seeds with ethanol and other anesthetics. Planta 145:507-510.

Went, F. 1953. Temperature effects on plant growth. Ann. Rev. of Plant Phys. 4:347-362.

Toole, E.H., V.K. Toole, H.A. Brothwick and S.B. Hendricks. 1955. Interaction of temperature and light on germination of seeds. Plant Physiol. 30:473-478.

Toole, V.K., E.H. Toole, H.A. Brothwick and A.G. Snow. 1962. Responses of seeds of *Pinus taeda* and *Pinus strobus* to light. Plant Physiol. 37:228-233.

Toole, V.K. 1973. Effects of light, temperature and their interactions on the germination of seed. Seed Sci. and Technol. 1:339-396.

VanDeWoude, W.J. and V.K. Toole. 1980. Studies of the mechanism of enhancement of phytochrome dependent lettuce seed germination by prechilling. Plant Physiol. 66:220-224.

Wareing, P.F. and P.F. Saunders. 1971. Hormones and dormancy. Ann. Rev. Plant Physiol. 22:261.