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Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*)

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Thirty years of cone production records for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) (two sites each) in the Cascade Mountains of Washington and Oregon were compared with basal area increment and weather records to determine relationships among weather, radial growth, and cone crop. Results show that the size of subalpine fir cone crops was negatively related to large crops and positively related to radial growth in the previous 2 years. Mountain hemlock cone crops were negatively related to a large cone crop and positively related to July or August temperature in the previous year. Radial growth in heavy cone years was inhibited more for subalpine fir than for mountain hemlock. Results are explained by differences in the location of cone production between species. It is concluded that global climate warming could result in fewer and more irregular cone crops for these species.

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Trente années de données sur la production de cônes de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) et de pruche de Patton (*Tsuga mertensiana* (Bong.) Carr.) qui furent récoltées dans deux sites pour chaque espèce dans les Cascades des états de Washington et de l'Orégon ont été comparées avec l'augmentation de surface terrière et les relevés météorologiques pour déterminer s'il y avait des relations entre les conditions météorologiques, la croissance radiale et la production de cônes. Les résultats ont montré que la production de cônes de sapin subalpin était reliée négativement à de fortes productions et positivement à la croissance radiale au cours des deux années précédentes. La production de cônes de pruche de Patton était reliée négativement à une forte production de cônes et positivement à la température des mois de juillet et août au cours de l'année précédente. Lors des années de forte production de cônes, la réduction de la croissance radiale était plus forte chez le sapin subalpin que chez la pruche de Patton. Les résultats s'expliquent par la différence entre les deux espèces dans le site de production des cônes. On peut conclure que l'effet d'un changement qui pourrait survenir dans le climat global amènera une production de cônes plus faible et plus irrégulière chez ces espèces.

[Traduit par la rédaction]

Introduction

Vegetation of the subalpine zone in the Pacific Northwest may be particularly sensitive to climatic change, because the distribution of tree clumps and meadows is determined by a number of factors responsive to climate, such as growing-season length and fire and soil moisture (Kuramoto and Bliss 1970; Franklin et al. 1971; Fonda 1979; Rochefort et al. 1994). Currently, climate acts through these factors to limit tree survival, however, other factors may become limiting should climate change. In particular, the potential of climate to affect cone production has been overlooked as a future constraint to tree establishment.

Cone production is critical to seedling establishment in the subalpine zone because seed supply and viability are not consistent through time (Zasada et al. 1992). Subalpine conifers of the western Cascade Mountains produce large cone crops at irregular intervals of approximately 3 years (Franklin 1968), and seeds are not viable in soil for more than 1–2 years (Archibold 1989). In addition, subalpine tree reproduction appears to be partly controlled by external factors such as climate, because cone crops often coincide on several species (Eis et al. 1965; Franklin 1968; McDonald 1992) and individuals (Kiss and Sziklai 1966) within the same region.

Several studies of conifers show that large cone crops occur 2 years after a cool cloudy summer (Lowry 1966; Van Vredenburch and La Bastide 1969; Eis 1973), 18 months after a cold winter (Eis 1973), and 1 year following a hot dry summer (Tiren 1935; Fraser 1958; Daubenmire 1960; Yanigihara et al. 1960; Van Vredenburch and La Bastide 1969; Brondbo 1970; Eis 1973; Ross 1988; Caron and Powell 1989). Climate is thought to interact with endogenous processes, including those responsible for past vegetative and reproductive growth, those involved in carbon production and storage (Matthews 1963; Van Vredenburch and La Bastide 1969; Eis 1973), and hormone levels (Sheng and Wang 1990; Ho 1991), at critical times such as bud differ-

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entiation. The process is sufficiently complex that simple relationships between individual variables and cone production have not been demonstrated (Ebell 1971; Jackson and Sweet 1972; Owens and Blake 1985).

The most abundant subalpine tree species in the subalpine zone of the western Cascade Mountains are subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) (Fonda and Bliss 1969; Henderson 1974; Franklin and Dyrness 1988). Subalpine fir occupies drier sites on south-facing slopes and in rain shadows; mountain hemlock exists in more mesic conditions (Henderson 1974; Franklin and Dyrness 1988). Both species exhibit the 2-year reproductive cycle typical of most temperate conifers, except most species of *Pinus* which have a 3-year cycle (Owens and Blake 1985).

Subalpine fir and mountain hemlock initiate reproductive buds in the year before cone production. Pollination occurs in late spring (subalpine fir, coastal British Columbia; Singh and Owens 1981) or early summer (mountain hemlock, coastal British Columbia; Owens and Molder 1975) of the cone year; cones are produced and seeds shed by autumn of the same year. Seed cones are found on the upper branches of both species, and pollen cones are produced on lower branches. The species differ in the types of buds that produce cones and flexibility of differentiation. Mountain hemlock seed cone buds develop from the initiation of apical vegetative buds on shoots that are at least 1 year old (Owens and Molder 1974, 1975); they rarely abort (Owens and Molder 1975) and are not reported to differentiate into vegetative buds. Subalpine fir seed cone buds can result from the initiation of undetermined apical, but more often, axillary buds on the upper surfaces of shoots (Owens and Singh 1982); they can abort, become latent, or differentiate into vegetative buds (Eis 1970).

We examined the influence of climate, history of radial growth, and past cone production on the size of cone crops of subalpine fir and mountain hemlock in the western Cascade Mountains. Regional as well as species differences are described. Because of the overlap of the differentiation and development of cones and the dependence of cone growth on carbon, direct and indirect climatic controls may not be straightforward. The existence of a multiyear record of weather and cone production for these two common species over a number of sites provided a unique opportunity to unravel some of the exogenous and endogenous factors associated with reproductive growth. Ultimately a better understanding of reproductive growth should improve our understanding of vegetative growth.

Methods

Study sites

Cone production data for subalpine fir and mountain hemlock (two sites each) were collected annually from 1962 to 1991 at locations in the central Cascade Mountains (Franklin 1968). Two of the four sites are located on opposite sides of a ridge in the Steamboat Mountain Research Natural Area (Gifford Pinchot National Forest, Washington, 46°08′21″N, 121°43′05″W). A subalpine fir site (SBF) (1524 m elevation, south aspect, 20–40% slope) included 15 surviving trees approximately 190 years old; a mountain hemlock site (SBH) (1615 m elevation, east-northeast aspect, 60% slope) included 14 surviving trees approximately 250 years old. The second subalpine fir site (SMF) is near Sand Mountain (Willamette National Forest, Oregon, 44°23′000″N, 121°55′18″W; 1585 m elevation, northwest aspect, 35% slope) and included 30 trees approximately 100 years old. The second mountain hemlock site (SPH) (Santiam Pass, Willamette National Forest, 44°24′57″N, 121°51′23″W; 1448 m elevation, 0% slope) included 14 trees approximately 290 years old. This site has been infested with spruce budworm (*Choristoneura fumiferana*) since 1986 (J.E. Means, personal observation). All trees were dominant or codominant.

