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GRADUATE COLLEGE

MAST FRUITING IN TREES: WHY AND HOW IN CEMBROID PINES

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BY

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MAST FRUITING IN TREES: WHY AND HOW IN CEMBROID PINES

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MAST FRUITING IN TREES: WHY AND HOW IN CEMBROID PINES

Frank Forcella

Major Professor: Paul G. Risser

ABSTRACT

A quantitative, 10-year, unit-area cone production sequence can be precisely estimated from a single brief visit to a Pinus edulis woodland. Such a sequence has applicability to natural resource managers and basic biologists alike. Good P. edulis (pinyon) seed crops are characteristically erratic, with only 1-3 occurring in a 10-year period.

If good seed crops precede one another, the second crop is invariably infested by obligate cone insects (and other animals). For this reason, consecutively good cone crops are not advantageous to pinyons. Instead, sporadic mast crops appear to confer survival to pinyon seeds. Cone and seed "predation" by animals may have been the evolutionary impetus for the development of mast fruiting behavior in trees.

Ecologically, sporadic mast crops are due to the exponential dependence of the initiation of ovulate cone primordia on erratically occurring low temperatures during the last week of August and/or the first weeks of September (2 years before crop maturity). The annual southerly migration of the stratospheric jet stream provides the requisite low temperatures at this time. Several other biotic events may be dependent upon these same low temperatures; included here are autumnal leaf senescence in temperate deciduous trees, and autumnal migrations of birds.

Pinus spp. cone crops are generally initiated by physiological stress (e.g. low temp., drought, low nitrogen availability etc.), where vegetative growth ceases prematurely, and generative growth processes commence. Environmental conditions initiating these stresses are always the logical opposites of the modal environments of the pine species.

Interspecific differences between P. edulis and P. monophylla, in regard to cone and canopy morphology, are consistent with the fact that the former is primarily infested by a relatively unmobile, obligate cone beetle (Conophthorus edulis; Scolytidae), whereas the latter primarily endures a mobile, obligate cone moth (Eucosma bobana; Tortricidae). Copious resin production by pinyon cones inhibits animal "predators" and microbial pathogens, but it equally inhibits subsequent decomposition of dead cones. Valuable plant nutrients are thereby securely locked into cone material that is highly resistant to degradation for several years. Consequently, these same nutrients are not available for use by the living trees. The ramifications of cone predation by animals span a range of biological subjects: physiology, biogeography, bioclimatology, microbial ecology, nutrient cycling and evolution.

CHAPTER 1

INTRODUCTION

Mast "fruiting", that is the occurrence in particular years of extraordinarily large fruit or seed crops, is characteristic of several plant taxa (Janzen 1971, 1976). The importance of this behavior to plants is not certain, but it profoundly affects animals, including humans, that are directly or indirectly dependent upon mast (Elton 1924, Formosof 1933, Lauckhart 1957, Svårdson 1957). In this report I shall detail the evolutionary impetus and ecological mechanism for mast crops, as I believe them to be, in one subsection of pine trees. To the best of my knowledge, these aspects of mast fruiting have not been previously resolved for any taxon. With due modification I believe my results can be extrapolated to other taxa, including prey animals. It is my hope that this report will aid biologists of many diverse backgrounds toward insights into the evolutionary development of physiological/morphological characters and the ecological manner in which these characters are expressed.

Pinyons, Pinus subsec. Cembroides, of warm and arid southwestern North America (Fig. 1) produce large-seeded ovulate cones that provide food for numerous animals (Phillips 1909, Frischknecht 1975). These strobili however, are not particularly dependable resources because of their highly variable annual production (Balda & Bateman 1971, Forcella 1978, Ligon 1978). Just how variable such production is has never been quantified, except for observations of "good" or "heavy" crops occurring in 1-3 out of 10 years, with very meager intervening crops (Phillips

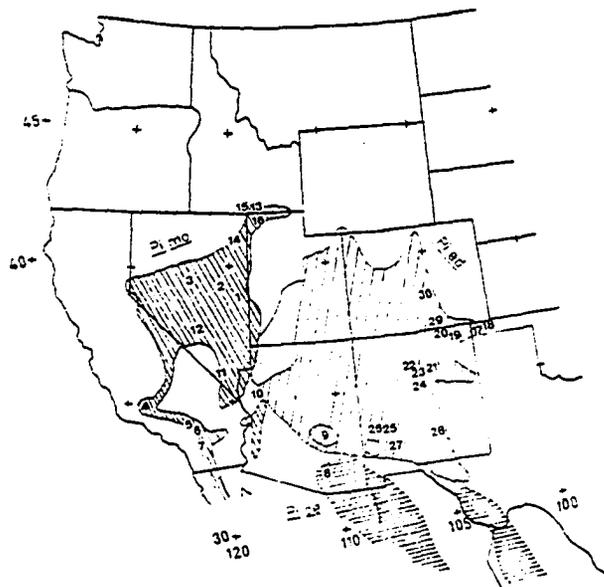
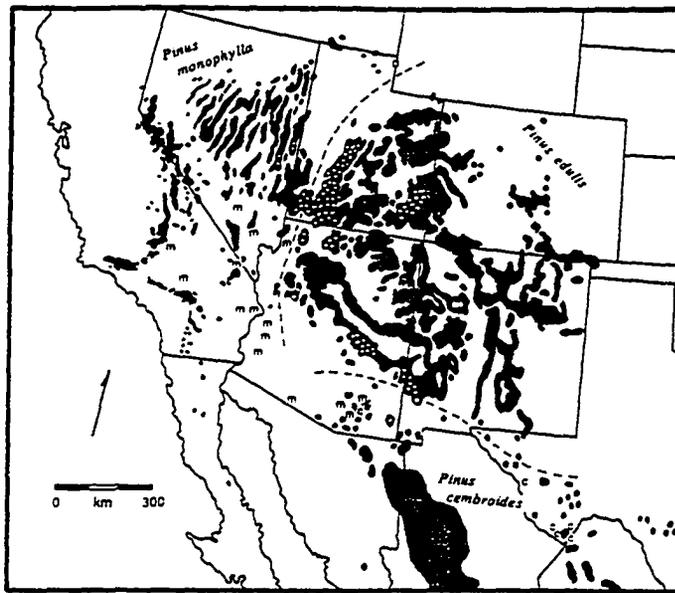


Figure 1. Upper map: Distribution of 3 major cembroid pines in USA and adjacent Mexico (from Van Devender & Spaulding 1979). Stippling represents areas of hybridization between *Pinus monophylla* and *P. edulis*. Lower map: Generalized distribution of 3 major cembroid pines and approximate locations of 30 sampled pinyon stands. Stands 1-16 were sampled in 1977, stands 17-30 in 1978. Stands 17-24 and 26-28 were analyzed for development and documentation of sampling methods (Forcella 1980a, see text); stands 17-24, 26 and 28 for animal/plant interactions; and stands 18-25 and 27-29 for relationship of cone crops and climate (each of these latter stands is near a U.S. Weather Bureau Station).

1909, Little 1938, Schopmeyer 1974). Not only has crop variability not been quantified, but no attention has been given to the more fundamental question of why pinyon crops are so variable from year to year. As implied above, there are two components to this question of mast crops: (1) the evolutionary impetus for their initial development, and (2) the current ecological mechanism for their actual production.

In the winter and spring of 1977 I was able to collect limited data and make preliminary observations on Pinus monophylla Torr. & Frem. (single-leaf pinyon) in the Great Basin and California (Forcella 1978). This allowed me to formulate hypotheses regarding precise quantitative estimation of pinyon cone crops, their yearly variability, and the evolutionary and ecological mechanisms for such variability. I tentatively concluded that: (1) a 10-year, unit-area, cone production sequence could be estimated from a single visit to a pinyon stand, (2) average cone crops might be accurately predicted from such an easily measured stand parameter as pinyon canopy coverage, (3) annual cone crops of stands were highly variable, with coefficients of variability (cv) averaging 100% (i.e. 1-3 good cone crops every 10 years, as had been observed earlier), and (4) consecutively good annual production was not advantageous for pinyon because this apparently allowed populations of cone- and seed-consuming animals to increase and devastate subsequent crops. This last conclusion was reasonable considering that: breeding success of some seed-consuming birds is dependent upon the availability of pinyon cones (Vander Wall & Balda 1977, Ligon 1978), some insects are entirely dependent upon these cones (Keen 1958), and

there was a significant correlation between the magnitude of animal depredation in the current year and the abundance of cones produced the previous year (Fig. 2). If this relationship was widespread taxonomically and geographically, and of long duration, then the characteristic variability of pinyon cone production may be a product of natural selection that developed through the following sequence of events: trees that produced cones every year supported large populations of cone- and seed-consuming animals and thereby produced few mature progeny, whereas trees with erratic production maintained small animal populations through low average annual cone production. These latter trees insured animal satiation and seed survival during the few and variable years of bountiful cone crops, but in the more numerous intervening years of poor cone crops they equally insured animal starvation. (Evidence for satiation is the occurrence of sound and presumably viable seeds that can be found on the ground in mid-winter after a mast crop.) Differential intensity of animal consumption thereby selected for erratically producing trees.

I was also curious as to the mechanism by which erratic crops were triggered or produced. Some pines produce consistent crops, for example P. banksiana, P. contorta (Lester 1967) and P. sylvestris (Svärdson 1957). In fact, the entire subsection Sylvestre, to which the above three species belong, seems to produce moderately abundant annual cone crops. In other pines regular cyclic reproduction occurs, every four years in P. monticola, for instance (Rehfeldt et al. 1971). This regular-

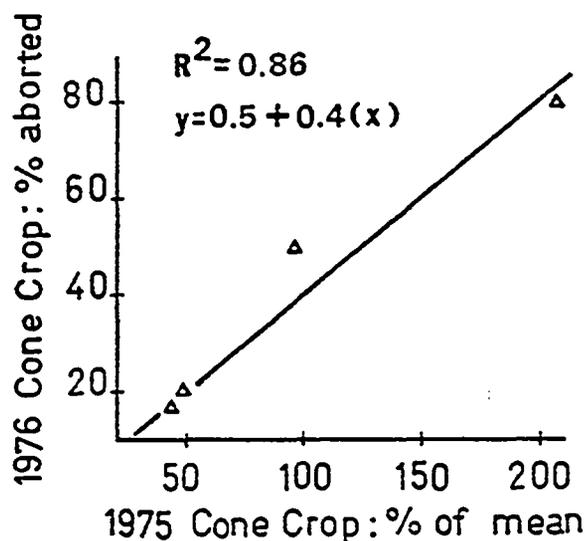


Figure 2. Relative utilization of pinyon cone crops by Eucosma bobana (pine-cone moth) larvae as a function of the magnitude of the previous year's crop. Ordinate represents percent of 1976 crop aborted from larval infestation. Abscissa represents 1975 crop as percent of 10-year cone production sequence for each Pinus monophylla community. If all cone predators (insects, rodents and birds) were included in the analysis the slope of the regression line would be about 0.5 (from Forcella 1978).

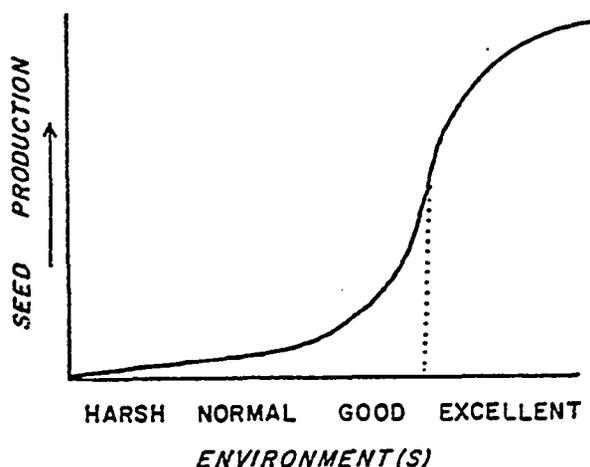


Figure 3. Original hypothetical model developed in 1977 for mechanism of erratic mast crop production in pinyon. Abscissa represents environment conducive to initiation of ovulate cone primordia in late August and/or early September two years prior to cone maturation. Average years produce meager cone crops, while only anomalous environmental years produce erratic mast crops.

ity is usually and logically explained by internal energy drains and restorations within the plants. But there is no intuitively obvious control mechanism for erratic production as in pinyons. Indeed, "erraticness" implies an uncontrolled mechanism. There is one possibility however. I guessed that production of pinyon cones (better stated as the successful initiation or development of ovulate cones, two years prior to cone maturation, from normally vegetative over-winter buds that form in mid-summer) was exponentially dependent upon some highly erratic environmental variable, probably involving local climate. Fig. 3 illustrates my original hypothetical model for cone production in pinyon. Here, most years at the time of primordia initiation would be average years, or nearly so, and would not be conducive to abundant cone production. But with the occurrence of anomalous weather an exponentially greater number of primordia would be induced. Thus mast crops would be as erratic as the anomalous weather conditions they require. I also assumed that with too extreme conditions the curve would at some point peak or level off; for example, if precipitation stimulated primordia, it is easily imagined that too much rainfall would cause soil flooding, anaerobiosis, and damage to actively respiring plant parts. Furthermore, since the American Southwest is characteristically hot and dry in summer, the only anomalous weather conditions that could hypothetically induce primordia would be cool and/or wet ones. Therefore, at the time of primordia initiation, August or September two years prior to cone maturation (Little 1938, Mirov 1967), cool and/or moist conditions were postulated

to be requisite for abundant cone production. If this were so it would be contrary to the environmental conditions assumed by other authors to stimulate cones in all other conifers (Eis 1976, Rehfeldt et al. 1971, and see reviews by Matthews 1970 and Jackson & Sweet 1972).

