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ENERGY DYNAMICS OF VEGETATIVE AND REPRODUCTIVE GROWTH IN SPANISH BAYONET (*YUCCA BACCATA TORR.*)

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ABSTRACT: *Yucca baccata* and *Yucca elata* are Chihuahuan desert plants which develop massive inflorescence stalks, large flowers and heavy fruits. A field study on the NMSU College Ranch found an average *Y. baccata* invests over 250 g of biomass (oven dry) into these reproductive structures, with about half of this in fruits. Its fruits are strongly affected by the yucca moth whose larvae develop inside the fruit and consume the maturing seeds.

A comparative laboratory study found the optimum net photosynthesis rate of *Y. baccata* leaves below 25°C, whereas *Y. elata* leaves had an optimum above 30°C, assuming equivalent moisture and irradiance levels. These physiological differences correlate well with their observed patterns of vegetative and reproductive growth. *Y. baccata* grows better in cooler seasons and sites than *Y. elata*.

A computer simulation study of reproductive and vegetative growth in *Y. baccata* indicated that an average-sized plant needs about 10–12% of its dry biomass as stored carbohydrates in order to produce an average-sized inflorescence with flowers and fruits. A lesser amount resulted in depletion of stored energy to less than 1%. Depending on environmental conditions, the simulation indicated that about three years were required to rebuild stored energy to the level needed for another reproductive effort.

Yucca baccata Torr. (Spanish bayonet) and *Yucca elata* Englem. (soaptree yucca) are common Chihuahuan desert succulents found in southern New Mexico. While both grow sympatrically in this region they differ in several important respects. *Yucca elata* is aborescent by a tall caudex and has a deep taproot, tall inflorescence stalk, dehiscent fruits and wind-dispersed seeds. In contrast, *Yucca baccata* has a short caudex, shallow root system, shorter inflorescence stalk, large indehiscent fruits and animal-dispersed seeds. The geographical distributions of the two species are also different. *Yucca elata* is common at lower elevations, 610–1250 m, in the eastern Sonoran and Chihuahuan

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409

deserts (McKelvey 1947). *Yucca baccata* is found at higher elevations and ranges from Texas to California and from Sonora and Chihuahua, Mexico, to Nevada, Utah and Colorado (Hastings, Turner and Warren 1972). Where both species occur, as on the Jornada range in southern New Mexico, *Y. baccata* is confined to washes along alluvial slopes. While occurring along washes, *Y. elata* is also common in desert grasslands (Campbell and Keller 1932, Little and Campbell 1943, and Buffington and Herbel 1965).

Growth patterns in relation to environmental factors have been investigated in *Y. elata* (Smith 1975, Smith and Ludwig 1976) who found vegetative growth closely tied to moisture availability during the growing season, but reproductive growth dependent on previous vegetative growth and stored energy reserves. Little is known, however, about *Y. baccata* and its growth and survival characteristics.

The primary focus of this study was to investigate the growth and reproductive patterns in *Y. baccata*. Energy demands of reproduction were studied by fields analysis and by simulation modeling. Rates of photosynthesis and respiration of leaf, flower and fruit tissues were measured to aid in the simulation modeling. The effect of herbivory on reproductive success was also considered. While concentrating on *Y. baccata*, comparative results for *Y. elata* were included.

METHODS. *Study Area.* Field data was collected on an alluvial fan (bajada) of Mt. Summerford at the north end of the Doña Ana Mountains located on the New Mexico State University Experimental Ranch. The ranch is adjacent to the USDA Jornada Experimental Range about 40 km NNE of Las Cruces, New Mexico. The bajada study site is a 25 hectare area previously used as part of the Desert Biome US/IBP Analysis of Ecosystems Program. This site is dissected by small washes (arroyos) which, besides yuccas, grow tarbush (*Flourensia cernua*), mariola (*Parthenium incanum*) and snakeweed (*Xanthocephalum sarothrae*). Plant nomenclature follows Correll and Johnston (1970).

Field Sampling. The study was initiated in early June, 1975 when *Y. elata* was beginning to flower and *Y. baccata* was in fruit. The percentage of reproduction in each species was determined on site. Though yuccas tend to grow in clumps, with many individuals arising from one parent, each individual leaf rosette in a clump is capable of reproducing and was therefore counted as a distinct individual. Inflorescence stalk heights and basal circumferences were measured and number of fruits counted. Fruit counts were made early in the reproductive process and again when fruits reached maturity, so that the rate of loss could be determined. For *Y. baccata* a third survey was made of remaining fruit a month after maturity in the beginning of August.