Data collection

Cones were counted annually on individual trees in July and August from fixed points using a spotting scope. Comparison of total cone production among trees could not be made because the proportion of the total crop that could be viewed from the counting point for each tree was not estimated. Counting mountain hemlock cones was difficult due to their small size, dense clusters, and retention for 2–3 years (Franklin 1968). This necessitated counting mountain hemlock cones early in the season so new, closed cones could be distinguished from old, open ones.

All living trees at the four sites were cored using an increment borer in August 1991. Two cores were taken at breast height (1.37 m) from cross-slope sides of the trees and stored in paper straws for transport. Cores were mounted in wooden blocks and sanded until individual tracheids could be distinguished. The highest quality core from each tree was used to determine annual increment to the nearest 0.01 mm using an incremental measuring machine equipped with a television camera and monitor. The machine is linked with digital encoder and microcomputer, which uses software to store ring-width measurements on disk by year for each core (Robinson and Evans 1980). Cores were cross-dated visually (Swetnam et al. 1985) and verified with a spline regression procedure, which also produced an annual growth index for each site (COFECHA; Holmes 1983). The growth index expressed annual deviation from long-term trends in basal area increment (BAI) for each site primarily owing to annual weather. The BAI, calculated using ring width and distance to the pith, was used to describe the growth of individual trees; DBH of the tree was used if the pith was not present. Cores from one tree at the SBF site were not used because rings could not be cross-dated.

Mean monthly temperature and total monthly precipitation were obtained for the western divisions of Washington and Oregon (WeatherDisc Associates, Inc. 1990). Divisional records provide the best description of conditions at any point within a region if data from a nearby weather station at the same elevation are not available (Fritts 1976). Average summer temperature in western Oregon (16.4°C) is higher than western Washington (14.0°C); average annual precipitation is higher in western Washington (221.5 cm) than western Oregon (174.7 cm).

Statistical analysis

Pearson correlation coefficients were used to compare site growth index values and cone crop with weather variables. Weather variables included mean monthly temperature and total monthly precipitation for the cone year and the previous 2 hydrologic years (beginning in October), or for a growth year and 7 months of the previous hydrologic year. Heavy cone crop years were excluded from the correlations of growth index and weather to avoid the negative effect of cone production on ring width (Morris 1951; Eis et al. 1965; Tappeiner 1969).

Stepwise multiple regression (SAS Institute Inc. 1988) was used to determine the relative importance (r^2) of predictor variables for cone crop size. Cone count had a negative binomial distribution in this study because many years had counts of zero. This distribution is not uncommon for count data (Mood et al. 1974) but there is no standard analysis (McCullheh and Nelder 1989). In addition, the data were autocorrelated with a lag of 3 years. A normally distributed nonautocorrelated response variable was obtained using the square-root transformation of total cone counts in years following two light cone crops for subalpine fir and one light cone crop for mountain hemlock. This

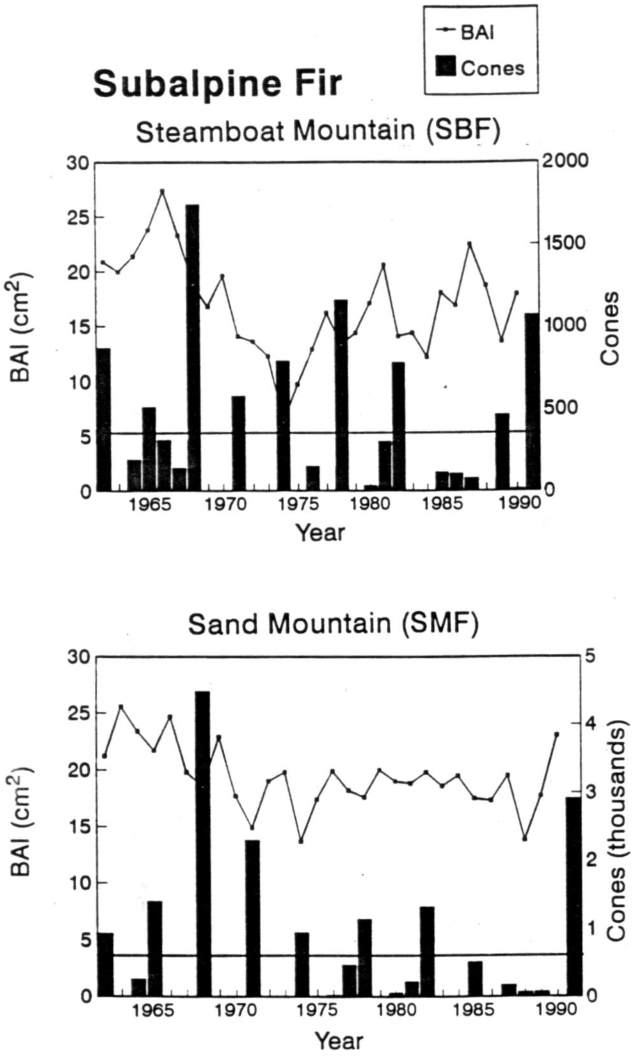

FIG. 1. Cone count (total cones for site) and mean basal area increment (BAI) for subalpine fir sites. Horizontal line differentiates between heavy and light cone crops.

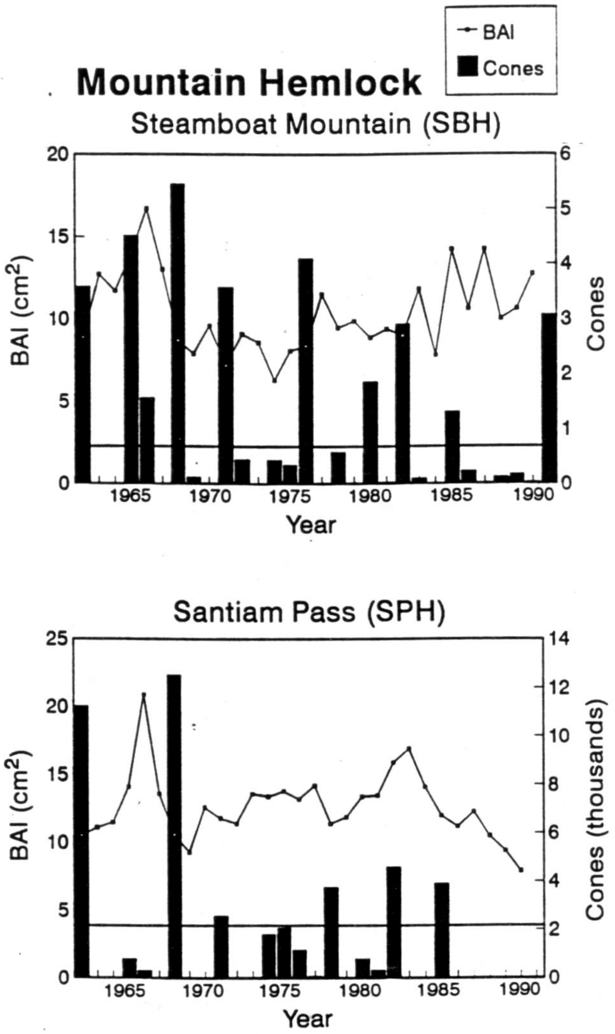

FIG. 2. Cone count (total cone for site) and mean basal area increment (BAI) for mountain hemlock sites. Horizontal line differentiates between heavy and light cone crops.