In winter 1978, armed with unsubstantiated techniques and ideas, I sampled several Pinus edulis Engelm. (Colorado pinyon) woodlands (Fig. 1) where I: (1) more fully developed and documented the adequacy of the sampling techniques (Forcella 1980a, Chapter 2), (2) analyzed several stands for cone crop/animal interactions (Forcella 1980b, Chapter 3), and tested the hypothetical exponential effect of climate on cone production (Forcella 1980c, Chapter 4).

After these analyses were completed I sought to compare my results, where pertinent and possible, with those of others in order to ascertain the breadth of my hypotheses and conclusions (Chapter 5). New insights arose, reinterpretation of published data for other pines was necessary, and a general synthesis of the mechanism for pine cone induction was attempted (Chapter 6). I have also investigated some broader biological implications associated with the same stimulus that initiates pinyon cone crops (Chapter 7), and its possible relevance to Earth history (Chapter 8). And, finally, I have briefly considered the evolutionary consequences of obligate cone insects in regard to interspecific divergence within pinyons (Chapter 9), and community processes such as nutrient cycling (Chapter 10).

CHAPTER 2

DETERMINATION OF PINE CONE PRODUCTION

Methods and Results. As cones abscise from the nodes of pinyon leader shoots (i.e., those shoots at the periphery of the canopy), scars remain on the shoots that can usually be distinguished for at least 8 years. If these scars are tallied by year, and cones and conelets (1st year cones) counted for all leader shoots in a stand (or if a representative sample of leader shoots is analyzed), then next year's potential crop, the current crop, crops of the preceding 8 years, and the variability of this 10-year sequence are known or estimated. A very similar, if not identical technique for examining P. sibirica cone production has been extensively used in central and eastern Asia (Shimanyuk 1963, Forcella 1980a).

Since counting abscission scars is a tedious task, especially on resinous pines, sampling a portion of the leader shoot population is desirable. I selected a 600 m² plot, considered representative of the stand, in each of 11 P. edilis/Juniperus spp. woodlands throughout New Mexico and western Oklahoma in January 1978 (Fig. 1). Most of these stands were chosen for proximity to U.S. Weather Bureau Stations (discussed in Chapter 4); others were sampled to fill geographic gaps in the distribution of sampled stands, while others were sampled simply because they were convenient. Within the plots I counted all potential cone-bearing leader shoots and measured canopy area of every tree. Canopy area was estimated as the product of pi times the squared average

of the greatest and least canopy radii. I arbitrarily chose 5-10 representative trees in each plot and counted the abscission scars, cones and conelets on 5-20 leader shoots in each of these trees. The sufficiency of the sample of leader shoots was examined through Chi-square analysis by comparing the sums of differences in annual production for each of 10 years between \underline{N} and the average of $\underline{N} + 1$ leader shoots ($\underline{N} = 1-19$). The first sampled stand (#17) was analyzed in this manner, and my analysis showed that Chi-square variability decreased to a near-stable level with a 4-5 leader shoot sample (Fig. 4). Subsequent analyses and results in both near and distant stands to #17 were comparable. The sufficiency of a 5-tree per stand sample was examined in 3 stands, each containing more than 10 trees, in the same manner as above with similar results (Fig. 5). Annual unit area cone production was then extrapolated from the cone and abscission scar counts by multiplying them by the ratio of total number of leader shoots per stand to number of sampled leader shoots. This resulted in an estimate of the 10-year cone production sequence for each stand. An example of such a sequence (Fig. 6) is for a pinyon stand (#21) near Las Vegas, New Mexico. Here, cone production averaged 2.1 ± 1.5 cones/m²/year, with 4 yearly crops well above average. Average coefficient of variability for all sampled stands was about 140%. It should be noted that good and poor crops did not follow any particular temporal pattern in stand 21, nor in other sampled stands. Most stands did produce mast crops in concert, however (i.e., 1969, 1974 and 1977 were mast years throughout the range

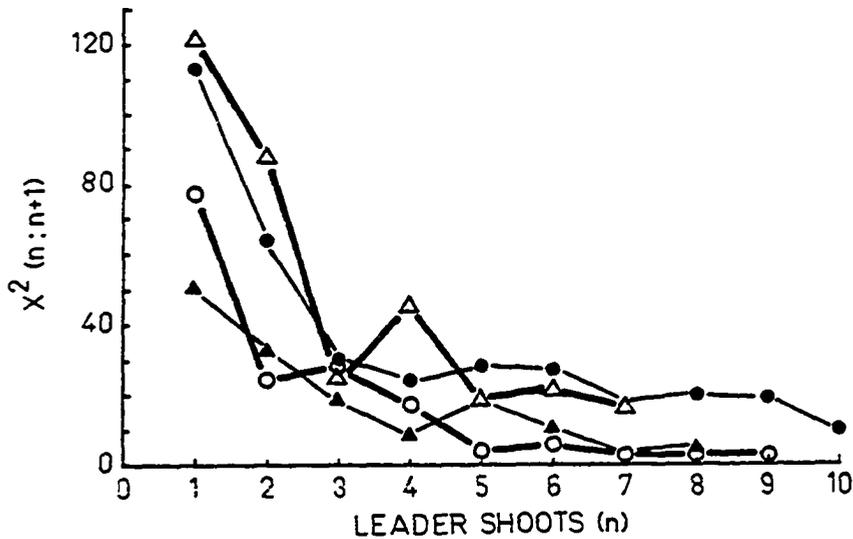


Figure 4. Representative relationship of Chi-Square values for the difference between \underline{n} and $\underline{n+1}$ leader shoot counts of pinyon cones and abscission scars (i.e., cone counts of 1 leader shoot compared with the average of 2 shoots, 2 with 3, 3 with 4, etc.) for 4 different trees in Stand 17. Since $\underline{X^2}$ variability stabilizes by 4-5 shoots, five leader shoots per tree is an adequate sample for estimating cone production in these trees. Results are identical for other stands.

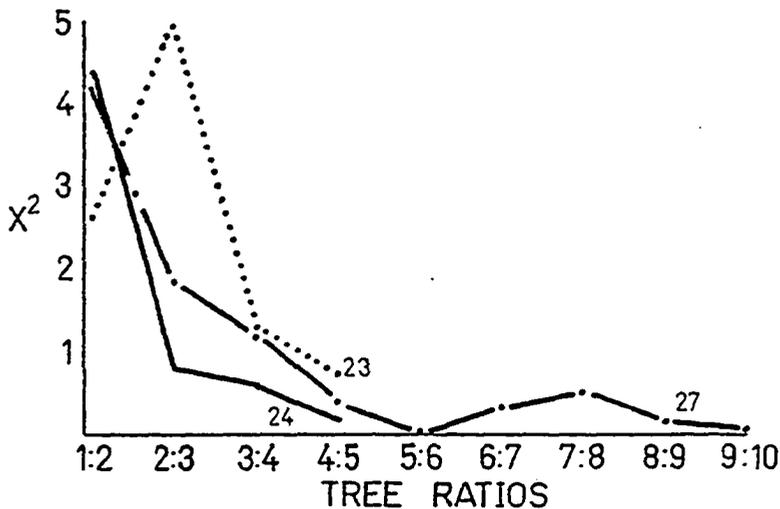


Figure 5. Representative relationship of Chi-Square values for differences between cone production estimates of \underline{t} and $\underline{t+1}$ trees in Stands 23, 24 and 26. Since $\underline{X^2}$ variability stabilizes at a sample size of 5 trees, such a sample is adequate for estimating total stand cone production.

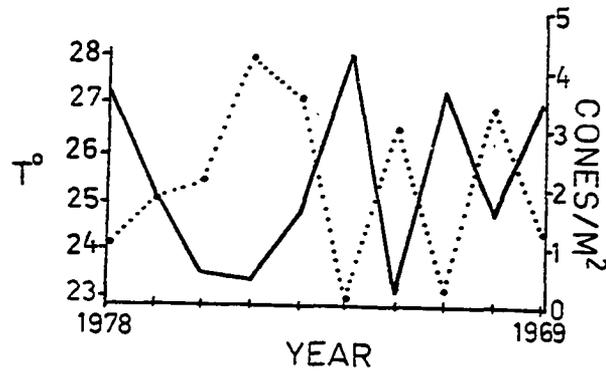


Figure 6. Representative 10-year cone production sequence for a pinyon community (Stand 21, near Las Vegas, New Mexico). Average cone production in this stand was 2.1 ± 1.5 cones/m²/year. The dotted line indicates mean maximum daily temperature at a near-by U.S. Weather Bureau Station for the time period corresponding to ovulate cone primordia initiation in pinyon (see Chapter 4).

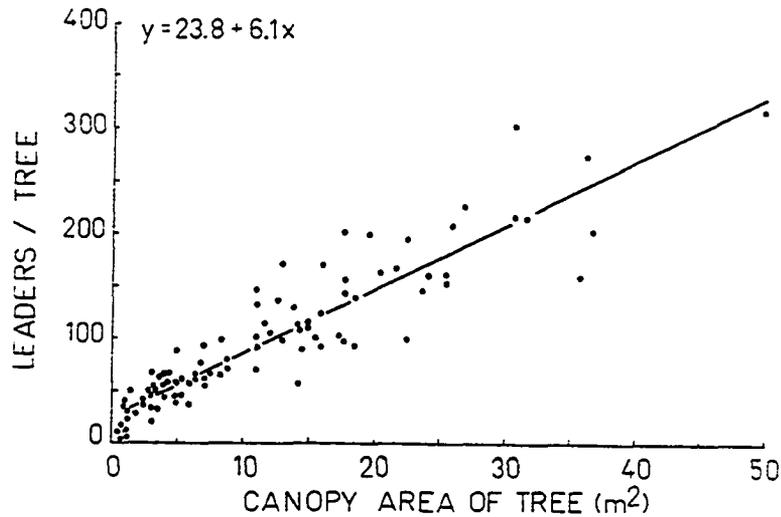


Figure 7. The number of potential cone-bearing leader shoots per tree in relation to the canopy area of the individual pinyons that supported them ($r^2 = 0.84$, $N = 103$). Sampled pinyons are from Stands 17-24 and 26-28.

of sampled stands). Cone production sequences for all 30 sampled pinyon stands, including P. cembroides, P. edulis and P. monophylla, are presented in Appendix 1.

Because recognition of potential cone-bearing leader shoots requires experience, and because counting hundreds of these items in each stand is time consuming, I sought a parameter of the tree that was correlated with leader shoot number and could be substituted for it in the future by others less familiar with pinyons. Since the number of leader shoots per tree versus individual tree canopy area was correlated ($r^2 = 0.84$, Fig. 7), stand canopy coverage (the sum of individual tree canopy areas) should predict leader shoot number per unit-area. If so, and if all pinyon leader shoot populations had similar potentials for cone production, then the average number of cones per m^2 should be correlated with stand canopy coverage. Mean (of 10 years) cone production and coverage were significantly correlated (Fig. 8). (One stand, #26, shown in Fig. 8 was atypical in other characteristics beside cone production: its soil was a Paleargid with a thick montmorillonitic clay horizon, its only juniper associate was Juniperus deppeana Steud., and juniper coverage was less than 0.1%. These characteristics differed strikingly from the remaining P. edulis stands which normally had: sandier soils, often with a petrocalcic horizon [Lithic Calciorthids]; J. monosperma [Engelm.] Sarg. or J. scopulorum Sarg.; and at least 1% juniper coverage.) The value of this linear relationship between mean production and stand canopy coverage is that it allows relatively easy calculation of the inherent

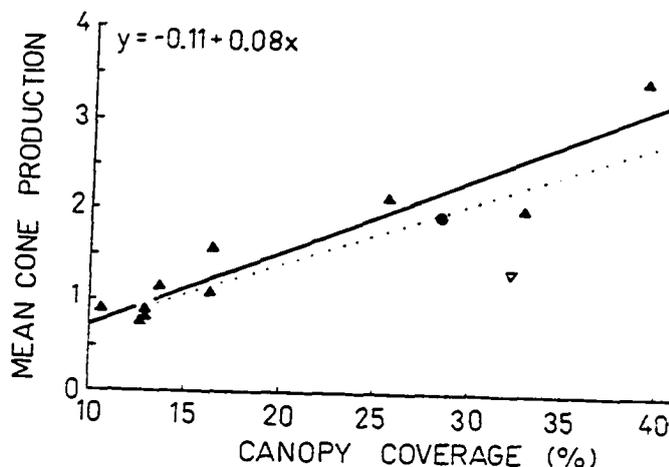


Figure 8. Average annual ovulate cone production per m^2 (\bar{x} of 1969-78 sequence) as a function of pinyon canopy coverage in stands 17-24 and 26-28. The solid regression line represents the best fit for 10 stands (solid triangles, $r^2 = 0.90$). The dotted line is the best fit for 11 stands including #26 (inverted, open triangle) ($r^2 = 0.72$, $y = 0.08 + 0.07x$). The solid circle is stand 10, a P. edulis/J. scopulorum community from NW Arizona that was sampled in January 1977; it was not used in the regressions, therefore it is a test of the regression model.

