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THE EFFECT OF LIGHT AND TEMPERATURE ON THE GERMINATION OF JACK PINE AND LODGEPOLE PINE SEEDS

BY

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INTRODUCTION

Germination of seeds is the initial, and under some circumstances, a critical step in the reproduction of forest stands by natural or artificial means. A fundamental knowledge of the ecology of germination of the seeds of the commercially important species is therefore essential to the forester practising the art of silviculture. Similarly, research workers in many fields of forest science will find it difficult to undertake experiments successfully if the germination requirements of the species under study are a matter of conjecture.

In studies with jack pine seeds (*Pinus banksiana* Lamb.) to determine the relationship between moisture content and germination, error variance was found that could best be explained by an uncontrolled light factor in the experiment. A few preliminary germination tests substantiated the observation, previously unreported, that the germination of this species is indeed subject to control by light. A series of experiments was then undertaken with jack pine seeds to determine:

1. The existence and characteristics of photo-control of germination.
2. The effect of incubation temperature on photo-control of germination.

A second, similar series of experiments was also undertaken with seeds of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) with the object of comparing the response of two closely related species under identical environmental conditions. The two species are very similar morphologically and in habit. Their ranges overlap in Alberta and natural hybridization occurs (Moss, 1949).

The main environmental factors affecting the initiation and rate of tree seed germination have long been held to be moisture, temperature and oxygen. Light, although proven in some early experiments to have an effect on the germination of a number of species, has generally been considered of secondary importance.

Recent discoveries in the physiology of growth and development have prompted studies into, *inter alia*, the role of light in the germination process. Results have shown that the seeds of a number of tree species are light sensitive in this matter, including among others:

Betula pubescens Ehr. (Black and Wareing, 1954)
Betula verrucosa Ehr. (Vaartaja, 1956)
Betula lutea Michx f. (Redmond and Robinson, 1954)
Ulmus americana L. (Toole et al, 1957)
Tsuga canadensis (L.) Carr. (Stearns and Olson, 1958)
Pinus virginiana Mill. (Toole et al, 1956)
Pinus sylvestris L. (Vaartaja, 1956)

Where the appropriate test has been carried out germination of the seeds of these species has been found to respond to light quality (germination promoted by red light, inhibited by far-red light), to single exposures of varying duration and/or to photoperiod (promoted by long photoperiods, inhibited by short pohtoperiods). In some experiments the response to light varied with the incubation temperature employed and with seed pretreatment such as chilling, soaking or scarification.

The series of tests described in this report are concerned with the ecology of germination rather than the physiology of germination. Nevertheless it was soon apparent that the responses, similar to those obtained by other workers investigating light effects on germination (Vaartaja, 1956; Borthwick, 1957), are similar also to those obtained by workers studying photo-control of growth parameters such as rooting (Shapiro, 1957), vegetative growth (Wareing, 1956) and flowering (Downs, 1956). These similarities, noted by Borthwick (1957) and others, strongly suggest a basic photomorphogenetic mechanism that may enter into many phases of plant growth and development.

A comprehensive hypothesis involving the action of light on the pigment phytochrome (Borthwick and Hendricks, 1960, 1961) has been recently advanced to explain the physiology of morphogenesis. Although the experiments with jack pine and lodgepole pine germination were not designed to further or test this hypothesis, interpretation of the results is greatly facilitated by reference to it. Consequently, a description of this hypothesis (hereafter referred to as the red, far-red reversion hypothesis) follows.

Appreciation of the nature of the photoreceptor and time measuring mechanism, leading to formulation of the red, far-red hypothesis, was accelerated by investigation of photomorphogenetic control over the germination of light-sensitive lettuce seeds. Flint and McAlister (1935) observed that red light promoted while far-red light inhibited the germination of this species. This effect was verified by Borthwick et al. (1952b) who also determined the response to be repeatedly reversible by irradiation with red or far-red light. Red light, with a maximum wave-length near 660 nm (nanometers, equal to millimicrons) promoted germination while far-red with a maximum near 730 nm inhibited germination. This was accepted as evidence for the existence of a photo-receptor pigment in two forms, red-absorbing and far-red-absorbing, each form convertible to the other in the wave-length range of its absorption peak.

At the present time, a simple working hypothesis has been proposed, incorporating the red, far-red conversion, to explain the mechanism of photoperiodic control (Borthwick and Hendricks, 1960, 1961).

$$\text{Pigment 660} \underset{\text{far-red light or dark}}{\overset{\text{red light}}{\rightleftharpoons}} \text{Pigment 730 (enzymatically active)}$$

The main characteristics of the reaction are summarized below.

1. The reaction is displaced to the right by red light, circa 660 nm. The reaction should be displaced to the right by daylight because sunlight is richer in red than in far-red light (Moon, 1940). Although sunlight contains both red and far-red light the pigment balance is at neither extreme but favours the right (Borthwick, Hendricks and Parker, 1952a).

2. The reaction is displaced to the left by far-red light, circa 730 nm.

3. There is evidence that P730 is the biologically active form, and that it has enzymatic properties (Hendricks et al., 1956; Borthwick and Hendricks 1960, 1961).

4. The reversible photoreaction is only slightly influenced by temperature between 43 F and 79 F (Borthwick et al., 1954).

5. In addition to being brought about by far-red radiation, reversion of P730 to P660 occurs spontaneously in darkness at a rate dependent upon the temperature (Borthwick et al., 1954). The rate of reversion of the pigment in darkness from the far-red-absorbing form to the red-absorbing form is considered the time measuring mechanism of the system.

6. The pigment has been assayed in living tissue and in solution and has been given the name phytochrome (Bonner, 1960, 1961; Butler et al., 1959). In this work speculation that the pigment might be a protein was reinforced.

7. The phytochrome obtained in solution exhibited photoreversibility in vitro but it did not undergo spontaneous reversion from P730 to P660 in darkness, leading to the hypothesis that reversion is not only thermal but enzymatic (Borthwick and Hendricks, 1960).

8. The reaction depends upon the extent of the interconversion of the phytochrome forms. If light is of mixed wavelength an equilibrium at intermediate pigment conversion is attained, the position depending upon the energy distribution in the various spectrum regions of the source rather than intensity (Borthwick et al., 1952a, b). Thus Garner and Allard (1926) noted that relatively low intensity incandescent light was effective in extending the natural photoperiod; Tincker (1925) found five foot-candles to be effective in extending daylength; and Withrow and Benedict (1936) got definite responses at less than one foot-candle of incandescent light. Effective light intensities for photoperiodic control of morphogenesis are therefore much lower than those needed for photosynthesis. Intensity is above saturation even in the shade on a cloudy day until well after sundown (Withrow, 1959).

9. High intensity radiation with red or far-red light does not necessarily produce the same results as low intensity radiation (Hendricks and Borthwick, 1959, a, b). The absorption bands of the two pigments overlap considerably; and high intensity light of appreciable band width will excite both forms even when the wavelength peak coincides with the absorption maximum of one form.

The series of experiments described in this report, for both jack and lodgepole pine, were confined to a single lot of seeds. It is recognized that ecotypic variation can be expected (Pauley and Perry, 1954; Vaartaja, 1954, 1962). It is also recognized that the response of germination to light and temperature is subject to environmental preconditioning after the seed is mature and perhaps during earlier stages of development as well (Rowe, 1964; Evenari, 1956; Koller et al., 1962; Koller, 1962). In view of the possibilities of ecotypic variation and preconditioning, a single seed lot can hardly be said to represent a species. Nevertheless it was considered unwise to introduce these sources of variation until the existence and basic characteristics of photo-control and the contribution of temperature are determined and more thoroughly understood. The information now obtained provides a reasonably sound basis for further studies which might well incorporate and assess these factors.

METHODS AND MATERIALS

Seed Origin and Quality

The jack pine seeds were collected in 1949 from plantations located in southern Ontario. They had been cleaned, and when obtained in 1958 had been in dry storage at 40 to 45 F. They were of high quality and purity with a germinative capacity of 91 per cent (based on germination and cutting tests of 10 samples of 100 seeds).

The lodgepole pine cones were obtained in October 1959 from two 90-year-old trees, at an elevation of 4,500 feet on the Kananaskis Forest Experiment Station (51° 00' N., 115° 10' W.), in the Subalpine Forest Region of Alberta (Rowe, 1959); they were stored in a cool, dry basement for a period of four months prior to extraction of seeds.

The cones were opened and the seeds extracted and cleaned in complete darkness, the purpose being to have seeds that had never been exposed to light, until the moisture content was down to approximately 5 per cent oven-dry weight. The cone scale resin bond was broken by a short immersion in water at 113 F (Clements, 1910; Cameron, 1953), and the cones dried in a small kiln, made light-tight by baffles, with intermittent forced air at a temperature of 110 F. Following extraction, the seeds were dewinged, cleaned in a small commercial seed cleaner and stored in a light-tight container at a temperature of 35 F. The lodgepole pine seeds were also of high quality and purity with a germinative capacity of 88 per cent (based on germination and cutting tests on 162 samples of 100 seeds).

Preliminary germination tests with both species indicated that prompt and near complete germination could be obtained without pretreatment for dormancy.

Temperature and Light Control

All germination tests were conducted in Jacobsen-type incubators. In this incubator, cards of blotting paper, supported on glass plates over a water reservoir, were used as a substratum. A continuous supply of moisture was maintained to the substratum by filter paper wicks extending into the reservoir. Temperature control was maintained by heating the water in the reservoir.

The incubators, equipped with Cenco-Dekhotinsky bimetallic thermoregulators mounted immediately below the substratum, were placed inside walk-in refrigerators equipped with independent temperature control. For constant temperature tests the refrigerator was maintained at a few degrees below the temperature desired for the incubator. This dual control system permitted temperature control to within $\pm$ 1 F, as measured by a mercury-in-glass thermometer mounted on moist substratum within the incubator.

