rub the seed between two pieces of wood.

FRANK GOUIN: Have you tried vinegar or tannic acid instead of sulfuric acid?

JOERG LEISS: Vinegar is a weak acid; however, sulfuric acid is not dangerous if handled properly.

RALPH SHUGERT: What is your treatment for *Taxus cuspidata*?

JOERG LEISS: Our seed is imported from Japan. We receive the seed by the end of January, treat with Terrachlor, and combine with an equal amount of moist sand and peat medium. The mixture is packed in shallow boxes, placed outside, and left until the spring two years following. Therefore 1986 seed will come out in the spring of 1988. You give them a cold, warm, then cold cycle before spring planting. You cannot speed it up.

PHOTOPERIODISM IN WOODY PLANTS AND ITS SIGNIFICANCE TO PLANT PROPAGATION AND PRODUCTION[1]

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Woody perennial plants which have developed in temperate regions have evolved intricate mechanisms to allow survival, competition, and reproduction. This has led to complicated, sophisticated mechanisms for starting and stopping growth at the appropriate times for best survival and growth. One of these mechanisms is the ability to sense the gradual seasonal changing of daylength or photoperiod that occurs because of the tilt of the earth's axis and its orbit around the sun. The higher the latitude the greater daylength changes between winter and summer. These photoperiod changes and their effects on flowering of greenhouse crops are reviewed in Post (35).

There are several early reports and reviews of woody plants responding markedly to daylength or photoperiod (12,25,36,43). One of the first of these in our Society was by Waxman (42). Nitsch (31), in his classic review, modified Chouard's (8) criteria and separated plants into response groups to photoperiod (see Table 1). He also listed as many

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woody species with photoperiodic studies as he could find and fit them into his classification groups. Numerous species that Nitsch listed have question marks as to their photoperiodic growth response group. This paper will offer explanations for the question marks and the significance of photoperiod for selecting and producing woody perennial plants in light of these explanations.

The first reason for conflicting reports regarding the photoperiodic classification of certain species reported by Nitsch (31), is that seedlings may respond to photoperiod differently than larger plants with more defined growth patterns. In addition to photoperiod, seasonal influences become important as the plant ages. The second and more significant reason is due to the phenomenon of photoperiodic ecotypes in a species. This has been recently studied extensively and has great significance not only to the production of woody perennial plants, but also to which ones to produce.

Seedlings vs. older plants. The vegetative growth response to increased photoperiod seems to be more active in seedlings than older plants. Hanover, *et al.* (18) found that newly germinated seedlings and one-year-old plants of *Picea pungens* grew continuously under 24 h days, but plants three or more years old formed terminal buds and ceased elongation after 4 to 6 weeks in the same light regime. Heide (20) reported that in *P. abies* longer photoperiods were needed for continuation or resumption of growth in second-year plants than for maintenance of uninterrupted growth in first-year seedlings. Junttila (24) observed that in *Salix pentandra*, smaller seedlings were less responsive to short days and formed a terminal bud when growth ceased, but large seedlings stopped growth sooner and aborted the shoot tip. Older plants of this species would form aborted shoot tips even under continuous light.

The maximum vegetative response to extended photoperiods depends on the absence of other limiting factors. If temperature, soil moisture, fertility, or any other growth factor is limiting, then a rapidly growing seedling can age prematurely and start responding to photoperiod in a different manner. This author (29) has had small tissue culture derived *Rhododendron* micropropagules, which are analogues to seedlings, stop growing because of a momentary stress period due to lack of watering in the greenhouse under long days. This changed these plants from an A response to a B response under Nitsch's classification in Table 1.

Photoperiodic ecotypes. An ecotype of a species is a genetic change that allows a group of plants of a species to adapt and compete favorably in a new environment (9). Woody plants in particular are likely to develop ecotypes because of their heterozygous genetic makeup and mechanisms to ensure cross-pollination. If the plants colonizing a new environment show major genetic rearrangements and major changes in outward appearance, then a new species or subspecies can be recognized. In many instances the outward changes are minor, but a plant's physiological response to the environment is altered. Development of ecotypes is a way of colonizing new areas by a species, and many woody perennial species have developed considerable ranges by this process (see Little, 26).

Table 1. Photoperiod and vegetative growth response of woody plant species classified by Nitsch (31).