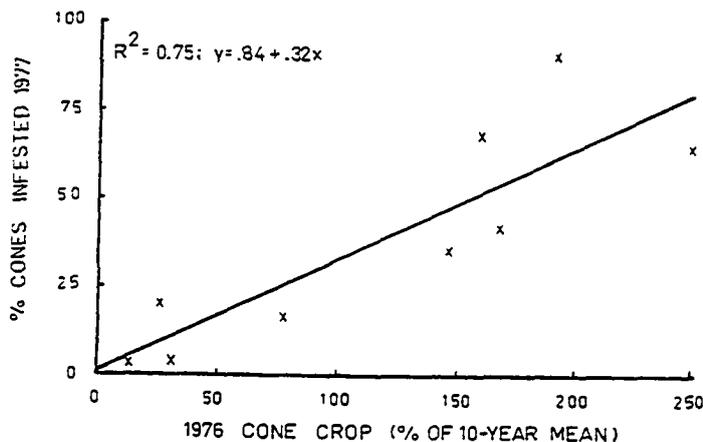


Figure 9. Effect of cone crop size in year $\underline{Y} - 1$ on the degree of insect infestation of cones in year \underline{Y} (cf. Fig. 2). Relationship suggests that consecutively good cone production is not advantageous for pinyons. Beetle populations apparently increase because of abundant food during first cone crop. Subsequently, their populations are sufficiently large to devastate the forthcoming cone crop. Samples are Stands 17-24 and 26-28. Organisms involved are Pinus edulis (Colorado pinyon) and Conophthorus edulis (pinyon cone beetle).

worth of pinyon woodlands in regard to long-term cone production. This should be useful to natural resource managers who may wish to evaluate impacts of modifications of pinyon/juniper vegetation on wildlife and local commerce.

Accuracy of this method can be evaluated by comparing the estimate of the most recent cone crop (1977 in this case) with a count of the most recently fallen cones (along with occasional cones that failed to abscise and remained in the trees) within the 600 m² plots. I made this comparison in 9 plots ($\underline{r}^2 = 0.69$; $F = 15.5$; $\underline{y} = 0.68 + 1.51\underline{x}$, where \underline{y} = abscission scar estimate in cones/m², and \underline{x} = fallen cones/m²). The slope of the regression equation indicated that the estimate of abscission scars consistently over-predicted the fallen cone count for 1977 by 50%. This discrepancy was due partly to burial, transport and/or obliteration of cones by birds and rodents (Vander Wall & Balda 1977, Forcella 1978). The relatively high \underline{r}^2 value suggested that the method was at least precise, if not accurate.

Conclusions of Cone Crop Estimation Technique. About 3 hours were required to estimate a 10-year, unit-area, cone production sequence in a typical pinyon/juniper woodland. The sequence included estimation of next year's potential crop, current production, crops of the preceding eight years, and variability of the sequence (e.g. Fig. 6). Use of the equation presented in Fig. 7, and a sample of not more than 25 leader shoots will allow estimation of the same production sequence in less than one

hour. The two forthcoming cone crops may be estimated in minutes, still using the equation in Fig. 7, if sampling is conducted in summer since both conelets and maturing cones can be counted. For example, if the average number of conelets per leader shoot was 1.0 for 10 pinyons, each with a canopy area of 20 m² and all occurring within a 1000 m² plot, then next year's potential crop would be estimated as follows:

$$1.0 \times 10 [23.8 + 6.1(20)] / 1000$$

or 1.46 cones/m². Furthermore, estimation of average annual cone crops was reliably predicted from simple calculations of stand canopy coverage (Fig. 8). Thus if natural resource managers desire average annual crop information, with the use of the equation in Fig. 8 and coverage data from aerial photographs, actual fieldwork may be unnecessary. However, with such high variability in annual production, average crop data has limited utility and will not reflect cone production of any particular year. The reason for such variability in production is that ovulate cone primordia are initiated only if anomalously cool temperatures occur during the last week of August and first weeks of September two years before cone maturity (see Fig. 6, and Chapter 4).

There are, to be sure, problems with the methods I have described. Production of summer shoots (Lanner 1976), though infrequent and obvious in the shoots I examined, may cause some difficulty in determining the correct age of cone scars. Cone buds or conelets may abort before maturity. This is especially true with two consecutively good cone crops, where the latter one is invariably infested with insects whose populations apparently initially increased because of

the first large cone crop (Forcella 1978, Chapter 3). Climatic anomalies may also cause abortion of conelets. Furthermore, the abscission scars left by these minute cones are not easily detected after about 2 years. Thus, abscission scar counts of potential crops in past years are undoubtedly underestimates. In some stands rodents, especially porcupines (Erethizon dorsatus), severely girdle tree trunks. Extensive senescence in the upper canopy results and surely biases the canopy/leader shoot and canopy/production equations. Nevertheless, the method appears adequate for estimation of a 10-year cone production sequence, and it is currently the only quantitative one available.

CHAPTER 3

PLANT/ANIMAL INTERACTIONS

Pinyon cone beetles, Conophthorus edulis Hopk. (Scolytidae), are obligate consumers of maturing (2nd-year) ovulate cones of Pinus edulis (Keen 1958). This fact raises the following questions: Are the numbers of this beetle and viable maturing cones necessarily inter-related? Does cone production in one year affect consumer populations and subsequent cone mortality in the next? If the answers to these questions are affirmative, as they seem to be for pinyon cone moths and P. monophylla (Fig. 2, Forcella 1978; and also for moths and P. resinosa, and beetles and P. lambertiana, Mattson [1971] and Keen [1958] respectively), then pinyons would appear to regulate their own cone mortality.

In order to evaluate the above questions for P. edulis, the extent of infestation of the 1977 cone crop was determined from the percent of beetle-aborted cones found within 600 m² plots in ten of the eleven stands discussed previously. This determination took into account both abscised cones and those that failed to abscise by the sampling date and remained in the trees. Predation of cone crops prior to 1977 could not be estimated due to rapid disarticulation of aborted cones dead for more than one year. The average number of beetles per cone was used to estimate unit-area beetle populations (these beetles are univoltine, the young are born in summer in cones and remain there till June of the next year when male/female pairs attack fresh maturing

cones [Keen 1958]).

Results and Conclusions. The relationship of current cone infestation to the magnitude of the previous year's cone crop is shown in Fig. 9. The correlation appears linear, and it is statistically significant ($F=21$, $p<0.05$) with attributable variability of 75%. Only 9 stands are plotted in Fig. 9. Pinyons in the tenth stand suffered only minor predation losses in 1977 even though the 1976 crop was quite large, about twice the 10-year average. But in contrast to the other stands, the (pre-infestation) 1977 cone crop was very small, about 1/6 of average, and it is possible that the scattered cones of this meager crop simply could not be efficiently located by the small and relatively immobile beetles (this may indicate that there is a threshold density, above which cones are subject to intense insect attack). The other ten stands produced near- or above-average crops in 1977 as did most pinyons throughout much of New Mexico and western Oklahoma. Thus it again seems that consistently high cone production has little selective advantage for pinyons since it apparently allows predator populations to increase and consume much of the potential progeny. Extraordinarily large cone crops followed by meager ones, or perhaps just consistently poor crops, would seem to be a more viable mechanism for pinyons to elude predation (Ligon 1978, Forcella 1978, cf. Janzen 1974).

The number of beetles per cone was rather variable, averaging 3.8 ± 5.3 (range 1-18). The highest unit-area concentration of beetles was in Kenton, Oklahoma, with an estimated population density of 6.4 beetles/m² (1.7 cones/m², 91% infestation). It is not surprising for

this pinyon stand to have had the highest beetle density since it is one of the most consistent annual producers of all stands examined. For example, the coefficient of variation (cv) for annual cone production in this stand was 84%, whereas average cv for other stands was $135 \pm 34\%$. With less variation in annual cone production the beetles in this stand should be able to maintain higher population densities on the average, and thus be able to more readily saturate cone populations in years with above normal crops. Again, this evidence suggests that high variability in annual cone production is evolutionarily desirable for pinyon. The question now is just how such variability is achieved by pinyons. This topic is discussed in the following chapter.

Another interesting aspect of the Kenton, Oklahoma pinyons is that they exist at the very eastern-most edge of the range of P. edulis (Fig. 1). I have limited data from other stands at the distributional limits of P. monophylla in Idaho, Utah, Nevada and California, and P. edulis in New Mexico that suggest all "edge" communities are characterized by relatively stable annual cone productivities (see Appendix 1). It may be that the climatic variables affecting cone production (Chapter 4) at the range limits of pinyon result in consistent annual production, and in turn high predator populations and reduced viable seed output. Possibly this reduction in seed production through enhanced predation is itself one of several factors delimiting the distribution of pinyon.

CHAPTER 4

ERRATIC CONE CROPS IN PINUS EDULIS: ECOLOGICAL MECHANISM

Eleven P. edulis woodlands in New Mexico, southeastern Colorado and extreme western Oklahoma (Fig. 1) were sampled for a 10-year cone production sequence (Chapter 2). Sampled stands were located as close as possible to U.S. Weather Bureau Stations; linear distances from stations to stands varied from 50 m to 5 km, and elevational differences were less than 250 m, with the weather station always being lower. Correlations of relative cone production for 1969-78 (date at crop maturity) and temperature (T, plural Ts) at the time of cone primordia differentiation (1967-76) were attempted. Since the exact time of primordia initiation was unknown (it occurs sometime in August and/or September; Little 1938, Mirov 1967), average monthly, biweekly and weekly daily maximum Ts were calculated for August and September and sequentially plotted against the cone crops they were hypothesized to produce two years hence. In a few cases T data for the months of June, July and October were also examined in the same manner. In addition, monthly precipitation data were also analyzed for association with cone induction.

Results. Cone crops were not correlated with monthly means of daily maximum T (except in one case), nor were they correlated with biweekly or weekly means for the first 3 weeks of August or the last 3 weeks of September. However, weekly or biweekly means for the last week of August (days 24-31) and/or the first weeks of September (days 1-7,

occasionally days 1-15) showed striking correlations with cone production. In Fig. 10 I have plotted cone crop versus T for all pinyon stands within 500 m of their respective weather stations. (T/cone crop plots for the remaining stands are discussed in Appendix 2.) The T/cone crop relationship in each stand follows a negative exponential curve (Fig. 10), and is statistically significant in 4 of 5 cases. Thus it appears that in years with average or above-average T, only meager cone crops are initiated. Most production occurs only in years when Ts during the end of August and/or beginning of September (two years before crop maturity) are roughly one standard deviation (sd) cooler than the mean (1967-76) T for that period (refer to bars and arrows along abscissae of Fig. 10). (Cool Ts are often associated with precipitation, but rainfall itself is not correlated with cone production.) Statistically, Ts equal to or less than one sd below the mean are expected to occur in 1.65 years of any 10-year period. This should result in 1-2 good cone crops every 10 years, which is in fact the case in most instances.

In two stands, Las Vegas (#21) and Kenton (#17), cone crops and Ts showed a more linear than exponential relationship. Consequently these stands produced more good cone crops than other stands. As mentioned previously, the Kenton site is at the eastern extreme of pinyon distribution, and near Las Vegas only scattered and sparse pinyon populations occur. In fact, Küchler (1967) does not map pinyon vegetation in the Las Vegas area. Though this locale is well within the limits of the species

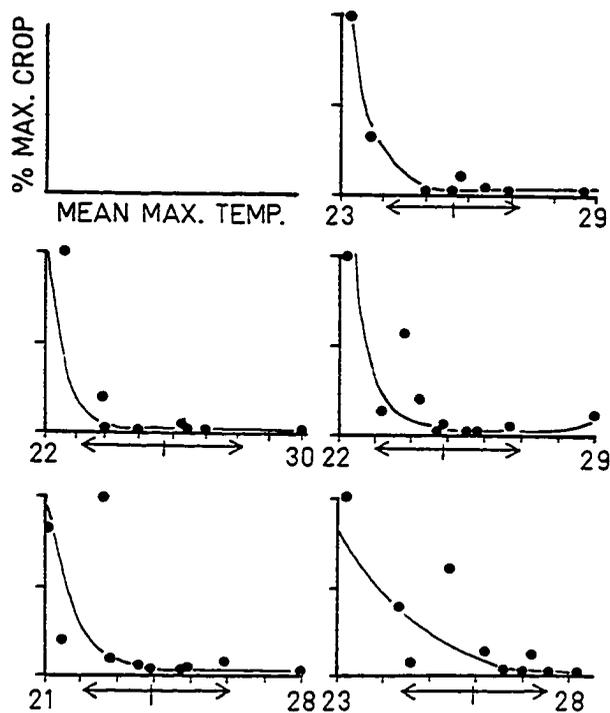


Figure 10. Exponential relationship of weekly or biweekly mean maximum daily temperature (T) during the time of cone primordia initiation to percent maximum cone production (C) two years later in five pinyon woodlands throughout New Mexico. All stands were within about 500 m of U.S. Weather Bureau Stations. Cone crop data from 1969-78, T data from 1967-76. Where less than 10 data points in graphs, T records were incomplete. Bars and arrows along abscissae represent mean $T \pm$ one standard deviation. From top to bottom and left to right, Weather Station, form of regression equation, correlation coefficient, and statistical significance (*, $p < 0.05$) for each pinyon stand are as follows: Mountain Park (Stand 28), $\ln C = 106.584 - 7.630T + 0.136T^2$, $r = .77$; Capulin Mt. Nat. Mon. (#19), $\ln C = 83.699 - 6.228T + 0.117T^2$, $r = 0.78^*$; Pecos Ranger Station (#23), $\ln C = 174.710 - 12.762T + 0.234T^2$, $r = 0.86^*$; Santa Fe College (#22), $\ln C = 170.380 - 12.868T + 0.244T^2$, $r = 0.80^*$; and Sandia Park (#24), $\ln C = 24.657 + 2.964T - 0.074T^2$, $r = 0.84^*$.

and has the outward appearance of typical pinyon habitat, its grass-land/woodland transition does not contain pinyon, except for a few small pockets as the stand I sampled. Thus both the Kenton and Las Vegas stands are "edge" populations of pinyons, and the local climate of these edge sites is apparently such that consistently good production results. As mentioned previously, such stands likely support large populations of cone-consuming insects (at Las Vegas, 1.4 beetles/m², the 4th densest stand), and the production of sound seed is thereby limited.

