AN ABSTRACT OF THE THESIS OF

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Title: EFFECT OF RED AND FAR-RED LIGHT UPON GROWTH OF DOUGLAS-FIR (PSEUDOTSUGA MENZIESII (MIRB.) FRANCO) SEEDLINGS

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Helge Irgens-Moller

The photoperiodic responses of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings grown from seed collected at Salmon Arm, British Columbia, Coconino National Forest, Arizona, and Southern Vancouver Island were studied. Plants were grown for 100 days under a 12-hour photoperiod at ?0° C. The effective length of the daily light and dark periods were altered by interruption at various times with different durations of red and far-red light.

Interruptions of darkness with ?, 15, and 30 minutes of red light increased the duration of growth, epicotyl and leaf lengths, and leaf numbers of all plants. Responses to these treatments increased as exposure times approached the center of the dark period. Exposures given equal times before or after the middle of darkness produced equal responses. Magnitudes of response

increased as exposure lengths increased. Both the nature and magnitude of response varied among seed sources.

Responses to 30 and 55 minutes of far-red light unexpectedly resembled those to red light. Apparently, excessive far-red light reversed the normal photoreaction of phytochrome and caused the accumulation of the active form (Pfr) of the pigment. Fifteen-minute exposures accelerated the onset of dormancy and reduced the growth of all plants.

Since responses to red light increased as exposure times approached the center of darkness, it appeared that each exposure produced similar Pfr concentrations and that dark conversion during the period of uninterrupted darkness determined the level mediating response. However, the dependence of response upon timing might also indicate that a particular Pfr concentration had to be present a specific length of time in order to produce a response. Consequently, responses were attributed to levels of Pfr activity not concentration.

Since all plants were grown in uniform environments, some proportion of the variation among seed sources is heritable and reflects their adaptation to the three habitats. Salmon Arm plants required larger, critical levels of Pfr activity for continued growth than Coconino plants. This difference seemed an expected result

since day lengths in northern areas are longer during the growing season. The critical requirement of Salmon Arm plants demonstrated that changes in day length are important in regulating their annual growth cycle. Such regulation would seem a prerequisite to survival for plants from an area of short growing seasons and large, abrupt seasonal changes in climate.

Vancouver plants had the lowest and least critical requirement for Pfr activity, indicating that changes in day length were of lesser importance in the control of growth periodicity. Such control would seem to be, and apparently is, of lesser selective value for plants from a coastal area having long growing seasons and gradual transitions between seasons.

Coconino plants resembled Salmon Arm plants in requiring a large, somewhat critical level of Pfr activity. This similarity reflects adaptation to the short growing season and seasonal extremes of climate characteristic of their mountainous, continental habitat. However, Coconino plants differed from the others in terms of their synchronous cessations and renewals of growth. This intermittent pattern of growth may reflect differences in the seasonal distribution of precipitation at the origins of the two continental sources. Summer rains constitute a greater portion of the annual rainfall in the Southern Rocky Mountains than in northern areas. Intermittent

growth under the long days of the growing season could permit dormancy if moisture was limiting, but could favor growth resumption if summer rains caused conditions to remain or become favorable.

Effect of Red and Far-Red Light Upon Growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) Seedlings

by

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INTRODUCTION

Since the discovery of photoperiodism by Garner and Allard (1920), considerable interest has developed in the effect of seasonal changes in day length upon plant growth and development. Numerous workers have reported the importance of these changes as reliable indicators of the seasons and as signals for the initiation of reproductive activities in herbaceous plants. More recently, it has been found that seasonal changes in day length also influence the timing of the annual cycle of vegetative growth in woody plants (Wareing, 1956). In the majority of woody species investigated, short days (12 hours or less) reduce growth and accelerate the onset of dormancy. On the other hand, long days increase the duration of growth. It is currently held that responses to changes in day length, either separately or in conjunction with other environmental factors, are important in the adjustment of growth and developmental periodicity to local climatic conditions. The vegetative processes affected include the duration of extensive growth, the onset and breaking of dormancy, the duration of cambial activity, leaf abscission, the development of frost resistance, and seed germination (Wareing, 1956).

In the middle latitudes, day length varies from about 9 hours

on the shortest day of winter to 15 hours on the longest day of summer, a difference of 6 hours (Leopold, 1964). However, the annual variation in day length increases with increasing latitude. Thus, the day length at a high latitude during the growing season exceeds that in areas nearer the equator. As a consequence of such differences, one would expect northern species or populations to exhibit different types and degrees of photoperiodic response than southern groups. That this is indeed the case has been shown by numerous workers. Vaartaja (1962) reported that intraspecific variation in photoperiodic response has been found in at least 31 tree species having wide latitudinal and geographical distributions in the North Temperate Zone.

Since a wide-ranging species such as Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) extends over a variety of latitudinal, climatic, and altitudinal zones, populations from various parts of its range are expected to differ in their response to changes in day length. Irgens-Moller (1962 and 1968) found such differences between several Douglas-fir populations. However, he was unable to characterize the response pattern of any one sample in detail since he maximized the number of populations examined and used only three day length regimes.

The objective of the present study was to describe the nature and degree of the response of three widely-separated Douglas-fir

populations to a variety of photoperiodic treatments. Emphasis was placed on characterizing the response pattern of plants from each population and on relating differences in response to differences in the environments of the three habitats. No attempt was made to describe the pattern of variation within the species since so few populations were sampled.

REVIEW OF LITERATURE

Light and Photoperiodism

Light reaching the earth from the sun provides the energy capital for the growth of all living systems. In addition, light intensity, quality, duration, and periodicity all influence the quality, quantity, and timing of plant growth. The following discussion is primarily concerned with these regulatory effects of light and the mechanisms underlying them.

In nature, day length or photoperiod varies with the season of the year and latitude. In the middle latitudes, day length varies from 9 hours in winter to 15 hours in summer (Leopold, 1964). The difference between the longest and shortest days increases with latitude. Unaware of the importance of these changes, early botanists largely held that temperature caused seasonal changes in the pattern of plant growth (Leopold, 1964). It remained for Garner and Allard (1920) to demonstrate the regulatory influence of day length. They established the concept that the relative length of day and night have a profound influence upon plant growth and reproduction, that is, the concept of photoperiodism. The consistent seasonal changes in day length at a given latitude provide a precise and reliable cue of the seasons for Temperate Zone plants.

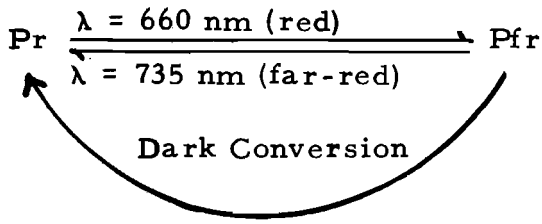
The Photoperiodic Mechanism

Few early experiments provided definitive answers as to how plants measured the duration of light and darkness. Hamner and Bonner (1938) reported one of the first important clues. They showed that a brief light period given during a long dark period nullified the otherwise inductive effect of a short day or long dark period and prevented the short-day plant, Xanthium pennsylvanicum Wall., from flowering. Interruption of the light period with darkness was without effect. The length of the uninterrupted dark period seemed to be the critical part of the 24-hour period. Hamner (1940) substantiated this by independently varying the length of the day and night. He found that the length of the light period was not nearly as critical as that of darkness.

Knowledge of the critical nature of dark period length and of the night-interruption effect permitted investigation of the light-sensitive system responsible for photoperiodic control. Borthwick, Hendricks, and Parker (1952) determined the action spectrum for the night-interruption effect in Xanthium sacchartum Wallr. Their results showed a maximum effect in the red region of the spectrum (630 to 660 nm). Far-red light (700 to 760 nm) had the same effect as a prolonged dark period, that is, it promoted flowering. Moreover, the effect of a red exposure was reversed by subsequent immediate

exposure to far-red light. The demonstration of similar action spectra and photoreversibility has indicated that the same mechanism influences at least 19 other growth responses in plants (Hendricks and Borthwick, 1963).

The reversibility of the photoreaction suggested that alternate red and far-red exposures converted a pigment from one form to another (Borthwick et al., 1952). They reasoned that exposure to sunlight during the day or to red light during the dark period converted the pigment to a far-red absorbing form. Moreover, it appeared that far-red light or darkness converted it back to the red-absorbing form. Hendricks, Borthwick, and Downs (1956) verified that red and far-red exposures did have reversible effects on a single pigment which could assume two forms, a red absorbing form (Pr) and a far-red absorbing form (Pfr). Hendricks and Borthwick (1963) summarized these facts in the following equation:



The Pfr form was found to be biologically active. For example, the inhibition of flowering in short-day plants by exposure to red light during darkness is readily reversed if far-red light is given immediately afterwards, but not if some time elapses between the

two exposures (Downs, 1956). He concluded that Pfr produced by the red exposure completed some critical function during the interval between exposures and was therefore the active form. Positive correlations between the mole fraction of Pfr and the degree of response have also been found (Hendricks and Borthwick, 1963).

Subsequently, the reversible pigment was isolated and named phytochrome (Butler, et al., 1959). Lane et al. (1963) demonstrated the presence of the pigment in extracts of green tissue from 20 species of herbaceous plants. In each case, its spectral properties were identical to those of pigment extracted from etiolated plants in the earlier study.

Hendricks and Borthwick (1963) proposed that plants measured time by the rate of dark conversion. The critical length of darkness required for a particular photoperiodic response was said to be equal to the time required for dark conversion to produce the required Pfr level. Evidence supporting this hypothesis was drawn from tests in which light was given at various times during the night. Harder and Bode (1943) demonstrated that red light caused maximum inhibition of flowering in the short-day plant, Kalanchoë blossfeldiana, when given at or shortly before the critical number of hours of darkness required for flowering. Similar results were reported for Xanthium by Salisbury and Bonner (1956). Evidence was also supplied from kinetic studies of dark conversion in vitro and in vivo

(Hendricks and Borthwick, 1963). However, there is also considerable evidence against this hypothesis. For example, if Pfr was gradually converted to Pr throughout the night and if its final concentration governed response, the amount of red light needed to saturate the reversal of response would increase the later it was given. However, Salisbury and Bonner (1956) showed that the amount of red light required to saturate the inhibition of flowering in Xanthium was the same after the fourth hour of darkness. They suggested that dark conversion was completed in the first four hours. Based on these and other results, Salisbury (1963) concluded that dark conversion was not the timer, but was preliminary to the operation of the actual timekeeping mechanism.

Bünning (1961 and 1964) suggested that time measurement was a function of the biological clock controlling other rhythmic processes. Two approaches have been used to demonstrate the involvement of endogenous rhythms. Hamner (1963) exposed the short-day plant, Biloxi soybean, to 72-hour cycles consisting of an initial 8 hours of light and 64 hours of darkness. When the dark period was interrupted with light at various times, three 12-hour periods were found during which light inhibited flowering. These periods corresponded to the latter half of the three 24-hour periods comprising the cycle. He also tested the effects of numerous cycle lengths on the flowering of soybean. Each cycle began with eight hours of light, but ended

with a variable length dark period. Response showed a rhythmic dependency upon cycle length with maximum flowering observed under 24-, 48-, and 72-hour cycles. Maximum inhibition occurred under cycles less than 24 hours, between 32 and 36 hours, and about 60 hours long. He concluded that rhythmic sensitivity to light was the method of measuring time.

Other work indicates that the role of the light period may not be merely the production of substrate. Meijer (1957 and 1959) found that red light given during the day permitted the short-day plant, Salvia occidentalis Sw., to flower even on long days. He also observed other interactions between light quality and the light period that could not be explained as photosynthetic effects. Könitz (1958) observed that exposure to red light during darkness inhibited flowering of the short-day plant, Chenopodium amaranticolor Coste and Reynier, but that exposure during the day promoted it. Each effect was reversed by subsequent far-red exposures. Exposures to far-red light alone produced opposite effects. Bünning (1959) interpreted these findings as evidence for rhythmic changes in pigment sensitivity. Kofranek and Sachs (1964) were unable to duplicate the results of Könitz (1958). However, they did observe that several races of C. amaranticolor responded differently to varying proportions of red and far-red light given during the daily light period. Salisbury (1965) considered such findings as analogies to rhythmic

phenomena since light can inhibit other rhythms at one time and stimulate them at other times. Salisbury (1965) reviewed other evidence that both the daily light and dark periods were important. He concluded, as had originally been proposed, that photoperiodism is a response to a periodic cycling of light and darkness and that the phytochrome system coupled the time measuring reaction to the environment.

Photoperiodism in Woody Plants

Garner and Allard (1923) included several woody species in their early studies of photoperiodism. They found that yellow poplar (Liriodendron tulipifera L.) went dormant when exposed to short winter days in the greenhouse. Similar plants given supplemental light to lengthen the days continued growth. They concluded that day length might be an important determinant of the onset and end of dormancy.

Kramer (1936) observed that sweet gum (Liquidambar styraciflua L.), post oak (Quercus stellata Wangenh.), and yellow poplar seedlings grew later in the autumn when the natural day length was increased by artificial light. Plants given day lengths shorter than the natural day went dormant early in the season. He also brought dormant plants into the greenhouse at mid-winter and found that exposure

to long days hastened growth resumption. He reported that photoperiod was clearly a factor in controlling the duration of growth.

Wareing (1950) observed the responses of one year old Scots pine (Pinus sylvestris L.) seedlings to various photoperiods. Exposure to 10-hour days produced earlier dormancy, fewer and shorter leaves per plant, and shorter plants than 15-hour days. Increases in growth, primarily caused by the longer duration of growth, were directly proportional to day length. Maximum stem growth occurred under 20-hour days, while further increases in day length decreased response.

Subsequent to these early studies, the photoperiodic responses of a variety of woody plants were investigated. Wareing (1956) reviewed the considerable volume of work and reported that day length affected a number of growth processes including germination, stem elongation, leaf growth, leaf abscission, duration of cambial activity, and the onset and breaking of bud dormancy.

According to Wareing (1956), day length influences the duration of extension growth in all but a few of the approximately 60 species tested. There seemed no exception to the rule that short days hastened the onset of dormancy, whereas long days delayed it and promoted elongation. Downs and Borthwick (1956) and Downs (1962) reached similar conclusions in their reviews, but emphasized that the character and degree of response differed greatly among species.

Numerous deciduous species and the Southern pines ceased growth under day lengths less than 12 hours (Downs, 1962). Other species such as Sitka spruce (Picea sitchensis (Bong.) Carr.) went dormant on day lengths of 14 hours or less. Still others, for example, Norway spruce (P. abies (L.) Karst.) and white spruce (P. glauca (Moench.) Voss) went dormant on day lengths as long as 16 hours. It seemed that northern species went dormant under longer days than southern species.

Downs and Borthwick (1956) found that most species ceased growth after about 28 days of short-day treatment. However, yellow poplar went dormant after only 10 days of treatment. At the other extreme, elm (Ulmus americana L.) continued gorwth until it had received over 140 short days.

Under 16-hour day lengths, pine and oak species went dormant shortly after treatment began, but quickly resumed growth (Downs, 1962). Pines continued this intermittent pattern of growth as long as 16-hour days prevailed. However, their growth was continuous on 14-hour photoperiods. Oaks eventually set a more permanent bud and would not resume growth even if long-day treatment was continued (Downs and Borthwick, 1956). The growth of catalpa (Catalpa bignonioides Walt.), dogwood (Cornus florida L.), and elm was continuous under 16-hour days. Douglas-fir and spruce grew continuously only under day lengths of 20 hours or longer

(Downs, 1962).

Wareing (1956) discussed the effects of photoperiod upon the resumption of growth. Generally, summer dormancies were easily broken. However, the ease with which winter dormancy could be broken varied with the species. Dogwood seedlings readily broke dormancy when exposed to long days (Borthwick, 1957). Long days did not break the dormancy of catalpa (Downs, 1962) or Scots pine (Borthwick, 1957) unless they had been given a cold period. Some species broke dormancy after chilling regardless of day length (Wareing, 1956). In other cases, long days hastened the breaking of chilled buds, demonstrating that the influence of photoperiod could be modified considerably by other environmental factors.

Downs and Piringer (1958) found that the effects of long days on plants from several pine species varied with age. Maximum juvenile growth occurred under 14- or 16-hour days, but the best growth of older material was obtained under continuous light.

Photoperiodic Mechanism of Woody Plants

The photoperiodic responses of herbaceous and woody plants seem to be controlled by a similar mechanism. Wareing (1950) showed that interruption of the daily dark period delayed dormancy and increased the growth of Scots pine seedlings. Zahner (1955) reported that interruption of 14.5-hour dark periods with 30 minutes

of white light doubled the growth of loblolly pine (P. taeda L.) and yellow poplar seedlings. The similarity of these results to those of Hamner and Bonner (1938) for short-day plants demonstrated the similarity of the underlying mechanisms. Nitsch (1957) observed that the growth of Weigela florida was inhibited by nine-hour days, but that exposure to one hour of weak light during the 15-hour dark period promoted growth. Response varied with the time of exposure. The largest response was observed when the exposure occurred at the middle of the dark period. This finding demonstrated that the length of the longest uninterrupted dark period was a critical part of the 24-hour period for woody plants just as Harder and Bode (1943) found for herbs.

Johnson (1965) provided clear evidence that phytochrome mediates the photoperiodic responses of woody plants. He grew Douglas-fir seedlings under 12-hour light periods and interrupted the complementary dark period with short periods of red and far-red light. Red light delayed the onset of dormancy whereas far-red light hastened it. Downs and Piringer (1958) found that fluorescent and incandescent lamps were equally effective in delaying dormancy. However, incandescent light produced taller pine seedlings than fluorescent light. The difference was attributed to the larger proportion of far-red radiation in the incandescent light. These results indirectly established the existence in woody plants of the same reversible

photoreaction that controls photoperiodic responses in herbs.

Intraspecific Variation in Photoperiodic Response

While some workers have described interspecific differences in the photoperiodic responses of woody plants, others have investigated intraspecific variation. Since plants cannot regulate their internal temperatures or escape from unfavorable changes in climate, their annual cycle of growth and development is necessarily correlated to the climate of their habitats. Adjustment to seasonal trends in local climate entails measuring time. Since seasonal variation in day length provides a reliable cue of the seasons, one would expect responsiveness to photoperiod to be of selective value. Furthermore, wide-ranging species would be expected to show intraspecific variation in this response.