Germination tests requiring alternating temperatures, e.g. 60 F night temperature and 80 F day temperature, were accomplished by locating incubators in two walk-in refrigerators, each maintained at the desired temperature. At the appropriate time the glass plates supporting substratum, seeds and wicks were moved from one temperature condition to the other. The temperature change by this method was necessarily abrupt.

The light source in all tests was 200-watt incandescent lamps yielding 40 to 50 foot-candles at the level of the substratum. Since the tests were conducted in the refrigerators the incandescent lamps were the only source of illumination.

All seed samples within the incubators were covered with glass petri dishes. When exclusion of all light was required the petri dishes were wrapped with aluminum foil. This method appeared to be satisfactory and at no time was there any evidence of light leakage. The temperature of illuminated seed samples was approximately 1 F higher (measured by fine-wire thermocouple) than that of samples within the same incubator from which radiation had been excluded by the foil wrapping.

Germination Test Procedure

All tests were conducted with samples of 100 seeds taken randomly after thorough mixing. During the counting of seed samples all damaged and obviously empty seeds were discarded in an attempt to maintain germinative capacity as high as possible. Except for a few samples maintained in continuous darkness all seeds were counted and handled in normal room light after it was assured that an air-dry moisture content of approximately 5 per cent of oven-dry weight had been reached.

The 100-seed samples were mounted on the moist substratum in the refrigerator and placed directly in the incubators. Approximately one minute passed between contact of the first seeds with the moist substratum and exclusion of light for those samples requiring continuous darkness.

The treatments of any particular experiment were randomly assigned to the samples and the samples were randomly assigned to positions within the incubator. The number of samples subjected to each treatment varied depending on the nature of the test and the supply of seeds. Either one or two samples were usually employed for jack pine tests while 3 samples of 100 seeds were used for all lodgepole pine tests.

The attribute measured was the percentage germination of the seeds in a specified period of time. A seed was considered germinated when growth of the radicle was sufficiently advanced that positive geotropism could be observed. Results are expressed for all jack pine tests as the percentage germination of all seeds in each 100-seed sample (apparent germination) and for lodgepole pine as the percentage germination of the sound, apparently healthy seeds of each 100-seed sample (real germination).

In those tests demonstrating very large treatment effects, statistical analyses to determine significance have not been considered necessary. In other cases all percentage germination data have been transformed using the arc-sine transformation and subjected to analysis of variance. If replicates of 100-seed samples were employed in the test, the analysis of variance followed standard procedure. If a single 100-seed sample was employed for each treatment, a theoretical error term, 821/100, applicable to the arc-sine transformation, was employed (Snedecor, 1956). Unless otherwise stated all effects discussed were significant at the 5% level.

The jack pine experiments were undertaken during the winter months of 1958-59 and 1959-60, the lodgepole pine experiments during the winter months of 1960-61 and 1961-62.

JACK PINE EXPERIMENTS

Experiment 1. The Effect of Incubation Temperature Under Continuous Light

The purpose was to determine the quality of the seeds, the rapidity of germination under presumably favorable conditions of continuous light, and the effect of varying temperature under continuous light. Tests were conducted at constant 60 F, 70 F, 80 F, alternating 80 F and 60 F (80 F for 16 hours, 60 F for 8 hours) and alternating 60 F and 80 F (60 F for 16 hours, 80 F for 8 hours).

The pattern of germination at each temperature level is shown in Figure 1. The percentage germination in 8 days at 70 F, 80 F, 60 F and 80 F, and 80 F and 60 F and in 14 days at 60 F is given in Table 1.

TABLE 1

Effect of temperature on total germination under continuous light.

Sample Number	Temperature				
	70 F	80 F	60 and 80 F	80 and 60 F	60 F
	Percentage germination in 8 days				in 14 days
1	87	89	85	95	83
2	87	83	86	88	90
3		91			85
4		90			
5		90			
6		89			
Mean	87	89	86	92	86

Germination commenced in 2 to 3 days and was largely complete in 8 days at all temperatures except 60 F. At 60 F germination was delayed until the sixth day but once initiated was rapid and complete in approximately 14 days.

There was no significant difference in total germination at any temperature level tested.

Discussion - Under continuous light, over the temperature range tested, jack pine seeds were not demanding in their temperature requirements. Lowering the temperature was effective in delaying germination, but once initiated, the rate and total amount of germination were similar at all temperature levels.

It is of interest to note that at constant 60 F, 70 F, and 80 F and alternating 80 F and 60 F approximately 120 degree-days above 50 F resulted in over 80 per cent germination. However, the temptation to generalize regarding energy requirements for germination is discouraged by the equally good results obtained at a much lower energy level in the alternating 60 F and 80 F test.

Exposure to continuous light should maintain the pigment phytochrome in the far-red-absorbing form favourable for germination. Since the photoreaction is only slightly influenced by temperature (Borthwick et al., 1954) the temperature effect observed (delay in germination at 60 F) probably results from slowing of subsequent temperature dependent stages in the germination process.

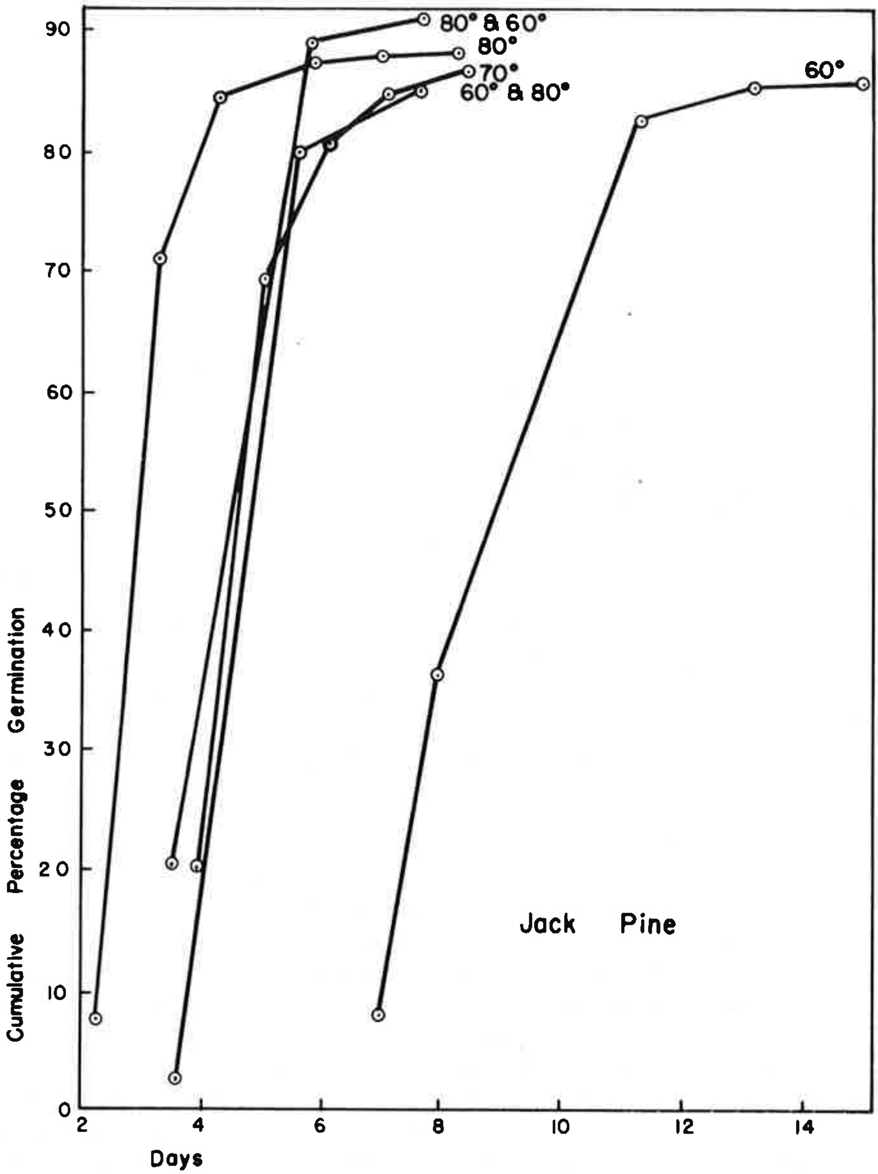

Figure 1. The effect of temperature under continuous light on the germination of jack pine seeds.

Experiment 2. Basic Light Test: Continuous Light vs. Continuous Darkness

This experiment was designed to test the hypothesis that light is required for the germination of jack pine seeds, and if so, that the requirement is temperature-dependent over a normal range of temperature. The temperature levels employed were constant 60 F, 70 F, 80 F, alternating 80 F and 60 F and alternating 60 F and 80 F. As in Experiment 1, the incubation period was 8 days for all temperature levels except 60 F for which a 14-day period was employed.

The results are shown in Table 2. The number following the germination percentage is the number of samples of 100 seeds contributing to the mean.

TABLE 2

Effect of Continuous Darkness on the Germination of Jack Pine Seeds at Various Temperatures

Light Treatment	Temperature				
	70 F	80 F	60 and 80 F	80 and 60 F	60 F
	Percentage germination in 8 days				in 14 days
Cont. light	87(2)	87(7)	86(2)	92(2)	86(3)
Cont. dark	16(2)	22(4)	12(2)	23(2)	20(2)

Germination was markedly reduced at all temperatures by the exclusion of light. It must therefore be concluded that light is required for the germination of a large percentage of these jack pine seeds and that this light requirement is unaffected by constant temperature between 60 F and 80 F or by alternating temperature between 60 F and 80 F.