Discussion. One might ask why the 24 August - 7 September period is the time of cone differentiation. Since it is the variability in T that seems to be required for strategic production of cone crops, the time for cone primordia induction should be a rather variable period of the growing season. To confirm this speculation I calculated the sd's of biweekly means of maximum daily T for 1 March through 30 September, 1967-76, for several pertinent weather stations (Fig. 11). Spring Ts are characterized by high, but steadily declining variability. Daily summer Ts are very stable until the last week of August and first week of September. At this time T variability increases dramatically. Such variability at the time of cone primordia initiation provides the T extremes that appear to be required by pinyon for mast crops, but provides these conditions seldomly and randomly enough so that they are infrequent and erratic. Mast crops, predator satiation and seed survival might thereby all be obtained by pinyon.

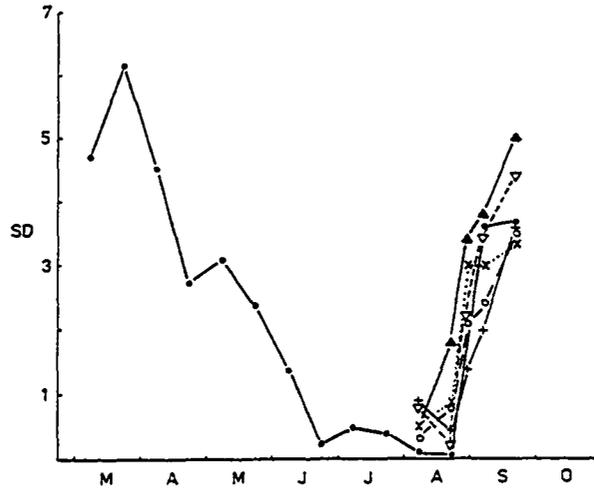


Figure 11. Relative variability of daily maximum temperature (standard deviations of biweekly means) during the approximate growing season from representative weather stations in or near pinyon vegetation. Data points are expressed for contiguous biweekly intervals except in late summer where overlapping biweeks more precisely depict the sudden rise in variability at that time. Symbols for pinyon stands are as follows: solid circles, Stand 17; open circles, 24; open triangles, 23; solid triangles, 22; plus sign, 19; and x, 27.

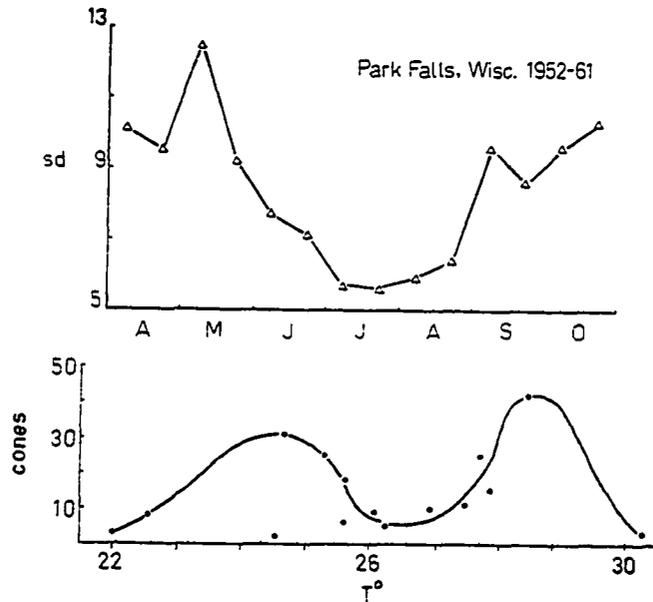


Figure 12. Lower graph: Approximate bimodal relationship between average Pinus resinosa cone crops from north central Wisconsin (1952-66) and mean maximum daily temperature 16-31 July (1950-64) in Park Falls, Wisconsin. Upper graph: Biweekly standard deviation of maximum daily temperature through the growing season for Park Falls, Wisconsin.

Since vernal T variability is as variable as that in autumn, or more so, why then are cones not initiated in spring? This is probably predetermined by the sequence of events during over-winter bud morphogenesis. The relative order of development within potential ovulate over-winter buds is: (1) leaves, (2) lateral buds, and lastly (3) ovulate primordia (Duff & Nolan 1958). Also over-winter buds in pinyon are not formed until July (Lanner 1976). Interestingly, this time is the most stable T period of the entire growing season (Fig. 11). Consistency in the production of over-winter buds seems beneficial and logical, as does the initiation of these buds at the most stable or "safest" period of the year.

Conclusions. The mechanism by which the traits of infrequency and randomness of pinyon cone crops are controlled is the overwhelming role played by anomalously cool temperatures for initiating abundant ovulate primordia during the period from 24 August through 7(15) September. The negative exponential relationship between cone primordia initiation and T characterizes this dependence. The period of successful initiation of cone primordia is also that time of the growing season when daily T variability increases suddenly from its summer-time low. This simultaneity hardly seems coincidental since high T variability provides the erratic conditions required for the advantageous production of erratic cone crops.

CHAPTER 5

CONE CROPS OF OTHER PINES

As my research progressed to the stage of Fig. 11, I felt relatively confident that I understood cone production in Pinus edulis and its conspecifics. But could my results be extrapolated to other distantly related pines? As mentioned previously for pinyon, results of most cone production investigations are stated in terms of poor, fair and good crops. Some quantitative data do exist, however. A particularly pertinent example is P. resinosa, red pine, of northeastern North America. Red pine is known to have erratic cone crops much like pinyon (Duff & Nolan 1958, Lester 1967). More interestingly, there are even suggestions that with two consecutively good red pine cone crops, the latter crop is devastated by obligate cone-insects (Mattson 1971).

Lester (1967) attempted to relate 15 years (1952-66) of cone crop data from several red pine trees scattered throughout northern Wisconsin to mean monthly temperatures two years prior to cone maturation. Temperature records were those of the nearest (undisclosed) weather stations to the trees. He found poor, but significant positive correlations between crops and both average July and August Ts. He concluded that primordia were stimulated by hot Ts in July because the correlation for that month was slightly higher.

Since my results with pinyon showed that only much shorter time intervals related meaningfully to cone production, and that primordia induction corresponds to a sudden increase in late summer T variability, I assumed that in Wisconsin either T variability might rise in July

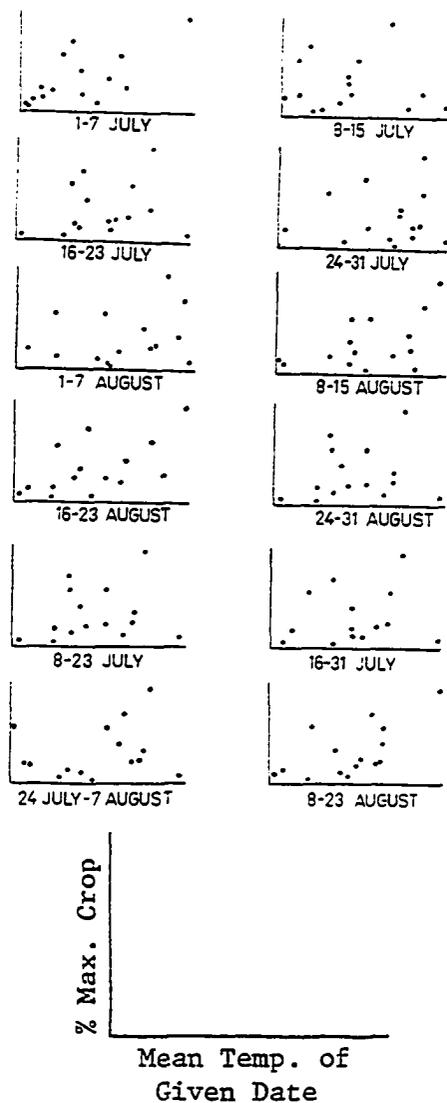


Figure 13. Sequential plots of mean maximum daily temperature (abscissa) and red pine cone production (ordinate) for weekly and selected bi-weekly intervals from July and August. Temperature data from Park Falls, Wisconsin (1950-64); cone data from 1952-66 (Lester 1967).

rather than late August, or that red pine primordia initiation actually takes place in August, but Lester's monthly averages obscured any relationship.

Park Falls Weather Station is situated in north-central Wisconsin and has a particularly good (i.e., complete) weather record. I calculated weekly, biweekly, and monthly means of maximum daily T for 1 July through 31 August (1950-64) for this representative station. I sequentially plotted these means against the yearly cone crop data given by Lester (Fig 13). In addition I calculated biweekly T variability for April through October. As in pinyon areas, T variability increases suddenly in late August (Fig. 12). Thus, primordia induction is probably not in response to anomalous T at this time. In fact, as Lester predicted from his mean monthly T correlations, there does appear to be a poor, but significant relationship between cone production and T during the first week of July. But equally significant linear relationships exist for the 3rd and 2nd & 3rd weeks of August (Fig. 13). Much more interestingly however, is cone production and T during 16-31 July (Fig. 12). Here the relationship appears bimodal, with cone production peaks at 24.5 and 29.0°C, and production troughs at 26.5° and at both warm and cold extremes. If Fig. 12 even approximates reality, this relationship is an extraordinarily efficient mechanism for initiation of erratic cone crops, given that such high variability is advantageous in regard to insect infestation. Not only can red pine utilize relatively low Ts for mast crop production as with pinyon, but high Ts as well. The more commonly experienced average Ts, however, produce only meager crops. Intui-

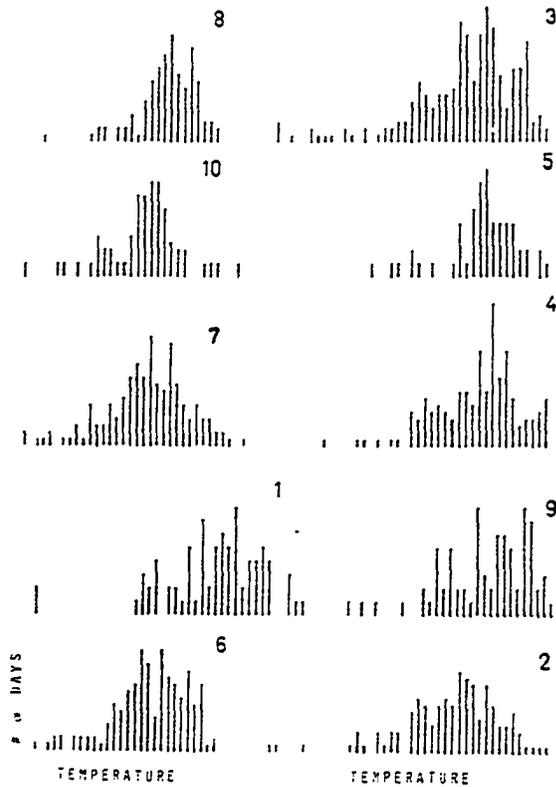


Figure 14. Frequency histograms of maximum daily temperatures during the time of cone primordia initiation and the number of days on which those temperatures were recorded in or near 10 pinyon stands. Most histograms are obviously skewed towards hot days (to the right). Actual numbers are not important in these graphs, but for perspective, smallest vertical lines represent either one or two days depending upon individual histogram, and temperatures vary as in Fig. 10.

tively, this appears a more advanced evolutionary system than that in pinyon. The question now is, with the severe animal depredation that pinyon incurs, why then has it not evolved the same mechanism for erratic mast production as red pine?

Having something more than a coldly objective regard for pinyon, relative to red pine, I felt confident that environmental constraints must have precluded the possibility of pinyon's use of both low and high T extremes for the initiation of cone bud primordia. Since pinyon floristically characterizes a desert climate, I hypothesized that frequency of daily Ts during the time of initiation in pinyon environments is skewed towards hot Ts. That is, extremely hot days are the mode in desert climates, thus there are no hot extremes. The only extreme days would be cold ones. If T distribution was completely random on the other hand, then frequency histograms of the number of days and maximum T recorded during those days would mimic a normal curve. I made such histograms for 10 pinyon stands (Fig. 14). In most cases the frequency distribution of days is skewed towards hot days, with comparatively few days being cool. Six of these distributions were tested statistically for randomness by the variance to mean ratio technique (Kershaw 1973). In all 6 cases the distributions were not random, and the probability of this lack of randomness having been due to chance alone was <0.005 . Thus there is some justification in concluding that pinyons are restricted to use of cool temperatures for primordia initiation because only cool Ts occur at frequencies low enough to stimulate advantageously infrequent mast crops.

Given this reasoning and suggestive data, complementary relationships must occur in red pine environments. That is, at the time of primordia initiation (16-31 July) the frequency distribution of daily Ts must approach a random distribution, thereby allowing red pine to fully utilize both "tails" of the normal curve for initiation processes. Fig. 15 depicts the daily T histogram for Park Falls, Wisconsin. It does indeed suggest a normal curve, relative to pinyon, though statistically its apparent randomness is not significant.

To this point I have shown a correlation of T extremes, or near extremes, to mast crops two years hence. But is the actual initiation of ovulate primordia due to extreme Ts, or to some much more general phenomenon?