Such variation has been found in a number of woody species. Pauley and Perry (1954) grew clones of black cottonwood (Populus trichocarpa Torr. and Gray) from a variety of latitudes under the natural day length regime of Weston, Massachusetts. Under these conditions, clones from high latitudes ceased height growth earlier than those from lower latitudes. The date of cessation for the various clones varied from June 20 to October 28. This degree of interclonal variation in one environment demonstrated that the differences were heritable. They also observed the dates of growth cessation

under the day length regime of Weston and a regime approximating that of Juneau, Alaska. Differences between responses to the two regimes were larger in clones from high latitudes. They concluded that day length was an important factor in the control of growth cessation and that local populations differed genetically in their response to it.

Vaartaja (1954) exposed Scots pine seedlings from two latitudes to 10- and 24-hour photoperiods. Northern seedlings grew much larger than those from lower latitudes under continuous light. However, the response was reversed under 10-hour days. Since day lengths are longer during the growing season at high latitudes, Vaartaja concluded that the responses reflected a heritable adaptation to the day length regime characteristic of each area.

Irgens-Moller (1958) obtained Douglas-fir seed from five localities in the Pacific Northwest and grew the seedlings under natural day lengths at Corvallis, Oregon. Plants from Vancouver Island grew several weeks later in the season than those from interior areas. Differences in the time of growth cessation were reflected by total height growth. Coastal seedlings were three to five times larger than those from a continental region, Salmon Arm, British Columbia, in the same latitudinal zone. He concluded that response to day length seemed to be an important factor in adjustment of the growth cycle to the growing season.

Seedlings from the same areas were grown under several day length treatments in a greenhouse (Irgens-Moller, 1958). The greatest responses to increases in day length were shown by Salmon Arm plants. For example, these plants produced 2.5 times as many leaves under a 19-hour photoperiod as under a 9-hour day. Similar treatment only slightly increased the duration of growth and the leaf production of Vancouver Island plants. The results demonstrated that considerable genetic diversity existed in Douglas-fir with respect to photoperiodic response.

Vaartaja (1959) examined the responses of seedlings from 38 species of forest trees to various photoperiods. The critical day length, that day length which significantly reduced growth below that attained under 18-hour days, was determined for each species and for seedlings from various parts of species ranges. A numerical expression of photoperiodic sensitivity was calculated by dividing the response in terms of height growth under long days by that for short days. A large ratio indicated large differences in response and high sensitivity. His results demonstrated that northern and continental species or subpopulations within species were more sensitive to changes in photoperiod and had longer critical day lengths than those from low latitudes or coastal areas. Intraspecific variation in these characters was noted in 15 of 17 species from 8 of 9 genera. This seemed adequate evidence to him that such variation

was common in wide-ranging forest tree species of the North Temperate Zone. The persistence of this variation under uniform environmental conditions demonstrated that the capacity to respond was genetically-determined. Vaartaja contended that the selective factors favoring the genes involved acted indirectly, that is, photoperiodic response was of selective value because it aided in protection against other environmental factors such as seasonal extremes of climate. He noted that such factors often change suddenly and vary inconsistently from year to year whereas seasonal variation in day length is consistent from year to year.

The photoperiodic responses of hemlock (Tsuga canadensis (L.) Carr.) seedlings were studied by Nienstaedt and Olson (1961). The seedlings were grown from seed collected at 30 locations representing a variety of latitudes and elevations. Under any given day length, seedlings from high latitudes or altitudes went dormant earlier and grew less than seedlings from low latitudes or altitudes. Regardless of seed source, height growth increased as day length increased. Critical day lengths were longest for northern seedlings.

Irgens-Moller (1962) collected seed from several Douglas-fir trees at each of 20 locations throughout the species range. Seedlings were grown under a 9-hour photoperiod and a similar regime extended to a 17-hour day by interruption of the dark period. Leaf number per plant, an estimate of height growth, was determined after three

months of treatment. Seedlings from continental areas such as Arizona, Colorado, Montana, and Idaho formed two to four times as many leaves under long days as under short days. Conversely, seedlings from coastal areas, Vancouver Island and Western Washington, formed only a few more leaves under the longer days. Consequently, the continental sources were considered most sensitive to changes in photoperiod.

Irgens-Moller (1968) grew Douglas-fir plants from three widely-separated areas under the natural day length of Corvallis, Oregon. The seed had been collected near Flagstaff, Arizona, on Southern Vancouver Island, and from Salmon Arm, British Columbia. Plants from the coastal area went dormant considerably later than plants from the continental regions. Arizona plants went dormant midway through the experiment, but over half of them resumed growth a short time later. When plants from the same three sources were grown under 16-hour photoperiods, the Vancouver plants remained active for most of the 90-day test period. The Arizona plants retained their intermittent growth pattern and, in fact, renewed growth twice under these conditions. Some of the Salmon Arm plants also renewed growth, but in smaller numbers and at irregular times. Under eight-hour photoperiods, continental plants went dormant earlier than Vancouver plants.

Irgens-Moller (1968) also observed that plants from other parts

of the Southern Rocky Mountains, New Mexico, Colorado, and Utah, grew intermittently under 16-hour days, whereas those from Northern areas, Montana, did not. He suggested that this variation was related to differences between the two areas in the seasonal distribution of precipitation. Normally, the Southern Rocky Mountains receive considerably more summer rainfall than more northerly area (Baker, 1944). Presumably, plants from the southern areas go dormant early if moisture conditions are limiting, but are able to resume growth should conditions either remain or become favorable.

MATERIALS AND METHODS

Test Populations

The Douglas-fir plants employed were grown from seed collected commercially in three widely-separated areas: Coconino National Forest, Arizona (Latitude, 35°N; Altitude, 8000 to 10,000 ft), Salmon Arm, British Columbia (51°N; 1500 to 2000 ft), and Southern Vancouver Island (49°N; 0 to 500 ft). The first two seed sources, northern and southern, continental sources respectively, fall within the population system referred to as var. glauca (Beissn.) Franco. The Vancouver Island source, a northern, coastal population, is var. menziesii.

The three sources were chosen for several reasons. First, the collection sites differed greatly in terms of latitude, topography, and climate. Second, each of the populations represented was formerly considered to be a separate taxonomic variety (Dallimore and Jackson, 1948). Last, they have been and are being employed in studies of intraspecific variation at Oregon State University. In this paper, each source will be referred to by the name of the location where the seed was collected, that is, by the terms Salmon Arm, Coconino, and Vancouver.

Culture of Plants

Seed was stored in a cold room at 2° C. At the start of each experiment, unstratified, imbibed seed was germinated in petri plates at 20° C and under a 12-hour photoperiod. When the emerging radicles were approximately 5 mm long, 26 seedlings were chosen at random and planted in metal cans (No. 10) containing a 75:25 mixture (by volume) of sandy loam and peat moss. The soil surface was covered with a half-inch layer of Perlite before planting to retard water loss and decrease the incidence of damping-off. This precaution and pre-germination were used to obtain a maximum number of plants per can and uniform populations.

Four replications, each containing an average of 23 seedlings (16 to 26 per can), were used per seed source and treatment. Newly-germinated plants were used in each test to avoid age differences, chilling requirements, and preconditioning effects. All plants were watered at four-day intervals and given a balanced fertilizer 50 days after planting. Four holes in the base of each can provided drainage.

Controlled Environment Chambers

Test plants were grown for 100 days under 12-hour photoperiods at a constant temperature of 20 ± 1.5° C. All but three experiments were performed in four identical controlled environment

chambers. The three exceptions were performed in an auxiliary unit described below. In the four main chambers, radiation during the light period was supplied by six cool white fluorescent tubes (General Electric: No. F48PG17·CW) and seven incandescent lamps (Sylvania: 100w/130v) located 10.5 inches above the plants.

The emission spectrum and energy output of this lamp combination were measured at plant level with a spectroradiometer (Instrument Specialties Company, Inc.: Model SR). The four chambers were identical in terms of these measurements (Figure 1). Total incident energy in the 380 to 750 nm region was 0.044 ± 0.0002 g cal·cm^{-2}·min^{-1}. These measurements, made after about 10 months or 3600 hours of service, were near minimal as lamps were replaced annually. The constant environment provided by the chambers permitted comparisons of experiments performed in individual units at the same or different times.

In several tests, plants were grown 17 inches below the chamber lights to accommodate experimental light units. This lowering reduced incident energy to 0.030 g cal·cm^{-2}·min^{-1}, but did not alter the spectral distribution of energy. In addition, the opaque light units permitted only diffuse light to reach the plants. The observed energy decrease plus some further reduction caused by shading may have affected developmental processes sensitive to light intensity.

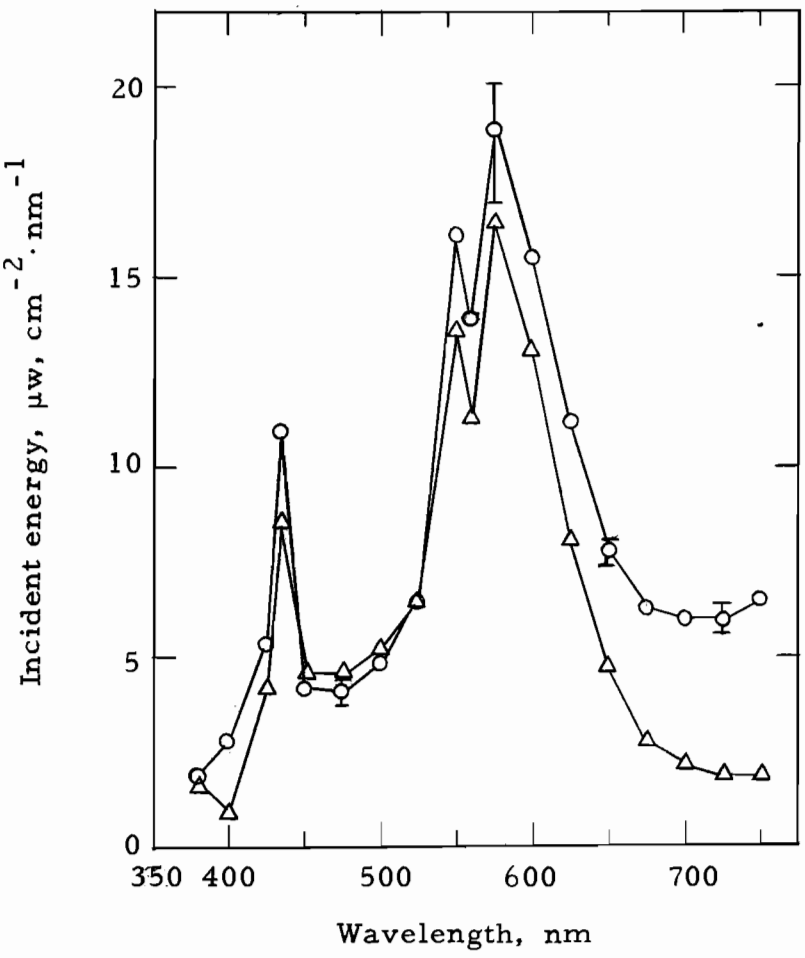


Figure 1. Spectral distribution of energy in the main (o) and auxiliary (Δ) growth chambers. Vertical bars denote the range of individual chamber measurements about the mean for the four main chambers.

With the exception of light, the environment of the auxiliary chamber corresponded to that of the main chambers. In the auxiliary unit, plants were located 45 inches rather than 10.5 or 17 inches below the light source. The lighting system consisted of 32 cool white fluorescent tubes (Ken Rad: No. F96T12/CW) and 11 incandescent lamps (Sylvania: 92w/125v). Total incident energy in the 380 to 750 nm region was 0.033 as opposed to 0.044 ± 0.002 g cal$\cdot$cm$^{-2}\cdot$min^{-1} for the main chambers. Although the spectra were similar over much of this range, they differed in the region of phytochrome absorbtion (Figure 1). Auxiliary chamber light contained less energy in both the red (660 ± 15 nm) and far-red (735 ± 15 nm) bands than main chamber light (Table 1). In addition, auxiliary chamber lights emitted a lower proportion of energy in the far-red band and had a far-red:red ratio half that of the main chambers. Since the balance or ratio of energy in the two bands determines response, the results of experiments performed in the auxiliary chamber were not compared directly to those from the main chambers.

Table 1. Energy content of red and far-red bands in spectra of two controlled environment chambers.

Chamber	Energy (g cal·cm^{-2}·min^{-1} × 10^{-3}) Red Band (660 ± 15 nm)	Far-Red Band (735 ± 15 nm)	FR/R Ratio
Main	3.0	3.0	1.0
Auxiliary	2.0	1.0	0.5

Red and Far-Red Light Sources

Test treatments consisted of interrupting the 12-hour light and dark periods at various times and with various durations of red or far-red light. Red light was supplied from six red-phosphor fluorescent tubes (Westinghouse: No. F30T8/R) suspended six inches above the plants. Far-red light was obtained by filtering light from ten tube-type incandescent lamps (Ken Rad: 40w/115-125v) through two layers of red cellophane (Dupont: No. 3135) and blue glass filters (Corning: No. 5850). Filters were six inches above the plant. Two lamps were placed above each of the five filters comprising the bottom of an otherwise light-proof plywood box. Boxes were fitted with fans and vents to prevent overheating. Periods of operation as long as one hour did not affect chamber air temperatures. The boxes shaded test plants during the light period.

The emission spectra of the red and far-red sources are shown

in Figure 2. Incident energy in the 550 to 800 nm region from red units was 0.008 g cal·cm^{-2}·min^{-1} at plant level. Energy in the region of maximum Pr absorbance, 660 ± 15 nm, was 0.002 g cal·cm^{-2}·min^{-1}. Although the red lamps emitted some energy beyond the region of Pr absorbance, the degree of impurity seemed negligible relative to the energy at 660 nm.

Incident energy in the 675 to 800 nm region from far-red sources 0.009 g cal·cm^{-2}·min^{-1}. Energy in the band specific for Pfr conversion, 735 ± 15 nm, was 0.002 g cal·cm^{-2}·min^{-1}. Little energy was emitted at wavelengths less than 675 nm. However, increasing amounts of energy were emitted at wavelengths beyond 800 nm. Although radiation at these and longer wavelengths has no specific effects upon plant growth, the proportion absorbed is converted to heat and may indirectly affect growth. As noted above, plants given far-red treatment received lower incident energies than other plants. This combination of factors was not common to other experimental treatments and may have produced responses in addition to the photoperiodic and formative effects of far-red exposures. Since these added effects could not be separated from those of far-red light, morphological data from such tests were not compared to those from control and red experiments.

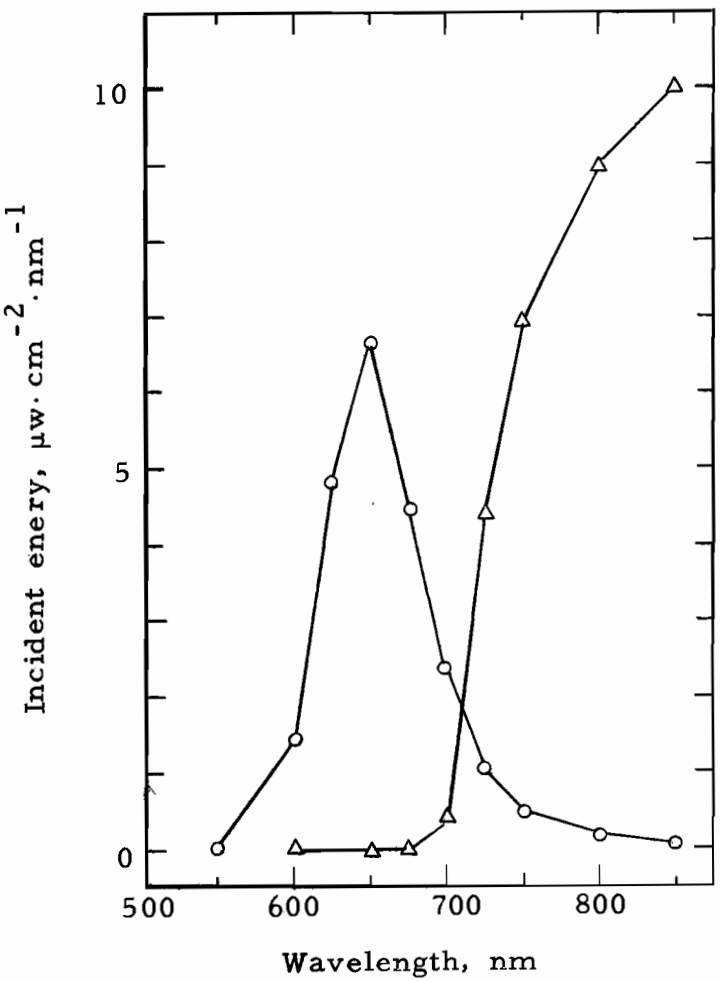


Figure 2. Spectral properties of the red (o) and far-red (Δ) light sources.

Observations and Measurements

Since the study spanned three years, some change in environment or population structure were expected over time. To monitor such change, a number of control experiments were performed. In the main chambers, a series of three were made; one each at the start, middle, and end of the study. Only one was performed in the auxiliary chamber as few tests were conducted in it.

Numbers of non-dormant plants were observed at five-day intervals. Frequent observation facilitated random rotation of the plants about each growth chamber. A seedling was considered non-dormant if its terminal bud was not enclosed in bud scales. Lateral bud development was not observed. Observations were expressed as percentages of non-dormant plants or activity per replication and averaged to obtain means for each treatment. Percentages were transformed to arc sine values for statistical analyses.

The number of active and dormant periods entered by individual plants was also recorded. Newly-germinated plants were considered active and in their first active period. After its first terminal bud was encased by bud scales, a plant was in its first dormant period. Upon breaking its second dormancy, a plant was active again, but in its third period of active growth. The number of plants in each active or dormant phase were summed over the four replications

per seed source and treatment and converted to percentages for comparison.

In some experiments, plants were cut off at the soil surface after treatment and pressed for the determination of leaf number, leaf length, and epicotyl length. Ten plants were randomly selected and measured from each replicate. Analyses of variance and calculated LSD values were used to test differences between responses to the various treatments (Steel and Torrie, 1960).