In July, 30 fruits and 15 inflorescence stalks from *Y. baccata* were harvested and dry and wet weights of fruit, seeds and stalks determined. Various insect larvae were found in the fruit. The percentage of seed destruction by larval

410

populations in the fruits was measured. Field data from Desert Biome studies and from Smith (1975) was used for comparative analysis.

Laboratory. Photosynthetic and respiration rates of various yucca organs were measured using a Gilson Differential Respirometer, which measures μl of O_2 exchanged per minute (Umbreit et al. 1964). Photosynthesis measurements were made using a diethanol amine buffer, which holds CO_2 partial pressure in the flasks constant. As respiration occurs during photosynthesis, readings represent net photosynthesis. Respiration was measured using a 10% KOH solution as a CO_2 trap.

Flowers and buds (10–15) were harvested in the field, immediately submerged in water, recut, and then transported to the lab. One flower or bud was placed in each flask. Fruits (11 *Y. baccata* and 10 *Y. elata*) were harvested in the field, brought into the lab and cut to fit the flasks. An effort was made to minimize structural damage by cutting along the carpels of the fruits. Seeds were generally included in each sample. *Yucca baccata* leaves (7) were cut with a cork borer into circles 2.13 cm in diameter. *Yucca elata* leaves (6) were cut into strips 2 cm long, with a blade, as they were too narrow to cut with a cork borer. Samples were placed in flakes with a few drops of distilled water and transported immediately to the lab.

Readings of photosynthetic and respiration rates were taken at 15, 25 and 35°C. Generally three replications of each reading were made at ten-minute intervals, but five-minute intervals were used at higher temperatures for flowers and buds where respiration was more rapid. A time interval of up to one hour was used between respiration and first photosynthesis readings. Light or irradiance levels were zero for dark respiration and constant at a level of about one-fourth full sunlight for net photosynthesis. Tissue water contents were assumed non-limiting with the experimental conditions used.
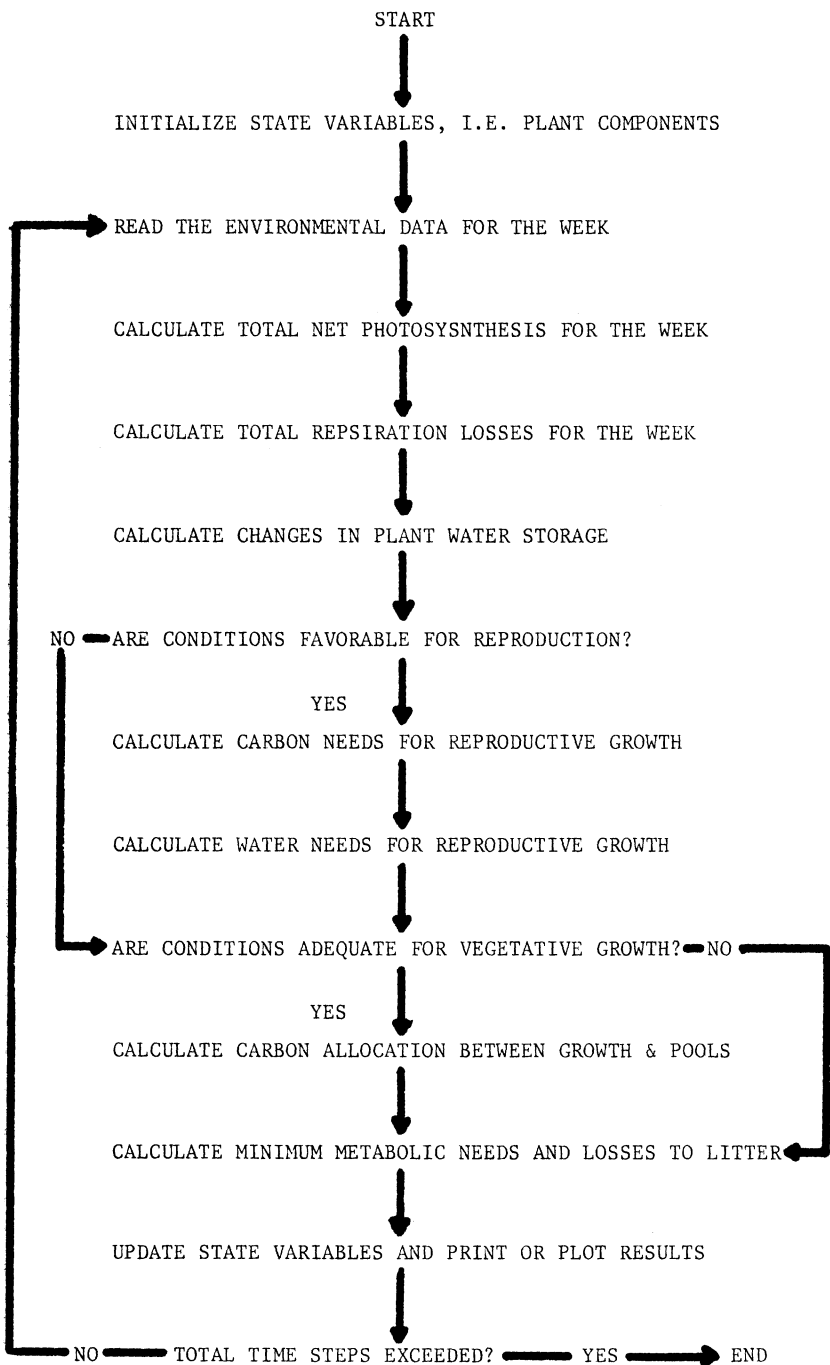
Data Synthesis. The results of the laboratory and field studies were used to develop a computer simulation model of carbon allocation in *Y. baccata* using CSMP (I.B.M.–SH19–7001). Specifically, the model was used to estimate the necessary size of mobile carbohydrate pools for vegetative and reproductive growth and the rates of loss and replenishment of these pools.