CHAPTER 6

PHYSIOLOGICAL INDUCTION OF OVULATE PRIMORDIA

Despite the cyclic nature of Pinus monticola (western white pine) cone production, the actual number of cones produced by the trees in the cool and mesic Pacific Northwest is stimulated by warm autumnal Ts and lack of precipitation (i.e., soil drought) (Rehfeldt et al. 1971, Eis 1976). Similarly, abundant cone primordia in P. ponderosa (ponderosa pine) are thought to result from hot mid-summer Ts in the cool northern Rocky Mts. (Daubenmire 1960), or hot April and May Ts in California (Maguire 1956; phenologically, April and May in California are equivalent to mid-summer elsewhere).

In the humid southeastern USA, cone crops of numerous pines are stimulated by soil drought, or the experimental equivalents thereof, i.e., root pruning and stem girdling (Hoekstra & Mergen 1957, and see general reviews by Matthews 1971 and Jackson & Sweet 1972).

I draw two general conclusions from information such as the above. (1) Cone crops are a product of successful primordia initiation (or development), which itself is dependent upon various environmental extremes, e.g. heat, cold, drought, and so on. (2) Environmental extremes that affect particular species are the logical opposites of the modal environment of the species existence. For example, pines of cool/wet northern climates are stimulated by warm/dry periods, crops of southeastern species are enhanced by droughts, and primordia in desert pines are initiated in response to cool Ts (e.g. pinyons).

An interesting, but indirect test of this 2nd conclusion is afforded by extensive horticultural use of pines. For instance, pinyons reproduce but rarely in their native environments, but when cultivated under cooler northern climates they "flower" and "fruit" well (Mirov 1956, Placerville, California, 38°44'N Latitude; Zabalin 1939, Crimea, 45 N). Reciprocally, all northern pines planted farther south flower abundantly (Mirov 1956). This phenomenon has, I believe, considerable potential economic utility for management of seed orchards. Though to date reciprocal transplantation of northern and southern pines for the expressed purpose of greater seed yield has neither been attempted nor suggested. I might add here a cautionary note: enhanced cone and seed production is a two-edged sword in that animal pests may become more problematic as cone production increases, as is the case in red pine and pinyon.

The first of the two general conclusions mentioned above was initially suggested by Duff and Nolan in their classic 1958 paper on the morphogenesis of red pine. They hypothesized a mechanism for primordia initiation. The suggestion was that a form of hormonal competition exists between vegetative and generative buds. If for some reason active vegetative processes were inhibited prior to the end of the growing season, cone primordia would then be initiated from the now-active generative buds. Perhaps because their suggestion was too speculative at that time, it has never been explicitly tested. It has, of course, become known subsequently that exogenously applied gibberellins often stimulate cone

production (Jackson & Sweet 1972). And very recently (Greenwood 1978) experimental inhibition of vegetative growth for the expressed purpose of inducing ovulate cone primordia has been examined in normally immature 3 year-old P. taeda (loblolly pine) seedlings. Cold temperature inhibition of vegetative growth significantly induced ovulate primordia in those seedlings. Apparently in ignorance of Duff and Nolan's work, Greenwood reiterated their hypothesis based on his more conclusive data. I believe the evidence presented earlier in regard to pinyon and red pine helps confirm the idea of stress-induced cone primordia initiation. More important ecologically however, is the degree (linear or exponential) to which primordia are dependent upon these stresses.

CHAPTER 7

DURIN'S DAY: TEMPERATE ZONE BIOLOGICAL TRIGGER

After I realized that the sudden increase in late summer temperature variability was not confined to pinyon environments (Fig. 11), but extended equally well to north-central Wisconsin (Fig. 12), I was forced to seek an explanation for such a consistent and widespread pattern. In doing so it became clear that this sudden rise in T variability was of hemispheric significance, and that its existence and consequences have never been explored to any degree, at least not by modern man. The actual increase in variability is due to the consistent annual migration and lowering of the stratospheric jet stream(s) from its high latitude summer-time position to its low altitude, low latitude winter-time location (Lamb 1972). The vacillating cold winds associated with this lofty air mass bring cool temperatures to the earth's surface. The actual time of migration apparently varies by one or two weeks from year to year. If early, then cool Ts may arrive in late August, if late, then about mid-September. Thus, over several years T variability begins to increase on about 24 August, with the change being quite noticeable by 1 September (see Figs. 11 and 12).

Curiously, information concerning such interesting meteorological consequences of a well known climatological event (i.e., jet stream migration) are not readily found in the pertinent literature. But there are intriguing suggestions that man has sensed this event for some time. In regard to our current calendar for instance, why does the 244th day of the year initiate the month of September? I, for one, can

easily imagine old and arthritic Latin patriarchs, perhaps Caesar himself, emphasizing the significance of our current 244th Gregorian-reformed day. In Britain, Saint Bartholomew, the harbinger of winter weather ("Saint Bartholomew, Brings in the cold dew") was formerly accorded a merry holiday of his own. The date: 24 August, of course (Book of Days). And those readers familiar J.R.R. Tolkein's The Hobbit, will appreciate the following passage between Thorin, the head dwarf, and Elrond:

"Then what is Durin's Day?" asked Elrond. "The first day of the dwarves' New Year," said Thorin, "is as all should know the first day of the last moon of August, on the threshold of winter."

In a more serious vein, it is known that both Julian and reformed Gregorian calendars were made and reformed to better correspond with agricultural phenology. Temperature variability, in general and in late summer, has considerable agricultural and biological impact, as I will attempt to document shortly. Indeed, Russian meteorologists have devised a synoptic seasonal calendar (Table 1) in order to better facilitate standardization of planting dates, harvesting dates etc. (Borisova & Rudičeva 1968). Not surprisingly, their Autumn begins on 23 August, and their High Summer lasts from 1 July through 22 August -- precisely the stable T period in Figs. 11 and 12.

I have yet to make a systematic search of the biological literature for phenomena that begin or end on or near 1 September, but as I became more cognizant (late August, 1978) of the potential significance of this date, I took note of any sudden biological changes occurring at this time. Also, during my usual perusal of the literature and attend-

Table 1. Synoptic seasonal calendar developed by Russian meteorologists for the U.S.S.R. Note the correspondence between seasons and temperature variability in Figures 11 and 12 (Borisova & Rudičeva 1968).

<u>Natural Seasons</u>	<u>Inclusive Dates</u>
Spring	10 March - 6 May
Foresummer	7 May - 30 June
High Summer	1 July - 22 August
Autumn	23 August - 15 October
Forewinter	16 October - 24 December
Winter	25 December - 9 March

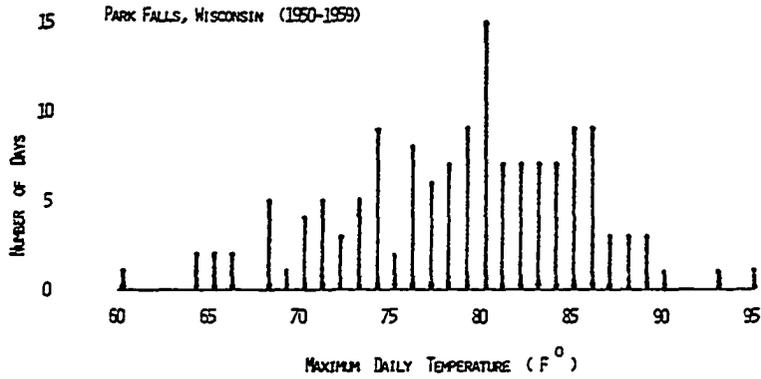


Figure 15. Frequency histogram for a 10-year period of 16-31 July temperatures (presumed time of primordia initiation in red pine) for Park Falls, Wisconsin. Though the histogram suggests a random distribution of temperatures, it does in fact depart significantly from randomness.

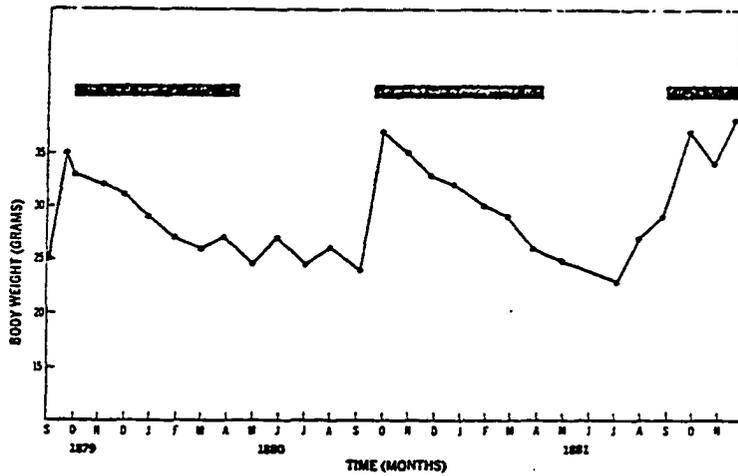


Figure 16. Weight changes in doormice due to accumulation of adipose tissue. Doormice kept in outdoor pens (from Rabus 1882, in Mrosovsky 1971).

ance at seminars, I was particularly attentive to phenological data. What follows is a brief outline of what I believe to be a plethora of biological events beginning or ending on or near 1 September.

Leaves of temperate deciduous trees begin synthesis of proteinases, and the exportation of protein degradation products to stems in preparation for autumnal leaf drop (Beevers 1975, see Spencer 1971 for review). This process is not strictly day-length dependent since it also occurs in greenhouse-grown trees with supplemental light (long days) (Howell & Weiser 1970).

Chlorophyll concentrations begin to decline in leaves of temperate trees (Moore 1965).

In preparation for winter hibernation, dormice begin rapid accumulation of adipose tissue (Fig. 16). Live weights nearly double from late August to late September (Rabus 1882, in Mrosovsky 1971).

Twig-girdling beetles pupate suddenly. In late September they metamorphose into adults and trap the amino acids rapidly being exported from senescing leaves of temperate trees by girdling the twigs to which the leaves are attached (Forcella 1980d).

Oklahomamourning doves begin their southerly migration (Lewis & Morrison 1978). They sometimes begin one week earlier, sometimes one week later. Hunting season begins on 1 September. If doves migrate in last week of August, hunting success is poor. If migration is delayed till early September, hunting success is good (Oklahoma City Times 1978).

Many other bird migrations begin at this same time. For instance, willow warblers end molt, accumulate fat and fly to southern Africa (from Europe), and this behavior is not day-length dependent (Gwinner 1977).

Acorns ripen on oak trees, and in past times passenger pigeons began flocking, being attracted to mast acorn crops (Janzen 1974).

Enzymatic machinery for carbon dioxide reduction begins in Sonoran Desert trees (Szarek & Woodhouse 1979), probably in response to the advent of autumnal precipitation, which itself is dependent upon the jet stream (see also, Wright 1979, for sudden rainfall increases in central Pacific Ocean).

Crickets invade the first floor of the University of Oklahoma's Botany Department (in which my office is located). I have noticed this for two consecutive years.

The ever-present summer-time stridulating of male cicadas ceases in Oklahoma.

Diptera in eastern Oklahoma forests become pleasantly inconspicuous, in striking contrast to two weeks previously. And associated with this, perhaps in a cause-and-effect manner, is the disappearance of spiders (excepting Frontinella) in these same forests.

Anthesis begins in the dominant panicoids of the Tall Grass Prairie.

This list is not exhaustive, nor is it restricted taxonomically. Organisms purportedly affected by late summer T variability range from gymnosperms to angiosperms, and arthropods to vertebrates. Variable late summer Ts do indeed appear to be a potent general biological trigger.

CHAPTER 8

RELEVANCE OF BIOLOGY TO CLIMATOLOGY

The most detailed relationship between organisms and Durin's Day that I have described is that involving erratic cone crops in pinyon. I assume that the strategic stimulation of ovulate cone primordia by infrequent, low temperature extremes during a two week period in late summer is a product of natural selection, with animal predation being the evolutionary impetus, and the annual migration of the stratospheric jet stream the provisioner of the requisite erratically low Ts. I also assume that natural selection requires lengthy time spans to result in such complex interactions. Given these assumptions, then I conclude that the jet stream has unwaveringly migrated from north to south at about the same time of year through an interval of time long enough for complex evolutionary processes to occur. Thus pine cones, those primitive ovulate reproductive strobili of phylogenetically ancient taxa, may well be able to tell us something about the history of our Stratosphere.

CHAPTER 9

INTERSPECIFIC DIVERGENCE IN PINYON: A CONSEQUENCE OF PREDATOR MOTILITY

It stands to reason that a single ecological factor applied continuously over many generations of a plant taxon will have pleiotrophic effects, morphologically and physiologically. Thus cone consumption by insects may not only be the selective impetus in pinyons for erratic cone crops, but for a number of other traits as well. Although to me,

some pinyon traits are obviously associated with cone predation, it is difficult to prove such purported character correlations. In most instances it is only with indirect evidence that these characters can be related. I shall briefly attempt this for pinyon in the following paragraphs.

Though Pinus edulis (Pied) and P. monophylla (Pimo) hybridize in their areas of overlap (Fig. 1), they have some rather distinct ecological/morphological characteristics. For example, average Pimo cones weigh about 13.6 grams, whereas those for Pied are only 4.3 g. Assuming that the massiveness of cones aids in the protection of seeds, then this difference in cone weights is important, perhaps. In the same light, average Pimo cones contain 14.3 seeds, and average Pied cones contain 7.6 seeds. The amount of protective cone material per seed is 0.95 g for Pimo and 0.56 g for Pied. Obviously, the strobili of these two pines differ considerably in these aspects.