Discussion - Failure of a large percentage of the seeds to germinate in continuous darkness is assumed to result from maintenance of phytochrome in the red-absorbing form, thus creating a block in the germination process.

The small percentage of seeds that germinated in continuous darkness provided germinants at the end of the incubation period of good colour and as large and thrifty as the seeds germinated under continuous light. Two explanations are possible. Either a small percentage of the seeds of this species are not subject to control by light or their light requirement has been satisfied by previous exposure. That such preconditioning is possible is shown in a later section of this report.

Experiment 3. Effect of a Single Light Exposure

The necessity of light for the germination of a large percentage of jack pine seeds was demonstrated in Experiment 2. In Experiment 3 the sensitivity of the photo-receptor system was investigated by exposing the seeds to various periods of light at the start of the incubation period and then completing the test in continuous darkness. The experiment was repeated at 60 F and 80 F with exposure and incubation given at the same temperature. The duration of exposure was measured from the placing of the dry seeds in the incubator.

If germination can be "triggered" by a single, initial light exposure it should also be delayed by a dark period given at the start of the test. This was demonstrated at 80 F by excluding light for various periods at the start of a test and then completing the incubation period in continuous light.

The effect of a single exposure provided at the start of the incubation period is shown in Table 3.

TABLE 3

The Effect of a Single Light Exposure of Varying Duration on the Germination of Jack Pine Seeds

Duration of exposure	Temperature	
	60 F	80 F
	Percentage germination in 14 days	Percentage germination in 8 days
Cont. dark	20 (2)	22 (4)
0.5 hrs.	No test	75
1 hr.	68	86
1.5 hr.	No test	92
2 hrs.	No test	84
2.5 hrs.	No test	82
3 hrs.	81	86 (2)
4 hrs.	79	84
6 hrs.	60	89
8 hrs.	80	No test
12 hrs.	80 (2)	84
16 hrs.	83	No test
24 hrs.	84	96
36 hrs.	No test	88
48 hrs.	76	80
72 hrs.	No test	86
Cont. light	86 (3)	87 (7)

At 80 F, the shortest exposure given, 30 minutes, resulted in a very marked increase in germination and a one-hour exposure resulted in complete germination. The same pattern of response was observed at 60 F but germination was considerably more erratic.

The effect of a single dark period provided at the start of the incubation period is shown in Table 4.

TABLE 4

The effect of a single dark period of varying duration on the germination of jack pine seeds

Duration of dark period	Test period		
	7 days	10 days	12 days
	Percentage germination		
3 hours	93	93	93
6 hours	89	89	89
12 hours	91	91	91
1 day	86	86	86
2 days	92	92	92
3 days	81	83	85
4 days	54	87	89

The delay induced by a dark period of up to 3 days' duration was insufficient to alter total germination obtained in 7 days. The delay induced by dark periods of 3 or more days is apparent however.

Discussion - The failure of dark periods of up to 3 days' duration to delay germination for a similar period probably results from an initial period of moisture imbibition common to all treatments. Resumption of growth of the embryo will not occur until adequate moisture is available. The effect of exposure to light or darkness, during the initial period of imbibition, on the amount of germination occurring in a specified period of time will be masked by this moisture requirement.

According to the red, far-red hypothesis, phytochrome, after being driven to the far-red-absorbing form by exposure to red light, reverts to the red-absorbing form in darkness at a rate depending on the temperature. Assuming this reversion takes place following a single exposure of the jack pine seeds to light, why does germination then occur in continuous darkness?

After promotion of lettuce seed (Lactuca sativa L) by red light and incubation at a suitable temperature, the germination process progresses in 12 hours beyond reversal by far-red light (Toole et al., 1953, 1957). With incubation at high temperatures, however, the seeds lose the ability to germinate in darkness, i.e., more rapid reversal of phytochrome to the red-absorbing form at the higher temperature prevents germination following a single exposure to light. It is probable that at the incubation temperatures employed with the jack pine seeds (60 F and 80 F) the germination process progressed beyond inhibition before reversal of phytochrome to the red-absorbing form could block germination.

Experiment 4. Determination of Threshold Moisture Content

Since dry seeds can be handled normally in daylight and still retain a light requirement, it seems reasonable to assume that the seeds do not become subject to light control until a threshold moisture content is attained. Further, since a one-hour exposure resulted in complete germination at 80 F (Experiment 3) it can be assumed that the threshold moisture content is attained in something less than one hour.

To determine the threshold moisture content for light control of germination the rate of imbibition at 80 F was determined for both jack pine and lodgepole pine seeds. This was done by placing seeds on germination blotters in the incubator and removing 3 samples of 100 periodically for moisture content determination. After removal (from the germinator) the seed samples were shaken in a beaker until surface dry (as evidenced by the lack of cohesion between seeds), weighed immediately, oven-dried at 220 F for 48 hours then reweighed. This procedure gave remarkably consistent results for replicate samples.

Air-dry moisture content of the seeds was 5 per cent. Moisture content increased very rapidly, reaching over 30 per cent in approximately 5 hours (Figure 2). At 80 F light becomes effective for most seeds within one-half hour of the start of imbibition and for all seeds within one hour. Reference to Figure 2 indicates that a moisture content of 10 to 20 per cent of dry weight is attained in that period.

Discussion - In this experiment the threshold moisture content could have been determined more precisely with more frequent sampling during the first hour of imbibition. Also, the effect of temperature on the rate of imbibition was not examined.

Germination was first observed at a moisture content of 53 to 54 per cent of dry weight. However, this is not to be construed as evidence that this moisture level is essential for the germination of jack pine and lodgepole pine seeds. Within limits, the moisture content at germination may merely reflect the physical conditions of the germination test such as substrate material, relative humidity, etc.

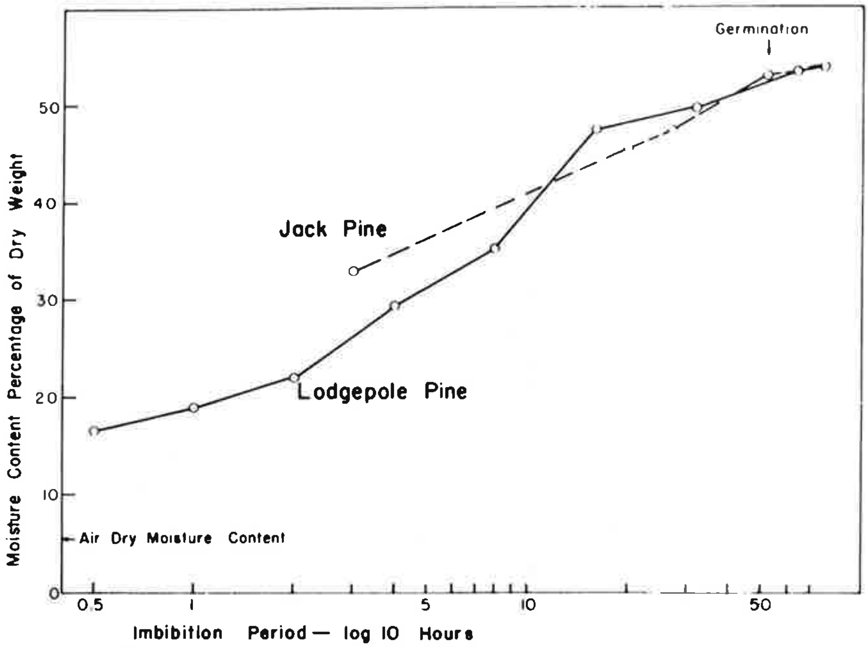

Figure 2. The rate of moisture imbibition of jack pine and lodgepole pine seeds at 80 F.

Experiment 5. Determination of the Sensitivity of the Photoreceptor System

The sensitivity of the system investigated in Experiment 3 was masked by the period of imbibition necessary before the threshold moisture content was attained. To test the sensitivity of the light reaction with seeds in a receptive condition, imbibition was permitted in darkness for periods of 2 hours and 24 hours and then the seeds were exposed to light for periods varying from 5 seconds to 32 minutes. The test was repeated at 80 F and 60 F with incubation periods of 8 days and 14 days respectively.

The results of this experiment are shown in Figure 3. While some seeds responded to exposures of only 5 seconds' duration, germination increased with duration of exposure, at both 60 F and 80 F, up to exposures of at least 2 minutes. Exposures longer than 4 minutes did not result in further significant increases in germination.

A given exposure was generally more effective at 80 F than at 60 F. This trend was surprisingly consistent considering the variability to be expected in the germinative capacity of the single, 100-seed samples receiving each treatment.

The period of imbibition prior to exposure, whether 2 hours or 24 hours, had little or no effect on the basic response to exposure.