RESULTS

Effect of Red Light

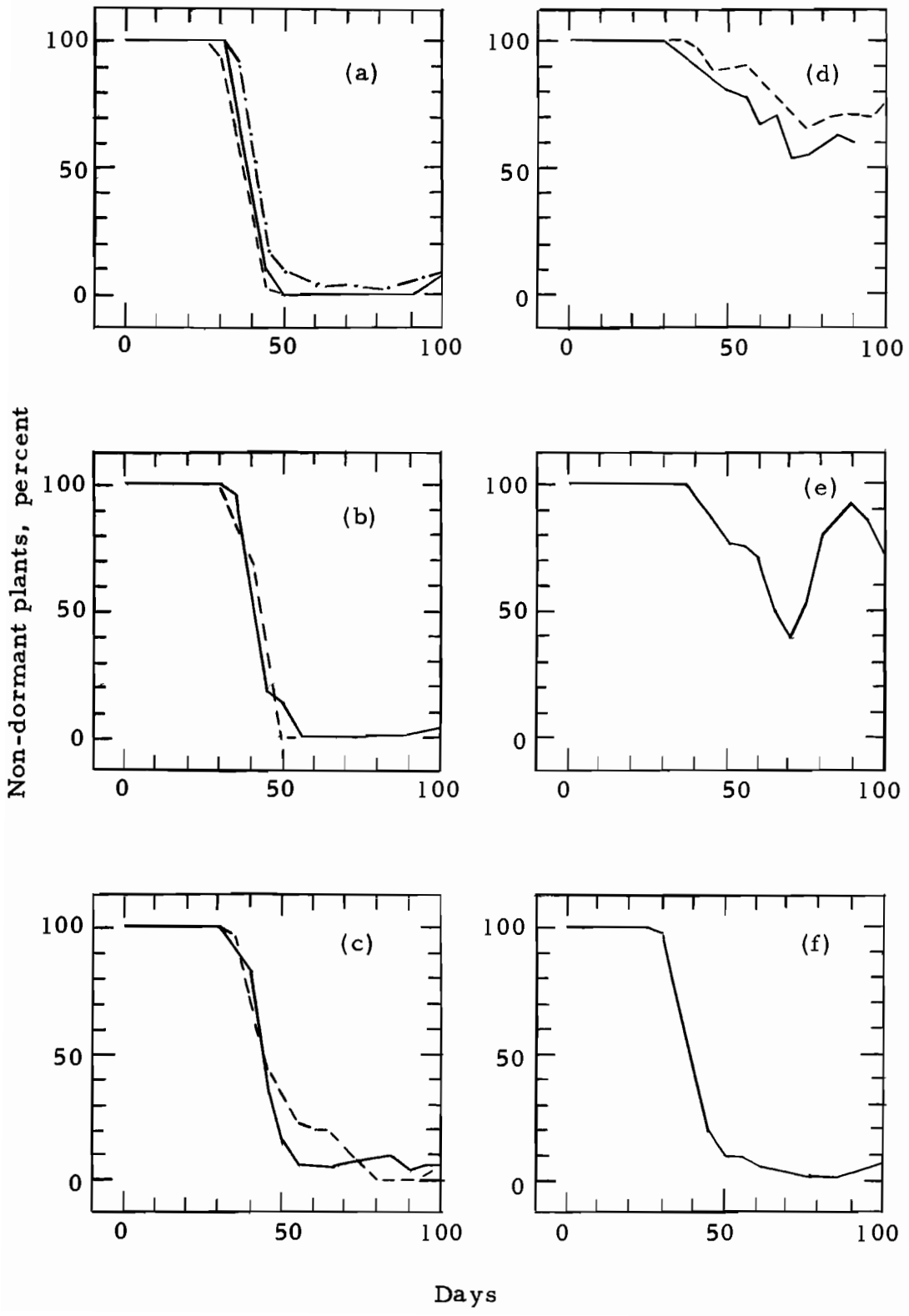
Phytochrome undoubtedly is involved in the physiological mechanism underlying the photoperiodic responses of woody plants. Since red light causes the conversion of Pr to Pfr, it was hypothesized that exposure to red light would cause accumulation of Pfr and responses similar to those of long photoperiods. Thirteen experiments were performed to test this hypothesis. Both the time and length of exposure were varied in order to evaluate differences between the responses of plants from the three sources. Individual treatments are described in Table 2. When several exposures are considered as a series, comparisons among responses are made relative to those of all controls. For specific comparisons, the control performed closest in time to the test concerned is used.

Effect of Thirty-minute Exposures

Duration of Growth. Salmon Arm plants in the control tests began to enter dormancy at about age 30 days (Figure 3a). In all three controls, activity decreased to minimum levels approaching zero percent between ages 50 and 60 days. A few plants subsequently broke dormancy and increased activity to an average of three percent

Table 2. Description of red light treatments

Exposure length (min)	Exposure time	Length of longest dark period (hours)	Response Observed			
			Percent non-dormant plants	Epicotyl length (mm)	Leaf number	Leaf length (mm)
30	12 PM	7.5	+	+	+	+
30	12 AM	12	+	+	+	+
Control	--	12	+	+	+	+
30	4 AM	8	+	+	+	--
30	10 PM	9.5	+	+	+	--
30	8 PM	11.5	+	+	+	--
30	6 AM	10	+	+	+	--
Control	--	12	+	+	+	--
30	7:30 AM	11.5	+	+	+	--
30	2 AM	6	+	+	+	--
Control	--	12	+	+	+	--
15	2 AM	6	+	--	--	--
2	2 AM	6	+	--	--	--


(a)
(b)
(c)
(d)
(e)
(f)
100
50
0
0
50
100
Non-dormant plants, percent
Days

at age 90 days. At that time, from 92 to 100 percent of the plants were in their first dormancy. Responses to 30 minutes of red light given immediately after the beginning or before the end of the dark period were similar to those of the controls (Figure 3b).

Salmon Arm plants given red light two hours after the beginning or before the end of darkness entered dormancy at age 35 days (Figure 3c). Minimum activities varying from zero to five percent were reached between ages 60 and 80 days as opposed to age 50 days under the treatments described above. Only small numbers of plants remained active or broke dormancy thereafter (Figure 3c). At age 90 days, approximately three percent of the plants were active. The majority of the plants (89 and 90 percent) were still in their first period of dormancy at that time.

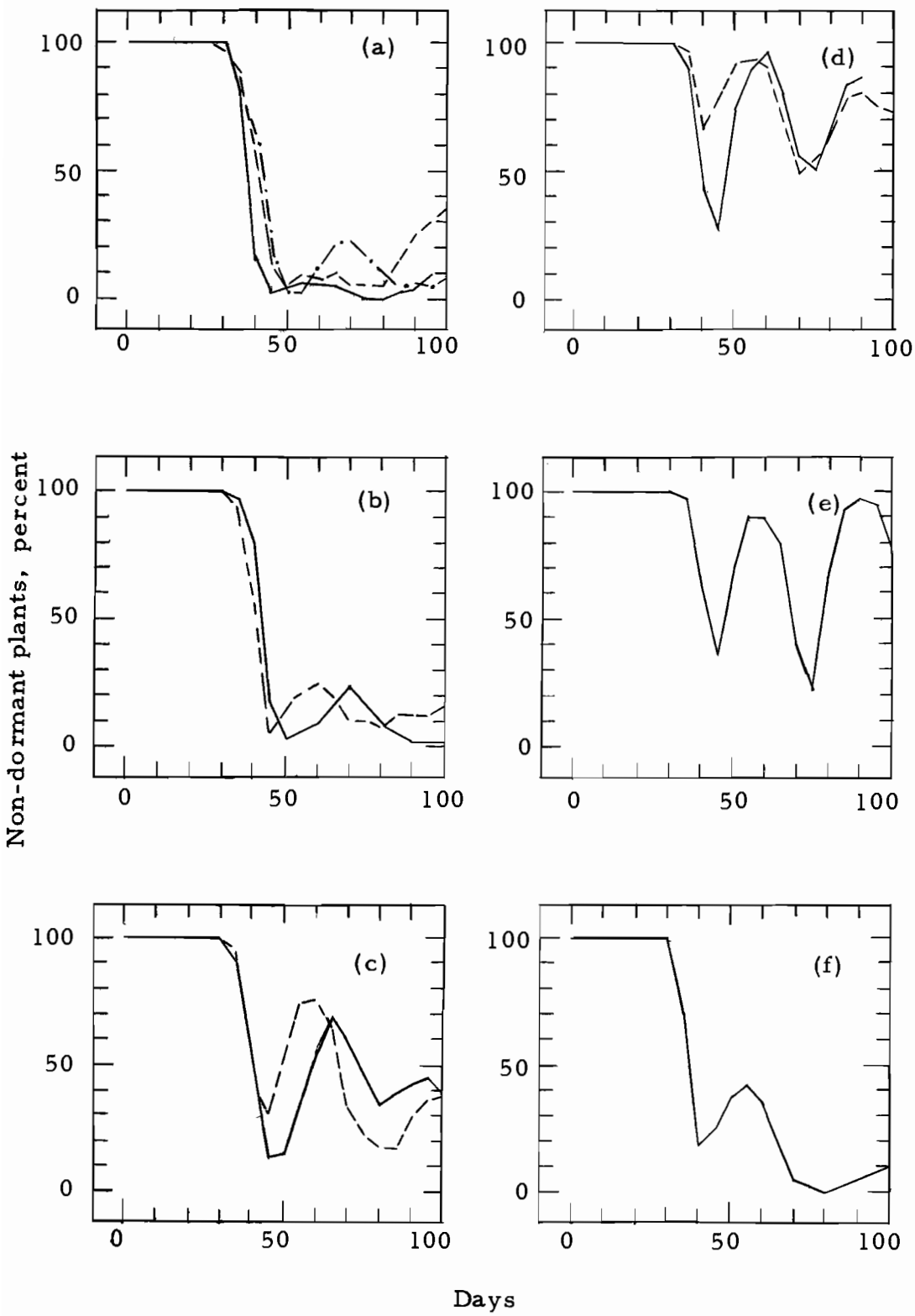
Salmon Arm plants exposed to red light two hours before or after the middle of the dark period also entered dormancy at age 35 days (Figure 3d). Numerous plants resumed growth shortly after entering dormancy. Since the infrequency of growth renewal was only slightly lower than that of cessation, activity decreased gradually in comparison to the rapid reductions noted for the other treatments. Minimum activities ranging from 53 to 65 percent were reached between ages 70 and 75 days (Figure 3d). Additional growth renewals increased activity to 60 and 72 percent at age 90 days under the treatments given two hours after and before the center of the dark period, respectively. Only 17 percent of the plants remained in the first period of dormancy at that time, while an average of 26 and 24 percent were in the second

period of active growth and in active and dormant periods beyond that, respectively.

Salmon Arm plants given red light at the center of the dark period began to enter dormancy at age 40 days (Figure 3e), five to ten days later than in all other experiments. Minimum activity (39 percent) was not reached until age 70 days. This minimum was considerably lower than when exposures were given two hours before or after the middle of darkness. In addition, nearly all of the plants that went dormant resumed growth within 20 days (Figure 3e). Activity at age 90 days (91 percent) exceeded that observed under all other treatments. At that time, only 8 percent of the plants were in the first period of dormancy, while 61 percent had broken the first dormancy and were in the second period of active growth. Only 13 percent of the plants entered or broke the second dormancy.

The response of Salmon Arm plants to red light given during the light period did not differ from that to the uninterrupted dark period (Figure 3f).

Coconino plants grown under the uninterrupted dark period began to enter dormancy at age 35 days (Figure 4a). Minimum levels of activity (two to four percent) were reached 10 to 15 days later. At age 90 days, activity varied from 4 to 26 percent. At that time, the majority of the plants (64 to 88 percent) had not broken the first dormancy, whereas only about one percent had broken the second.


(a)
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100
50
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50
100
Non-dormant plants, percent
Days

Coconino plants given red light immediately after the beginning or before the end of the dark period entered dormancy at the same time (age 35 days) as control plants (Figure 4b). Minimum activities of five and three percent were reached at age 45 and 50 days. A frequency of growth resumption larger than that in the controls increased activity to approximately 24 percent between ages 60 and 70 days. A large proportion of these plants subsequently entered a second period of dormancy. By age 90 days, activity was reduced to an average of seven percent. Approximately 73 percent of the plants were in the first period of dormancy and 4 percent had broken the second period of dormancy at that time.

Coconino plants exposed to red light two hours after the beginning or before the end of darkness entered dormancy at age 35 days (Figure 4c). Minimum activities ranging from 14 to 31 percent were reached at age 45 days. A large proportion of the plants quickly broke dormancy thereby increasing activity to about 73 percent between ages 60 and 65 days (Figure 4c). The frequency of growth renewal exceeded that observed in the tests previously described. Subsequently, the plants entered a second period of dormancy. By age 80 or 85 days, activity was reduced to second minima of 17 and 34 percent (Figure 4c). This second period of dormancy was broken by fewer plants than the first. At age 90 days, activity varied from 28 to 43 percent. Thirteen to 20 percent

of the plants had not broken their first dormancy at that time, whereas 18 to 24 percent had broken their second dormancy.

Coconino plants given red light two hours before or after the middle of the dark period began to enter dormancy at age 35 days (Figure 4d). Minimum activities were reached by age 45 days and varied from 26 to 66 percent. A high frequency of growth renewal increased activity to a mean of 95 percent between ages 50 and 60 days (Figure 4d). A second minimum level of activity (about 50 percent) was reached between ages 70 and 75 days. This second period of dormancy was also broken by large numbers of plants as shown by the second increase in activity to a mean of 84 percent at age 90 days (Figure 4d). By that time, nearly all of the plants had broken their first dormancy and approximately 56 percent had broken their second dormancy.

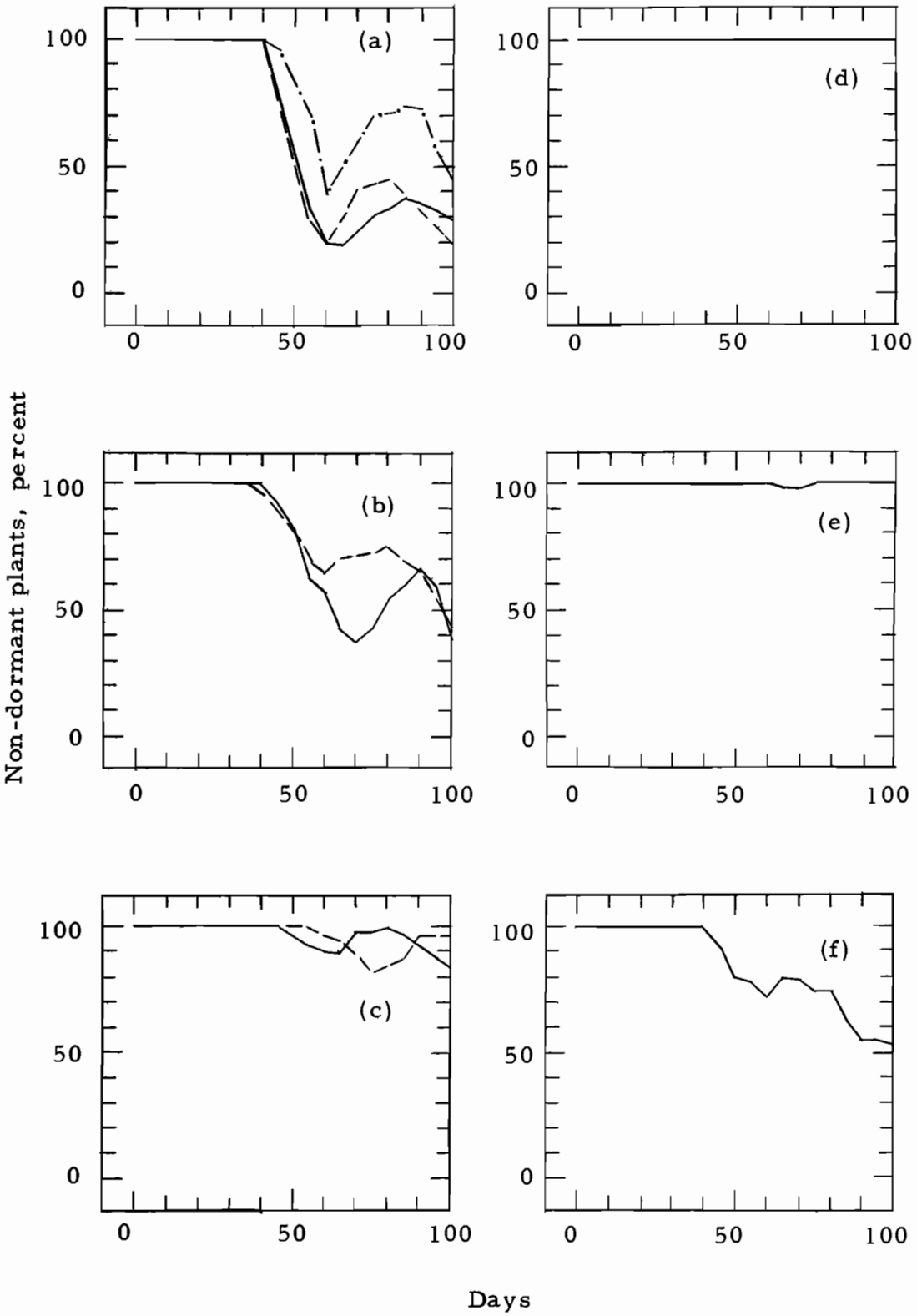
Coconino plants exposed at the center of darkness entered dormancy at the same time (age 35 days) as plants from the other tests (Figure 4e). Minimum activity (38 percent) was reached at age 45 days. Within 15 days, large numbers of plants broke dormancy and increased activity to 91 percent. Most of these plants subsequently entered a second period of dormancy and activity dropped to 22 percent at age 75 days (Figure 4e). Subsequently, numerous plants broke both the first and second dormancies, increasing activity to a second maximum of 97 percent at age 90 days.

This maximum occurred earlier and was larger than under most other treatments. By age 90 days, 69 percent of the plants had broken their second dormancy.

Coconino plants given red light two hours before the middle of the light period began to enter dormancy at age 35 days (Figure 4f). Minimum activity (18 percent) was reached at age 40 days. Within 15 days, growth renewals increased it to 42 percent. The number of plants that broke the first dormancy was considerably larger than in the controls. After age 55 days, most of the plants went dormant again and activity gradually declined to five percent at age 90 days (Figure 4f). At that time, 52 percent of the plants had not broken the first dormancy and practically none the second.

Vancouver plants grown under uninterrupted dark periods began to enter dormancy at age 40 days (Figure 5a). Minimum levels of activity were reached in all three tests at age 60 days and ranged from 18 to 39 percent. The considerable number of seedlings which remained active throughout the experiment and which resumed growth resulted in activities varying from 33 to 73 percent at age 90 days (Figure 5a). The number of plants that remained active until that time ranged from 9 to 27 percent.

When red light was given immediately after the beginning or before the end of the dark period, the onset of dormancy occurred at the same time (age 40 days) as in the controls (Figure 5b).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50
0
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50
100
Non-dormant plants, percent
Days

Minimum activities of 65 and 38 percent were reached at about age 65 days. Percentage activity at age 90 days was 66 percent as compared to the generally lower values of the controls. Forty-nine and 23 percent of the plants exposed near the beginning or near the end of darkness, respectively, remained active throughout the experiment.