A general flow chart of the *Y. baccata* simulation model is shown in Fig. 1, and a source listing is available upon request. The plant components or state variables modeled were: leaf, stem (caudex), taproot (tuber), fine-roots, inflorescence stalk, flowers, fruits and the carbon and water storage pools. Environmental data for the bajada site from March 1973 to March 1974 was used to drive the simulation starting with initial values taken from plants previously measured (Ludwig et al. 1975).

The first time-dependent calculation (weekly steps) was net photosynthesis, which uses our laboratory temperature rates and irradiance and water content rates from Neales et al. (1968). The limiting factor approach was used, where maximum photosynthetic rates for the given temperature, irradiance and plant water content are first determined and then the minimum or most limiting of these three rates is taken as the rate for net CO_2 fixation.

Respiration rates of leaf and reproductive tissues were experimentally determined as a function of temperature. The respiration rates of caudex, tuber and fine lateral roots are assumed to be proportional to the leaf respiration rate, and were given values of 1%, 1% and 5%, respectively.

Plant water storage was a function of precipitation, transportation and water

411

START

↓

INITIALIZE STATE VARIABLES, I.E. PLANT COMPONENTS

↓

→ READ THE ENVIRONMENTAL DATA FOR THE WEEK

↓

CALCULATE TOTAL NET PHOTOSYSNTHESIS FOR THE WEEK

↓

CALCULATE TOTAL REPSIRATION LOSSES FOR THE WEEK

↓

CALCULATE CHANGES IN PLANT WATER STORAGE

↓

NO ← ARE CONDITIONS FAVORABLE FOR REPRODUCTION?

YES ↓

CALCULATE CARBON NEEDS FOR REPRODUCTIVE GROWTH

↓

CALCULATE WATER NEEDS FOR REPRODUCTIVE GROWTH

↓

→ ARE CONDITIONS ADEQUATE FOR VEGETATIVE GROWTH? ← NO →

YES ↓

CALCULATE CARBON ALLOCATION BETWEEN GROWTH & POOLS

↓

CALCULATE MINIMUM METABOLIC NEEDS AND LOSSES TO LITTER ←

↓

UPDATE STATE VARIABLES AND PRINT OR PLOT RESULTS

↓

NO ← TOTAL TIME STEPS EXCEEDED? → YES → END

412

use for growth. It was assumed that a total of 2.5 cm of precipitation must occur within the week before water uptake by the lateral roots occurs. Transpiration rates were approximated from data of Neales (1973). Water use for growth and maximal storage capacities were based on water content measurements of the plant parts.