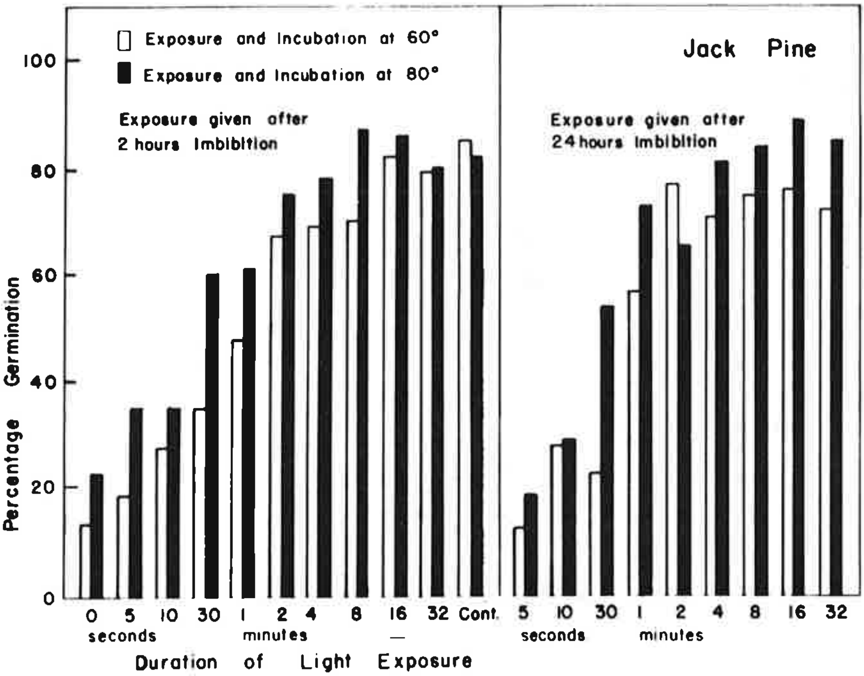

Figure 3. The effect of a single exposure of varying duration on the germination of jack pine seeds at 60 F and 80 F.

Discussion - In the experiments with lettuce seeds the response to a given light exposure varied with time of imbibition preceding exposure. The promotion of germination owing to a fixed irradiance with red light increased for 8 to 10 hours and then remained constant until about 20 hours, after which the amount of stimulation decreased rapidly. The inhibition of germination with a fixed irradiance of far-red also remained constant for imbibition times of 10 to 20 hours but increased after 20 hours (Borthwick et al., 1954). A similar effect has not been demonstrated for jack pine seeds. Complete germination of this species was obtained with a single brief exposure following imbibition periods of 2 hours and 24 hours.

Experiment 6. Persistence of Stimulation by a Single Light Exposure

In the previous experiments it was found that the light requirement of jack pine seeds could be satisfied by a single short exposure provided at the start of the germination period. It is of interest to know whether a single exposure satisfies the light requirement for any length of time or whether return to an air-dry condition negates the effect. To investigate this possibility seeds were exposed to light for 2 hours in the incubator (an exposure sufficient to completely satisfy the light requirement) then removed and air-dried for periods of 24 and 72 hours. Both periods were found sufficient to permit the seeds to return to an air-dry moisture content of 5 per cent. The seeds were then returned to the incubator and germination tests conducted at 80 F in continuous darkness. In the event that treatment was partially effective or had altered the light requirement of the seeds, single exposures of 1 to 48 hours' duration and continuous light were also included in the test.

The results are presented in Table 5.

TABLE 5

The effect of a single exposure followed by air drying on the germination of jack pine seeds.

Duration of exposure	Period of drying after 2-hour exposure	
	24 hours	72 hours
	Percentage germination in 8 days	
Cont. dark	83	90
1 hour	81	86
3 hours	86	84
18 hours	83	81
36 hours	88	83
48 hours	86	No test
Cont. light	87	87

Complete germination was obtained in continuous darkness after air drying for 24 and 72 hours. The stimulation afforded by the single exposure persisted after seeds were returned to an air-dry condition.

Discussion - Persistence of the effect of a single exposure to light, after return of seeds to an air-dry condition is an excellent example of preconditioning. Apparently seeds exposed to light either by accident or intentionally, while above the threshold moisture content, are thereafter capable of germination in continuous darkness. The researcher unaware of this possibility may misinterpret the results of germination experiments or the action of such standard pretreatments as cold soaking or stratification.

Removal of the seeds from the source of moisture after 2 hours of exposure to light and rapid return to an air-dry moisture content apparently renders the seeds physiologically inactive and the phytochrome is "fixed" in the far-red-absorbing form. Germination can then proceed in continuing darkness without additional irradiation.

Experiment 7. The Effect of Photoperiod on the Germination of Jack Pine Seeds.

The effect of photoperiod was investigated at 60 F, 70 F, and 80 F constant, alternating 60 F and 80 F and alternating 80 F and 60 F. At 60 F and 70 F, photoperiods of 2 hours to 22 hours were tested while at 80 F and the alternating temperatures, only the basic short (8-hour) and long (16-hour) photoperiods were tested. As in previous experiments a 14-day incubation period was employed at 60 F, and an 8-day period at all other temperatures. Short photoperiods were given at 80 F and long photoperiods at 60 F in the alternating 60 F and 80 F test and *vice versa* in the alternating 80 F and 60 F test.

The results are shown in Table 6 for all temperatures and in Figure 4 for tests conducted at 60 F and 70 F.

Photoperiod was ineffective in controlling germination at all temperatures above 60 F. At 60 F, however, photoperiods of 2 to 10 hours were similar in effect to continuous darkness. Germination increased sharply with 12-hour and 14-hour photoperiods and was complete with photoperiods of 16 hours or longer.

Photoperiodic control of the germination of jack pine seeds becomes effective between 70 F and 60 F. Germination at 70 F or higher or with alternating temperatures between 60 F and 80 F is not subject to photoperiodic control, unless continuous darkness is considered a photoperiodic treatment.

Discussion - The results of this and previous experiments demonstrate a puzzling characteristic of light control of germination. At 60 F the germination of jack pine seeds is complete in continuing darkness following a single brief exposure to light given at the start of the germination period, but does not respond to a daily light exposure of 2 to 10 hours' duration.

According to the red, far-red reversion hypothesis, phytochrome reverts in darkness from the far-red absorbing form at a rate dependent upon the temperature. The reversion should be more rapid and the effect more pronounced at 70 F and 80 F than at 60 F. Why then is photoperiod effective only at the lower temperature?

TABLE 6

The effect of photoperiod and temperature on the germination of jack pine seeds

Duration of daily exposure	Temperature				
	60 F	70 F	80 F	60 and 80 F	80 and 60 F
	in 14 days	Percentage germination in 8 days			
0 hours	20 (2)	16 (2)	22 (4)	12 (2)	23 (2)
2	28 (2)	86 (2)			
4	26 (2)	86 (2)	80		
6	18 (2)	82 (2)			
8	22 (3)	84 (2)	84 (2)	84 (2)	90 (2)
10	28 (2)	84 (2)			
12	49 (2)	86 (2)			
14	74 (2)	84 (2)			
16	83 (3)	85 (2)	82 (2)	90 (2)	86 (2)
18	85 (2)	89 (2)			
20	82 (2)	89 (2)	80		
22	86 (2)	90 (2)			
24	86 (3)	87 (2)	87 (2)	86 (2)	92 (2)

The germination of fully promoted lettuce seeds progressed in 12 hours beyond reversal by light (Toole et al., 1953). The rate of which "escape" occurs probably also depends on the temperature. Although a similar process has not been demonstrated for jack pine seeds, its assumption provides a reasonable explanation for germination under short photoperiods at the higher temperatures.

Reversion of phytochrome in darkness from the far-red-absorbing form to the red-absorbing form, at a rate dependent upon temperature is considered the clock mechanism in photoperiodic control of growth (Borthwick et al., 1954). The possibility of escape of the germination process at a rate also dependent on the temperature suggests that the light period in a cycle plays an equally significant role. With such a complex system it is most difficult to determine the controlling stage in the process for any specified photoperiod and temperature regime.

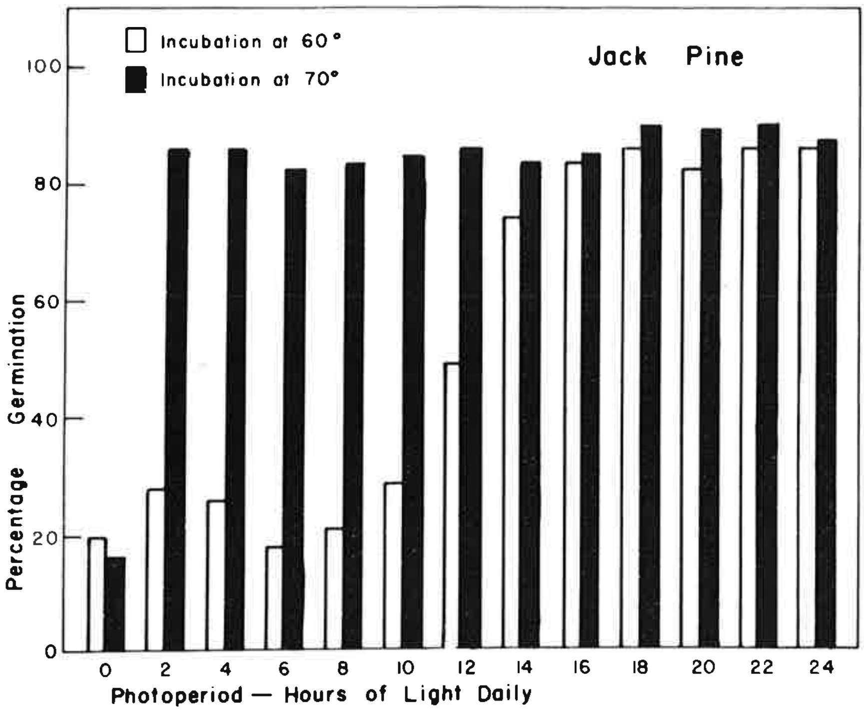

Figure 4. The effect of photoperiod at 60 F and 70 F on the germination of jack pine seeds.

Experiment 8. The Independence of Stimulation by a Single Exposure and by Daily Exposure

The previous tests have demonstrated that germination can be promoted at 60 F by either a single exposure of a few minutes' duration or by long photoperiods and that germination can be inhibited by continuous darkness and short photoperiods. Experiment 8 was designed to determine whether photoperiodic control is possible with seeds that have no basic light requirement; that is, with seeds capable of germination in continuous darkness.