Exposures given two hours after the start or before the end of the dark period caused Vancouver plants to enter dormancy at about age 55 days (Figure 5c), 15 days later than the control plants. While the majority of plants remained active, small numbers entered dormancy at irregular intervals. At age 60 days, 91 to 96 percent of the plants were active in contrast to the low levels of the controls. Although the timing and frequency of growth renewal varied somewhat between tests, activity was increased to about 94 percent at age 90 days in both cases (Figure 5c). The percentage of plants that had remained active until that time varied from 76 to 82 percent.

Vancouver plants largely remained active when exposed to red light two hours before, two hours after, or at the middle of the dark period (Figure 5d and e). Less than five percent of these plants went dormant and these few resumed growth within 15 days. All plants were active at both age 60 and 90 days (Figure 5d and e).

Vancouver plants given red light during the light period began to enter dormancy at age 40 days (Figure 5f), the same time as

control plants. At age 60 days, activity was 72 percent as compared to 100 percent when exposures were given at a comparable time during darkness and 18 to 39 percent in the controls. Further growth cessations decreased activity to 56 percent at age 90 days (Figure 5f). Forty-eight percent of the plants remained active throughout the test.

According to these results, exposure to 30 minutes of red light during the dark period increased the number of active plants and the duration of growth above the levels of controls. However, the several treatments affected plants from each source differently. Salmon Arm plants exposed at or near the center of darkness went dormant later than controls or plants given red light near the ends of the dark period. In addition, fewer plants went dormant and greater numbers broke dormancy under exposures given near the middle of darkness. Responses to exposures at or near the center differed much more from those of controls than did those to exposures at other times. The frequency and regularity of growth cessation and renewal when exposures were given at the center of darkness exceeded that under exposures two hours before or after the center. Consequently, this treatment increased the uniformity of response in addition to delaying dormancy and increasing activity to the greatest extent.

Unlike plants from the other sources, Coconino plants entered the first dormancy in large numbers and at the same age irrespective

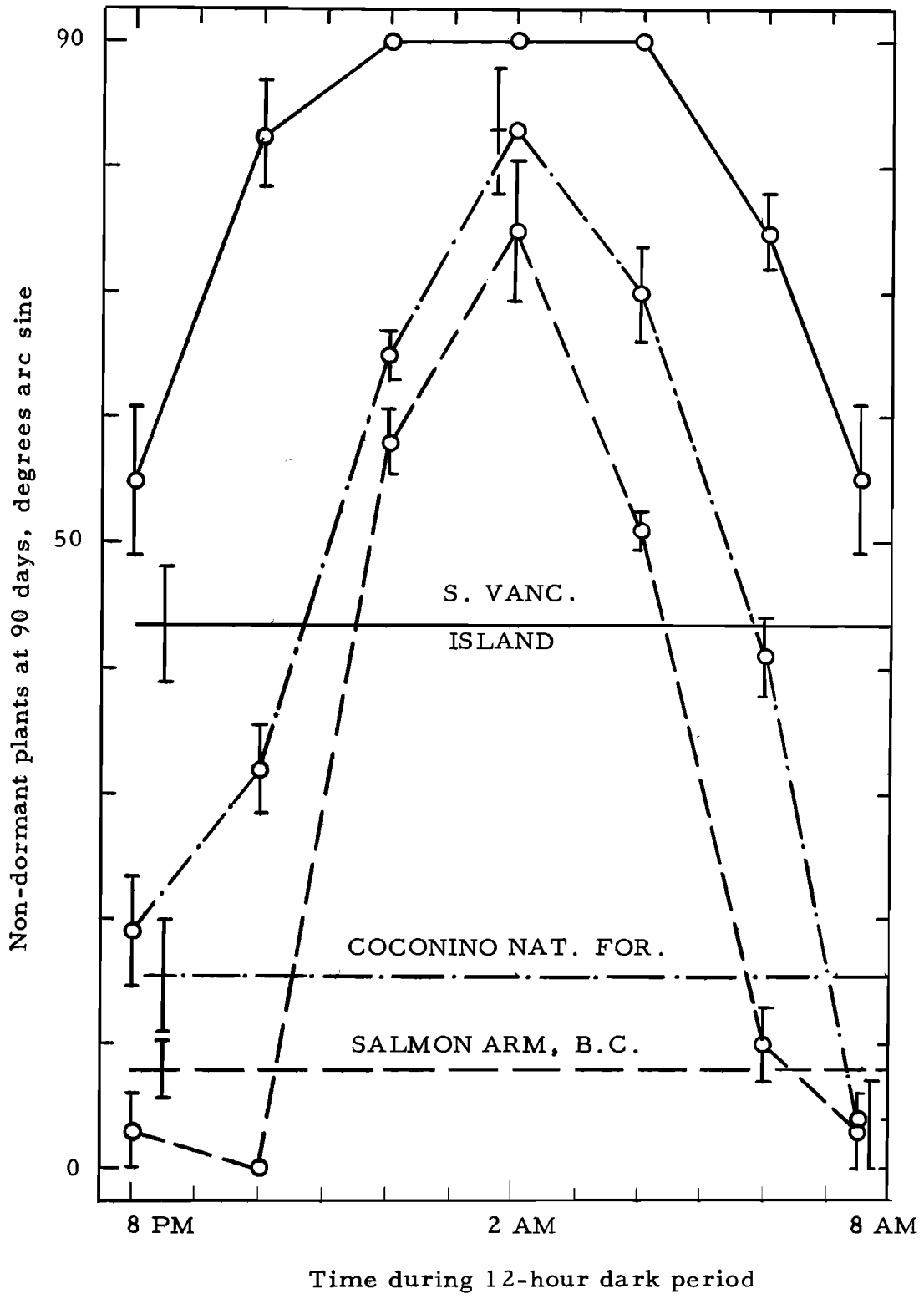
of treatment. While few plants broke dormancy in the controls or when exposures were given near the ends of the dark period, variable numbers of plants entered and broke two consecutive dormancies in the other tests. The number of plants involved, the number of recurrent active periods, and the synchrony of response increased as the time of exposure approached the center of the dark period. Aside from Salmon Arm plants exposed at the center of darkness, intermittent growth was common only to Coconino plants. The responses of Coconino plants differed less between treatments than those of Salmon Arm plants, but more than those of Vancouver plants.

Regardless of treatment, Vancouver plants went dormant later than plants from the two continental sources. Exposure to red light delayed the onset of dormancy and the delay increased as the time of exposure neared the middle of the dark period. Fewer plants went dormant and larger numbers resumed growth when red light was given than in the controls. Unlike plants from the continental sources, those from Vancouver tended to remain active. Maximum numbers of plants remained active when exposed at or near the center of the dark period. However, increases in response as exposure times neared the center were gradual as compared to the larger differences noted for Salmon Arm and Coconino plants.

The response of Salmon Arm plants to red light given during

the light period was identical to that of controls. As evidenced by the larger number of plants resuming growth, Coconino plants exhibited a greater response than Salmon Arm plants. The response of Coconino plants resembled that to exposure at the ends of the dark period. Although exposure during the light period did not delay dormancy, fewer Vancouver plants went dormant than in the controls. The number of plants remaining active throughout the test approximated that when exposures were given at the ends of the dark period. In this sense, the response of Vancouver plants exceeded those of plants from the other sources. Generally, exposure during the light period had effects similar to those during darkness.

Differences between treatment effects within seed sources and between the responses of plants from each source were examined further by comparing percentages of activity at a given age. The percentage of active Salmon Arm and Vancouver plants changed only slightly between age 85 and 95 days (Figure 3 and 5). Coconino plants were either at constant levels of activity or near the peak of their second growth renewal at age 90 days (Figure 4). Consequently, comparisons were made at age 90 days. Percentage activity was converted to degrees arc sine, averaged over the four replications of each treatment, and plotted against the time during the dark period at which the exposure occurred (Figure 6). Despite variation among the responses of control plants, the three controls


90
50
0
Non-dormant plants at 90 days, degrees arc sine
S. VANC.
ISLAND
COCONINO NAT. FOR.
SALMON ARM, B.C.
8 PM
2 AM
8 AM
Time during 12-hour dark period

of each source were pooled.

This method of analysis confirmed that maximum response occurred when red light was given at the center of the dark period (Figure 6). Moreover, response decreased in a symmetrical manner as the time of exposure departed from the center of the dark period. For example, the percent of Coconino plants active when the exposure was given two hours before the middle of the dark period (81 percent) was essentially equal to that when the exposure occurred two hours after the center (87 percent). The curve shapes and positions confirmed that the pattern of response varied among sources.

The nature of the observed responses clearly resembles those of plants from the same sources to 16-hour photoperiods (Irgens-Moller, 1968). Consequently, exposure to red light did produce magnitudes of Pfr action approximating those produced by longer photoperiods. The symmetry of the curves in Figure 6 indicates that the level of Pfr activity increased as the time at which the exposure was given approached the center of the dark period. Presumably, each exposure produced similar amounts of Pfr, but the quantity ultimately involved in mediating response depended upon the length of darkness available for subsequent dark conversion to the inactive Pr form. Consequently, each exposure appeared to divide the 12-hour dark period into two periods, the longest of which

governed the onset and breaking of dormancy.

Comparisons between the responses to various lengths of uninterrupted darkness provided a useful method for evaluating differences between the responses of the three sources. The arc sine values representing activity at age 90 days were subjected to single-factor analyses of variance. Treatments in which replications had equal responses were excluded as their variances were zero.

In each of the three analyses, light treatment effects were highly significant (Appendix, Tables 1 to 3). Calculated LSD values (one percent level) were used to test differences between treatment means. The responses of Salmon Arm plants to any two exposure times symmetrical about the center of the dark period were equal (Table 3). However, response to 6 hours of uninterrupted darkness significantly exceeded that to dark periods 7.5 hours or longer. The effects of 7.5- and 8-hour periods were greater than those of longer dark periods. Responses to dark periods from 9.5 to 12 hours long were the same.

The responses of Coconino plants exposed at any two times symmetrical about the center of darkness did not differ (Table 3). Uninterrupted intervals of darkness varying from 6 to 8 hours in length had similar effects. However, responses to these treatments significantly exceeded those of dark periods 9.5 hours and longer. Consistent differences were not found between responses to dark

Table 3. Effect of dark period length upon the percentage of non-dormant plants at age 90 days. Data transformed to degrees arc sine.[1]

Seed source	Hours of uninterrupted darkness				
	6.0	7.5 8.0	9.5 10.0	11.5	12.0
Salmon Arm	75.00	(57.97)[3] (51.06)	0.00[2] 9.47	2.88 3.01	11.98 12.20 0.00[2]
Calculated LSD (1%) = ±13.38					
Coconino	82.66	64.61 69.99	(31.80) (40.77)	19.00 4.11	14.65 26.42 5.90
Calculated LSD (1%) = ±19.06					
Vancouver	90.00[2]	90.00[2] 90.00[2]	82.40 (74.80)	(54.84) (55.07)	(59.21) (33.72) (36.14)
Calculated LSD (1%) = ±20.19					

1 Observations are means of four replications, each containing an average of 23 plants.

2 Observation excluded from analysis.

3 Brackets denote the shortest dark period that significantly reduced activity below the level of the six-hour interval.

periods varying from 9.5 to 12 hours.

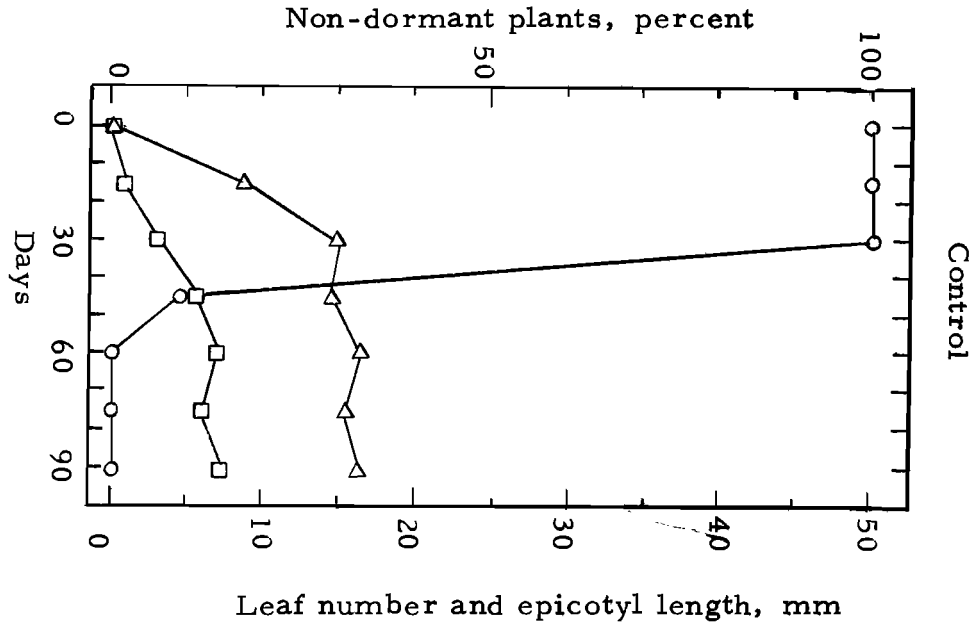
The responses of Vancouver plants to any two exposure times symmetrical about the middle of the dark period were equal. Although responses to 6-, 7.5-, and 8-hour dark periods were excluded from the analysis, they did not appear to differ significantly from those to 9.5- and 10-hour intervals. However, the effect of the 9.5-hour dark period exceeded those of longer periods of darkness. As a result of variation among the responses of control plants, consistent differences were not found between responses to dark periods 11.5 hours and longer.

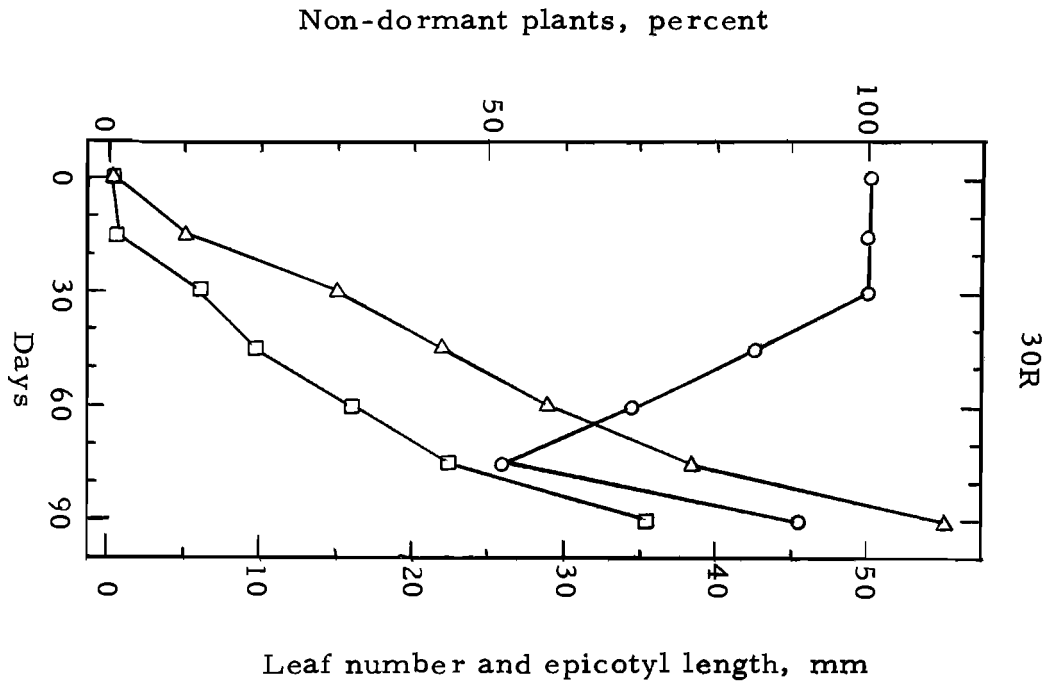
Differences among the responses of Salmon Arm plants to the shorter dark periods exceeded those for the other sources. Intervals of uninterrupted darkness as short as 7.5 or 8 hours significantly reduced the activity of Salmon Arm plants below the level observed under the shortest dark period. The responses of Coconino plants did not differ as greatly as those of Salmon Arm plants, but varied more than those of Vancouver plants. The length of darkness which clearly inhibited the active growth of Coconino plants was about 10 hours, two hours longer than that for Salmon Arm plants. Unlike the responses of Coconino and Salmon Arm plants, those of Vancouver plants increased gradually as the length of uninterrupted darkness decreased. A 10- or 12-hour dark period was the shortest interval that significantly reduced activity.

Epicotyl Elongation and Leaf Production. In Douglas-fir germinants, the apical meristem simultaneously forms leaves and elongates as the growing season progresses (Allen, 1947). Consequently, epicotyl length and leaf number would seem dependent upon the duration of active growth. As noted previously, duration of growth was inversely related to the length of the longest uninterrupted dark period. One would therefore expect a similar relationship for epicotyl length and leaf number. These hypothesized relationships were examined by periodically measuring increases in epicotyl length and leaf number and by taking similar measurements at age 100 days.

In the first instance, one group of Salmon Arm plants was grown under uninterrupted dark periods, while a second received red light at the center of the dark period. The groups consisted of four replications, each containing 23 plants. At 15 day intervals, three plants were chosen at random, cut off at the soil surface, and measured. Data are presented in Figure 7. Populations given similar treatments supplied data on trends in percentage activity (Table 2).

On or shortly after the day that control plants began to enter dormancy (age 35 days) both epicotyl elongation and leaf production ceased (Figure 7). Although plants given red light also entered dormancy at age 35 days, fewer plants were involved (Figure 7).


Non-dormant plants, percent
0
50
100
Days
0
30
60
90
0
10
20
30
40
50
Control
Leaf number and epicotyl length, mm


Non-dormant plants, percent
0
50
100
Days
0
30
60
90
0
10
20
30
40
50
30R
Leaf number and epicotyl length, mm

Most of these plants broke dormancy between ages 75 and 90 days. The epicotyl lengths and leaf numbers of plants given red light continued to increase throughout the test. Consequently, epicotyl length and leaf number were directly related to the duration of growth and inversely related to the length of the dark period.

(a) Epicotyl Elongation: The relationship between epicotyl length at age 100 days and the length of the dark period was examined for each seed source (Table 4). A two-factor analysis of variance (Appendix, Table 4) showed that seed source, treatment, and interaction effects were highly significant. Calculated LSD values (one percent level) were used to test differences between treatments.