Another interesting distinction between the two species is the annual average number of cones produced per leader shoot. This is an index of cone density and availability for infestation. The values are 0.05 for Pimo and 0.08 for Pied. Thus Pimo produces 0.63 times fewer cones per leader shoot per year than Pied.

The number of leader shoots per square meter of tree canopy is another index of cone density. This index can be calculated by regressing leader shoot number per tree against tree canopy area. The slope of the regression line is the index. This was done for 49 Great Basin Pimo trees and 103 Pied trees (Fig. 17). The slope for Pimo was 4.3, and

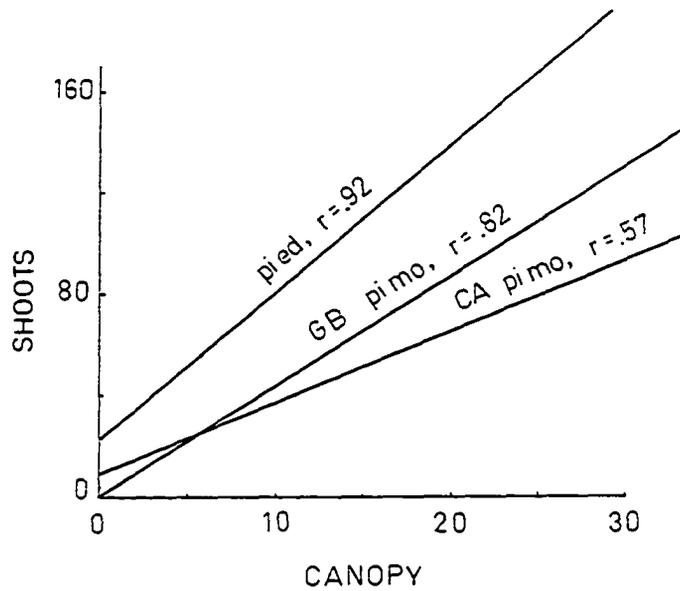


Figure 17. Number of potential cone-bearing leader shoots per tree and canopy area of the trees supporting these shoots. Pinus edulis (pied) from New Mexico and Oklahoma, P. monophylla (GB pimo) from the Great Basin, and P. monophylla (CA pimo) from southern California. All regressions statistically significant. (Canopy area in m².)

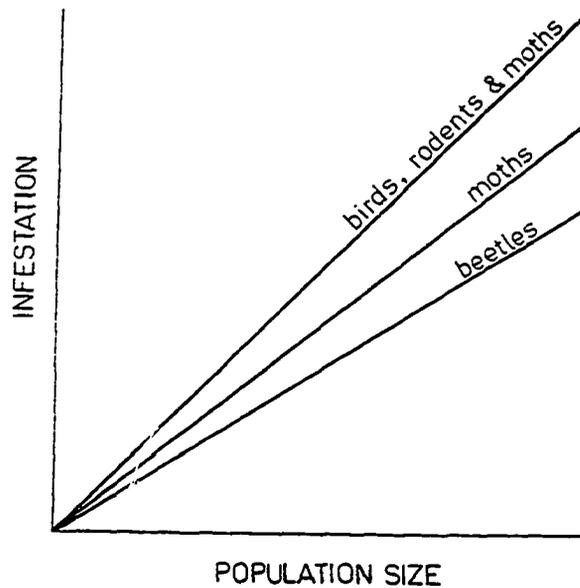


Figure 18. Relative infestation rates (slopes of lines) for cone-consuming animals of different inherent mobilities. Rates increase as mobility increases. Line slopes taken from Fig. 9 and Forcella (1978). Population sizes estimated from number of cones available for consumption one year previous to measurement of infestation.

that for Pied was 6.1. This indicated that Pimo produced 2/3 as many leader shoots per unit-area of canopy as Pied.

A summarization of these several comparisons follows: Pinus edulis produces many leader shoots, many small cones per leader shoot, and few poorly-protected seeds per cone; Pinus monophylla produces few leader shoots, a few large cones; and many well-protected seeds per cone. Why?

Again, if it is assumed that animal predation is a significant ecological problem for pinyon (both Pimo and Pied), and that it has been so for a sufficiently long time, then cone density is an important tree characteristic. Animals would expend more time and energy seeking cones in low density crops than in high density crops. It would be particularly advantageous for trees susceptible to highly mobile animals to produce a few leader shoots and few cones per leader shoot, but pack those few scattered cones with many well-protected seeds. This of course describes P. monophylla. We could predict then that the major obligate cone predator of Pimo would be motile in comparison to that for Pied. Such an insect is the Tortricid moth, Eucosma bobana (Forcella 1978), and it is indeed highly motile relative to the major pest of Pied, a particularly small (1.5-2.0 mm in length) Scolytid beetle.

I believe that such predator motility as suggested above is significant for the trees. I have one last piece of circumstantial evidence for this. In Fig. 18 I have plotted the degree of infestation of cone populations on year Y + 1 as compared to the estimated predator population size (estimated from number of cones providing food resource

on year Y). Infestation rate increases with the motility of the consuming animals.

CHAPTER 10

LONG-TERM NITROGEN RETENTION IN DECOMPOSING PINYON CONES

Resin inhibits microbial activity. For instance, conifer needles are protected from decomposition by fungi by the abundant resin they contain (Millar 1974), and I have shown a similar relationship for resin and microbial decomposition of pinyon cones (Forcella 1979). In this latter case, cones are somewhat resistant to decomposition for perhaps 4 years; subsequently, decomposition accelerates rapidly. By-and-large however, decomposition is rather slow; 8 year-old cones for example are still 56% of their initial weight. Since these cones contain recyclable nutrients, resin retardation of decomposition seems counterproductive for the trees (assuming that more nutrients would be advantageous for the trees). What follows is an attempt to quantify nutrient retention by pinyon cones on a unit-area basis. As nitrogen is probably the most important plant nutrient, I have chosen it as the model. Furthermore, I shall discuss the trade-offs of merits and demerits of resinous cones.

I determined the macro-Kjeldahl nitrogen concentrations of three sets of decomposing cones of known age that had been previously analyzed for carbon loss (Forcella 1979). These cones had been decomposing for 0, 3 and 8 years in a pinyon/juniper woodland 15 km ENE of Aragon, New Mexico (stand 26). Nitrogen as percent dry weight of these cones was: 0 yr, 0.59 ± 0.06 ; 3 yrs, 0.53 ± 0.05 ; and 8 yrs, 0.61 ± 0.06 ($n = 4$ for

each set). Though C:N ratios remain relatively constant over time, ca. 175:1, carbon is continuously being lost from these cones, e.g. 3-yr cones are 93%, and 8-yr cones 56% of their original mass. Given an average new cone mass in this stand of 5.5 g (less seeds), calculation of N as a percent of initial cone concentration is possible. Relative to the original cones, current N in decomposing cones was: 0-yr, $100 \pm 10\%$; 3-yr, $84 \pm 8\%$; and 8-yr, $58 \pm 6\%$. In Fig. 19 these values are presented in graphical form. Residual N content of cones appears to be a linear function of time (if means are used as data points then, $r^2 = 1.0$, $F = 22016$, $p < 0.01$). By extrapolation of the straight regression line, cones are predicted to be free of N, hence thoroughly decomposed, 19 years after they fell from the trees. The extinction coefficient for cone N is 5.24% per year, and N half-life in cone litter is about 9.5 years.

I also determined a 9-year cone production sequence (1969-77) in this stand. By knowing the number of cones produced per m^2 over this time period in addition to the expected residual N in these same now-decomposing cones or cone remnants, I was able to calculate the total residual cone N/m^2 for this 9-year sequence. Table 2, somewhat reminiscent of demographic Life Tables, shows the stepwise results of the calculations involved in obtaining this unit-area N value. Residual N in cones of the nine preceding cone crops was $0.354 \text{ g}/m^2$. Since pinyon canopy coverage in this stand was 32.5%, there was $1.09 \text{ g } N/m^2$ pinyon canopy.

Determination of total N in all cone litter from 19 years of de-

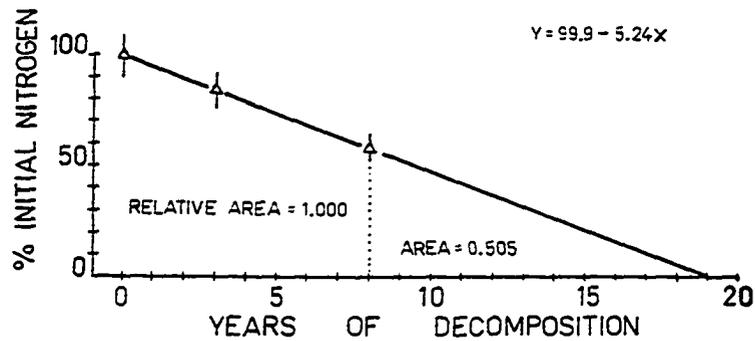


Figure 19. Loss of nitrogen from pinyon ovulate cones over time. Abscissa is number of years since cone maturation (i.e. since year of cone crop). Ordinate is cone nitrogen as a percent of that in original cones. Vertical bars represent ± 1 standard deviation unit. For relative areas refer to text. Extinction coefficient for nitrogen is the slope of the line, 5.24% loss per year. Nitrogen half-life is estimated as 9.5 years.

Table 2. Calculation of residual nitrogen in decomposing cones from a 9-year cone production sequence of a pinyon-juniper stand 15 km ENE of Aragon, New Mexico (Stand 26).

Year of cone crop	1977	1976	1975	1974	1973	1972	1971	1970	1969
Years of decomposition	0	1	2	3	4	5	6	7	8
No. cones produced per m ²	4.00	1.91	0.09	3.41	0.23	0.05	0.18	0.09	3.00
Original cone mass (g/m ²)	22.0	10.5	0.5	18.8	1.3	0.3	1.0	0.1	16.5
Original cone nitrogen (g/m ²)	.130	.062	.003	.111	.008	.002	.006	.001	.097
% original N (from Fig. 19)	100.0	94.7	89.4	84.2	78.9	73.7	68.5	63.2	58.0
Current residual N (g/m ²)	.130	.059	.003	.093	.006	.002	.004	.001	.056
Cumulative Residual N (g/m ²)	.130	.189	.192	.285	.291	.293	.297	.298	.354 ^{1/}

^{1/} Current residual N from 9 preceding cone crops = 0.354 g/m² (or 3.54 kg/ha). Pinyon canopy coverage in this stand was 32.5%; if only area under pinyon cover is considered, then current N in cone litter is 1.09 g/m².

composing cones is made by adding the "known" amount in the first eight years of decomposition (0.354 g/m^2) to the expected amount in the remaining 11 years. This is easily accomplished by comparing areas underneath the curve in Fig. 19. If 0-8 year-old cones have a relative residual N content of 1.0, then expected N under the 9-19 year portion of the curve has an area of 0.505, and a calculated residual N value of $0.505 \times 0.354 = 0.178 \text{ g/m}^2$. Total residual N for all 19 cone crops is therefore 0.53 g/m^2 ground surface, or 1.64 g/m^2 pinyon canopy. This is equivalent to 5.3 and 16.4 kg N/ha respectively. Considering the scarcity of nitrogen fixing leguminous plants, the prevalence of bare ground ($50 \pm 10\%$, $n = 9$), and the lack of a continuous and substantial litter layer in pinyon/juniper vegetation, these values may be substantial. (To date, I can find no data in the literature to which I can compare these figures.)

Pinyon cones are subject to extensive destruction by animals, especially insects, as discussed earlier. More than 9% of the dry weight of pinyon cones is benzene-soluble resin (Forcella 1979), which makes handling more than a few of them with bare hands an unpleasant task. Even with gloves it is difficult; within a short time the gloves' fingers tenaciously bind, forming paws of once dexterous digits. Imagine the difficulties this must impose upon less technologically oriented animals. Indeed, I have often seen dead or dying obligate cone insects trapped in cone resin. And Clark's nutcrackers can frequently be observed rubbing clean their beaks after encounters with resinous cones. I contend that the physical and chemical (i.e., toxic terpenes, etc.) properties of cone resin are deterrents to animal depredations (in the case of bird

seed consumption/seed dispersal, resin may curtail precocious feeding). This contention is not restricted to pinyon, but includes an entire section of Pinus. The two sections of the genus seem to have different mechanisms for lessening cone destruction by animals. The hard or Diploxyton pines have rigid cones, with spine- or prickle-tipped umbos on their scales (cf. Smith 1970), and their cones have abundant tannin (pers. observation). White, soft or Haploxyton pines on the other hand, lack these features. For comparative purposes, I collected cones of seven species of pines representative of the USA, and determined their resin contents by leaching them in benzene for 24 hours. A large difference between the two groups of pines is apparent (Table 3). Average resin content of Haploxyton pines was $11.6 \pm 4.2\%$, and for Diploxyton pines it was $2.2 \pm 2.2\%$. I conclude from these data and from several field observations that cone resin content is a reasonably invariant trait distinguishing the two pine sections, and in regard to animal and microbial disturbance, that high resin levels in white pines compensate for lack of rigidity, armament and phenolic derivatives so characteristic of hard pines. White pines pay an ecological price for such potential protection however. In pinyon's case, this price involves the long-term retention of valuable plant nutrients in microbially resistant ovulate cones. I have stated elsewhere (Forcella 1980b) that ramifications of prolonged animal "predation" of pinyon cones span a range of biological subjects, including physiology, geography, bioclimatology and evolution. I might add here morphology, microbial ecology and nutrient cycling as well.