Seeds were placed in the incubator and permitted to imbibe moisture for 2 hours while exposed to light. This treatment satisfies the basic light requirement insofar as the seeds are then capable of germination in continuous darkness. Other seeds were handled in exactly the same manner except that no light was permitted during the 2-hour imbibition period. These seeds therefore retained their basic light requirement and would not germinate in continuous darkness. Both groups of seeds were then air-dried and subjected to germination tests at 60 F to determine their susceptibility to photoperiodic control.

Two photoperiods were tested, 18 hours and 6 hours, applied over an incubation period of 14 days.

The results are shown in Table 7.

TABLE 7

The effect of photoperiod at 60 F after triggering

Photoperiod	Seed pretreatment	
	2 hours light	No light
	Percentage germination in 14 days	
Cont. dark	78 (2)	23 (2)
6 hours	20 (2)	18 (2)
18 hours	87 (2)	86 (2)

The two-hour light exposure given prior to germination was effective, resulting in a high germination percentage in continuous darkness. The control seed also behaved as expected with continuous darkness and short photoperiod inhibiting germination. The point of interest is that at 60 F a short photoperiod is effective in inhibiting the germination of seeds capable of germination in continuous darkness.

Discussion - Retention of sensitivity to photoperiodic control by seeds capable of germination in continuous darkness, although useful as information, does not imply a different mechanism of control in each case. The pigment system, driven to the promotive form by an exposure to light should be maintained in the promotive form if return to an air-dry condition takes place more rapidly than reversion to the inhibitive form, or if exposure to light is continued during drying. If incubation is then resumed in continuous darkness the germination process is initiated with the pigment system in its promotive form and germination occurs. If incubation is resumed with short photoperiods inhibition is induced by reversion of the pigment during the first dark period to the red-absorbing form.

Experiment 9. The Effect of Number of Daily Exposures on Jack Pine Germination

Previous experiments have resulted in the observation that at 60 F a single exposure of only a few minutes' duration promotes germination in the dark while a daily exposure of up to 10 hours' duration inhibits germination. The question arises whether or not the inhibition induced by the short photoperiods is a function of the number of daily exposures received. To investigate this, daily exposures of 4, 8, 12 and 16 hours were given for periods of 1 to 5 days, followed by incubation in continuous darkness.

Percentage germination obtained in 14 days is shown for each treatment in Table 8.

TABLE 8

The effect of number of daily exposures on the germination of jack pine seeds

Duration of daily exposure	No. of consecutive days that exposure is given				
	1	2	3	4	5
	Percentage germination in 14 days				
4 hours	78	66	86	72	52
8 hours	80	80	77	71	45
12 hours	81	81	81	85	73
16 hours	83	83	68	71	65

Although the data are erratic, a high percentage germination resulted from a single exposure regardless of duration or from repeated exposures of 12 and 16 hours' duration, as expected. The inhibitory effect of short, 4- and 8-hour exposures is not apparent except for the seeds which received 5 consecutive exposures of this duration.

Discussion - Although the test was not continued beyond the 14-day period specified, examination of the seeds and germinants at that time indicated that the low germination following 5 days of short photoperiod had resulted from delay and that additional germination would occur. It was concluded that the inhibiting effect of short photoperiods occurs only as long as the daily exposures continue. Cessation of the daily exposures and continuation of incubation in either continuous light or darkness will result in the initiation of germination. The effect is the same as that of "triggering" germination by a single exposure with the last exposure received acting as the triggering mechanism.

Experiment 10. The Effect of Length of Dark Period on the Germination of Jack Pine Seeds at 60 F.

It has been demonstrated in previous experiments that continuous darkness following an initial exposure of short duration does not inhibit germination at 60 F, while daily periods of darkness longer than 12 hours' duration (short photoperiod) do inhibit germination. This seemingly contradictory result was investigated further by subjecting seeds to dark periods of varying duration by interruption with short, 20-minute exposures. Dark periods of 4, 8, 12, 24, 48 and 72 hours were tested. Each test was initiated by a dark period of appropriate length.

Total germination 14 days after the first light exposure is shown in Table 9. The progression of germination is illustrated in Figure 5.

TABLE 9

The effect of length of dark period on the germination of jack pine seeds at 60 F

Sample	Length of dark period - hours							
	4	8	12	16	20	24	48	72
	Percentage germination in 14 days from first exposure							
1	83	85	85	75	73	40	62	58
2	87	82	82	79	68	41	61	70
Mean	85	84	84	77	70	40	62	64

In each test there was visual evidence of germination approximately 6 days following the initial 20-minute exposure; a normal lag for an incubation temperature of 60 F. Dark periods of 4, 8 and 12 hours' duration resulted in complete germination while dark periods of 16, 20 and 24 hours' duration resulted in increasing inhibition. To this point the effect is comparable to inhibition induced by shortened photoperiod. However, germination shows evidence of recovery with dark periods in excess of 24 hours' duration, and from previous tests, would be complete under conditions of continuous darkness following the first exposure.

Discussion - In Experiment 3 it was argued that germination occurs in continuing darkness, after a single brief irradiation, because the germination process proceeds, at some temperatures, sufficiently fast to escape the inhibition resulting from reversion of phytochrome to the red-absorbing form. The results of Experiment 10 do not support this argument. Inhibition presumably associated with reversion of phytochrome is indeed evident, reaching maximum effectiveness with dark periods of 24 hours' duration, but recovery of germination with dark periods in excess of 24 hours' duration indicate that this state of inhibition is short-lived.

The results of this experiment suggest that reversion during the dark period may not be a simple thermal reaction. Determination of the exact nature of

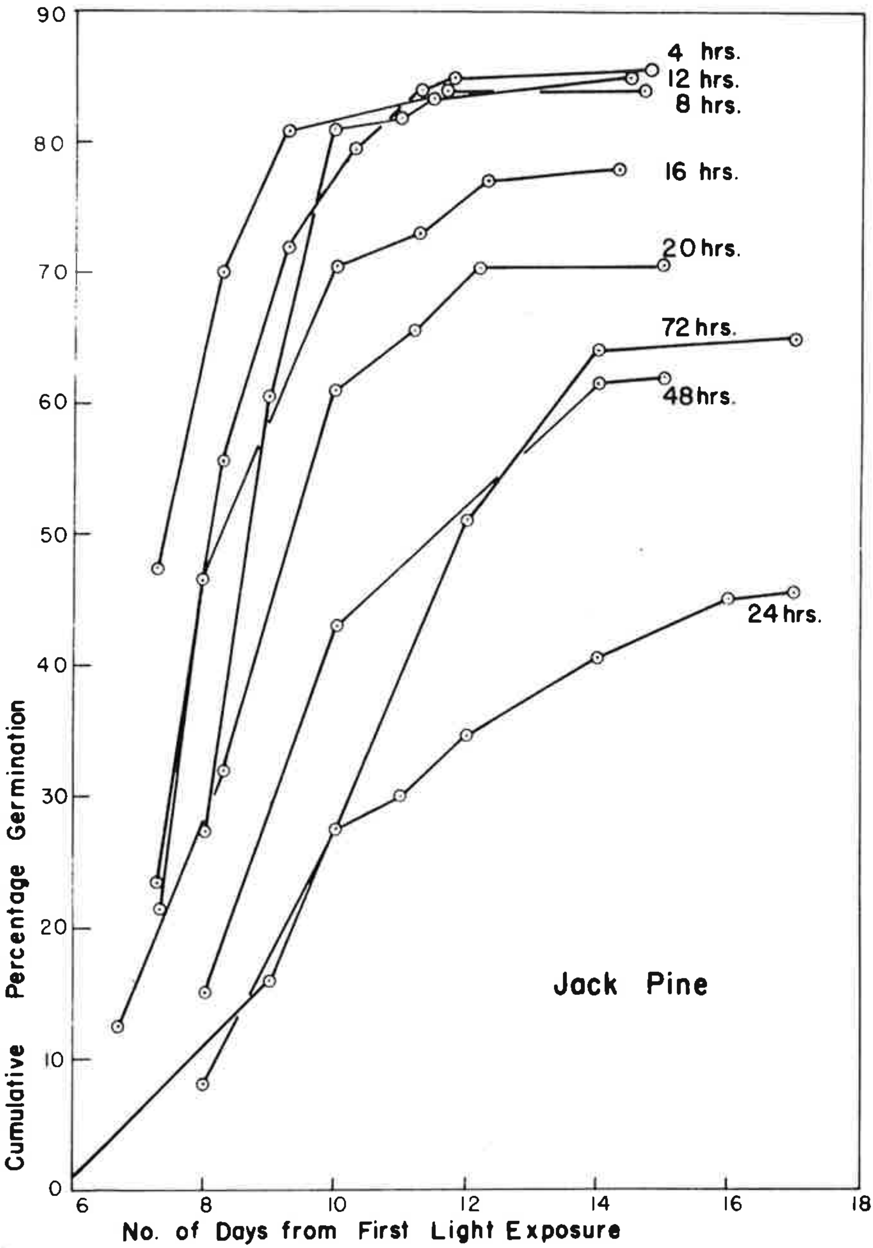

Figure 5. The effect of repeated dark periods of varying duration on the germination of jack pine seeds at 60 F.

the reversion process during the dark period and the mechanism by which photoperiodic behaviour is modified by temperature should be most rewarding.

In Experiment 10, repeated 16-hour and 20-hour dark periods, created by interruption with 20-minute light exposures resulted in relatively good germination when compared to that obtained by 16-hour and 20-hour dark periods provided in association with the 8-hour and 4-hour light exposures of a normal 24-hour cycle. This observation emphasizes again that, although spontaneous reversion of phytochrome during the dark period undoubtedly plays an important role in photoperiodic control of germination, processes depending on the duration and temperature of the associated light period are not less significant.