In order for reproduction to be initiated, a photoperiod of over eleven and one-quarter hours must occur and the carbon and water storage pools must both exceed minimum thresholds, the sizes of which were under investigation. Once reproduction was initiated, the amount of carbon mobilized each week to provide for growth of the reproductive structures depended on the length of time from initiation, with the total reproductive phase taking about ten weeks to reach mature fruits. Fruits then go through an extended period of loss to herbivores of about nine weeks.

If the conditions for reproduction were not favorable, then vegetative growth was possible if the carbon and water storage pools exceeded minimum thresholds. Otherwise the plant was assumed to be dormant and only maintaining minimal metabolic demands. Losses to litter through death and herbivory increased during periods of rapid vegetative growth (Smith 1975).

RESULTS AND DISCUSSION. *Reproductive Growth*. In early June 1975, a survey of 1358 individuals of *Y. baccata* indicated that 7.7% had produced inflorescence stalks, with 6.0% bearing fruits (Table 1). The stalks without fruits were already withered. There was an average of 7.7 fruits per plant having viable inflorescences. By July, this had dropped to 5.6 fruits, the latter figure indicating the number of fruits reaching maturity in 1975. Fruit production in 1973 was about half that of 1975. In addition, inflorescence stalks were larger and flowers heavier in 1975.

In terms of biomass, energy costs per *Y. baccata* plant for reproduction (inflorescence + flower + fruit), were about 250 g in 1975. There were also additional costs due to respiration, but some of this is offset by photosynthesis under good conditions. Most of the energy for reproductive growth comes from previously stored carbohydrates, with some from current leaf photosynthesis. The relative contributions from these various sources were investigated by the simulation model as discussed below.

In comparison, the *Y. elata* populations had higher proportions of individuals reproducing, with about 36% in 1975 (Table 1). Furthermore, the inflorescence stalks were larger, a higher percentage of the stalks had fruit, and the number of fruits per stalk was greater at maturity. While *Y. elata* has smaller fruits than *Y. baccata*, the total

Fig. 1. General flow chart of the *Yucca baccata* computer simulation model.

413

TABLE 1

Reproduction characteristics of Yucca baccata *and* Yucca elata *for 1973 and 1975. Data for 1973 from either Smith (1975) or Desert Biome data. Means and standard errors given where appropriate and available.*

Reproductive Characteristics	Yucca baccata		Yucca elata	
	1973	1975	1973	1975
Percent of population forming inflorescences	36	7.7	67	36
Inflorescence stalk length (cm) per plant	61 ± 1.2	66 ± 1.2	195	178 ± 3.5
Inflorescence stalk biomass (g) per plant	60	67	331	*
Percent of population forming fruits	14	6	57	34
Number of fruits per inflorescence prior to maturity	*	7.7 ± 1.1	13	22 ± 1.2
Number of fruits per inflorescence at maturity	3.2 ± 0.5	5.6 ± 0.9	9	19 ± 1.4
Mean fruit biomass (g) per fruit	22	28 ± 3.2	23	*
Total fruit biomass (g) per plant	77	158	299	446
Mean seed biomass (g) per fruit	*	7.9 ± 0.9	10	*

* Data not available.

seed weight per fruit is greater in *Y. elata* since *Y. baccata* fruits have a thick, fleshy covering.

In 1973, compared to 1975, *Y. baccata* and *Y. elata* both had a higher percentage of plants reproducing. However, their reproductive effort, in terms of mature fruits per plant, was lower in both species. This may have been due to lower precipitation and hence poorer vegetative growth prior to reproduction. Based on observations on *Y. elata* (Smith 1975) it is likely that only the largest, most vigorous plants would reproduce in 1975 after reproducing in 1973, due to the time required for rebuilding stored energy reserves needed for reproduction. Since about two-thirds of the *Y. elata* population reproduced in 1973, this could account for the reduced reproduction in this species in 1975. As 36% of the *Y. baccata* population reproduced in 1973 and only 8% in 1975, it is likely that there was no overlap of reproducing individuals in this species. On this site, *Y. baccata* may need longer time periods to build up sufficient energy reserves for costly reproduction (see below).

Herbivore Effects on Reproduction. Herbivory of mature, indehiscent fruits in *Y. baccata* is essential in order for seeds to be dispersed. Thus, of primary concern are the effects of herbivory on the fruits before they are fully mature and destruction of seeds before they can be dispersed. In 1975, the number of fruits per inflorescence

414

dropped from 7.7 in June to 5.6 in July (Table 1), indicating about a 25% loss by maturity. Herbivory continued throughout July and by August only a few fruits remained (generally highly parasitized) and stalks were withered.