response variable accounted for the possibility that large cone crops inhibit cone production in subsequent years (Tiren 1935; Owens 1969; Ebell 1971; Caron and Powell 1989) by eliminating years with low BAI following heavy cone crops. Heavy cone crops were defined as those with more than 18% of the maximum observed crop. This level designated approximately half of crops as heavy at all sites, and separated classes at natural break points (see Figs. 1 and 2).

Predictor variables included the sum of basal area increment in the previous two years ($BAI_{-1,-2}$), and previous July ($JULT_{-1}$) and August temperature ($AUGT_{-1}$). These weather variables were selected because they have been associated with cone production in other studies (Tiren 1935; Fraser 1958; Daubenmire 1960; Yanagihara et al. 1960; Van Vredenburch and La Bastide 1969; Brondbo 1970; Eis 1973) and because they were correlated with cone production in preliminary data analysis for this study. The BAI of previous years was chosen to represent growing season quality and to indicate carbohydrate storage, which may influence cone production (Owens 1969; Ebell 1971; Eis 1973). The BAI was summed for 2 years because the values for individual years were significantly correlated ($p < 0.05$). Regression models were evaluated for total cone counts for each site (four sites, 30 years) and for individual trees (15–30 trees/site, 30 years).

Multiple regression was also used to predict growth index from temperature and precipitation using variables that explained the greatest amount of variance (highest r^2 value). Weather–growth regressions for each site were based on BAI measured for low cone years during the period of record to obtain a predictive equation for growth based on weather alone. This regression was used to predict growth for the heavy cone years, and residuals were used to examine the effect of cone crop on growth.

Results

Comparisons between BAI and cone production of subalpine fir (Fig. 1) and mountain hemlock (Fig. 2) showed that trees had better radial growth and the largest cone crops at all sites in the first decade of the 30-year record. Late snowmelt at Steamboat Mountain in 1974 resulted in small BAI for both species, but especially subalpine fir. A spruce budworm infestation resulted in small BAIs at site SPH in the late 1980s.

Site totals and tree averages of cone years did not differ between species (Table 1). However, the data from Steamboat Mountain indicate that mountain hemlock stands (SBH) may be able to produce more crops than subalpine fir (SBF) at the same site during the same time period. Individual trees had fewer cone crops compared with sites, especially at the youngest site (SMF). All sites except SMF had at least 1 year in which all trees produced cones.

Cone crops coincided more closely within species than between species or among sites (Fig. 3), although at least

TABLE 1. Number of years during the 30-year study in which cone production was greater than zero by site, and the proportion of individual trees contributing cones in those years for n trees per site

	No. of cone years			Trees contributing cones	
Site n	Site total	Tree average	Tree range	Average (%)	Range (%)
		Subalpine fir			
SBF 14	19	14	12–17	75	14–100
SMF 30	19	11	1–16	57	3–97
		Mountain hemlock			
SBH 14	25	16	14–21	65	7–100
SPH 14	16	13	11–15	81	7–100

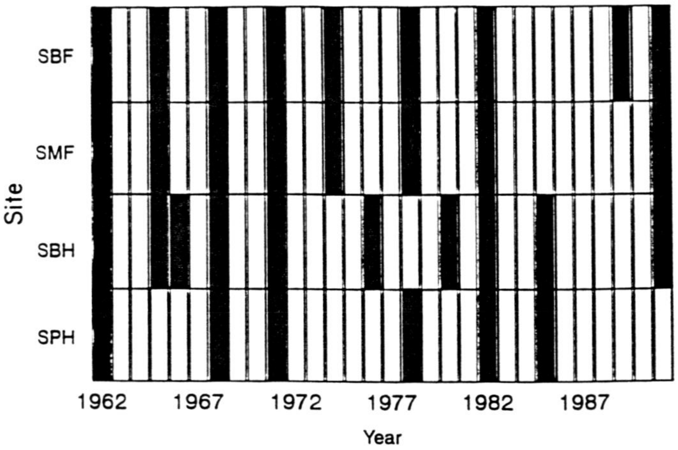

FIG. 3. Occurrence of heavy cone crops (solid bar) at four sites during 1962–1991.