LODGEPOLE PINE EXPERIMENTS

This series of experiments was undertaken to determine whether the light and temperature effects observed for jack pine were also operative for lodgepole pine. The only major change in procedure with lodgepole pine seeds was the exclusion of all light during extraction, cleaning and initial handling of the seeds. This precaution was taken to avoid the possibility of accidental exposure to light while seed moisture content was above the threshold level.

Experiment 1. The Effect of Incubation Temperature Under Continuous Light

The initial experiment was undertaken to determine the quality of the seeds, the rapidity and pattern of germination under continuous light and the effect of varying temperature under continuous light. The tests were conducted at constant temperatures of 60 F, 70 F, 80 F and 90 F, alternating 60 F and 80 F, and 60 F constant for 4 days followed by 90 F constant for the remainder of the test.

The pattern of germination at each temperature level is shown in Figure 6 and the percentage germination in 12 days is given in Table 10.

The optimum constant temperature for germination of lodgepole pine was 70 F. This is in agreement with the findings of Bates (1930). Alternating temperatures bracketing 70 F gave equally good results.

Temperatures higher than 70 F constant resulted in earlier initiation but greatly reduced amount of germination. The effect was evident at 80 F but most pronounced at 90 F.

A constant temperature of 60 F is obviously well below the optimum for this species.

Excellent results were also obtained at 60 F for 4 days followed by 90 F.

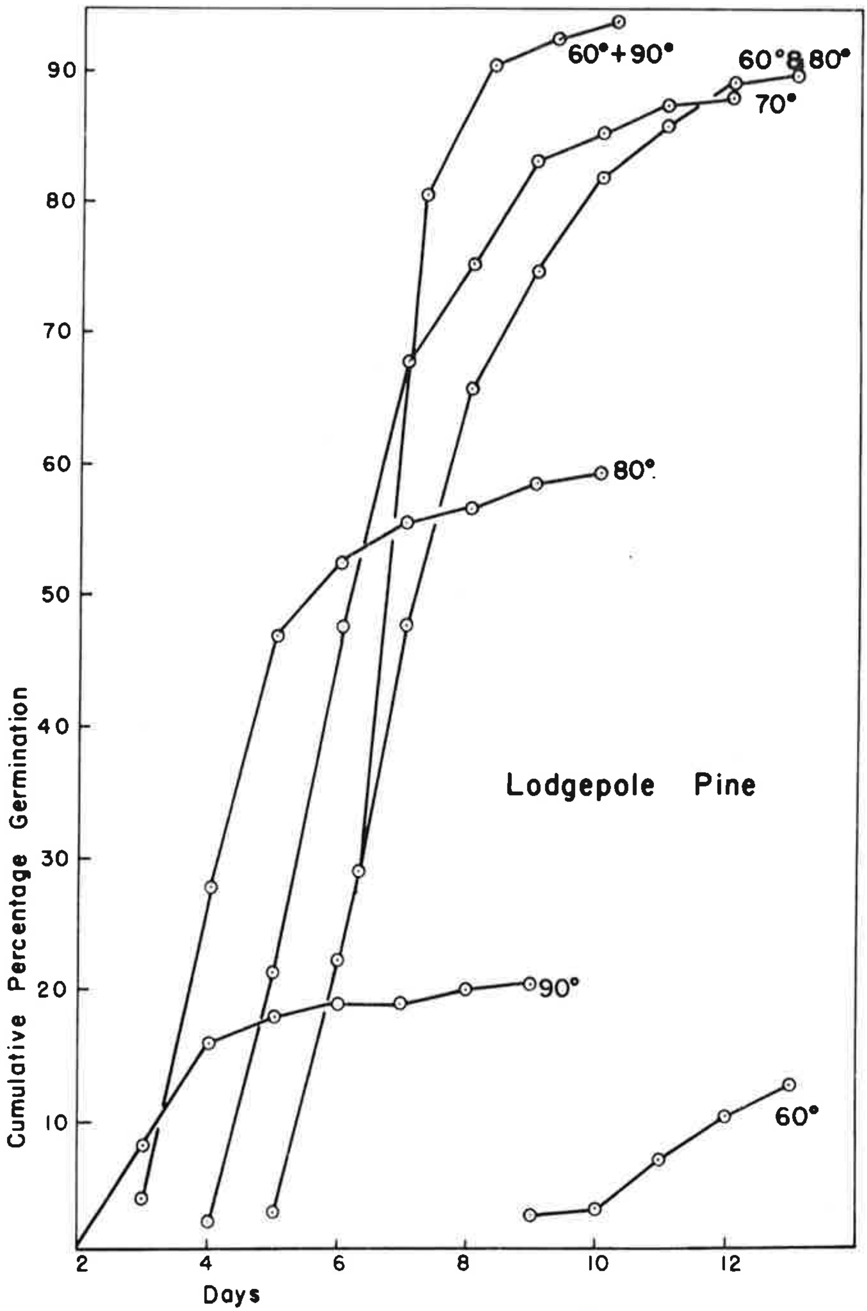

Figure 6. The effect of temperature under continuous light on the germination of lodgepole pine seeds.

TABLE 10

Effect of temperature on total germination under continuous light

Sample no.	Temperature					
	60 F	70 F	80 F	90 F	60 and 80 F	60 + 90 F
	Percentage germination in 12 days					
1	13	84	57	21	84	97
2	9	92	65	24	93	93
3	8	88	56	16	93	92
Mean	10	88	59	20	90	94

Discussion - The results of the test initiated at 60 F and completed at 90 F are startling. They suggest a two-stage process for germination with each stage having a different optimum temperature range. The first stage requires temperatures in the neighbourhood of 60 F to 70 F while the second requires temperatures of 70 F to 90 F. Overlapping at 70 F permits good germination at this temperature while constant temperatures above or below this level fail to satisfy the requirements of either stage in the germination process.

Lodgepole pine proved to be more exacting in its temperature requirements than jack pine. Whereas complete germination of jack pine seeds was obtained at 60 F, 70 F and 80 F, temperatures above or below 70 F resulted in a marked reduction in the germination of lodgepole pine seeds.

Experiment 2. Basic Light Test: Continuous Light vs. Continuous Darkness

This experiment was designed to test the hypothesis that light is required for the germination of lodgepole pine seeds and if so, that the requirement is temperature dependent over a normal range of temperature. The temperature levels employed were constant 60 F, 70 F, 80 F, and 90 F; alternating 60 F and 80 F and 60 F for 4 days followed by 90 F.

In the above test, the lodgepole pine seeds, although extracted and dried to air-dry moisture content in complete darkness, were thereafter handled in normal room light. An additional test was undertaken at 70 F to determine whether light exposure after air-dry moisture content is attained can promote germination. Three samples of 100 seeds were held in complete darkness throughout extraction, cleaning and germination.

Germination at all temperatures was markedly reduced by the exclusion of light (Table 11).

TABLE 11

Effect of continuous darkness on the germination of lodgepole pine seeds at various temperatures

Light	Incubation temperature					
	60 F	70 F	80 F	90 F	60 and 80 F	60 + 90 F
	Percentage germination in 12 days					
Cont. light	10	88	59	20	90	94
Cont. dark	1	6	6	3	6	6

The effect of exposure to light after the seeds have attained air-dry moisture content is shown in Table 12.

TABLE 12

Effect of exposure to light after air-dry moisture content is attained

Treatment	Sample no.			
	1	2	3	Mean
	Percentage germination in 12 days at 70 F			
Light after air-dry	7	5	6	6
No light	1	0	2	1

These results indicate that a very small percentage of seeds can be induced to germinate by exposure to light after an air-dry moisture content is attained.

Discussion - A relatively large proportion of the jack pine seeds were capable of germination in continuous darkness. Unfortunately it was not possible to determine for jack pine the effect of exposure to light after air-dry moisture content was attained. Judging from the results of this test with lodgepole pine however, it is possible that most of the jack pine germination in continuous darkness can also be attributed to light-exposure while air-dry.

Experiment 3. Effect of a Single Light Exposure

The effect of single light exposures varying in duration from 30 minutes to 8 hours was tested at the temperature levels employed in Experiments 1 and 2. In this experiment the same temperature level is maintained throughout the exposure and incubation period.

The results are summarized in Table 13. At the temperatures obviously unfavourable for the germination of this species (60 F and 90 F), a single exposure of up to 8 hours' duration had no significant effect on germination. At temperatures favourable for germination, a single light exposure resulted in a significant increase in germination.

Germination increased with the duration of exposure at 70 F and 80 F. However, a single light exposure of up to 8 hours did not result in germination equal to that obtained under continuous light at any temperature tested.

TABLE 13

The effect of a single light exposure of varying duration on the germination of lodgepole pine seeds

Duration of exposure	Exposure and incubation temperature					
	60 F	70 F	80 F	90 F	60 and 80 F	60 + 90 F
	Percentage germination in 12 days					
Cont. dark	1	6	6	3	3	6
30 min.	No test	No test	10	6	No test	No test
1 hour	No test	No test	26	8	No test	No test
2 hours	0	53	35	6	38	55
4 hours	1	55	44	7	40	No test
8 hours	1	59	50	8	36	No test
Cont. light	10	88	59	20	90	94

*Exposure given at 80 F

Discussion - Although both lodgepole pine and jack pine germination responded to a single exposure of light, the degree of response, and the effect of incubation temperature on the response, varied considerably between the two species. For jack pine, complete germination was obtained from a single exposure of only a few minutes' duration at all temperatures tested, whereas complete germination of lodgepole pine seeds could not be obtained by a single exposure of up to 8 hours' duration at any temperature tested. In addition, significant increases in the germination of lodgepole pine seeds as a result of a single exposure of light could be obtained only at incubation temperatures at or near the optimum for this species.