Table 3. Resin content of mature cones (less seeds) of 7 pines species from throughout the conterminous USA*. Haploxyton pines are the soft or white pines; Diploxyton are hard, red or yellow pines.

	Percent Resin ± std. dev.	Sample No.
HAPLOXYLON		
<u>P. albicaulis</u>	9.0 ± 1.5	10
<u>P. edulis</u>	9.4 ± 0.2	10
<u>P. strobiformis</u>	16.5 (15.9 & 17.0)	2
Average	11.6 ± 4.2	
DIPLOXYLON		
<u>P. contorta pygmaea</u>	0.1 ± 0.2	5
<u>P. echinata</u>	1.7 ± 0.7	10
<u>P. muricata</u>	0.7 ± 0.5	5
<u>P. rigida</u>	5.4 ± 1.0	10
Average	2.2 ± 2.2	

* Collection locations and dates for this material were as follows: P. albicaulis, SW Montana-NW Wyoming, Sept. 1978; P. edulis, W New Mexico, Jan. 1978; P. strobiformis, S New Mexico, Jan. 1978; P. contorta and P. muricata, coastal California, Nov. 1978; P. echinata, SE Oklahoma, Sept. 1978; P. rigida, Long Island NY, August 1978.

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APPENDIX 1

In the event that my estimates of pinyon cone production in various areas in the Southwest may be useful to others, I have appended here the following information for each sampled stand: approximate location (referenced to the nearest named landmark), brief community description, average annual cone production, 10-year cone production sequence with coefficient of variation (Fig. A-1), and a map relating coefficients of variation for cone production to geographic distribution and the general range limits of pinyon (Fig. A-2).

Stand 1. Nevada, Sacramento Summit of Snake Mts. Pinus monophylla (22% coverage), Juniperus osteosperma (20%), Artemisia arbuscula (+, present), Ephedra nevadensis (+). Limestone substrate. 0.94 ± 0.56 cones/m²/yr.

Stand 2. Nevada, Little Antelope Summit of White Pine Mts. P. monophylla (11%), J. osteosperma (19%), Purshia tridentata (+), A. arbuscula (+). Volcanic substrate. 0.28 ± 0.18 cones/m²/yr.

Stand 3. Nevada, Bob Scott Summit of Toiyabe Mts. P. monophylla (30%), J. osteosperma (2%), A. tridentata (10%), Oryzopsis hymenoides (+). Granitic substrate. 1.83 ± 1.73 cone/m²/yr.

Stand 4. California, Mt. Pinos, Sierra Madre (San Rafael) Mts. P. monophylla (56%), Quercus dumosa (20%), Q. chrysolepis (+), Cercocarpus betuloides (+). 1.89 ± 1.82 cones/m²/yr.

Stand 5. California, San Gabriel Mts., on Rt. 2 about 8 km SSW of Cajon Summit. P. monophylla (37%), A. tridentata (15%), Yucca brevifolia (5%), Sytanion hystrix (10%), Purshia glandulosa (+), Fremontia californica (+). Granitic alluvium. 0.69 ± 0.68 cones/m²/yr.

Stand 6. California, San Bernardino Mts., about 10 km W of Big Bear City. P. monophylla (52%), Juniperus californica (5%), A. tridentata (15%), P. glandulosa (+). Quartzite substrate. 1.50 ± 1.95 cones/m²/yr.

Stand 7. California, Pinyon Flat of San Jacinto Mts. P. monophylla (26%), J. osteosperma (+), P. glandulosa (+), Bernardia incana (+), Quercus chrysolepis (+). Gneiss substrate. The crowns of all trees in this stand appeared old and unproductive. 0.26 ± 0.20 cones/m²/yr.

Stand 8. Arizona, Santa Catalina Mts., about 25 km NE of Tucson. Pinus cembroides (67%), Juniperus deppeana (20%), Arctostaphylos pringlei (10%). $9.98 \pm$ cones/m²/yr.

Stand 9. Arizona, Sierra Ancha Mts., N of Globe. Hybrid of P. monophylla and P. edulis (34%), Juniperus erythrocarpus (5%), Rhus ovata (20%), Q. dumosa (5%), Yucca schottii (5%), Arctostaphylos pringlei (5%). 1.03 ± 1.32 cones/m²/yr.

Stand 10. Arizona, Juniper Mts., about 15 km SW of Seligman. P. edulis (27%), Juniperus scopulorum (25%), Purshia glandulosa (5%), Bouteloua gracilis (+). Limestone substrate. 1.25 ± 1.84 cones/m²/yr.

Stand 11. Nevada, east slope of Charleston (Spring) Mts. P. monophylla (48%), Artemisia tridentata (5%), Simmondsia chinensis (5%), Yucca schottii (+), Arctostaphylos pringlei (+). Limestone substrate. 0.76 ± 0.84 cones/m²/yr.

Stand 12. Nevada, Toquima Mts., about 13 km S of Manhattan. P. monophylla (16%), J. osteosperma (7%), A. tridentata (5%), P. glandulosa (5%). Granite substrate. This stand was heavily infested with mistletoe. 0.61 ± 0.86 cones/m²/yr.

Stand 13. Idaho, Goose Creek Mts., 2 km N of Almo. P. monophylla (17%), J. osteosperma (19%), A. arbuscula (10%), Oryzopsis hymenoides (r, rare). Granitic substrate. 0.72 ± 0.39 cones/m²/yr.

Stand 14. Nevada, Toand Mts., about 26 km SW of Montello on Rt. 30. P. monophylla (13%), J. osteosperma (20%), A. arbuscula (5%), Agropyron spicatum (2%), O. hymenoides (+), Cercocarpus ledifolius (+). Deep secondary lime deposit. 0.10 ± 0.12 cones/m²/yr.

Stand 15. Idaho, Goose Creek Mts., 4 km E of City of Rocks. P. monophylla (39%), J. osteosperma (3%), A. tridentata (+), A. spicatum (+). Quartzitic and Alaskitic (granitic) substrate. 0.52 ± 0.61 cones/m²/yr.

Stand 16. Utah, Black Pine Mts., about 5 km E of Strevell, Idaho (stand probably on state line). P. monophylla (13%), J. osteosperma (30%), A. spicatum (2%), Poa sanbergii (2%), Oryzopsis hymenoides (+). Calcic lacustrine deposit (from Glacial Lake Bonneville, perhaps). 0.34 ± 0.32 cones/m²/yr.

Stand 17. Oklahoma, about 1 km ESE of Kenton. P. edulis (16%), J. monosperma (5%), Quercus undulata (5%), Yucca glauca (5%), Bouteloua gracilis & curtipendula (5%). Sandstone substrate. 1.57 ± 1.27 cones/m²/yr.

Stand 18. Oklahoma, about 1.5 km E of Kenton. P. edulis (16%), J. monosperma (10%), Bouteloua gracilis (10%), Yucca glauca (3%), Andropogon scoparius (2%), Quercus undulata (1%). Sandstone substrate. 1.08 ± 1.19 cones/m²/yr.

Stand 19. New Mexico, adjacent to Capulin Mt. Nat. Mon. entrance.

P. edulis (13%), Juniperus scopulorum (10%), Q. undulata (15%), Fallug-

ia paradoxica (+), Bouteloua gracilis (40%). Basaltic substrate. 0.77 ± 1.20 cones/m²/yr.

Stand 20. New Mexico, about 4 km WNW of Raton. P. edulis (11%), Juniperus monosperma (r), F. paradoxica (10%), Yucca baccata (+), Bouteloua curtipendula (30%). Sandstone substrate. 0.89 ± 1.66 cones/m²/yr.

Stand 21. New Mexico, Sangre de Cristo Mts., about 2 km S of Las Vegas Hospital. P. edulis (26%), J. monosperma (5%), Pinus ponderosa (5%), B. gracilis (30%), B. curtipendula (20%), Nolina microcarpa (+). 2.13 ± 1.50 cones/m²/yr.

Stand 22. New Mexico, 500 m E Santa Fe College. P. edulis (14%), J. monosperma (25%), Yucca glauca (15%), Hilaria jamesii (+). Granitic bajada. 1.14 ± 1.71 cones/m²/yr.

Stand 23. New Mexico, Sangre de Cristo Mts., 200 m W of Pecos Ranger Station. P. edulis (33%), J. monosperma (5%), Bouteloua gracilis (15%), Festuca arizonica (+). Arkosic sandstone substrate. 2.02 ± 3.23 cones/m²/yr.

Stand 24. New Mexico, Sandia Mts., 50 m SE of Sandia Park Weather Station. P. edulis (40%), J. scopulorum (10%), J. deppeana (+), Q. undulata (2%), Q. gambelii (+), Fallugia paradoxica (1%), Bouteloua gracilis (3%). Mixed arkose and limestone substrate. 3.45 ± 4.79 cones/m²/yr.

Stand 25. New Mexico, Magdalena Mts., 5 km E of Magdalena. P. edulis (10%), J. monosperma (10%), J. deppeana (r), Bouteloua gracilis (50%), F. paradoxica (+). Mixed colluvium of quartzite and arkose. Unit-area data not gathered in this stand.

Stand 26. New Mexico, Tularosa Mts., 15 km ENE of Aragon on Rt. 12.

P. edulis (33%), J. deppeana (5%), J. monosperma (r), Bouteloua gracilis (40%), Chrysothamnus nauseosus (5%). Andesitic parent material forming a heavy clay (Paleargid) soil. CaCO₃ at 50 cm. 1.30 ± 1.61 cones/m²/yr.

Stand 27. New Mexico, Pinos Altos Mts., about 4 km N of Fort Bayard. P. edulis (13%), J. deppeana (10%), Bouteloua gracilis (20%), Nolina microcarpa (+), Yucca baccata (r). 0.82 ± 0.97 cones/m²/yr.

Stand 28. New Mexico, Sacramento Mts., about 1 km E of Mountain Park. P. edulis (13%), J. monosperma (3%), F. paradoxica (20%), Nolina microcarpa (3%), Yucca baccata (+), Quercus undulata (+). Limestone substrate. 0.85 ± 1.70 cones/m²/yr.

Stand 29. Colorado, about 2 km S of Trinidad. Field notes lost after recording relative cone crop sequence. (P. edulis/J. monosperma community.)

Stand 30. Colorado, near Florence. Field notes lost after recording relative cone crop sequence. (P. edulis/J. monosperma community.)

APPENDIX 2

Figures A-3 and A-4 present temperature/cone crop relationships for all appropriately sampled pinyon stands that were greater than 1 km from their respective weather stations. There are four points I wish to emphasize concerning these figures. 1) As noted earlier, in two stands (17 & 21; Fig. A-3) the T/cone crop relationship was linear rather than exponential, and this may be a consequence of the "edge" locations of the stands (Fig. A-2). 2) Stands 20 and 25 (Fig. A-3) suggest that Ts may sometimes be too cool, thereby destroying or not inducing cone primordia. Though parts of each curve are exponential as originally predicted, these data suggest overall bell-shaped (25) or hyperbolic (20) curves for T and cone crops. 3) The T range in Stand 25 (Fig. A-3) in southern New Mexico is only about 2°C. This extremely narrow T distribution for differential initiation of cone primordia serves well its purported purpose of inducing mast crops or cone failures. Because of this I currently see no justification for excluding T variability from also acting as a biological trigger in sub-tropical and tropical environments, where such variability is normally less than in average temperate zone communities. 4) The weekly or biweekly T means used in the correlations of Figs. A-3 and 10 are quite arbitrary time units. During the original data calculations I used the 24-31 August and 1-7 September intervals as a convenience. I do not expect biological phenomena to adhere strictly to my choices of time. Although it does appear that anomalously cool Ts during those two weeks correlate well with mast crops, the actual stimulation of cone bud primordia by low temperature might occur in a much shorter time. An excel-

lent example of this 4th point is Stand 29 from Trinidad, Colorado. Here 9 of 10 cone crops fit a negative exponential curve, using 1-7 September mean maximum T as the abscissa (Fig. A-4, upper graph). The tenth cone crop (1978), with 89% maximum production, is unexpectedly associated with relatively high Ts during 1-7 Sept. 1976; a very meager crop would have been predicted. However, during 8-10 Sept. 1976, daily maximum Ts dropped quite suddenly by 10°C, and then rose just as suddenly on 11 Sept. and held steady thereafter. It was these 3 anomalously cool days in 1976 that probably initiated the mast crop in 1978. But this relationship is obscured by using mean Ts for predetermined time intervals such as 1-7, 7-15 or 1-15 September. There is a modest correspondence between cone crops and mean T for 1-10 Sept. (Fig. A-4, lower graph). Other examples of this kind are apparent in my data. If the 3 or 4 coolest consecutive days between 24 August and 7(15) Sept. were plotted against cone crops the results might be superior to those in Figs. 10 and A-3, but I am not confident I could justify this action to my colleagues. Thus Figs. 10, A-3 and A-4 (upper), using weekly or biweekly means, represent a happy median.