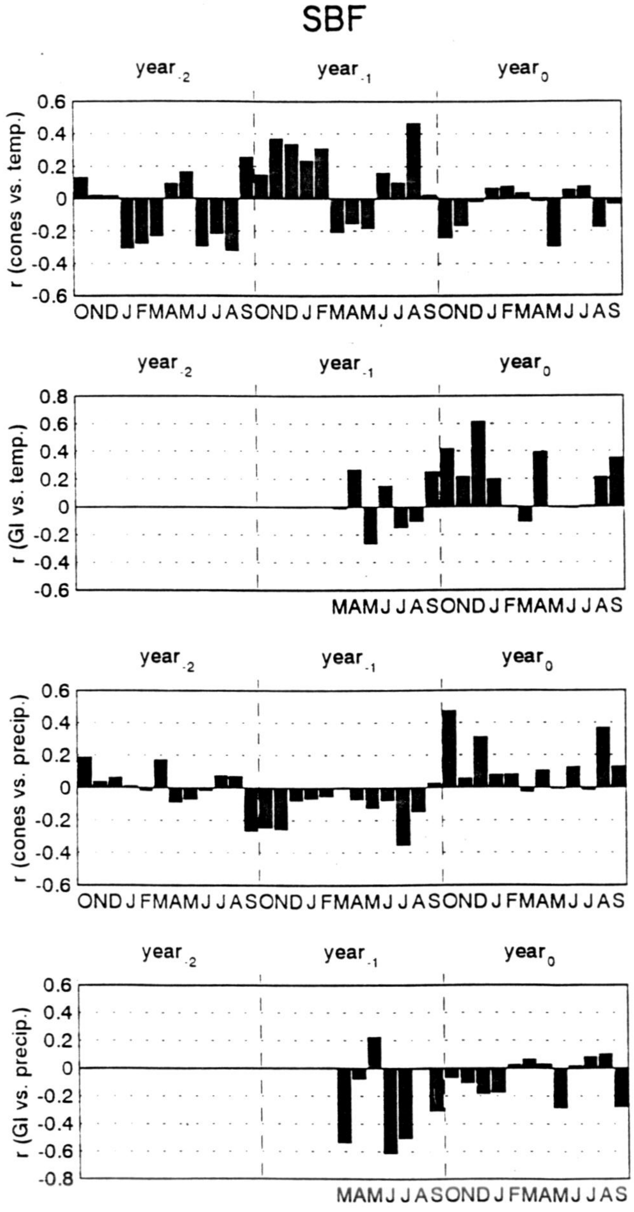

FIG. 4. Correlations of cone crop size and growth index (GI) with climate variables for subalpine fir at Steamboat Mountain.

three sites had synchronous crops in 6 years during the sample years. Large cone crops were produced most consistently at 3-year intervals during the 1960s and early 1970s. Subalpine fir cone crops occurred at 3-year intervals from 1962 through 1974, and at 4-year intervals from 1975 through 1982. Mountain hemlock cone production had a weak 3-year periodicity from 1962 through 1971.

Correlations of cone crop in any year (year$_0$) with climate variables in that year, and the previous 2 years (year$_{-1}$ and year$_{-2}$; Figs. 4–7) showed similar patterns for both tree species; correlations of growth index with climate variables varied with region (Washington vs. Oregon). Cone production for both species was associated with: (*i*) a cool, wet summer in year$_{-2}$; (*ii*) followed by a warm, dry fall and winter, a cool spring, and warm dry summer year$_{-1}$; (*iii*) followed by a cool, wet winter.

Radial growth was greater in response to dry conditions throughout the previous 19 months except in July and August in both years. Then, increased precipitation was associated with higher growth indices. In addition, high growth indices were associated with a previous warm fall and winter at Steamboat Mountain (SBF and SBH) and warm conditions in late winter and spring followed by a cool summer in Oregon (SMF and SPH). In general, conditions that were conducive to good radial growth in the previous year were also conducive to a large cone crop in the current year. Weather conditions associated with a large cone crop in the current year were not associated with good radial growth that year. This effect is independent of the effect of cone crop on radial growth because heavy cone years were excluded from the growth index – weather relationships.

Years were classified by the pattern of heavy or light cone

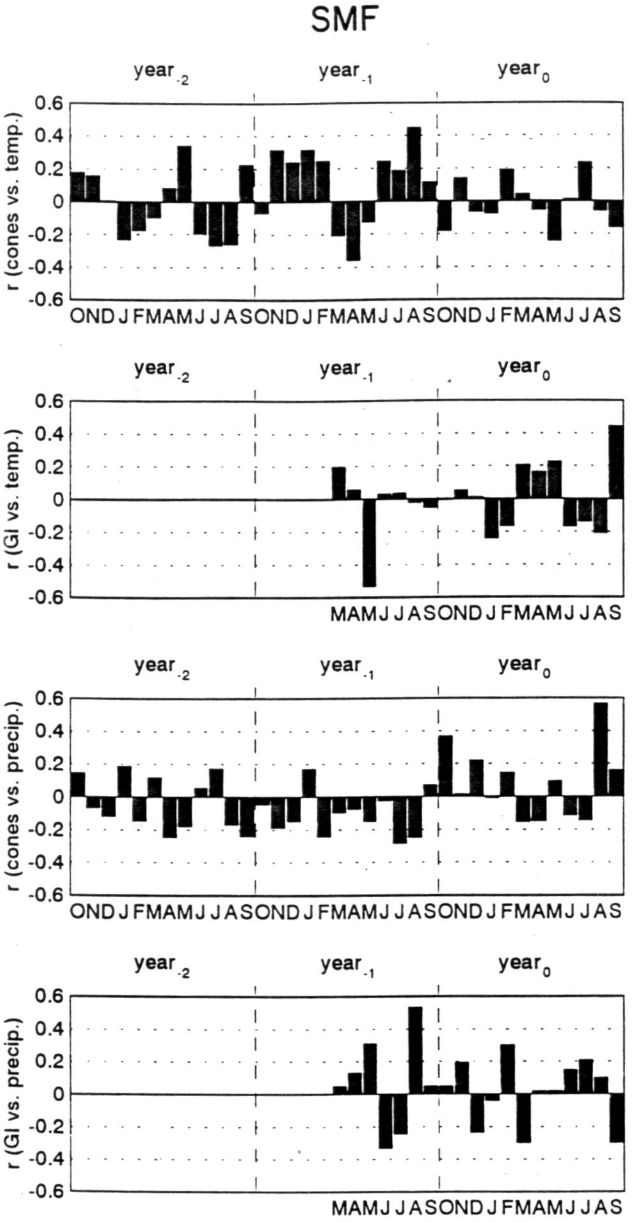

FIG. 5. Correlations of cone crop size and growth index (GI) with climate variables for subalpine fir at Sand Mountain.