Experiment 4. The Effect of Temperature During Exposure

Failure to obtain complete germination of lodgepole pine seeds with a single exposure of light prompted an additional test to determine if the effect of temperature during a single exposure is of any significance. A single exposure of 16 hours' duration was given at 60 F, 70 F, 80 F and 90 F, followed by incubation in continuous darkness at 70 F. The germination results are given in Table 14.

TABLE 14

The effect of temperature during a single exposure on the germination of lodgepole pine

Sample no.	Temperature during 16-hour exposure			
	60 F	70 F	80 F	90 F
	Percentage germination in 12 days at 70 F			
1	56	52	51	44
2	56	49	47	47
3	58	52	47	34
Mean	57	51	49	42

With an incubation temperature of 70 F, the differences in germination attributable to the temperature at which exposure is given are small. Nevertheless the difference between exposure at 60 F and 90 F is significant at the 5 per cent level and it can be concluded that within very broad temperature limits, germination decreases with increase in temperature during exposure.

It is of interest to note that increasing the duration of exposure from 8 hours (Table 13) to 16 hours' duration (Table 14), with an exposure and incubation temperature of 70 F, did not result in an increase in germination.

Discussion - Maintenance of any given temperature during the first 16 hours of incubation may have effects on the rate and amount of germination completely unassociated with exposure to light during the same period. There is therefore a distinct possibility of misinterpretation in this experiment. Until additional evidence is obtained caution should be used in attributing significance to the effect of temperature during exposure.

Experiment 5. The Effect of Single Exposures of Varying Duration at 60 F

In view of the increase in germination obtained by a 16-hour exposure given at 60 F, a test was conducted to determine whether further increases in the duration of exposure at this temperature might result in additional increases in germination. To this end, seed samples were exposed, at 60 F, to 1, 2, 3, 4 and 5 days of light and then incubated in total darkness at a temperature of 70 F.

The germination results are given in Table 15. Increasing the duration of exposure at 60 F from 1 to 3 days had no effect on germination. Exposures of 4 and 5 days resulted in a significant increase in germination however, and with 5 days' exposure, germination was close to being complete for this lot of seeds.

TABLE 15

The effect of exposures of varying duration at 60 F followed by incubation at 70 F on the germination of lodgepole pine seeds

Sample no.	Duration of exposure at 60 F - days				
	1	2	3	4	5
	Percentage germination in 12 days at 70 F				
1	52	67	59	79	77
2	59	47	59	70	71
3	56	61	57	69	76
Mean	56	58	58	73	75

Discussion - In this test it is questionable whether exposure to light for the first 4 or 5 days differs significantly from exposure to continuous light under the same conditions, for it is highly likely that by the fourth or fifth day the germination process has progressed beyond control by light.

Significant increases in the germination of lodgepole pine seeds have been obtained by a single exposure to light and by varying the temperature at which the exposure is given. However, for reasons not yet known, all attempts to obtain complete germination of this species by a single exposure have been unsuccessful.

Experiment 6. Duration of Stimulation by a Single Light Exposure.

To determine the persistence of stimulation by a single light exposure, 3 samples of 100 seeds were given 8 hours of exposure and imbibition, returned to air-dry moisture content and stored for a period of 1 month. Germination tests were then conducted in continuous darkness at 70 F. The results are summarized in Table 16.

TABLE 16

The effect of a single 8-hour exposure followed by storage on the germination of lodgepole pine seeds in continuous darkness

Treatment	Sample			
	1	2	3	Mean
	Percentage germination in 12 days at 70 F			
No exposure - no storage	7	5	6	6
8 hours light - no storage	61	64	53	59
8 hours light - 1 month storage	40	53	53	49

The stimulation afforded by the single 8-hour exposure at 70 F was still evident 1 month after treatment. Although there is a suggestion of a reduction in germinative capacity with storage the difference is not significant statistically.

Discussion - It has been demonstrated, for both lodgepole pine and jack pine seeds, that stimulation by a single exposure persists for some time after treatment. Additional testing will be required to establish permanency of stimulation, which may be of considerable practical importance.

Experiment 7. The Effect of Photoperiod on the Germination of Lodgepole Pine Seeds.

The effect of photoperiod was investigated at 60 F, 70 F, 80 F and 90 F constant, alternating 60 F and 80 F, and 60 F for 4 days followed by 90 F.

Only two photoperiods were tested, long (16 hours) and short (8 hours). A 12-day incubation period was employed at all temperature levels.

The results are shown in Figure 7. Daily exposure to light, 8 or 16-hours duration, resulted in a significant increase in germination (as compared to continuous darkness) at all temperature levels tested. However, lengthening the photoperiod from 8 to 16 hours was effective only at 70 F and alternating 60 F and 80 F. It is apparent from these data that the germination of lodgepole pine seeds is also subject to photoperiodic control and the degree of control is temperature dependent.

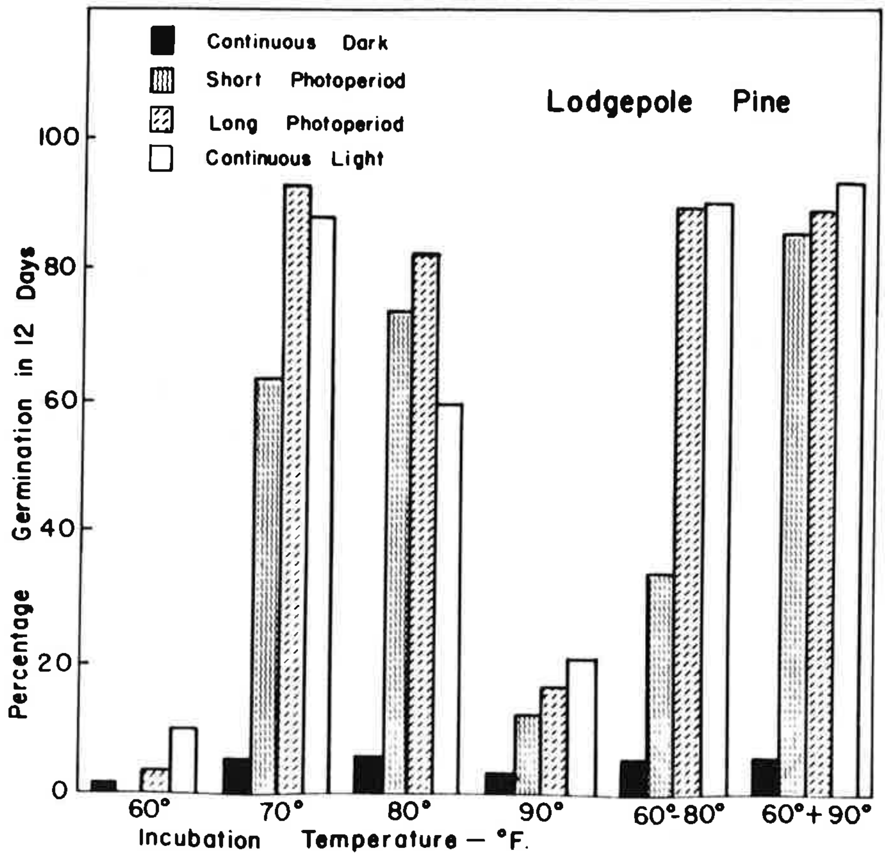

Figure 7. The effect of photoperiod at various temperatures on the germination of lodgepole pine seeds.

Discussion - These data contain several puzzling features:

1. Unlike the jack pine results, both the long and short photoperiods resulted in significant increases in germination at all temperature levels.

2. Long photoperiods were significantly better than short photoperiods only at those temperatures optimum for germination under continuous light (70 F and alternating 60 F and 80 F) whereas photoperiod was effective for jack pine seeds at 60 F only; a temperature considerably below optimum for the species.

3. At 60 F, followed by 90 F, complete germination was obtained with short photoperiods as well as with long photoperiods and continuous light.

4. At a constant temperature of 80 F both long and short photoperiods resulted in significantly better germination than continuous light.

No explanation or hypothesis is offered that would account for these phenomena. The puzzling response of lodgepole pine germination to photoperiod, plus the failure to obtain complete germination by a single exposure renders very difficult any attempt to interpret these results by reference to the red, far-red hypothesis in its present simple form.

Similar difficulties have been encountered with other species. The seeds of Pinus virginiana Mill. responded to exposure to red light when held at 77 F but not when held at 68 F or 86 F. Also, some block in the germination process prevents complete response to the photoreaction at 77 F. However, if imbibition for 24 hours preceding irradiation is at 41 F and if incubation after irradiation is at 77 F, germination is complete (Toole et al., 1956). It is evident that much is to be learned about the interaction of light and temperature in the physiology and ecology of germination. Meanwhile, unqualified statements of the temperature or light requirements for germination are of little value.

COMPARISON OF THE RESPONSE OF JACK PINE AND LODGEPOLE PINE

Light is effective in controlling the germination of both jack pine and lodgepole pine seeds. Both species respond to single exposures and to photoperiod, and the response in both species is temperature dependent. Marked differences have been demonstrated however in the degree of response to any given temperature or light treatment. The most significant features of this variation are noted below.

1. Under continuous light the jack pine seeds were considerably less sensitive to temperature control than lodgepole pine seeds. Complete germination

was obtained for jack pine seeds at constant 60 F, 70 F and 80 F while the germination of lodgepole pine seeds was reduced by constant temperatures above or below 70 F.

2. A two-stage germination process was not demonstrated for jack pine. Considering the greater tolerance of this species to temperature, it is probable that wider range of temperatures would have to be investigated to demonstrate the presence or absence of this phenomenon.