Based on field observations, it appeared fruit herbivory was largely due to woodrats (*Neotoma albigula* and *Neotoma micropus*) and rabbits (*Lepus californicus and Sylvilagus auduboni*). Woodrats have the ability to climb up the inflorescence stalks and eat the fruit. Rabbits primarily consume the fruits on plants with inflorescence stalks close to the ground and not well-protected by the sharp-pointed, bayonet-like leaves. Often they consume only the fleshy outer walls of the fruit leaving the seeds exposed for dispersal.

The primary insect herbivore on *Y. baccata* was the yucca moth. Larvae were found in 60% of the fruits collected. Eggs are deposited in the ovary when the yucca moth pollinates the flower and the larvae develops inside the fruit. They eat their way through a row of seeds as the fruit matures and then burrow out, drop to the ground, burrow into the soil and pupate over winter. Of the seeds in infected fruits, 27% were consumed by yucca moth larvae, with an average of 7.5 larvae per fruit.

Galls, formed by Diptera larvae and parasitized by Hymenoptera, were found in 82% of the fruits. On the average, about 5% of the mesocarp was infested with small galls. The Diptera larvae and pupae were much more abundant than the Hymenoptera. Although the larvae did not appear to have any direct effect on the seeds, they may have had an indirect effect on seed dispersal, as herbivores sometimes avoided heavily parasitized fruits.

Coleoptera larvae were found on fewer fruits (18%) but their effect was greater. The larvae most often found were probably Tenebrionidae. Adult Tenebrionidae were observed at the base of the plants. Fruits affected became dark brown and rotten. Larvae appear to eat the mesocarp which then becomes infected with bacteria and fungi and this infection spreads to the seeds. Larvae may also infect inflorescence stalks which then become rotten and break. Two other species of Coleoptera larvae were occasionally found. Infestation by these larvae may also lead to fruit rot.

Ants are also abundant on the inflorescences, flowers and fruits of both yucca species prior to maturity. They appear to feed on sap and nectar.

Vegetative Growth and Herbivore Effects. The production of new leaves in *Y. baccata* varies with environmental conditions (Fig. 2).

415

Growth is slowest in seasons with the lowest rainfall, e.g. summer of 1971. There may be two peaks of new leaf growth, one in the spring and another in the fall, e.g. 1972.

In mature plants, death of old leaves about equals new leaf production. In reproducing plants, leaf growth ceases, which has also been shown for *Y. elata* (Smith 1975). After reproduction, a new leaf apical meristem must be formed. There is usually a delay in meristem formation until the summer or fall rains begin. Only individuals showing good vegetative growth reproduce.

Plants with severe herbivore damage did not give evidence of reproducing. The chief herbivores on leaves of *Y. baccata* appear to be woodrats. In a survey of 50 plants, 35% of the leaves had been eaten down to about 25 cm in length.

Photosynthesis and Respiration Rates. The respiration rates for *Y. elata* buds and flowers were 2, 5 and 9 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ at 15, 25
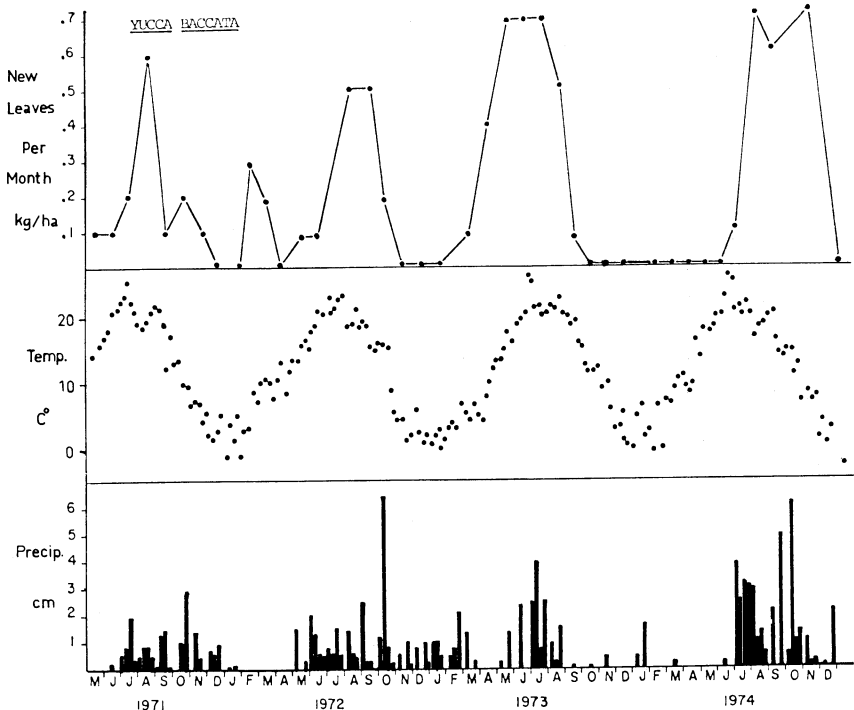