The epicotyl lengths of Salmon Arm plants given dark periods of approximately equal length did not differ significantly (Table 4). However, responses to 6- or 8-hour periods were significantly greater than those to dark periods 9.5 hours or longer. Differences among plants grown under dark periods varying from 9.5 to 12 hours or given red light during the light period were not significant.

Coconino plants given equal lengths of darkness grew to similar heights (Table 4). Response to 6- and 8-hour dark periods significantly exceeded that to 11.5 and 12 hours of darkness. However, responses to the former treatments did not differ from that to 9.5- and 10-hour dark periods. A consistent pattern of differences was not found between dark periods longer than 9.5 hours. Response to

Table 4. Effect of dark period length upon epicotyl length (mm) at age 100 days.[1]

Seed source	Hours of uninterrupted darkness					
	6.0	7.5 8.0	9.5 10.0	11.5	12.0[2]	12.0
Salmon Arm	44.2	44.2	(13.6)[3]	11.0		9.3
		40.4	(14.2)	8.3	10.2	9.0
						7.0
Coconino	22.7	23.2	16.4	(7.4)		(6.7)
		25.8	20.9	(5.4)	8.7	(9.1)
						(4.4)
Vancouver	78.7	71.0	81.4[4]	(53.9)		(48.8)
		78.8	87.3[4]	(38.4)	58.4	(28.2)
						(23.9)
	Calculated LSD (1%) = ±13.4					

1 Observations are means of four replications, each containing ten plants.

2 The dark period was 12 hours long in this treatment, but 30 minutes of red light were given 4 hours after the beginning of the light period.

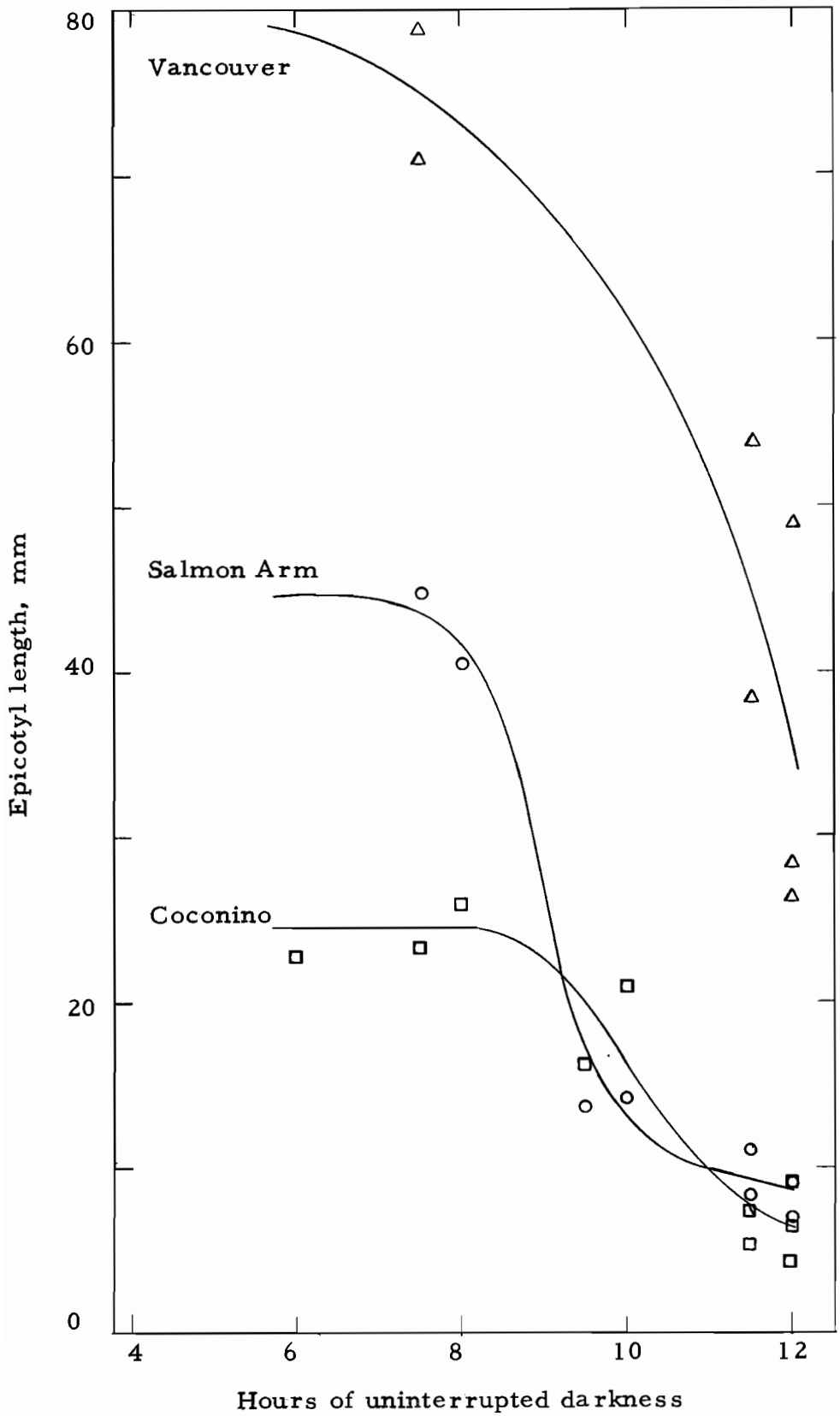
3 Brackets denote the shortest dark period that significantly reduced growth below the level under six hours of darkness.

4 Vancouver plants given these treatments grew 10 to 20 days longer than other plants and were excluded from the analysis.

red light given during the light period was not significantly different from that to the longer dark periods.

The epicotyl lengths of Vancouver plants given 6- to 8-hour dark periods were similar, but significantly greater than those of plants given 11.5 and 12 hours of darkness (Table 4). Since plants given 9.5- and 10-hour dark periods were harvested 10 to 20 days after all other plants, their responses were not included in the analysis. Consistent differences were not found between the heights of plants given 11.5- and 12-hour dark periods. Response to red light given during the light period was equal to or slightly larger than that to 11.5- and 12-hour dark periods.

Generally, the epicotyl lengths of Vancouver plants exceeded those of plants from the interior sources. Salmon Arm and Coconino plant heights differed only when dark periods were about ten hours long. Irrespective of source, epicotyl elongation increased as the length of uninterrupted darkness decreased. These findings inferred that the significant interaction term (Appendix, Table 4) resulted from variation between sources in the degree of response. When data from Table 4 were plotted against dark period length (Figure 8), the nature of the interaction became apparent. Changes in the response of Salmon Arm plants were abrupt and clearly-defined. Coconino plants exhibited a response pattern similar to that of Salmon Arm plants, but changes in response were more gradual. While Vancouver plants had the greatest range of response, the increases caused by successively shorter dark periods were more gradual than for the other two sources. The shortest dark period that significantly reduced epicotyl length below that produced by the 6-hour dark period was


80
60
40
20
0
Vancouver
Salmon Arm
Coconino
Epicotyl length, mm
4
6
8
10
12
Hours of uninterrupted darkness

shortest for Salmon Arm plants (9.5 or 10 hours), intermediate for Coconino plants (11.5 to 12 hours), and longest for Vancouver plants (11.5 or 12 hours).

(b) Leaf Production: Leaf numbers were determined by counting fully-elongated leaves exclusive of the terminal tuft and lateral branches on ten plants from each replication. A two-factor analysis of variance demonstrated that source, treatment, and interaction effects were highly significant (Appendix, Table 5). Calculated LSD values (one percent level) were used to test differences between treatments.

The leaf numbers of Salmon Arm plants given dark periods of approximately equal length did not differ significantly (Table 5). Leaf production by plants given 6- to 8-hour dark periods significantly exceeded that under 9.5-hour or longer dark periods. Differences among the responses of plants given dark periods varying from 9.5 to 12 hours or given red light during the light period were not significant.

Coconino plants given equal length dark periods had similar leaf numbers (Table 5). Significant differences were not found between responses to dark periods varying from 6 to 10 hours. However, leaf number in these cases significantly exceeded that under 11.5 and 12 hours of darkness. No significant increase above that for 11.5- and 12-hour dark periods occurred when red light was given during the light period.

Aside from the variation between controls, the leaf numbers of Vancouver plants grown under equal length dark periods were similar (Table 5). Leaf production under 6- or 8-hour dark periods significantly exceeded that under 11.5 or 12 hours of darkness. Data

Table 5. Effect of dark period length upon leaf production at age 100 days.[1]

Seed source	Hours of uninterrupted darkness					
	6.0	7.5 8.0	9.5 10.0	11.5	12.0[2]	12.0
Salmon Arm	55.8	49.2	(23.2)[3]	21.1	19.5	19.8
		49.3	(23.1)	18.9		20.2
						18.5
Coconino	49.3	46.4	42.7	(22.5)	24.4	23.7
		49.8	44.1	(22.4)		28.6
						17.6
Vancouver	74.2	62.8	78.2[4]	(60.5)	54.4	(56.1)
		68.0	74.8[4]	(51.4)		(45.0)
						(36.5)
	Calculated LSD (1%) = ±11.6					

1 Observations are means of four replications, each containing ten plants.

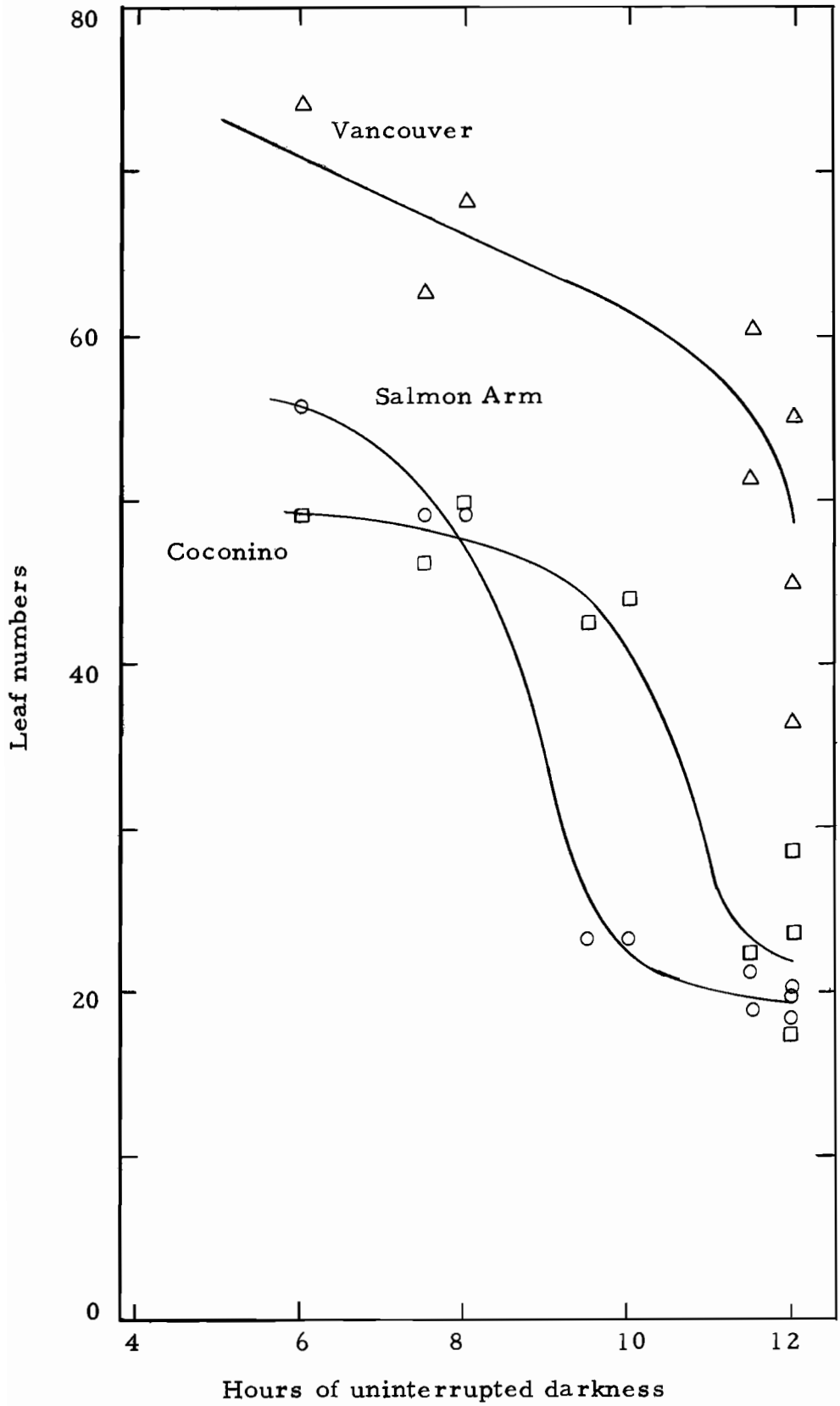
2 The dark period was 12 hours long in this treatment, but 30 minutes of red light were given four hours after the beginning of the light period.

3 Brackets denote the shortest dark period that significantly reduced leaf production below the level under six hours of darkness.

4 Vancouver plants given these treatments grew 10 to 20 days longer than other plants and were excluded from the analysis.

from the 9.5- and 10-hour tests were not analyzed. A consistent pattern of significant differences between dark periods varying from 7.5 to 12 hours was not apparent. However, response appeared to increase by relatively small, but variable increments with each successive reduction in dark period length. Response to red light given during the light period was generally equal to that for dark periods ranging from 7.5 to 12 hours.

Irrespective of treatment, Vancouver plants had more leaves than plants from the other sources. The responses of Salmon Arm and Coconino plants were similar except under 9.5- and 10-hour dark periods. Regardless of source, leaf production increased as the length of the longest uninterrupted dark period decreased. The pattern of response for each seed source (Figure 9) indicated that the significant interaction term (Appendix, Table 5) was caused by differences in the degree of response. Salmon Arm plants exhibited large, abrupt increases in leaf number (Figure 9). On the other hand, leaf production by Vancouver plants increased gradually. The response of Coconino plants was intermediate. The shortest dark period that significantly reduced leaf number below that under the 6-hour dark period was shortest for Salmon Arm plants (9.5 or 10 hours), intermediate for Coconino plants (11.5 hours), and variable, but longest for Vancouver plants (11.5 or 12 hours).


80
60
40
20
0
Leaf numbers
Vancouver
Salmon Arm
Coconino
4
6
8
10
12
Hours of uninterrupted darkness

(c) Sensitivity Ratios: Regardless of the response measured, consistent differences were found among sources in the degree of response to particular treatments and the pattern of response over the various treatments. Numerical expressions of these differences were obtained by calculating a sensitivity ratio for each source (Vaartaja, 1959). Ratios were calculated by dividing the epicotyl length and leaf number of plants given interrupted dark periods by that for control plants. Since maximum response occurred under six-hour dark periods, data from that test and the concurrently-performed control were used (Table 6).

Sensitivity ratios larger than unity denote a positive or stimulatory effect. A large ratio indicates a large difference between responses and high sensitivity. Salmon Arm plants were the most sensitive to red light and changes in the length of the dark period (Table 6). In agreement with earlier conclusions, Coconino plants were intermediate in sensitivity and Vancouver plants were least sensitive.

Leaf Elongation. Previous analyses demonstrated that epicotyl length and leaf number increased as the length of the longest uninterrupted dark period decreased and that the pattern of response depended upon seed source. Differences in response to 30 minutes of red light were further examined in terms of leaf elongation. Measurements were made on plants given red light four hours after the

Table 6. Sensitivity of epicotyl elongation and leaf production to thirty minutes of red light given at the center of a twelve-hour dark period.

Seed Source	Epicotyl Elongation (mm)					Leaf Production				
	Treatment				Sensitivity ratio 30 R/ control	Treatment				Sensitivity ratio 30 R/ control
	30 R		Control			30 R		Control		
	Mean	Std error of mean	Mean	Std error of mean		Mean	Std error of mean	Mean	Std error of mean	
Salmon Arm	44.2	±2.5	7.0	±0.4	6.3	55.8	±2.5	18.5	±0.4	3.0
Coconino	22.7	±0.8	4.4	±0.4	5.2	49.3	±1.1	17.6	±0.8	2.8
Vancouver	78.7	±2.7	23.9	±5.0	3.3	74.2	±3.0	36.5	±3.9	2.0

beginning of darkness (12 PM), given a similar exposure four hours after the beginning of the light period (12 AM) and grown in a concurrent control test (Table 7). Fully-elongated leaves were measured to the nearest mm.

A two-factor analysis of variance showed that seed source and treatment effects were significant at the one percent level, while the interaction term was significant at the five percent level (Appendix, Table 6). Differences between treatments were tested with calculated LSD values (one percent level).

Table 7. Effect of red light upon leaf length (mm) at age 100 days.[1]

	Treatment		
Seed Source	Red Exposure at 12 PM	Red Exposure at 12 AM	Control
Salmon Arm	18.7	15.6	15.1
Coconino	15.8	13.9	13.2
Vancouver	23.8	23.6	22.5

Calculated LSD (1%) = 2.1

[1]Observations are means of four replications, each containing ten plants.

Exposure to red light during darkness significantly increased the leaf lengths of Salmon Arm and Coconino plants (Table 7). This treatment did not increase the leaf length of Vancouver plants. Irrespective of source, exposure to red light during the light period did

not significantly affect leaf length. As in the case of epicotyl length and leaf number, Salmon Arm plants were the most responsive.

Résumé. Irrespective of seed source, the duration of growth and leaf production of plants given red light at or near the center of the dark period resembled those of plants grown under 16-hour photoperiods (Irgens-Moller, 1962 and 1968). These results support the hypothesis advanced earlier that exposure to red light would produce magnitudes of Pfr action approximating those of longer photoperiods. Since the responses observed in the present study varied with the length of uninterrupted darkness, the data suggest that each exposure produced equal amounts of Pfr and that dark conversion diminished this quantity to that amount ultimately active in the biochemical and physiological reactions underlying the differing responses. One might then conclude that each source required a particular concentration of Pfr for continued growth. This interpretation seems reasonable in view of results reported by Hendricks and Borthwick (1963).

However, the present data do not exclude a number of other possible explanations from consideration. For example, the dependence of response upon the length of uninterrupted darkness may indicate that the required amount of Pfr must be present a specific length of time in order to produce a given response. Furthermore, the differing responses of plants from the three sources to

exposures of equal duration and timing could indicate that the rate of dark conversion or the catalytic efficiency of a given quantity of Pfr differs among sources. On the other hand, diurnal variation in phytochrome sensitivity seems an unrealistic explanation since the same type of response was observed regardless of whether the exposure was given during the light or dark period.