Plant response	Class	Examples
I. Long days prevent the onset of dormancy		
1. Short days cause dormancy		
a. Long days cause continuous growth	A	*Weigela, Populus*
b. Long days cause periodic growth	B	*Quercus, Rhododendron*
2. Short days do not cause dormancy	C	*Juniperus, Thuja*
II. Long days do not prevent dormancy onset	D	*Buxus, Syringa*

One of the changes in physiological response of major survival value to a plant species is the response to changes in daylength in the environment. This genetic change allows a species to colonize different latitudes or different altitudes by new photoperiodic ecotypes. The growth responses of interest here are the induction of growth cessation, bud maturity, and dormancy by shortening days in the autumn. This phenomenon was reported by Weiser (45) to be necessary for the first stage of hardiness induction of *Cornus sericea.* Hummel, *et al.* (23) found that *C. sericea* plants of ecotypes from 65°N and 62°N underwent this first stage hardiness induction at a shorter night (longer day) than those collected from 42°N latitude. This was under genetic control as shown by crosses being intermediate in response. Donselman and Flint (10) reported that both stages of hardening, the first stage being induced by short days, increased more rapidly in northern than in southern sources of *Cercis canadensis.* Aronsson (2) found photoperiod was more important than temperature in the fall hardening of *Pinus sylvestris.* Although other factors may be important for some geographic hardiness of other species (1,3,15), plants in Nitsch's class A or B would probably be hardened by shortening days in the autumn.

Several studies have measured the response of ecotypes from several latitudes and their growth response to photoperiod (4,11,15,17,27,34,39,40,46), although hardiness was not tested. The photoperiod at which growth stopped generally decreased with decreasing latitude. Trees with extensive southern latitude ranges may reach a point where vegetative growth does not respond to photoperiod. This was found for

Liquidambar styraciflua by Williams and McMillan (46) and *Taxodium distichum* by Flint (personal communication).

Heide (19) in a major study of *Picea abies* from five different latitudes found major interactions of temperature, photoperiod, and latitude in the critical photoperiod for growth of seedlings. The growth response at lower temperatures to increased photoperiod was not as strong as higher temperatures; i.e., the critical photoperiod for growth was increased at lower temperatures. Pauley and Perry (32,33) collected seeds of *Populus trichocarpa* from several latitudes and grew them at Weston, Massachusetts. The growth cessation in the fall was correlated with the latitude or daylength and frost-free season of the native habitat. They further found this character was under multigenic control as F_1 hybrids from a north-south cross were intermediate to their parents in growth cessation at the latitude of Weston, Massachusetts.

Altitude can also play a major role in photoperiodic ecotype response. Harborg (17) and Heide (19) reported that critical photoperiod for growth response of Scandinavian trees and shrubs was longer for seed sources from a high altitude than those from a low altitude at the same latitude. McCreary, *et al.* (28) reported a similar response for Douglas fir although the latitude also varied slightly with elevation.

Photoperiod and plant production. The response of plants to photoperiod and photoperiodic ecotypes has several important ramifications in the production of woody plants for the landscape. This phenomenon is primarily important in seedling production, but can be an important consideration in clonal propagation, particularly with the newer micropropagation techniques. The photoperiodic considerations can be divided into two areas — selection of native plant sources, and methods of accelerating production.

Selection of plants to be propagated. The selection of seed source is very important for those plant species that have native ranges over several degrees of latitude and considerable changes in altitude at the same latitude. At higher altitudes fall freezing temperatures occur earlier. There have been several papers showing the importance of seed source for production of woody plant species out of their native region. Heit (21) in an early paper before this Society, and Flint (14) later, state that consideration of seed source is second only to which species to propagate. However, the sale of seedlings by seed source, except for a few species, is hard to find in nursery catalogues. Plant material manuals tend to stress species, clones, and maximum hardiness range and say little about ecotypic or geographical variation. An important exception is by Flint (16) who gives a range of hardiness in his plant descriptions.

An example of importance of seed source is illustrated in the production of Douglas fir for Christmas trees in central Illinois as Heit (22) had earlier found in New York State. Dr. Jokela, of the Forestry Department, University of Illinois, had planted several trees from Arizona and New Mexico seed sources that grew rapidly compared to other local trees of unknown sources. Several seed sources also were obtained from Dr. Widemoyer, Department of Forestry and Horticulture, New Mexico State University, and grown in Urbana, Illinois. The growth of these trees proved markedly different, as shown in Table 2. The seed source trees from lower elevations grew twice the height of some of the others, although considerable variation was noted even within a seed source of good growth. The superior growth of some of these trees was due to growth later into the summer: the classic photoperiodic ecotypic response.

Table 2. Seeds from several sources in Arizona and New Mexico started in a greenhouse in deep tubes and grown with incandescent lights from 12 p.m. to 4 a.m. and seedlings grown in a bed for two summers (height of seedlings measured at the end of the second summer).