Fig. 2. Vegetative growth patterns of *Yucca baccata* in relation to precipitation (cm) and temperature (mean weekly minimums) patterns.

416

and 35°C, respectively. These rates are similar to those for creosotebush (*Larrea tridentata*), the dominant shrub on the site, which has rates of 2–4 and 4–6 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ at 25 and 35°C, respectively (Cunningham, pers. comm.). Unfortunately *Y. baccata* buds and flowers were not available, since fruits were already formed when this phase of the study was initiated. As the bud and flower structures are similar, *Y. elata* respiration rates were used in the *Y. baccata* simulation model.

Rates of net photosynthesis and respiration of fruit and leaf tissues at different controlled temperatures are shown in Fig. 3. The maturing fruits of both *Y. baccata* and *Y. elata* have green walls and show slight net photosynthesis. A comparison of these rates in these two species illustrates some interesting physiological differences. Net photosynthesis of *Y. baccata* fruits is lower and peaks around 25°C, whereas *Y. elata* peaks around 35°C. Corresponding to these physiological differences, *Y. baccata* is typically found in cooler sites, e.g. higher elevations, and reproduces about a month earlier in the spring than *Y. elata*.

Leaf photosynthesis and respiration rates in *Y. baccata* and *Y. elata* are quite similar in range. The net photosynthesis peak for *Y. baccata* is lower, at around 25°C. Leaf respiration rates are slightly higher in *Y. elata*. A rough estimate of gross photosynthesis (combining net photosynthesis and respiration rates) falls within the range generally reported for succulents (Mooney 1972).

Crassulacean Acid Metabolism (CAM) has been identified in *Agave americana* (Neales et al. 1968, Neales 1973) and it was considered a possibility for yuccas (Bender et al. 1973), as later confirmed for both *Y. baccata* and *Y. elata* by Syvertsen et al. (1976). The presence of CAM would influence an interpretation of our results in two principle ways. First, the rates of the light reaction would be highest under a regime of low night, high day temperatures; a condition not included in our experimental design. Second, instead of a constant level of photosynthesis in daylight, rates in CAM plants vary throughout the day (Neales et al. 1968). The first results in an under-estimate of photosynthesis, but the second would tend to over-estimate production in our model; thus the two tend to cancel each other. Also, but of relative minor importance, CAM plants have the ability to internally recycle carbon from catabolism, which does not represent new carbon fixed from external sources (Szareck et al. 1973). Even though CAM may occur in yucca leaves under certain conditions, it is doubtful that yucca fruits exhibit CAM since they develop when high night temperatures occur.
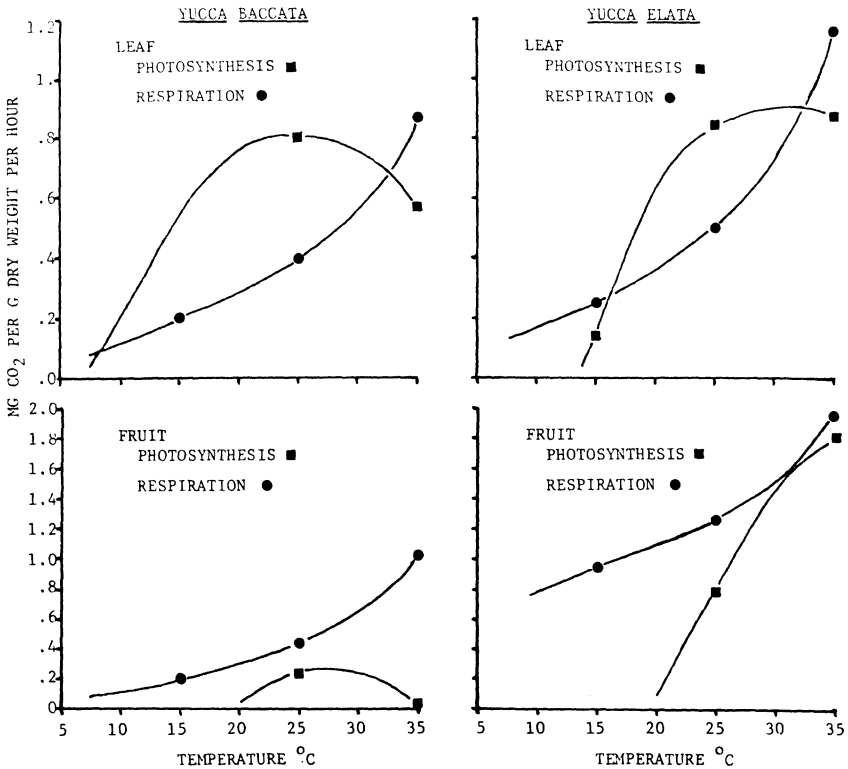
417