Although several of the alternative explanations cannot be distinguished between with certainty on the basis of the present data, the different responses and variation in them can be attributed to a common factor, the relative or apparent level of Pfr activity. Thus, the degree of response, whether measured as the duration of growth, the percentage of active plants at a given age, epicotyl length, leaf number, or leaf length, reflects the level of Pfr activity produced by each treatment. Similarly, the response pattern and sensitivity of each source reflect the level of Pfr activity required for growth and the relative importance of changes in Pfr activity.

The level of Pfr activity required for the continued growth of Salmon Arm plants, as evidenced by the lack of response to long dark periods (8 to 12 hours), exceeds that required by Coconino and Vancouver plants. The large, abrupt changes in response and the high sensitivity of Salmon Arm plants demonstrate a requirement for a high and sharply-defined or threshold level of Pfr activity. Levels of Pfr activity below this threshold are clearly inadequate

and levels above it tend to yield responses of relatively the same magnitude. Coconino plants apparently require an intermediate level of Pfr activity, but resemble Salmon plants in that a threshold level, although somewhat less pronounced, seems evident. On the other hand, the relatively uninhibited growth of Vancouver plants under longer dark periods demonstrates that their requirement for Pfr activity was the lowest. The rather gradual increases in response as the length of darkness was decreased and the low sensitivity of Vancouver plants indicate that these plants did not have as critical a requirement as the other sources.

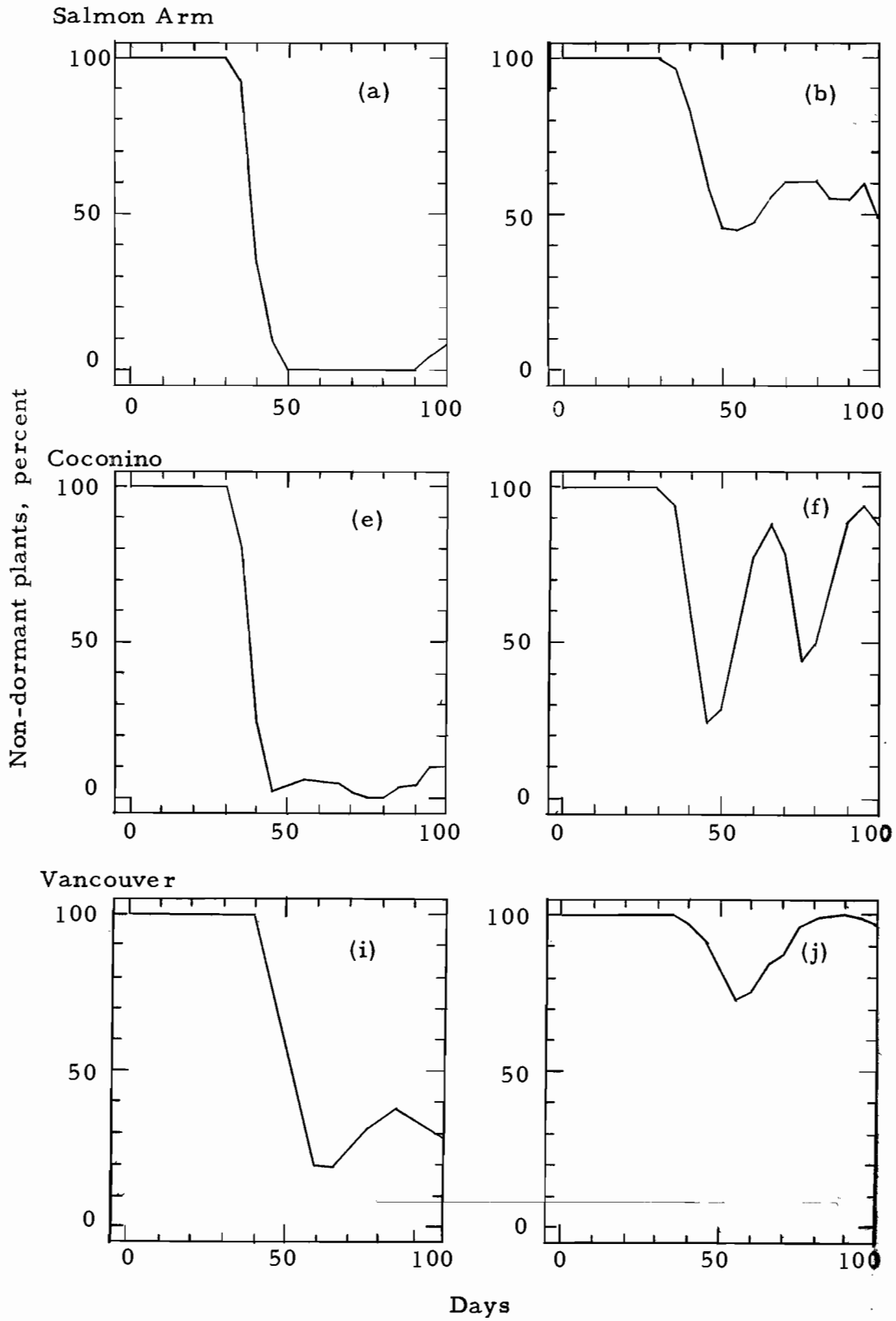
Effect of Two- and Fifteen-Minute Exposures

Regardless of seed source, maximum responses to red light were observed when the interruptions were given at the middle of the dark period, that is, when the longest uninterrupted dark period was six hours long. Presumably, exposure to red light at such times increased Pfr activity to levels approximating those maintained during the short dark period complementary to long photoperiods. One would therefore expect shorter or less energetic exposures given at the same time to produce lower levels of Pfr activity and cause weak red effects. Correspondingly, any differences among seed sources with respect to the minimum required level of Pfr activity would also become evident.

To test these hypotheses, it was most practicable to vary exposure length. The 2- and 15-minute exposures employed were given such that the longest period of continuous darkness was six hours long (Table 2). Since both experiments were performed shortly after both a control and the 30-minute test, comparisons could be made among all experiments.

Salmon Arm plants given the 2-minute exposure began to enter dormancy at the same time (age 35 days) as the controls (Figure 10a and b). Minimum levels of activity were also reached at a similar time (age 55 days) but the level in the 2-minute experiment (45 percent) exceeded that in the control (zero percent). Under the 2-minute treatment, frequent, but irregularly occurring growth renewal increased activity to 61 percent at about age 75 days (Figure 10b). Although activity declined to 55 percent at age 90 days, 32 percent of the plants were in their second period of active growth.

Under the 15- and 30-minute exposures, Salmon Arm plants began to enter dormancy at age 40 days (Figure 10c and d). Although minimum activities were reached at similar times under the 2- and 15-minute treatments, the latter exposure reduced activity to a lower level, 38 percent, as compared to 45 percent (Figure 10b and c). Minimum activity (39 percent) in the 30-minute test was not reached until age 70 days (Figure 10d), 15 to 20 days later than in all other experiments. The frequency of growth renewal exceeded that of both


Salmon Arm
Coconino
Vancouver
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
100
50
0
0
50
100
Non-dormant plants, percent
Days

the 2- and 15-minute treatments. Activity at age 90 days was 75 and 91 percent under the 15- and 30-minute exposures, respectively. Sixty-one percent of the plants given 30-minute exposures were in their second period of active growth as compared to 49 percent for the 15-minute treatment.

Coconino plants given the 2-minute and control treatments began to enter dormancy at age 35 days (Figure 10e and f). Minimum activities of 24 and 2 percent, respectively, were reached at age 45 days. By age 65 days, 88 percent of the plants given red light were active again (Figure 10f). Subsequently, a second period of dormancy occurred and activity decreased to 44 percent at age 75 days. Growth renewal of plants in both the first and second periods of dormancy increased activity to 89 percent at age 90 days. At that time, 67 percent of the plants had broken their second dormancy, whereas 88 percent of the controls had not yet broken their first dormancy.

Coconino plants under the 15- and 30-minute exposures also entered dormancy at age 35 days (Figure 10g and h). Minimum activity (50 percent) was reached at age 50 days in the 15-minute experiment as compared to 30 percent at age 45 days under the longer exposure. In the 15-minute test, numerous plants broke dormancy, thereby increasing activity to 83 percent at age 70 days. By age 85 days, some of these plants entered a second period of dormancy and activity decreased to 60 percent (Figure 10g).

Irregular growth renewal increased activity to a high of 83 percent at age 100 days, slightly after maxima were reached in the 2- and 30-minute tests. Generally, the frequences of growth cessation and renewal were greatest under the 30-minute treatment. At the end of the experiments, 50 and 69 percent of the plants had broken their second dormancy under the 15- and 30-minute exposures, respectively.

Vancouver plants given two minutes of red light began to enter dormancy at the same time (age 40 days) as controls (Figure 10i and j). However, minimum activity (73 percent at age 55 days) was both greater and reached earlier in the 2-minute test than in the control (18 percent at age 65 days). In addition, growth renewal under the 2-minute treatment increased activity to 100 percent at age 90 days as compared to 35 percent in the control (Figure 10i and j). Fifty-nine percent of the former plants remained active throughout the test, whereas only nine percent of the controls did.

Vancouver plants exposed to 15 minutes of red light entered dormancy in smaller numbers (two percent) and at a later time (age 55 days) than those given the 2-minute or control treatments (Figure 10k). All plants broke dormancy by age 75 days and remained active thereafter. Ninety-eight percent were active throughout the test. The effects of the 15- and 30-minute exposures were identical except that the latter treatment delayed dormancy about ten

days longer (Figure 10k and l).

Résumé. In agreement with the hypothesis advanced earlier, decreases in exposure length produced weaker responses. The reduction in response varied with the seed source. For example, longer exposures delayed dormancy in Salmon Arm plants and increased the frequency and regularity of growth renewal. Differences between the responses of Salmon Arm plants to the various exposure lengths were considerably greater than those for Coconino and Vancouver plants.

The percentage of Coconino plants which resumed growth one or more times was greater under all red treatments than in the control. Only minor variation in the timing and magnitude of the recurrent growth renewals was found among exposure lengths. Plants given the 15-minute treatment deviated somewhat from the typical pattern, but this may have been caused by the use of a substitute observer.

Under the longer exposures, Vancouver plants went dormant later than in the control. Both total activity and the percentage of plants remaining active throughout the tests were directly proportional to exposure length. Responses to the 15- and 30-minute exposures were equal, but somewhat greater than that to the 2-minute exposure.

Since exposures as short as two minutes produced responses

similar to those of the longest exposure, the level of Pfr activity required for the growth of Coconino and Vancouver plants was apparently quite low. On the other hand, the level of Pfr activity required by Salmon Arm plants seemed considerably larger. The apparent requirements of the three sources deduced from these experiments thus agree with those deduced from the experiments described earlier, in which exposures were given at various times during the dark period. The larger and abrupt increases in the response of Salmon Arm plants demonstrate that their requirement for Pfr activity is not only the largest, but also that it is a threshold-type requirement. The more gradual changes in the response of Coconino plants suggest that they do not have as critical a requirement as Salmon Arm plants. This characteristic of the Coconino source was also evident from previous experiments. Vancouver plants either did not have a sharply-defined requirement or it was below the levels of Pfr activity produced by the treatments tested.

Effect of Far-Red Light

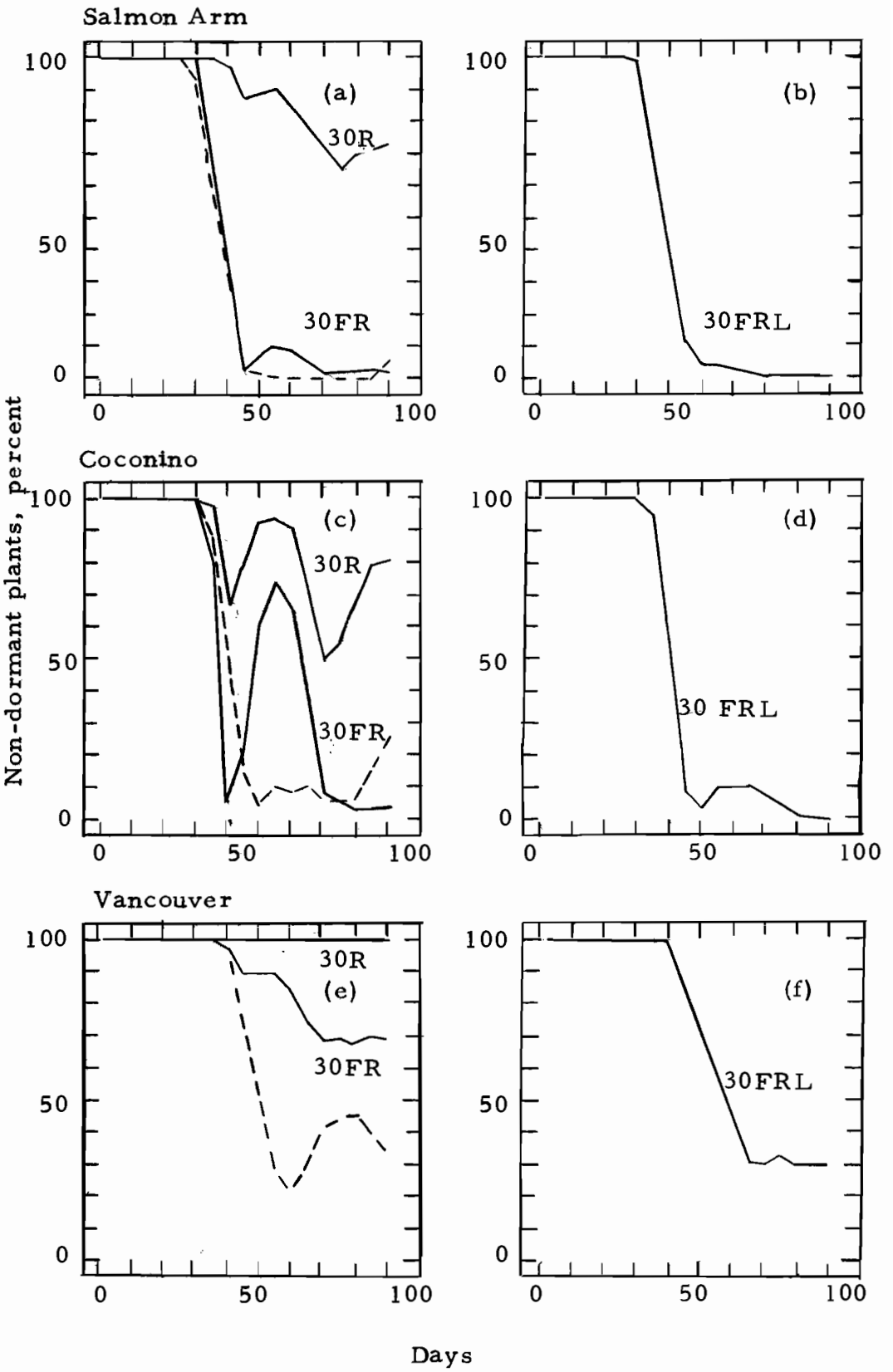
As described earlier, interruption of the dark period with red light delayed the onset of dormancy and stimulated rapid renewal of growth after short dormant periods. Photoconversion of Pr to Pfr by red light presumably caused these effects. Consequently, one would expect far-red interruptions to convert Pfr to Pr and thereby

hasten the onset of dormancy and inhibit growth renewal even more than uninterrupted 12-hour dark periods. To test this hypothesis, plants from all three sources were given 2, 15, 30 and 55 minutes of far-red light. Results of these experiments and an associated control are described below.

Effect of Thirty-Minute Exposures

Salmon Arm plants given 30 minutes of far-red light two hours before the middle of the dark period began to enter dormancy at age 35 days, five days later than control plants (Figure 11a). A small number of plants resumed growth and increased activity to ten percent at age 55 days. Most plants went dormant again, but a few remained active thereafter. Although generally similar to the control, this treatment caused more and earlier growth renewals. When a similar far-red exposure was given two hours before the middle of the light period, response was essentially identical to that of the control (Figure 11b).

Plants from the Coconino source given far-red light during darkness and the control treatment began to enter dormancy at age 35 days (Figure 11c). By age 40 days, only six percent of the far-red-treated plants were active. However, dormancy was quickly broken and 74 percent of the plants were active again within 15 days, whereas activity in the control remained at about ten percent. A


Salmon Arm
Coconino
Vancouver
(a)
(b)
(c)
(d)
(e)
(f)
30R
30FR
30FRL
30 FRL
Non-dormant plants, percent
Days
0
50
100

second period of dormancy reduced activity to four percent at age 90 days. Sixty-eight percent of the far-red-treated plants broke the first dormancy and 4 percent the second, while only 36 percent of the control plants broke the first and none the second dormancy. Coconino plants given far-red light during the light period entered dormancy at approximately the same age as control plants (Figure 11c and d). Both treatments produced similar minimum activities at age 50 days. Subsequent behavior was also similar except that fewer plants renewed growth under far-red treatment. Only 11 percent of those plants broke dormancy as compared to 36 and 72 percent under the control and dark period interruption respectively.

Vancouver plants exposed to far-red light during darkness began to enter dormancy at age 40 days, but did not reach minimum activity (68 percent) until age 70 days (Figure 11e). Control plants entered dormancy at the same age, but reached a minimum (21 percent) ten days earlier. Percentage activity under far-red treatment exceeded that of the control at all times after the onset of dormancy. Forty-seven percent of the far-red-treated plants remained active throughout the test as opposed to 13 percent in the control. When the exposure was given during the light period, the onset of dormancy also occcurred at age 40 days (Figure 11f). The level and time of minimum activity approximated that of the control. Nineteen percent of the plants remained active as compared to 13 percent of the

control plants.

Comparisons of these findings to those observed when red light was given at a comparable time (Figure 11a, c, and e) showed that far-red light did not cause the expected response. For example, Salmon Arm plants given far-red light during darkness went dormant later than controls. In addition, far-red light stimulated earlier and more growth renewal. Similar results were obtained for Coconino plants. Furthermore, the number of far-red-treated Coconino plants breaking the first dormancy exceeded that under the control and approximated that under red treatment (Figure 11c). Fewer Vancouver plants went dormant when given far-red light than in the control. In addition, a higher percentage of the plants remained active throughout the test. Regardless of seed source, exposure to 30 minutes of far-red light two hours before the middle of darkness produced effects analogus to those of red light. Far-red light given during the light period gave results essentially identical to those of the controls.