State	National Forest	Ranger District	Elev. (ft)	Growth (cm[1])	Size range (cm)
AZ[2]	Kaibab	North Kaibab	8,800	13.7 ± 4.4	8-20
NM	Carson	Canjilon	9,800	15.5 ± 5.3	6-28
AZ	Coconino	Unknown	8,000	21.0 ± 6.1	9-32
NM	Santa Fé	Las Vegas	8,100	21.1 ± 4.2	13-30
NM	Santa Fé	Santa Fe	Z 730[3]	23.5 ± 5.8	5-36
AZ	Apache-Sitgreaves	Chevelon	8,500	24.0 ± 10.2	13-49
NM	Carson	Jemez	7,600	24.7 ± 7.6	5-39
AZ	Apache-Sitgreaves	Unknown	8,000	25.1 ± 5.2	18-33
AZ	Apache	Black River	7,700	26.9 ± 8.2	6-43
NM	Gila	Reserve	Z 180[3]	29.7 ± 11.3	11-60

[1] Mean growth of 36 plants ± standard deviation of the mean.
[2] AZ = Arizona; NM = New Mexico
[3] Seed collection zone; elevation unobtainable.

Another example of seed source importance is *Liquidambar styraciflua* (sweet gum). There appears to be considerable variation of hardiness in the local sweet gum trees during the unusually cold winters that central Illinois has had the last few years. Numerous trees have died-back and some were killed to the ground, while numerous other trees experienced no damage. This is possibly related to seed source, although this is difficult to prove. These trees are 20 to 40 years old and came from various local nurseries which obtained seedlings from a variety of sources. There are several ways to solve this problem. First, seed could be collected from the northern-most latitude in the Midwest or from even hardier local trees and grown by local nurseries or contracted to a seedling grower. Another alternative is to choose several of the better local trees and micropropagate them (37) as superior central Illinois clones.

Photoperiod and plant production. Numerous nurseries are using extended daylengths to produce large, rapidly-growing seedlings which are reported to survive transplanting better. Hanover, *et al.* (18) have reported anywhere from 0 to 800% increase in growth of seedlings in a greenhouse using continuous light, high moisture and fertility, vs. normal seedbed-grown seedlings. Tinus (38) grew seedlings of several seed sources of Douglas fir and Englemann spruce in a greenhouse and found growth increased from 50 to 600% depending on the latitude of collection and photoperiodic treatment. Witte, *et al.* (47) have reported in past Society *Proceedings* responses of several woody species but sweet gum and European white birch did not respond. They may not have had the proper photoperiodic ecotype of these species (46).

Both light type and duration may have a major influence on production response. Cathey and Campbell (5,6) found that woody plants were most sensitive to incandescent light of five vision lighting sources tested. Tinus (38) found a variation in response of photoperiodic ecotypes to maximum daylength with some ecotypes of Douglas fir and Englemann spruce doing better with 21-h days than 24-h days. All ecotypes did even better if they received a light break of one minute out of 15 throughout the dark period (cyclic lighting (7) or flashlighting (43) and incandescent light at 270 lux was more efficient than cool white fluorescent light at 950 lux for this response. It would appear from this and other studies that incandescent light would be the best light source for obtaining continuous vegetative response, and flash lighting (43) would save on energy cost for the accelerated greenhouse production of photoperiodically responding woody plant seedlings or micropropagules.

SUMMARY

Nitsch's photoperiodic class of a woody species can vary with the ecotype or even between seedlings and older plants. The continuous vegetative growth of seedlings of many woody species under extended days can be used to produce accelerated seedlings or micropropagated plants and save considerable time in the seed or transplant bed. The length of day or photoperiod is the strongest controlling force of many woody

plant species with native ranges into the higher latitudes. Photoperiodic ecotype has to be considered when deciding on the length of photoperiod necessary for accelerated production of particular species. To obtain a seed source for maximum growth and hardiness in a specific location, photoperiodic ecotypes must be considered for plant species with native ranges in several latitudes or different altitudes at the same latitude. Care should be taken to match photoperiod and first frost to the area where the plants are to be grown if local hardy seed sources are not available.

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COMPANION GRASSES IN NURSERY PRODUCTION

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We at Forrest Keeling Nursery are involved in our third year using companion grasses as an integral part of our field-grown seedling production program. Introduction of selective grass herbicides has rendered this program a valuable asset to seedling production.

Primary reasons for using companion grasses at Forrest Keeling have been: erosion control; stabilization of mulching materials; prevention of crusting of mulch materials; and protection from a number of spring weather conditions including torrential rains, desiccating winds, and late spring frosts.

GRASSES USED AND THEIR CONTROL

After experimenting with several grasses we have determined the best two for our program are annual rye grass for summer and fall-seeded nursery crops and oats for spring-seeded nursery crops. It is important to note that fall seeded oats, as historically practiced in the nursery industry, fail to