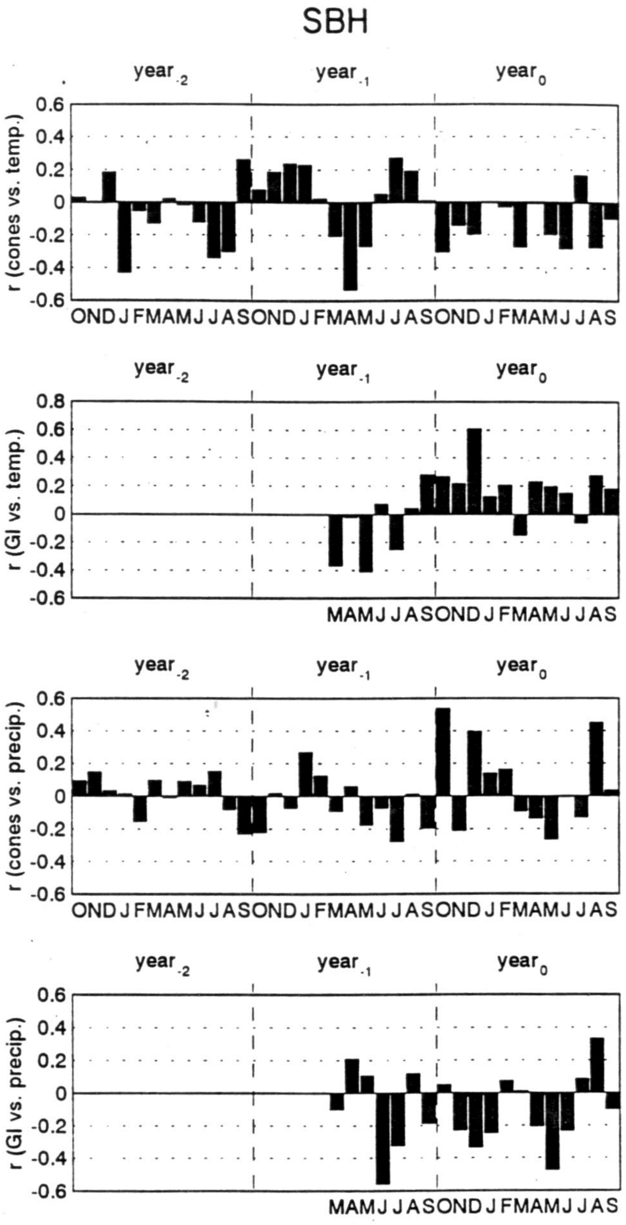

FIG. 6. Correlations of cone crop size and growth index (GI) with climate variables for mountain hemlock at Steamboat Mountain.

crops in the 2 previous years (Table 2) to examine the effect of past cone production on the current year's cone crop. The majority of cone crops and the highest average cone crops occurred in years following two low cone crops for both species. Subalpine fir cone crops were at least 50% smaller in years preceded by a heavy crop in either of the previous 2 years. Results from SBH show that mountain hemlock cone production was small in years preceded by only one heavy crop. These results suggest that the influence of previous cone crops lasts for two years for subalpine fir and one year for mountain hemlock.

The relative importance of growth, indicated by BAI, and previous summer temperature in predicting cone crop varied between tree species (Table 3). Cone production for subalpine fir in years following two light crops was predicted best by $BAI_{-1,-2}$ at both sites ($p < 0.03$ SMF, $p < 0.10$ SBF), although $AUGT_{-1}$ was also significant ($p < 0.03$) at SMF, the site with younger trees. Results from individual trees were consistent with site patterns. Significant ($p < 0.03$) predictor variables for cone crop size of mountain hemlock included $JULT_{-1}$ at SBH, and $BAI_{-1,-2}$ and $JULT_{-1}$ temperature at SPH. Results from individual trees at both hemlock sites show summer temperature in the previous year as more important than the previous 2 years' BAI for predicting cone crop in mountain hemlock.

The strength of the association of previous BAI, especially in $year_{-2}$, and previous summer temperature with cone crop is emphasized by the case of 1968, which was the year of highest cone production for all four sites and 57% of individual trees. It was preceded in 1967 by the highest August temperature recorded during the study period at all sites, and in 1966 by the greatest BAI for three sites (SBF, SBH, and SPH) and the second greatest for the fourth (SMF).

When multiple regression was used to predict radial growth from weather variables using data from light cone crop years, the expected value of the residuals is zero. A trend in residuals when growth is predicted for heavy cone years

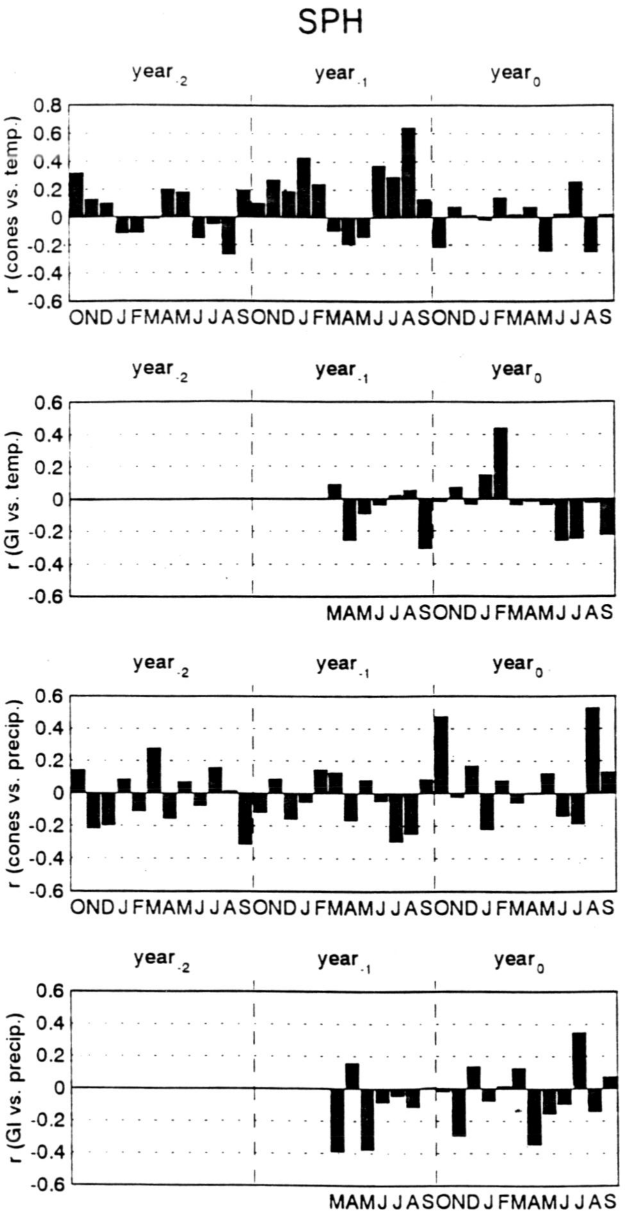

FIG. 7. Correlations of cone crop size and growth index (GI) with climate variables for mountain hemlock at Santiam Pass.

TABLE 2. Distribution and size of cone crops in years having one of four crop histories

	Cone crop history[a]			
	LL	HL	LH	HH
Subalpine fir				
SBF				
No. of years	14	8	8	0
No. of cone years	12	5	2	—
Cone years (%)	86	62	25	—
Mean cone crop (site)	621	313	157	—
Mean cone crop (tree)	44	22	11	—
SMF				
No. of years	16	7	7	0
No. of cone years	14	3	2	—
Cone years (%)	88	43	29	—
Mean cone crop (site)	1206	106	2	—
Mean cone crop (tree)	40	4	0	—
Mountain hemlock				
SBH				
No. of years	13	8	8	1
No. of cone years	13	5	7	0
Cone years (%)	100	62	88	—
Mean cone crop (site)	1775	1786	343	—
Mean cone crop (tree)	127	127	25	—
SPH				
No. of years	18	6	6	0
No. of cone years	14	1	1	—
Cone years (%)	78	17	17	—
Mean cone crop (site)	3205	767	5	—
Mean cone crop (tree)	229	55	0	—

[a] LL, two light crops; HL, heavy crop followed by a light crop; LH, light crop followed by a heavy crop; HH, two heavy crops. Light cone crops are defined as those with less than 18% of the maximum observed crop.

using the equation based on light cone years was used to indicate an effect of cone crop on growth. Residuals for heavy cone crop years at the subalpine fir sites (Fig. 8) were negative on average (SBF = −1.18; SMF = −0.53); the residuals in heavy cone years at the hemlock sites were closer to zero than subalpine fir (SBH = −0.20, SPH = −0.40) (Fig. 9). The negative residuals at the end of the SPH record correspond to a spruce budworm outbreak.