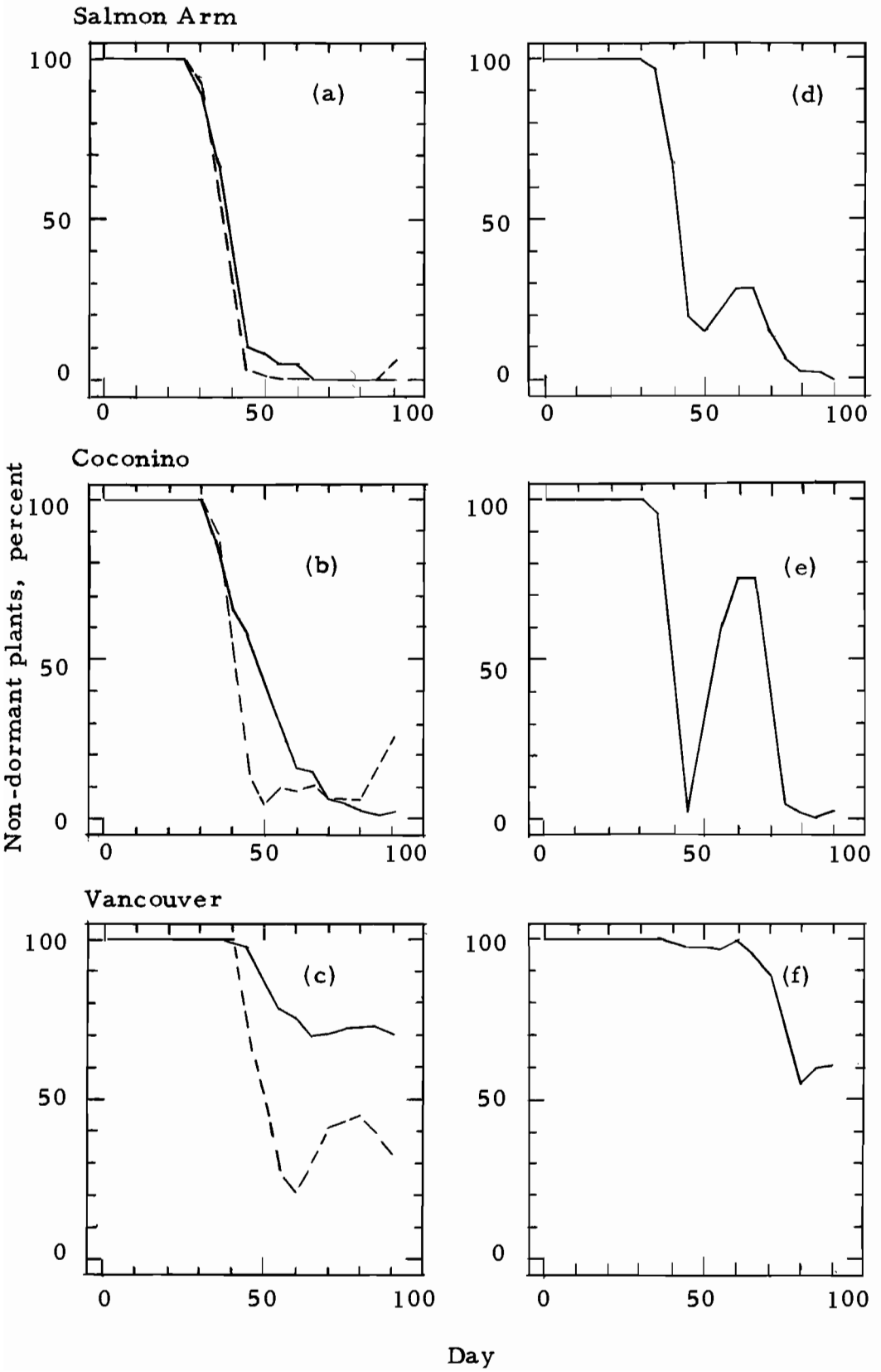
These unexpected results may be explained by several properties of phytochrome. The two forms of the pigment have overlapping absorbancies (Hendricks and Borthwick, 1963). In addition, the quantum efficiency for Pr conversion is four times that for the reverse reaction. As a result of Pr absorbance in the far-red region and the greater efficiency of conversion, exposure to high

intensity or to long durations of low intensity far-red light drives the reaction toward Pfr rather than in the opposite, expected direction. The consequent accumulation of Pfr, the physiologically active form, results in a red response. Such behavior has been noted for several responses in a number of species (Hendricks and Borthwick, 1963).

Effect of Two- and Fifty-five-minute Exposures

An experiment employing a 55-minute far-red exposure was performed in order to confirm that the 30-minute exposures did produce red effects. It was hypothesized that a longer duration would yield an ever stronger red effect. In addition, an attempt was made to find an exposure length sufficiently short to avoid overdose complication, yet long enough to effect photoconversion. For this purpose, a two-minute exposure was used.

Effect of Fifty-five-minute Exposures. Salmon Arm plants given 55-minute far-red exposures two hours before the middle of darkness began to enter dormancy at age 35 days (Figure 12d). This was five days later than control plants, but at the same time as plants given the 30-minute treatment. Activity was reduced to a minimum of 15 percent at age 50 days, but growth renewal increased it again to 28 percent at age 60 days. Growth renewal occurred at the same time as in the 30-minute test, but involved more plants than either


Salmon Arm
Coconino
Vancouver
(a)
(b)
(c)
(d)
(e)
(f)
100
50
0
0
50
100
Non-dormant plants, percent
Day

the 30-minute or control treatments.

Coconino plants entered dormancy at the same time (age 35 days) and in the same proportions as under the 30-minute exposure and the control (Figure 12e). Although activity decreased to 2 percent at age 45 days, growth renewal increased it to 75 percent within 15 days. This response paralleled that to the 30-minute treatment. A second period of dormancy reduced activity to two percent at age 90 days (Figure 12e). Seventy-three percent of the plants broke the first dormancy and two percent the second. These percentages were similar to those for the 30-minute exposure.

Only a small number of Vancouver plants entered dormancy at age 40 days (Figure 12f). Equal frequencies of cessation and renewal maintained activity at approximately 97 percent until age 65 days. Minimum activity (55 percent) was reached at age 80 days as compared to 68 percent at age 70 days and 21 percent at age 60 days under the 30-minute and control treatments, respectively. A percentage of plants equal to that observed under the 30-minute exposure (47 percent) remained active throughout the test.

Regardless of source, the 55-minute treatment had a somewhat stronger red effect than the 30-minute exposure. This confirms that far-red exposures 30 minutes or more in length reversed the normal reaction of phytochrome to far-red light.

Effect of Two-minute Exposures. Salmon Arm plants given two

minutes of far-red light two hours before the middle of darkness began to enter dormancy at the same time (30 days) as control plants (Figure 12a). Activity decreased rapidly to ten percent at age 45 days and then gradually to zero percent at age 65 days. These and later levels of activity were similar to those in the control, but somewhat lower than those under longer far-red exposures. In addition, fewer plants (two percent) broke dormancy than under any other treatment.

Coconino plants began to enter dormancy at age 35 days (Figure 12b). Although activity decreased rapidly to 15 percent at age 65 days, small numbers of plants broke dormancy at irregular intervals both before and after this time. Minimum and mid-experiment levels of activity approximated those of the control. Fewer plants (3 percent) were active at age 90 days than in the control (26 percent). The percentage of plants breaking the first period of dormancy (29 percent) was lower than in any other test.

Vancouver plants entered dormancy at the same age (age 40 days) as control plants (Figure 12c). Minimum activity (69 percent) was reached at age 65 days. The lower minimum of the control (21 percent) was reached five days earlier. Equal frequencies of cessation and renewal after age 65 days maintained activity at approximately 70 percent until age 90 days. Fifty-seven percent of the plants remained active during the test. This percentage was similar to

that of longer far-red exposures (47 percent) and greater than that of the control (13 percent).

In populations from the continental sources, the 2-minute exposure reduced activity and growth renewal to levels equal to or slightly less than those of the control. Vancouver plants responded somewhat differently in that levels of activity were greater than in the control. However, high, and possibly differential, mortality in one replication under the 2-minute treatment may have caused this difference. Consequently, the behavior of plants from the other sources was considered a better indication of response.

Effect of Fifteen-minute Exposures

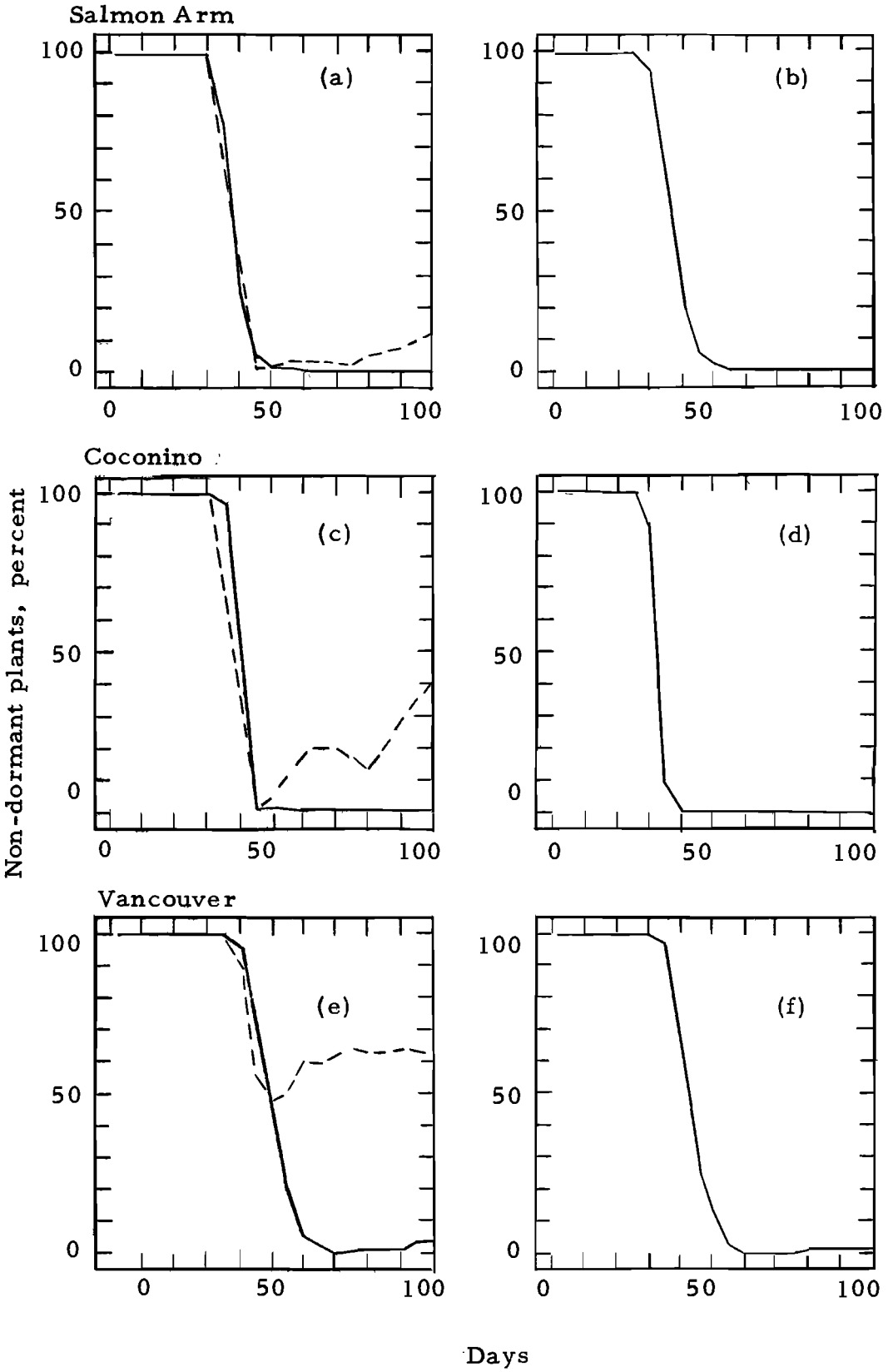
Since 30- and 55-minute far-red exposures produced red effects and 2-minute treatments did not cause obvious far-red effects, 15-minute exposures were tested. To evaluate the effect of exposure timing, 15-minute treatments were given either two hours before the middle of the dark period (12 PM) or immediately after the darkness began (8 PM). Since these tests were performed in the auxiliary chamber, their results cannot be directly compared to those from far-red tests in the main chamber. However, the responses observed in the different chambers can be compared relative to their respective controls.

Salmon Arm plants grown under the uninterrupted dark period or given 15-minute far-red exposures began to enter dormancy at

ages 30 or 35 days (Figure 13a and b). Under both far-red treatments, all plants were dormant at age 60 days. Control seedlings also showed a rapid, early decline in activity, but growth renewal gradually increased it to eight percent at age 90 days (Figure 13a). Eleven percent of the control plants resumed growth whereas far-red-treated plants never broke dormancy.

Coconino plants began to enter dormancy at age 35 days under the control and far-red exposures given near the middle of the dark period (Figure 13c). The plants given far-red light shortly after darkness entered dormancy five days earlier (Figure 13d). Regardless of treatment, low levels of activity were reached at age 40 to 45 days. Plants given the far-red treatments were all dormant at age 60 days. However, growth renewal increased activity in the control to 21 percent by that time. While a number of control plants entered a second dormant period, others remained active or resumed growth, thereby increasing activity to 29 percent at age 90 days. Fifty-three percent of the controls broke dormancy at least once, whereas all plants given far-red light remained dormant.

Vancouver plants entered dormancy at age 35 days regardless of treatment (Figure 13e and f). In far-red experiments, all plants were dormant by age 70 days and largely remained so. Thirty percent of the control seedlings remained active throughout the experiment and large numbers broke their first dormancy so that activity


Salmon Arm
Coconino
Vancouver
(a)
(b)
(c)
(d)
(e)
(f)
100
50
0
0
50
100
Non-dormant plants, percent
Days

was increased to 63 percent at age 90 days (Figure 13e).

Résumé. The results of the 2- and 15-minute far-red experiments showed that short exposures generally hastened the onset of dormancy and prevented growth renewal. These findings agreed with the expected response to far-red light in that they were opposite those for the 30- and 55-minute treatments. With the exception of plants from Vancouver Island, the effects of the 2- and 15-minute treatments were similar when compared relative to their respective controls. However, 15-minute exposures were somewhat more effective in preventing growth renewal by Coconino plants. In addition, Salmon Arm and Vancouver plants reached complete dormancy earlier under the 15-minute treatments. Consequently, the 2-minute exposure was probably close to the minimum duration capable of inducing a far-red response. Plants from all sources began to enter dormancy and were all dormant at a slightly earlier age under far-red exposures immediately after the beginning of darkness than under far-red treatment near the middle of the dark period. However, the data did not supply adequate evidence that these differences were significant.

Effect of Far-Red Light on Epicotyl Elongation and Leaf Production

Little difference in terms of percentage activity was found between responses to 15 minutes of far-red light given at two times

during darkness. Since tests with red light showed that epicotyl length and leaf number varied with the time of interruption, it followed that these determinations might also be used to discern differences between the far-red exposure times. Plants given far-red treatment in the auxiliary chamber did not have the spindly, etiolated appearance of those given similar treatment in the main chambers. Consequently, controls and plants given far-red light in the former chamber could be compared. Determinations of epicotyl length and leaf number were made as previously described.

Two-factor analyses of variance on the data summarized in Table 8 showed that seed source, light treatment, and interaction effects were highly significant (Appendix, Tables 7 and 8). Calculated LSD values (one percent level) were used to test differences between treatment means. Regardless of source, the epicotyl lengths and leaf numbers of plants given far-red light were significantly lower than those of control plants (Table 8). No significant differences were found between the two far-red treatments with respect to leaf number. However, plants from all sources had fewer leaves when far-red light was given at the beginning of the dark period. Similarly, this treatment produced the greater reduction in epicotyl length, but the difference was significant only in the case of Vancouver plants. It appeared that far-red response, unlike that to red light, did not vary with the time of interruption.

Table 8. Effect of exposure to fifteen minutes of far-red light at two times during the dark period upon epicotyl length (mm) and leaf number at age 100 days.[1]

Epicotyl Length (mm)				Leaf Number		
Treatment				Treatment		
Control	15 FR at 12 PM	15 FR at 8 PM	Seed Source	Control	15 FR at 12 PM	15 FR at 8 PM
8.7	3.8	1.8	Salmon Arm	19.6	12.4	7.7
9.3	2.0	1.4	Coconino	26.8	12.0	8.0
53.0	12.8	8.2	Vancouver	67.0	21.1	16.8
Calculated LSD (1%) = ±4.5				Calculated LSD (1%) = ± 6.0		

1 Observations represent means of four replications, each containing ten plants.

However, the differences could be biologically meaningful since the lack of significance may reflect an inadequate sample size. Further tests must be made before a definite conclusion can be drawn.

Since responses were qualitatively alike, the significant interactions (Appendix, Table 7 and 8) indicated that the degree of response varied among sources. A numerical expression of these differences was obtained by calculating the ratio; response to far-red treatment at the beginning of darkness over response to the uninterrupted dark period (Table 9). Since Vancouver plants exhibited the largest reductions and the smallest ratios, they were the most sensitive to far-red exposures. The smallest reduction occurred in the case of Salmon Arm plants. The sensitivity of Coconino plants approached that of plants from Vancouver Island. This ranking of sources was opposite that under red treatments (Table 6). In other words, Salmon Arm plants were the least sensitive to far-red light, but the most sensitive to red light when compared to Coconino and Vancouver plants.

Resume. The low sensitivity of Salmon Arm plants to far-red light suggested that the level of Pfr activity required for their active growth was larger than that for the other sources. As inferred by their early and continued dormancy, the level of Pfr activity produced by the 12-hour dark period of the control was not adequate. Consequently, a further reduction by exposure to far-red light had

Table 9. Sensitivity of epicotyl elongation and leaf production to fifteen minutes of far-red light given near the beginning of a twelve-hour dark period.

Seed Source	Epicotyl Elongation (mm)				Sensitivity ratio	Leaf Production				Sensitivity ratio
	Treatment					Treatment				
	15 FR		Control			15 FR		Control		
	Mean	Std error of mean	Mean	Std error of mean	15 FR/ control	Mean	Std error of mean	Mean	Std error of mean	15 FR/ control
Salmon Arm	1.8	±0.3	8.7	±0.3	0.21	7.7	±0.5	19.6	±0.6	0.39
Coconino	1.4	±1.1	9.3	±1.2	0.15	8.0	±0.6	26.8	±1.7	0.30
Vancouver	8.2	±0.7	53.0	±2.8	0.15	16.8	±0.8	67.0	±3.9	0.25

little effect, whereas the increase in Pfr activity caused by red exposures, particularly those given near the center of darkness, had pronounced effects.