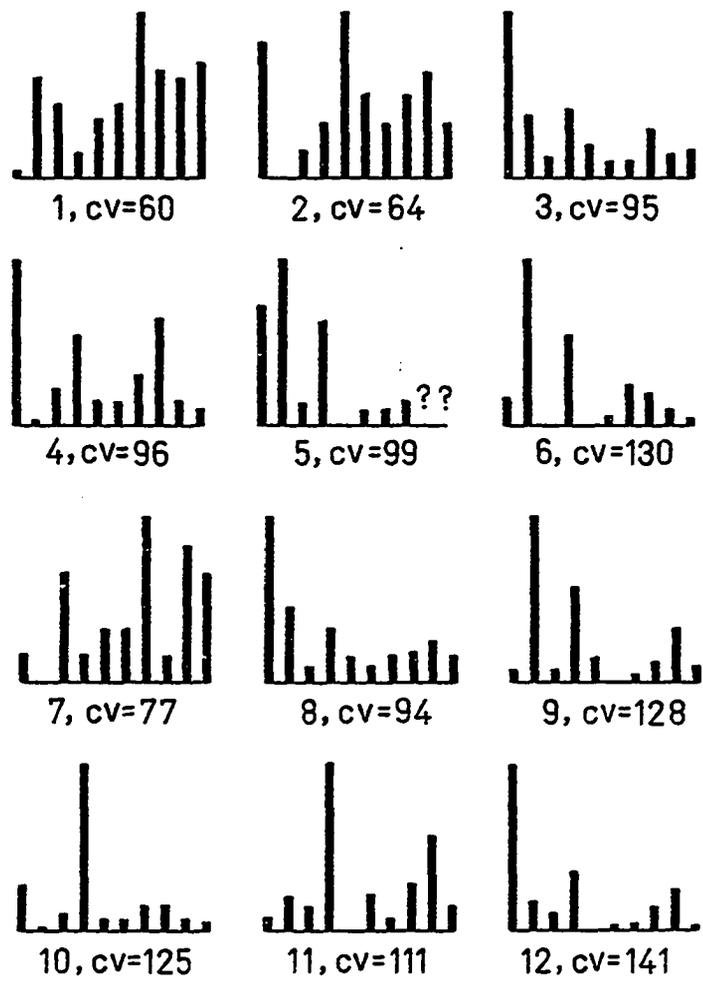


Figure A-1. Relative annual cone production of 30 pinyon stands throughout southwestern USA. Stands 1-16, years of cone maturation 1977-68, left to right. Stands 17-30, years of cone maturation 1978-69, left to right. Coefficient of variation, cv.

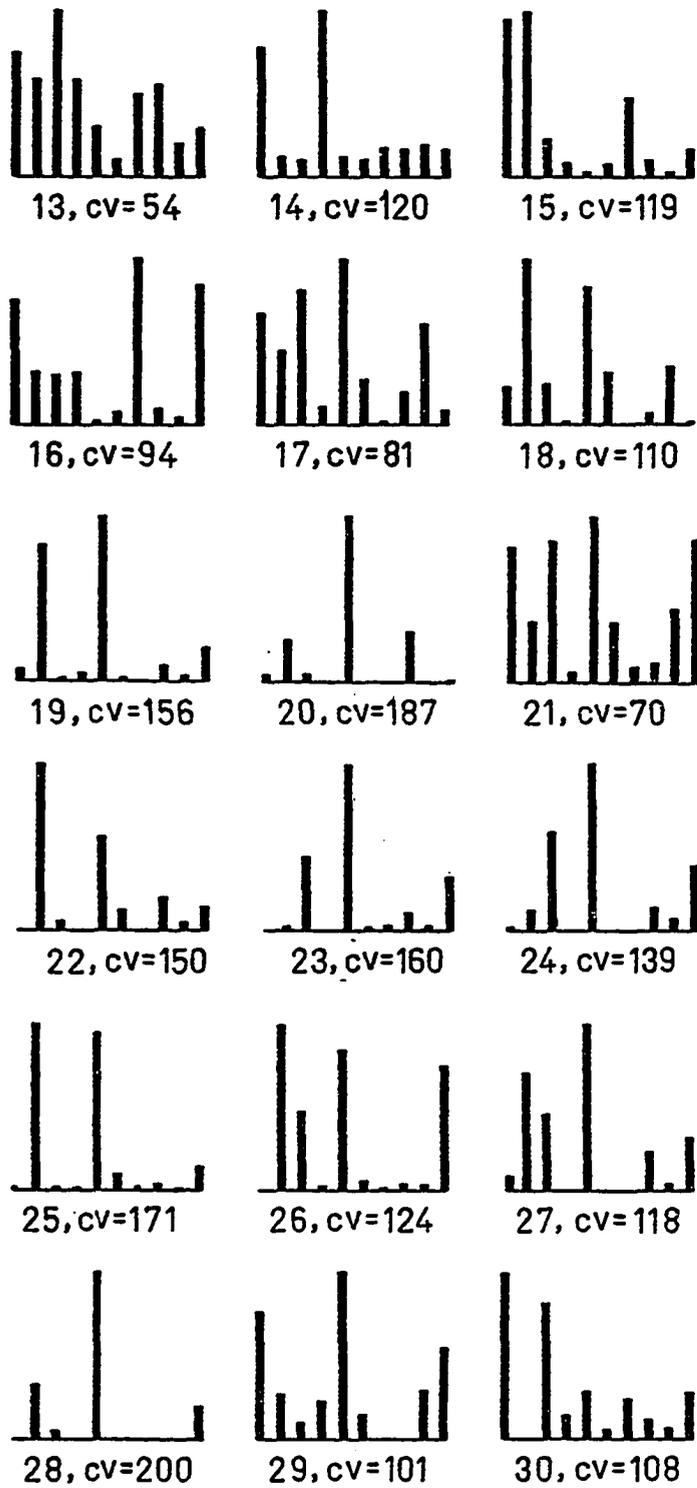


Figure A-1. Continued.

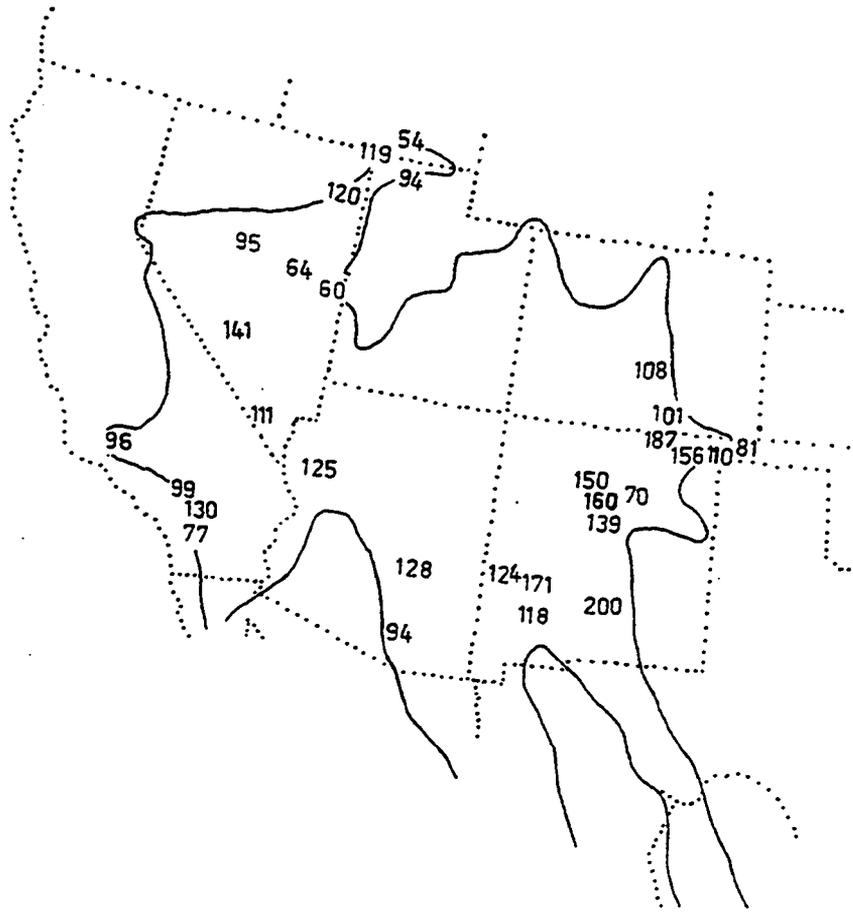


Figure A-2. Distribution of variability in annual pinyon cone production (coefficients of variation) for 30 pinyon communities, and the highly generalized range of pinyon.

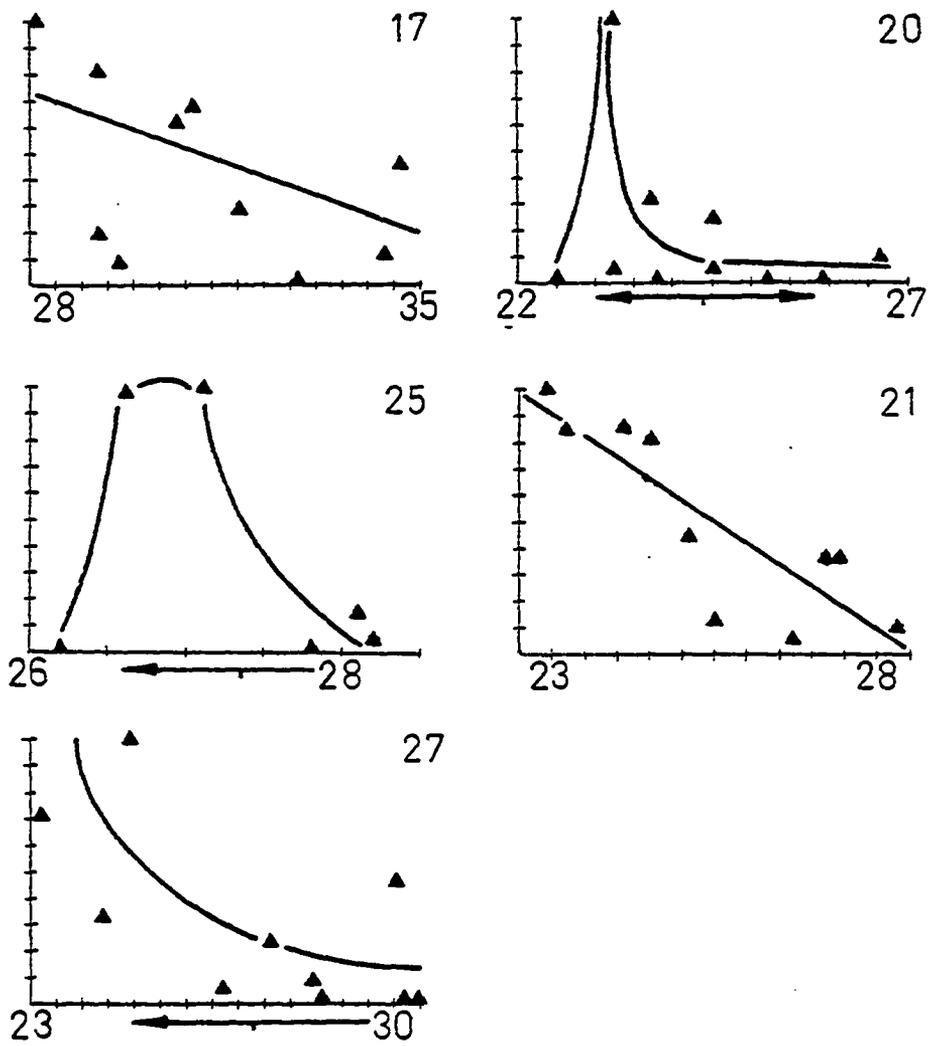


Figure A-3. Cone production in 5 pinyon stands and mean weekly or bi-weekly temperature during the time of primordia initiation. All stands greater than 1 km from respective weather station. Cone crops from 1978-69. Stands and temperature-time periods (1976-67) follow: 17, 24-31 August; 20, 24 August - 15 September; 21, 24 August - 7 Sept.; 25, 1-7 Sept.; 27, 1-7 Sept. Bar and arrows along abscissa represent mean $T \pm 1$ standard deviation. In graphs with less than 10 data points, T records incomplete. Ordinate represents percent maximum cone production.

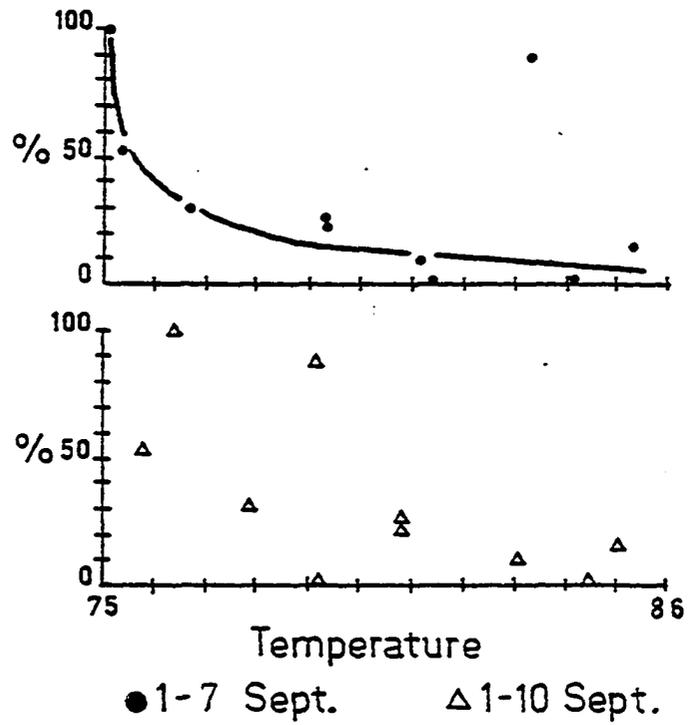


Figure A-4. Cone production and mean maximum daily temperature ($^{\circ}$ F) for Stand 29 (Trinidad, Colorado; about 2 km from weather station). Cone crops, 1978-69; temperatures, 1976-67.