Discussion

Relationships among weather, cone production, and radial growth

Associations between weather and cone production have been described for a variety of conifer species with 2-year reproductive cycles (Table 4). Our results agree with some relationships and contradict others. The cool conditions in year$_{-2}$ important to cone crops of subalpine fir and mountain hemlock in our study (Figs. 4–7) agree with cool, wet conditions in year$_{-2}$ seen for lowland Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). These conditions may be associated with increased photosynthesis because July temperatures are often above optimum for Douglas-fir (Salo 1974). Increased photosynthesis may have a positive influence on reproductive bud initiation in year$_{-1}$ in response to increased carbohydrate storage (Matthews 1963) or from greater initiation of leaf primordia, thereby providing more axillary sites for cone bud initiation in the following year (Owens and Blake 1985). Cool, wet weather in July and August is associated with good radial growth for subalpine fir and mountain hemlock at the Oregon sites; only July and August precipitation is important at the Washington sites where average temperature is lower. Apparently, conditions resulting in good radial growth by reducing moisture stress in year$_{-2}$ are associated with good cone crops.

Our results show that warm, dry weather in the year of reproductive bud initiation is associated with large cone crops in subalpine fir and mountain hemlock (Figs. 4–7) as it is in many other conifer species with 2-year reproductive cycles (Table 4), and flowering trees (Jackson and Sweet 1972; Owens and Blake 1985; Zasada et al. 1992). Temperature has potential to act through many mechanisms because it affects metabolic processes, including photosynthesis, nutrient and water uptake, and resource utilization, all of which may affect the ability of a tree to produce cones (Owens and Blake 1985). Temperature is also associated with high light levels, which may stimulate cone production (Winjum and Johnson 1964; Smith and Stanley 1969;

TABLE 3. Predictor variables for cone crop size in year following two light cone crops (subalpine fir) or one light cone crop (mountain hemlock)

		Site total		Individual trees	
Site	n	Variable	Partial r^2	Variable	Mean partial r^2
		Subalpine fir			
SBF	14	$BAI_{-1,-2}$	0.203	$BAI_{-1,-2}$	0.060
				$AUGT_{-1}$	0.055
SMF	15	$BAI_{-1,-2}$	0.477	$BAI_{-1,-2}$	0.140
		$AUGT_{-1}$	0.263	$AUGT_{-1}$	0.083
				$JULT_{-1}$	0.012
		Mountain hemlock			
SBH	21	$JULT_{-1}$	0.296	$JULT_{-1}$	0.131
				$BAI_{-1,-2}$	0.015
SPH	23	$BAI_{-1,-2}$	0.335	$AUGT_{-1}$	0.194
		$JULT_{-1}$	0.149	$BAI_{-1,-2}$	0.035
				$JULT_{-1}$	0.027

NOTE: All predictor variables are $p < 0.03$, except for SBF, which is $p < 0.10$. Variables are listed by their partial r^2 values for sites, and by partial r^2 values averaged across cores for variables with $p < 0.05$ for at least one core. Signs of all predictors are positive.

Brondbo 1970; Simpson and Powell 1981). High temperatures may also result in moisture stress, which has been shown to stimulate reproductive bud initiation (Matthews 1963; Ross 1988) as have other stresses such as girdling and wounding (Owens and Blake 1985).

In contrast to others, we found a positive relationship between cone production and a warm, dry winter 18 months before cone crop (year$_{-1}$; Figs. 4–7), while a cold winter is associated with good cone production in low-elevation species (Eis 1973; Table 4). A cold signal is thought to trigger physiological processes that result in cone production in low-elevation species; it may be available every year to high-elevation species. A longer growing season resulting from a warm winter with low snowpack may be more important at high elevations. In addition, the requirement for a warm winter just prior to a cone crop that has been observed in other studies (Lowry 1966; Eis 1973) is only weakly supported here.

We can also use correlations of weather with growth index (based on BAI) and cone crop to evaluate radial growth in years preceding heavy cone crops. Good radial growth in subalpine fir and mountain hemlock is associated most consistently with a warm, dry winter and spring, presumably because the reduced snowpack provides a longer growing season. This relationship has been previously seen for subalpine fir (Colenutt and Luckman 1991; Villalba et al. 1992; Peterson 1993) and other subalpine species including Engelmann spruce (*Picea engelmannii* Parry) (Colenutt and Luckman 1991; Villalba et al. 1992; Peterson 1993), subalpine larch (*Larix lyallii* Parl.) (Graumlich and Brubaker 1986; Colenutt and Luckman 1991; Peterson 1993), and mountain hemlock (Graumlich et al. 1989). The comparison between conditions favoring growth index with those favoring cone crop suggest that a warm dry winter 18 months preceding cone crop should be associated with good radial growth in year$_{-1}$ (Figs. 4–7). In contrast, the tendency of growth index and cone crop to have opposite-signed correlation coefficients with weather variables in year$_0$ (Figs. 4–7) suggests that a heavy cone crop may be associated with poor radial growth in the cone year. This result is based on climate alone, without considering the production cost of cones, which also reduces radial growth (Morris 1951; Eis et al. 1965; Tappeiner 1969).

Endogenous and exogenous factors affecting cone production

Reviewers have concluded that reproduction in trees is determined by interactions among endogenous and exogenous factors (Jackson and Sweet 1972; Puritch 1972; Owens and Blake 1985; Ross and Pharis 1985) whose complexity is magnified in conifers because cone development proceeds over several years, which increases the likelihood of failure from stochastic events. Exogenous factors include supplies of raw materials and energy, which are determined primarily by climate. Endogenous factors include nutrient (both carbon and minerals) and hormone levels, which are determined by history of growth and reproduction in response to exogenous factors. Few studies of the effect of climate on cone production have separated the influence of endogenous from exogenous factors; the work by Rehfeldt et al. (1971) is an exception.