As in the case of red exposures, the level of Pfr activity required for the stimulation of growth in Coconino plants appeared to be intermediate. The magnitude of activity, growth renewal, epicotyl elongation, and leaf production for Vancouver plants under control conditions suggested that the minimum level of Pfr activity required for their growth was the lowest. Increasing the level by means of exposure to red light therefore had only slight effects. However, a reduction in Pfr activity by far-red treatment had a proportionately greater effect than the increases caused by red exposures. The conclusions drawn from far-red experiments concerning variation among seed sources in terms of apparent Pfr activity requirements agree with those drawn from the results of the red tests.

DISCUSSION AND CONCLUSIONS

The proportion of phytochrome in the Pfr form at the close of a daily light period has been estimated to be between 70 and 90 percent (Downs, 1962). He contended that a portion of this amount was converted back to Pr during darkness and that less than ten percent of the total pigment would be Pfr following a dark period of sufficient length. If the pigment remains predominantly in the Pr form for an appreciable length of time, woody plants cease extension growth and enter dormancy. That is, short days or long dark periods accelerate the onset of dormancy since the amount of Pfr present is low. Long days or short dark periods, on the other hand, produce and maintain higher Pfr levels and cause opposite responses.

Since the pigment is photoreversible between the two forms, treatments which preferentially increase or decrease the Pfr level should produce opposite effects. In the present study, an attempt was made to increase and decrease Pfr levels by exposing Douglas-fir plants to red and far-red light, respectively. The results of tests in which plants were exposed to 30 minutes of red light at various times during a 12-hour dark period showed that red light increased the duration of growth, epicotyl length, leaf number, and leaf length irrespective of seed source. Since these results agree with those found for similar populations grown under 16-hour days

(Irgens-Moller, 1962 and 1968), they are clearly long day responses. They also agree with the effects of long days on numerous other woody species as described previously.

Such findings indicate that exposure to red light caused the photoconversion of Pr to Pfr. Since the magnitude of the individual responses increased as exposure time approached the center of the dark period, one might conclude that each exposure produced equal amounts of Pfr and that this concentration was reduced by dark conversion to a variable extent depending upon the length of uninterrupted darkness. The amount of Pfr left after the respective actions of photoconversion and dark conversion had taken place appeared to govern the degree and type of response. The early dormancy and reduced growth caused by 15-minute exposures to far-red light confirmed that the responses were caused by changes in Pfr levels. These considerations suggest that the mechanism involved is similar to that outlined by Downs (1962). However, the dependence of response upon exposure timing in the case of red light could also be interpreted as evidence that the concentration of Pfr produced by photoconversion and dark conversion had to be present a specific length of time in order to produce a given response. A clear distinction between these two possible types of mechanisms cannot be made on the basis of the present data. Instead, response appeared dependent upon both a concentration and time factor. Consequently,

changes in the magnitude of a given response could not be considered proportional to an increase or decrease in Pfr concentration. It seemed more appropriate to consider responses and variation in them as being related to a relative or apparent level of Pfr activity.

By measuring a number of responses and the patterns of response exhibited by plants from each seed source, an attempt was made to deduce the relative levels of Pfr activity required to maintain or stimulate their growth. The large increases in percent activity, epicotyl length, and leaf number in Salmon Arm plants as 30-minute exposure times approached the center of the dark period demonstrated that the level of Pfr activity required for the continued growth of these plants was greater than that characteristic of plants from the other sources. The magnitude of differences between responses to exposure lengths varying from 2 to 30 minutes confirmed this conclusion.

Furthermore Salmon Arm plants exhibited little or no increase in response under dark periods longer than ten or shorter than eight hours, but showed large responses under dark periods between these lengths. These findings suggested that its required level of Pfr activity was high and also characterized by a sharp threshold. Evidence in support of these conclusions was also obtained from experiments using far-red light. By virtue of an unexpected reversal of the photoreaction, the longer far-red exposures produced red effects in Coconino and Vancouver plants, but had little stimulatory effect on Salmon Arm plants. That is, the Pfr activity produced by 30- and 55-minute far-red exposures was inadequate to noticeably affect

the growth of Salmon Arm plants, thus indicating their high requirement. In addition, Salmon Arm plants were relatively insensitive to 15-minute far-red exposures. It appeared that the Pfr activity maintained by 12-hour dark periods was below the required level. Consequently, further reduction in the level by photoconversion had little effect. It was concluded that Salmon Arm plants required a high and critical level of Pfr activity for normal growth and development and that such a level could be produced and maintained by day lengths of 14 to 16 hours.

The relatively large increases in percent activity, epicotyl length, and leaf number as the exposure times approached the center of the dark period indicated that the level of Pfr activity required by Coconino plants was lower than that for Salmon Arm plants. However, the moderate sensitivity of Coconino plants, the smaller changes in response as the length of uninterrupted darkness decreased, and the definite but lesser change at the critical length of darkness indicated that they had a threshold requirement but that it was not as critical as that for Salmon Arm plants. Furthermore, the similarity of responses to exposure lengths from 2 to 30 minutes at the middle of the dark period demonstrated that the required level of Pfr activity was lower and less critical than that observed for Salmon Arm plants and that it was satisfied by exposures shorter than two minutes.

The results of experiments using far-red light also demonstrated that the requirement of Coconino plants was lower than that for Salmon Arm plants. The effects of 30- and 55-minute far-red exposures upon Coconino plants were intermediate between those on

Salmon Arm and Vancouver plants. That is, the levels of Pfr produced by these treatments were sufficient to produce noticeable responses, but not as great as those produced by 30-minute red exposures. The sensitivity of Coconino plants to 15-minute far-red exposures was intermediate. This far-red treatment induced complete and permanent dormancy in these plants. However, the difference between this response and the percentage activity of control plants was intermediate between the minor reduction in the response of Salmon Arm plants and the greater reduction in the response of Vancouver plants. It was concluded that the level of Pfr activity produced and maintained by the control treatment approached the required level, but was sufficiently below it to prevent continued growth. Consequently, reducing this level with far-red exposures had observable, but less pronounced, effects than similar treatments had on Vancouver plants. These considerations and that the degree of reduction in percent activity exceeded that for Salmon Arm plants support the conclusion that Coconino plants required intermediate levels of Pfr activity. The requirement of Coconino plants appeared to be similar to that produced and maintained by a 12- to 14-hour day length.

Percentage activity, epicotyl elongation, and leaf number of Vancouver plants were increased by gradual increments as 30-minute red light exposures approached the center of the dark period. These observations and the marked similarity of responses to

exposures at or near the center of the dark period suggested that the level of Pr activity required by Vancouver plants was lower than that for Salmon Arm and Coconino plants. The slight changes in response to exposures varying from 2 to 30 minutes substantiated this conclusion. The sensitivity of Vancouver plants to red light was the lowest of the three sources tested. The low sensitivity and the gradual, almost linear increase in response as exposure times approached the center of the dark period indicated that the requirement of Vancouver plants was not only lower than that for the other sources, but also was less critical, that is, a threshold was not apparent.

As noted earlier, the responses of Vancouver plants to long far-red exposures resembled those to red light more than did the response of the other sources. Since these treatments appeared to have caused a reversal of the normal photoreaction and had little effect on plants from the other sources, they probably did not produce large quantities of Pfr. Consequently, the observable response of Vancouver plants to the activity of these quantities indicates that their requirement was low. While Vancouver plants were the least sensitive to red light, they were the most sensitive to far-red light. As noted previously, the control treatment produced a Pfr activity approaching the required level. Since exposures to 15 minutes of far-red light caused a larger reduction in the response of Vancouver

plants than in those of the other sources, the level of Pfr activity in the controls was not sufficiently below the required level to severely inhibit growth. Further reduction in this level and response were therefore possible. This confirmed that Vancouver plants had a lower requirement and that they did not possess as critical a requirement as the other sources. It is possible, however, that the present study did not include treatments capable of diminishing Pfr activity to levels which would have resulted in an observable threshold. Vancouver plants appeared to require the lowest and least critical requirement of all three sources. The Pfr activity produced and maintained by 12- to 14-hour day lengths seemed to satisfy this requirement.

In the present study, exposure of plants from the three seed sources to red light during the daily light period had little or no effect. The responses of Coconino and Vancouver plants to this treatment resembled those to exposures during the dark period, but were considerably less. This observation indicates that the levels of Pfr during the remainder of the light period and at the beginning of the dark period were increased. As a result, Pfr activity during the dark period apparently exceeded that in control plants. Since the increased Pfr activity was sufficient to cause noticeable effects only in Vancouver and Coconino plants, this supports the conclusion that these sources had lower and less critical

requirements than Salmon Arm plants.

A similar conclusion emerged from the results of experiments in which 30 minutes of far-red light was given during the daily light period. Although the effects of these treatments were weak, they resembled red effects just as did those of similar exposures to far-red light during the dark period. In both cases, Vancouver and Coconino plants were affected more than Salmon Arm plants.

In the present study, the effect of both red and far-red exposures during the light period were similar in nature to those of similar exposures during darkness. Consequently, there did not appear to be a rhythmic change in pigment sensitivity as was postulated by Könitz (1958) and Bünning (1959). Instead, these results agree with those of Downs and Piringer (1958) and Meijer (1957 and 1959), who found that photoperiodic responses depended upon the quality of light period radiation as well as the relative length of the light and dark periods.

The results of exposure to red light during the light period indicate that increases in the proportion of red light during the daily light period delay dormancy and increase growth of Douglas-fir seedlings. As noted above, the degree of response varied with the seed source. These findings may have implications for the practicing forester. The light received by plants grown in a clearing contains a greater proportion of red light than that received by

plants grown under a forest canopy (Hendricks and Borthwick, 1963). Although the importance of this difference is presently unknown, the performance of young Douglas-fir plants in the field might be affected by light quality.

Since test plants were grown in a uniform environment, some proportion of the variation among the different responses and the Pfr activities underlying them is heritable. Only by growing plants under a number of different environments each having a common photoperiod is it possible to assess the relative importance of photoperiodic response as a factor in the regulation of growth. Nevertheless, the differences in the responses and Pfr requirements of the three seed sources reflect to some extent the degree and nature of adaptation to selective factors operative at their origins. Since the seed sources represent populations from markedly different latitudinal, altitudinal, and climatic areas, it should not be surprising that each has developed a different means of adjusting its growth cycle to seasonal trends in climate.

The response pattern of plants from the northern continental source, Salmon Arm, demonstrated that they required a high and critical level of Pfr activity. Their growth was significantly reduced by Pfr activities similar to those produced by day lengths approximately two hours longer than that reducing the growth of plants from the southern, continental source, Coconino. This variation in day

length requirement seemed an expected result since day lengths at the latitude of the northern source are longer during the growing season. This agrees with the results of other workers who found that the critical day lengths for northern species and subpopulations generally exceeded that for southern plants (Vaartaja, 1959; Nienstaedt and Olson, 1961). In addition, the coastal source, Vancouver, had a lower and less critical requirement than the continental source, Salmon Arm. Since these sources represent populations from the same latitudinal zone, they have essentially the same day length regimes during their growing seasons. Despite these similarities, the growth of the Salmon Arm plants was inhibited by day lengths about two hours longer than those inhibiting the growth of the coastal sources. Similar differences between the day length requirements of continental and maritime populations of forest trees have been reported by other authors (Irgens-Moller, 1958 and 1968; Vaartaja, 1959).

The level of Pfr activity required by Salmon Arm plants was larger and more critical than that of plants from the other sources. This critical requirement demonstrated that photoperiodic response was of considerable importance in regulating the growth and development of Salmon Arm plants. These plants represented populations native to a region in a high latitude characterized by a short growing season and large seasonal extremes of climate (Chapman, 1952). In

such an environment, relatively strict control of growth by response to changes in day length would seem a logical outcome.

The Pfr requirement of Vancouver plants was lower than and less critical than those of the continental sources, indicating that day length was of lesser importance in the control of growth. The coastal climate of Vancouver Island is characterized by a long growing season, mild winters, and gradual seasonal changes of climate (Chapman, 1952). Under such conditions, the regulation of the growth cycle by changes in day length would seem to be and, apparently, is of lesser selective advantage.

Although from a lower latitude, Coconino plants resembled Salmon Arm plants in that they required a threshold level of Pfr activity for continued growth. This similarity reflects the adaptation of Coconino plants to the short growing season and abrupt changes between seasons characteristic of its high altitude, inland habitat. However, Coconino plants differed from the other sources in terms of their cyclic growth behavior. Under treatments which produced Pfr activities equal to or greater than the minimum requirement, Coconino plants continued growth by entering and breaking a series of short dormant periods.

Irgens-Moller (1968) found that a similar pattern of intermittent growth, though of lesser amplitude and regularity, could be induced in plants from near the Salmon Arm source, but only under

long days and fluctuating day and night temperatures. Similarly, the present study demonstrated that the regularity of growth renewal by Salmon Arm plants was increased only by the most extreme red treatment. Regardless of the conditions employed, this growth pattern was absent from Vancouver plants. In the present study, Coconino plants exhibited cyclic behavior under day lengths as short as 14 hours even though temperature was held constant. Irgens-Moller (1968) found that fluctuating temperatures increased the uniformity of response. He also reported that at least one cycle of cessation and renewal occurred when Coconino plants were grown outdoors at Corvallis, Oregon. The above considerations indicate that the intermittent growth pattern of Coconino plants is under strong genetic control.

Provided that other factors are not limiting, Coconino plants have the capacity to cease and renew growth at least twice under day lengths of 14 hours or longer. It is possible that this growth pattern may be a mechanism to avoid drought. Sixty-four percent of the annual rainfall in the Southern Rocky Mountains occurs during the summer, whereas only 29 percent occurs during that season in more northerly areas (Baker, 1944). If day lengths are sufficient to maintain the required level of Pfr activity, the intermittent growth pattern could permit growth beyond the first dormancy provided that summer rains are adequate and

properly-timed. Further evidence that this pattern of growth is related to differences in the seasonal distribution of rainfall was provided by Irgens-Moller (1968). He found that plants from the Southern Rocky Mountains exhibited cyclic behavior, while those from northern areas did not.

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Appendix Table 1. Single-factor analysis of variance on percentage of non-dormant Salmon Arm plants at age 90 days.[1]

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F ratio
Total	35	25,985.8864	--	--
Treatment	8	24,724.7207	3090.5901	66.16**
Error	27	1,261.1657	46.7098	--

** Significant at the 1% level.
Standard Error of Difference = ±4.83
Calculated LSD (1%)= ±13.38

[1] Data transformed to degrees arc sine.

Appendix Table 2. Single-factor analysis of variance on percentage of non-dormant Coconino plants at age 90 days.[1]

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F ratio
Total	43	33,838.1384	--	--
Treatment	10	30,667.1679	3066.7168	31.92**
Error	33	3,170.9705	96.0900	--

** Significant at the 1% level.
Standard Error of Difference = ±6.93
Calculated LSD (1%) = ±19.06

[1] Data transformed to degrees arc sine.

Appendix Table 3. Single-factor analysis of variance on percentage of non-dormant Vancouver plants at age 90 days. [1]

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F ratio
Total	31	10,547.4097	--	--
Treatment	7	8,047.5308	1149.6472	11.04**
Error	24	2,499.8789	104.1616	--

** Significant at the 1% level.
Standard Error of Difference = ±7.22
Calculated LSD (1%) = ±20.19

[1] Data transformed to degrees arc sine.

Appendix Table 4. Two-factor analysis of variance on epicotyl lengths of plants from three seed sources exposed to 30 minutes of red light. [1]

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F ratio
Total	131	90,771.47	--	--
Treatment	32	85,754.22	2,679.82	52.88***
Seed Source	2	53,741.74	26,870.87	530.21***
Light	10	23,157.39	2,315.74	45.69***
Interaction	20	34,357.61	1,717.88	677.93***
Error	99	5,017.25	50.68	--

***Significant at the 0.1% level.
Standard Error of Difference = ±5.03
Calculated LSD (1%) = ±13.4

[1] Observations were means of ten plants selected at random from each of four replications per seed source and treatment.

Appendix Table 5. Two-factor analysis of variance on leaf numbers of plants from three seed sources exposed to 30 minutes of red light.[1]

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F ratio
Total	131	50,339.90	--	--
Treatment	32	46,574.69	1,455.46	38.27***
Seed Source	2	24,818.88	12,409.44	326.29***
Light	10	17,329.95	1,732.99	45.57***
Interaction	20	4,425.86	221.29	5.82***
Error	99	3,765.21	38.03	--

***Significant at the 0.1% level.
Standard Error of Difference = ±4.36
Calculated LSD (1%) = ±11.6

[1]Observations were means of ten plants selected at random from each of four replications per seed source and treatment.

Appendix Table 6. Two-factor analysis of variance on leaf lengths of plants from three seed sources exposed to red light.[1]

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F ratio
Total	35	604.4764	--	--
Treatment	8	574.0089	71.7511	63.59***
Seed Source	2	525.0739	262.5370	232.66***
Light	2	37.0872	18.5436	16.43***
Interaction	4	11.8478	2.9620	2.62*
Error	27	30.4675	1.1284	--

***Significant at the 0.1% level. *Significant at 5% level.
Standard Error of Difference = ±0.75
Calculated LSD (1%) = ±2.1

[1]Observations were means of ten plants selected at random from each of four replications per seed source and treatment.

Appendix Table 7. Two-factor analysis of variance on epicotyl lengths of plants from three seed sources exposed to 15 minutes of far-red light. [1]

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F ratio
Total	35	8501.2900	--	--
Treatment	8	8357.7500	1044.7188	196.51***
Seed Source	2	3257.8467	1628.9234	306.40***
Light	2	2823.6517	1411.8258	265.56***
Interaction	4	2276.2516	569.0629	107.04***
Error	27	143.5400	5.3163	--

***Significant at the 0.1% level.
Standard Error of Difference = ±1.63
Calculated LSD (1%) = ±4.5

[1]Observations represent means of ten plants selected at random from each of four replications per seed source and treatment.

Appendix Table 8. Two-factor analysis of variance on leaf number of plants from three seed sources exposed to 15 minutes of far-red light. [1]

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F ratio
Total	35	10,652.1164	--	--
Treatment	8	10,402.7889	1300.3486	140.88***
Seed Source	2	3,140.7206	1570.3603	170.14***
Light	2	4,752.2439	2376.1220	257.43***
Interaction	4	2,509.8244	627.4561	67.98***
Error	27	249.3275	9.2344	--

***Significant at the 0.1% level.
Standard Error of Difference = ±2.15
Calculated LSD (1%) = ±6.0

[1]Observations represent means of ten plants selected at random from each of four replications per seed source and treatment.