3. A substantially higher percentage of jack pine seeds was without a light requirement. This may reflect a basic difference between the two species or may be a result of the precautions taken with the lodgepole pine seeds to avoid exposure to light during extraction, cleaning and handling.

4. Jack pine seed germination responded to a single exposure of light at 60 F, 70 F and 80 F while lodgepole pine responded at 70 F and 80 F but not at 60 F or 90 F.

5. Complete germination of jack pine seeds was obtained by a single light exposure of 2 to 4 minutes' duration at all temperatures tested while complete germination of lodgepole pine seeds could not be obtained at any temperature tested by a single light exposure of up to 5 days' duration.

6. Both species responded to a daily light exposure at all temperatures tested. However, the duration of the daily exposure (photoperiod) was significant for jack pine seed germination at 60 F only, while photoperiod was significant for lodgepole pine at 70 F and alternating 60 F and 80 F.

7. At temperature levels at which photoperiod was effective, the degree of inhibition resulting from short photoperiods varied markedly between the two species. A short photoperiod with jack pine resulted in no more germination than obtained with continuous darkness while a short photoperiod with lodgepole pine seeds resulted in much greater germination than obtained in continuous darkness.

DISCUSSION

Throughout this report, reference has been made to the red, far-red reversion hypothesis of growth control. Another hypothesis, related to the germination of seeds involves the action of endogenous rhythms. Bünning (1936, 1958, 1959a, b, c, 1960a, b, 1961) maintains that endogenous oscillation is the basis of photoperiodic response and that it activates cellular responses that in turn cause rhythmic changes in the light sensitivity of cells. The existence of a large number of regularly recurring oscillatory changes in biological parameters of plants (and animals) is no longer in doubt (Wolf, 1962). It is argued, however, that apparently endogenous rhythms may actually be driven by external, unrecognized environmental cycles such as very weak magnetostatic and electrostatic fields and possibly by radio frequency fields (Brown, 1962).

Features of the endogenous rhythm system that are of particular significance to photoperiodic control of growth are:

1. Circadian rhythms (period length of approximately 24 hours, Halberg, 1959), are often lacking in plants that have been maintained under constant conditions and can be frequently induced by a single stimulus, e.g., a short light exposure (Bünning, 1931, 1958; Ball and Dyke, 1954).

2. The initiation and maintenance of rhythms can be accomplished by red light and antagonized by far-red light (Bünning and Lörcher, 1957; Lörcher, 1958).

3. The free-running circadian rhythms in all plants are only slightly influenced by temperature (Went, 1962).

4. Circadian rhythms capable of self-sustenance for many cycles may obtain precise timing by synchronization with, or entrainment by, extrinsic phenomena such as cycles of day and night or high and low temperatures (Bünning, 1958). The laws and limitations governing this entrainment are known (Bünning, 1958; Chovnick, 1960).

5. Interference with the 24-hour environmental signal can result in disease and death. In young tomato plants it is sufficient to have either a temperature or a light intensity cycle for normal development and growth but it must be circadian to be effective (Went, 1962).

It is evident from this brief description that the responses of jack pine and lodgepole pine seeds to the various light and temperature treatments in this series of experiments may possibly be interpreted by reference to the known characteristics of endogenous circadian rhythms. For a detailed account of the present state of knowledge on this subject the reader is referred to the proceedings of recent conferences on rhythmic functions in living systems (Wolf, 1962; Chovnick, 1960; Withrow, 1959b).

The proponents of the red, far-red hypothesis of photomorphogenetic control have concentrated on the photo-aspects, such as the effects of light quality, light intensity, action spectra and existence and functions of the pigment mechanism and sometimes have neglected the significance of periodism in the system. The proponents of endogenous rhythms have, on the other hand, stressed periodism and given less attention to the photo-aspects. Bünning (1960b), although admitting that a photomorphogenetic pigment is involved in photoperiodism, does not believe that the pigment reaction is the basic time-measuring mechanism. Rather, it is proposed that endogenous rhythms cause cyclical changes in conditions controlling pigment-linked processes. For a discussion on the possible interrelationships between hypotheses involving the pigment system, endogenous rhythms, photoperiodism and thermoperiodism the reader is referred to Romberger (1963).

The existence and function of the pigment phytochrome and the red, far-red hypothesis of light control was largely the result of research with light-sensitive lettuce seeds. Similar responses to those obtained with lettuce seeds, and with jack and lodgepole pine seeds in this study, have been obtained with seeds of Betula pubescens Ehrh. (Black and Wareing, 1957; Vaartaja, 1956). However, chilling birch seeds in moist storage removed the light requirement. Further, Black and Wareing (1955) showed that birch seeds from which the pericarps had been removed germinated well in comparison to intact seeds, and Black (1956) found that merely scratching the seed coat or increasing the oxygen tension improved germination. Leaching with water for a period of 4 weeks was also shown to have a marked effect on the photoperiodic responses. Redmond and Robinson (1954) found that a water extract of Betula lutea Michx. f. seeds and seed coats inhibited germination almost completely in the dark but only partly in the daylight and suggested that the role of light involved photochemical destruction of an inhibitor. An explanation of these phenomena which would also accommodate the phytochrome hypothesis or the action of endogenous rhythms has yet to be presented.

The importance of light and the length of the daily light and dark periods in controlling vegetative growth of many herbaceous species and a number of woody species has been generally recognized since the work of Garner and Allard (1920, 1923, 1925). Further effects in woody plants were observed by Nitsch (1957a, b), Vaartaja (1954, 1960) and Wareing (1949, 1950a, b, 1951, 1956). From the work done to date the generalization can be made that long photoperiods, or short dark periods, promote vegetative growth whereas short photoperiods inhibit growth and induce dormancy. Extension growth, leaf growth and cambial activity of Scots pine (Pinus sylvestris L.) are known to be prolonged by long photoperiods while growth cessation, bud formation and dormancy are promoted by short photoperiods (Wareing, 1949, 1950a, b, 1951; Downs and Borthwick, 1956). Similarly, Giertych and Farrar (1961) have demonstrated that long photoperiods delay winter bud formation and increase height, total dry weight, leaf weight and root weight of jack pine and lodgepole pine seedlings.

Continued advances in the field of growth control, as reflected in the hypotheses concerning the existence and function of phytochrome and biological rhythms present exciting possibilities in the applied biological sciences such as forestry. Basic information of this type will certainly hasten the solution of problems such as species distribution and variation and be of great assistance to the forest geneticist in his programme to develop a superior growing stock. The silviculturist and forest ecologist will be provided with a much sounder understanding of the relationships between the tree, at all stages of development, and the environment, and will therefore be better equipped to develop and manage the forest. Many examples can be cited. For instance, there is a growing interest in ball planting (bullet planting, tube planting) (McLean, 1959; Walters, 1961; Williamson, 1964) as an efficient, practical method of reforestation. To be successful, this technique will require economic, mass culture of seedlings in individual small containers, with a very high degree of success. This will not be possible without a precise knowledge of the light and temperature requirements during the germination and seedling stages of development.

SUMMARY

A series of experiments was undertaken to determine the existence and characteristics of photo-control of the germination of seeds of jack pine and its dependence upon temperature. A second, similar series of experiments was also undertaken with lodgepole pine in order to compare the germination response of two closely related species under similar environmental conditions.

The jack pine results are summarized below:

1. Under continuous light (50 foot-candles, incandescent) germination was rapid and complete in seven to eight days at incubation temperatures of 70 F and 80 F and alternating temperatures about this level. Germination was also complete at 60 F but at this temperature a 14-day incubation period was required.

2. Germination was markedly reduced at all temperatures by the exclusion of light. No evidence was obtained that would indicate interaction between incubation temperature and ability to germinate in continuous darkness.

3. Light did not become effective in controlling or "triggering" germination until a threshold moisture content of approximately 10 to 20 per cent of dry weight was attained. This moisture content was reached in approximately 30 minutes during imbibition from a free-water surface.

4. When the threshold moisture content was attained, a single exposure of only 5 seconds' duration was sufficient to induce the germination of some sensitive seeds and an exposure of 2 to 4 minutes provided complete germination at all temperatures tested.

5. The stimulation provided by a single exposure was persistent for at least three days. The seed retained the ability to germinate in continuous darkness if returned to an air-dry condition.

6. Photoperiod was effective in controlling the germination of jack pine seeds but this control was subject to a temperature interaction. At 60 F short photoperiods of two to ten hours' duration inhibited germination while photoperiods of 16 hours or longer promoted germination. At constant temperatures of 70 F and 80 F and alternating 60 F and 80 F germination was complete regardless of photoperiod.

7. The inhibitory effect of short photoperiods occurs only as long as short photoperiods are provided. Cessation of short daily exposures was followed by germination.

8. At temperatures at which photoperiod was effective, repeated dark periods of 12 to 24 hours' duration were increasingly inhibitive. However, dark periods in excess of 24 hours' duration were progressively less inhibitive.

The response of lodgepole pine seeds to photo-control was found to be similar in all major respects to that of jack pine seeds. Both species responded to single exposures, and to photoperiod; and the response of both species to photoperiod was temperature dependent. However, marked differences were demonstrated in the degree of response to certain temperature and light treatments. Germination of lodgepole pine seeds showed a strong optimum at temperatures around 70; also, photoperiod affected germination only at similar temperatures. While a single exposure to light produced a definite increase in germination, no single exposure permitted complete germination to occur.

The results conform in major aspects to the red, far-red reversion hypothesis, and to the hypothesis incorporating the action of endogenous circadian rhythms.

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Germination of both species was reduced at all temperatures by the exclusion of light, but could be promoted by either a single exposure or by daily exposures greater than a minimum length. A strong interaction was evident in the light and temperature requirements of both species.