With only 30 years of cone-crop data, many explanatory variables to differentiate, and data requiring nonstandard analysis, we attempted to separate endogenous and exogenous factors in stages. First, the endogenous effect of previous cone production was examined (Table 2). When years that had been strongly influenced by a previous cone crop were removed from further consideration, the importance of exogenous and other endogenous factors could be examined using multiple regression. We limited our examination of climatic effects to variables ($JULT_{-1}$, $AUGT_{-1}$) that are correlated with cone production in our study, were found important by others (see Table 4), and are associated with a critical stage of cone bud initiation. In addition, we included the influence of endogenous assimilate status by using history of radial growth ($BAI_{-1,-2}$) as a surrogate.

Vegetative and reproductive growth share the same resources, and a variety of evidence indicates that one occurs at the expense of the other (Powell 1977). Cone crops are associated with a decrease in increment growth in trees (Morris 1951; Eis et al. 1965; Tappeiner 1969) and in individual branches that have abundant cones compared with those that do not (Smith and Stanley 1969). Trees may have

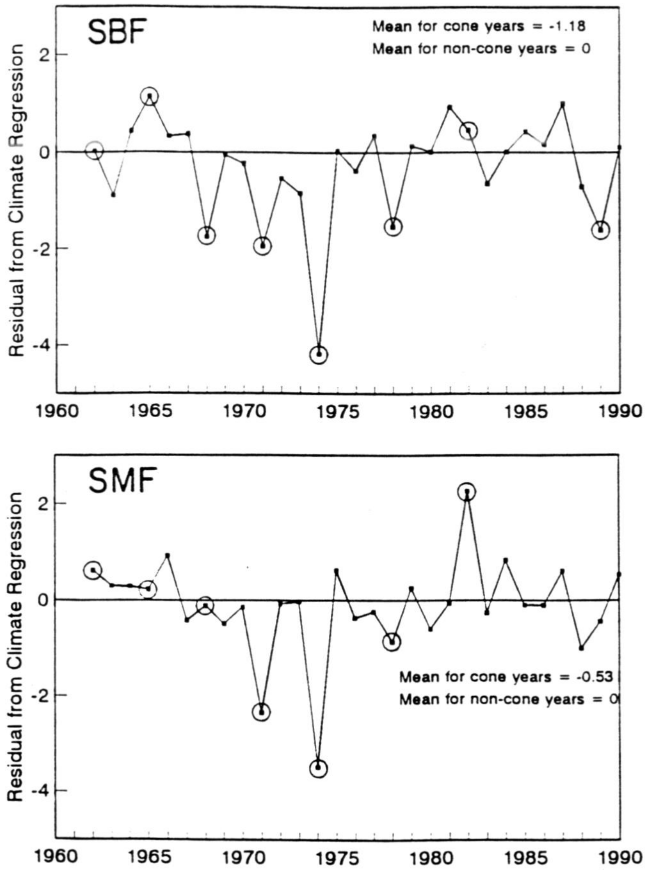

FIG. 8. Residuals from regression equation predicting basal area increment (BAI) from climate variables for subalpine fir sites. The regression equation was developed using years with no cones or light cone crops. Circles indicate heavy cone crops.

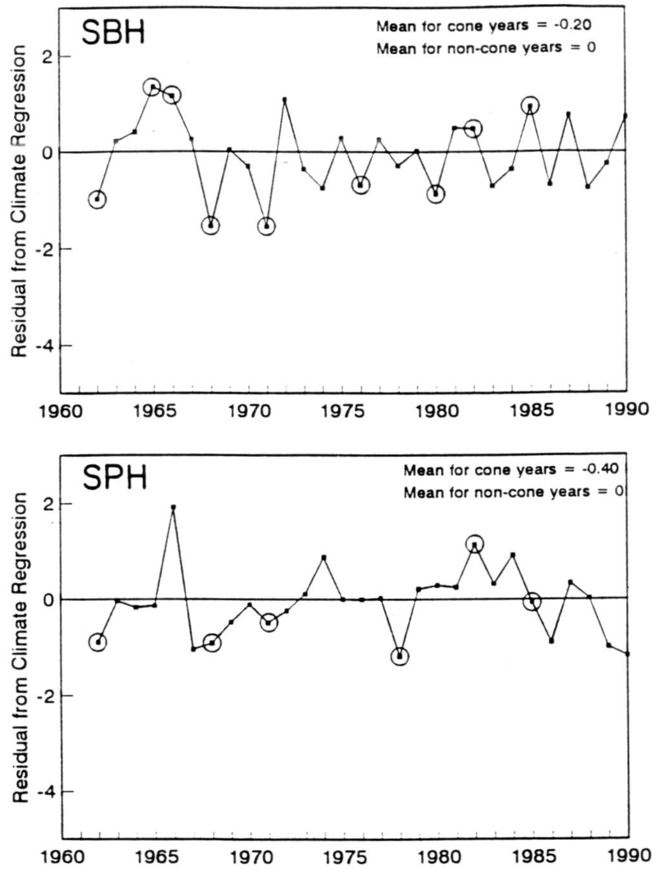

FIG. 9. Residuals from regression equation predicting basal area increment (BAI) from climate variables for mountain hemlock sites. The regression equation was developed using years with no cones or light cone crops. Circles indicate heavy cone crops.

a genetic predisposition to producing large cone crops or growth but not both (Linhart and Mitton 1985). Cone production competes with vegetative growth because cones are strong sinks for carbohydrate and nitrogen reserves at the expense of vegetative structures (Dickman and Kozlowski 1970; Rook and Sweet 1971), and because cone buds differentiate in place of vegetative buds. Conditions that enhance carbohydrate concentrations in shoots (e.g., increased light or phloem blockage by girdling) or inhibit vegetative growth (e.g., water stress during shoot elongation) are associated with large cone crops (Ross and Pharis 1985). Lags between cone crops have been attributed to the need to replenish reserves (Owens 1969; Ebell 1971) or the fact that cone buds cannot differentiate in years with cone development and vegetative growth already in competition for resources (Smith and Stanley 1969). In spite of this evidence, studies have failed to show a connection between cone production and soluble sugar or total carbohydrate content of shoots (Ebell 1971; Ross and Pharis 1985). It has been shown, however, that carbohydrate determinations for entire shoots do not represent carbohydrate levels at individual buds (Takeda et al. 1980).

Our results show a stronger relationship between radial growth and cone production for subalpine fir than mountain hemlock. This is supported by the importance of $\mathrm{BAI}_{-1,-2}$ as a predictor variable for cone production (Table 3), the large negative residuals from the climate regression in heavy cone years (Figs. 8 and 9), and the apparent need for 2 years between heavy cone crops for subalpine fir (Table 2). In contrast, radial growth was not an effective predictor variable for mountain hemlock cone production except in the case of SPH, which had a period of poor growth without cone crops due to spruce budworm infestation. The importance of growth was not supported by the analysis of individual trees at SPH. Furthermore, mountain hemlock BAI in heavy cone years did not deviate consistently from the prediction based on climate, and a lag of only 1 year was necessary between heavy cone crops.

Differences between species in the relationship between radial growth and cone production cannot be explained by greater relative commitment of resources represented by cone crops of either species. Franklin and Carkin (1974) stated that total production at these sites could be estimated by 2.0 (mountain hemlock) or 1.7 (subalpine fir) times the median cone count. When this equation is applied to total cones produced over 30 years at SBF and SBH (Table 2), two healthy, mature stands with equal numbers of trees, the result shows that mountain hemlock produced four times as many cones as subalpine fir (4222 vs. 1042 cones). However, subalpine fir cones have 4.5 times greater volume than mountain hemlock cones on average (Harlow and Harrar 1969 for subalpine fir; Sudworth 1968 for mountain hemlock). Assuming equal densities, the total investment in cone crops may not be very different between species.

Growing-season length limits the potential resources which can be allocated to growth and reproduction. Mountain hemlock is more competitive on sites with deeper snowpack

TABLE 4. Climatic conditions associated with cone production in conifer species having 2-year reproductive cycles (Owens and Blake 1985)

Period	Mechanism	Species	Reference
Cool, wet June, July, and August (year$_{-2}$)	Associated with good growth	Douglas-fir Grand fir	Lowry 1966; Van Vredenburch and La Bastide 1969; Eis 1973 Eis 1973
Cold December, January, and February (year$_{-1}$)	Exposure to low temperature is required for many physiological processes	Douglas-fir Grand fir	Eis 1973 Eis 1973
Moist, cloudy, cool March and April (year$_{-1}$)	Associated with seed cone differentiation	Douglas-fir Grand fir Subalpine fir	Lowry 1966; Van Vredenburch and La Bastide 1969; Eis 1973 Eis 1973 Henderson 1974
Drought, May and June (year$_{-1}$)	Increase in carbohydrates; cone differentiation associated with cessation of vegetative elongation; conditions reduce chance of abortion	Douglas-fir Grand fir Subalpine fir	Ebell 1967, Van Vredenburch and La Bastide 1969; Eis 1973 Eis 1973 Henderson 1974
Warm, dry summer (year$_{-1}$)	Cone differentiation associated with cessation of vegetative growth which may result from drought stress; carbohydrates may also be involved	Douglas-fir Black spruce Engelmann spruce Japanese larch Norway spruce Grand fir White spruce	Lowry 1966; Van Vredenburch and La Bastide 1969; Eis 1973 Caron and Powell 1989 Ross 1985 Yaniġihara et al. 1960 Tiren 1935; Fraser 1958; Brondbo 1970; Lindgren et al. 1977 Eis 1973 Ross 1988
Warm winter (year$_0$)	No freeze damage; warmth for seed and pollen formation	Douglas-fir Grand fir	Lowry 1966; Eis 1973 Eis 1973
Sunny, dry April	Time of pollination	Douglas-fir	Eis 1973
Sunny, warm June and July (year$_0$)	Susceptible to frost damage	Douglas-fir	Lowry 1966

than subalpine fir, and therefore experiences later snowmelt. In spite of the relatively short growing season at mountain hemlock sites, cones crops that do not appear to affect radial growth. Development of cones from apical buds may insure that resources normally allocated to foliar growth are used for reproduction by limiting terminal vegetative growth. Also, the apical position prevents cones from intercepting photosynthate flowing from foliage to the trunk. Hence, resources for radial growth may not be greatly affected. In addition, mountain hemlock experiences only partially preformed growth, which allows it to produce more foliage to compensate for reproductive growth in years when resources are abundant. The SPH mountain hemlock site, where insect infestation resulted in poor growth and an absence of cone crops, illustrates that stress can result in poor radial growth and cone production.

Subalpine fir experiences generally longer growing seasons and exhibits a slightly different strategy for reproduction. Subalpine fir cone crops are comprised of fewer, large cones, whose production is more detrimental to radial growth. Cones develop only from lateral buds, where they can act as sinks for photosynthates moving from new foliage to the trunk. In addition, vegetative growth is preformed in subalpine fir, so compensatory foliage cannot be produced if conditions are suitable. However, commitment of buds to reproduction is flexible; buds can abort prior to differentiation, or become latent or form shoots at the differentiation stage. The high cost of producing cones may explain the fact that conditions associated with large cone crops in year$_0$ are also associated with good radial growth in year$_{-1}$ (Figs. 4 and 6).

Global climate change, cone crop, and seedling establishment

Heavy cone production is associated not only with greater numbers of seeds, but also with a greater proportion of viable seed (Noble and Ronco 1978; McDonald 1992). Small cone crops of subalpine fir may include as little as 7% filled seed while large crops can have 50% filled seed (Noble and Ronco 1978). Therefore, it seems that large crops are necessary for significant seedling establishment to occur. In addition, seeds of these species are thought not to persist for more than one (subalpine fir) or two (mountain hemlock) seasons in the soil (Archibold 1989), so large cone crops must occur fairly frequently to replenish the seed bank.

Subalpine fir requires good radial growth in the 2 previous years and mountain hemlock requires a warm summer in the previous year to produce large cone crops. The predicted effect of global climate change is for an increase in mean annual temperature of 2.0°C above the preindustrial level by 2025 if present trends in greenhouse gas emissions continue (IPCC 1990). This change could meet the needs of both species by lengthening growing seasons and providing warmer July and August temperatures. However, the effect of precipitation on growth and cone production is crucial because precipitation patterns and amounts determine depth of winter snowpack and degree of summer drought. Moreover, some cool, wet periods are associated with large cone crops. Unfortunately, precipitation is not predicted with certainty by existing climate models (IPCC 1990). It is possible that the growing season will be defined in the future by earlier meltout but earlier dormancy due to drought stress in summer. These conditions may have no net effect on cone crop, assuming there is some adjustment in conifer phenology.

Mean annual temperature during the 1980s was greater than any decade since continuous weather records began ca 1870 and may be part of a long-term warming trend (IPCC 1990). There were fewer and less regionally synchronized cone crops at our study sites during this time period. However, there were several episodes of seedling establishment at several sites in the Cascade Mountains during the 1980s (Little et al. 1993; R.M. Rochefort, unpublished data). This can be explained if viable seed persists in the soil longer than previously thought, or if growing conditions are more limiting than the number of seeds even when cone crops are light. We conclude that climate, through its effects on cone production, is not likely to limit the establishment of trees in subalpine meadows in the near future, even though cone production by subalpine conifers may be lower and more variable if future climate is warmer.

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