Fig. 3. Net photosynthesis and respiration rates for leaf and fruit tissues of *Yucca baccata* and *Yucca elata* at 15, 25 and 30°C. The rates are expressed in mg CO_2 flux per g dry weight of tissue per hour. The CO_2 flux is positive, i.e. fixation, for net photosynthesis and negative, i.e. loss, for respiration.

Water requirements. Since the inflorescence and fruits of both *Y. baccata* and *Y. elata* are quite succulent, the water requirements for reproduction were considerable. The following tissue water contents were determined for *Y. baccata*: fruits — 4x; inflorescence stalks — 2.5x; leaves — 2.6x; and roots — 3x. These contents were assumed to closely reflect water requirements for the growth of these new tissues, realizing that at maturity water contents may decrease. Transpiration rates for reproductive tissues were not available, thus this additional water requirement was not considered. Water contents of leaves and roots were used as a guide to the potential water storage of these species.

Yucca baccata Computer Simulation Model. A reproductive and vegetative growth simulation model was developed for *Y. baccata* in

418

order to estimate the dynamics of the mobile carbohydrate pools under given environmental conditions. The initial conditions for the simulation are based on an individual excavated in 1971 by one of us (Ludwig), which had 424 and 83 g of live and dead leaf biomass, respectively. Its short caudex only weighed 10.5 g, whereas its large tuberous root weighed 798 g, both dry weights. It's smaller, diffuse lateral roots system weighed about 36 g. Based on the water content data, it was estimated that the total water storage pool was about 3000 g. The initial carbon storage pool was set at 150 g, approximately 12% of total dry weight.

Reproductive and growth patterns were examined for a one year simulation starting with the March 1973 environmental conditions, initial plant biomass states and the functions for photosynthesis and respiration rates of plant organs. As shown in Fig. 4, the biomass of all plant vegetative organs increased by a few grams in the first five weeks of the spring. Then the plant initiated reproduction as the following threshold conditions were met: carbon storage pool exceeded 10% of dry weight; the water storage pool exceeded 75% of potential; the photoperiod exceeded 11.25 hours; and the mean night temperature exceeded 3°C. There was a rapid increase in inflorescence biomass followed by a quick buildup of flower biomass in about two weeks. At peak flowering, approximately 16.5 g carbon per 100 g flower dry biomass was being respired. Then fruits began to develop rapidly, reaching peak biomass at about week 15. During fruit growth, fruit net photosynthesis only slightly exceeds night respiration.

As reproductive biomass builds, the level of the carbon pool drops rapidly from 150 g to about 15 g. After peak fruit biomass, the carbon pool begins to rebuild and by the end of the growing season (in early fall on week 36), the pool was rebuilt to about 50 g. During the winter, respiration loss exceeds photosynthesis gain and the carbon pool drops to just below 40 g by spring, i.e. the end of the simulation.

Based on these simulation results, which followed a series of trial simulations where we adjusted the carbon pool threshold in order to achieve results similar to field measurements, it would take about three years for the carbon pool to rebuild to the level required for another reproduction, based on the 1973–74 environmental condition. Further, the mobile carbon pool must be about 10 to 12% of the total structural biomass in order to achieve the energy demands of reproduction, given the functions, assumptions and environmental conditions used in this simulation. In a simulation study of *Larrea*, Cunningham and Reynolds (1977) used a mobile carbon pool of 7% of the vegetative struc-
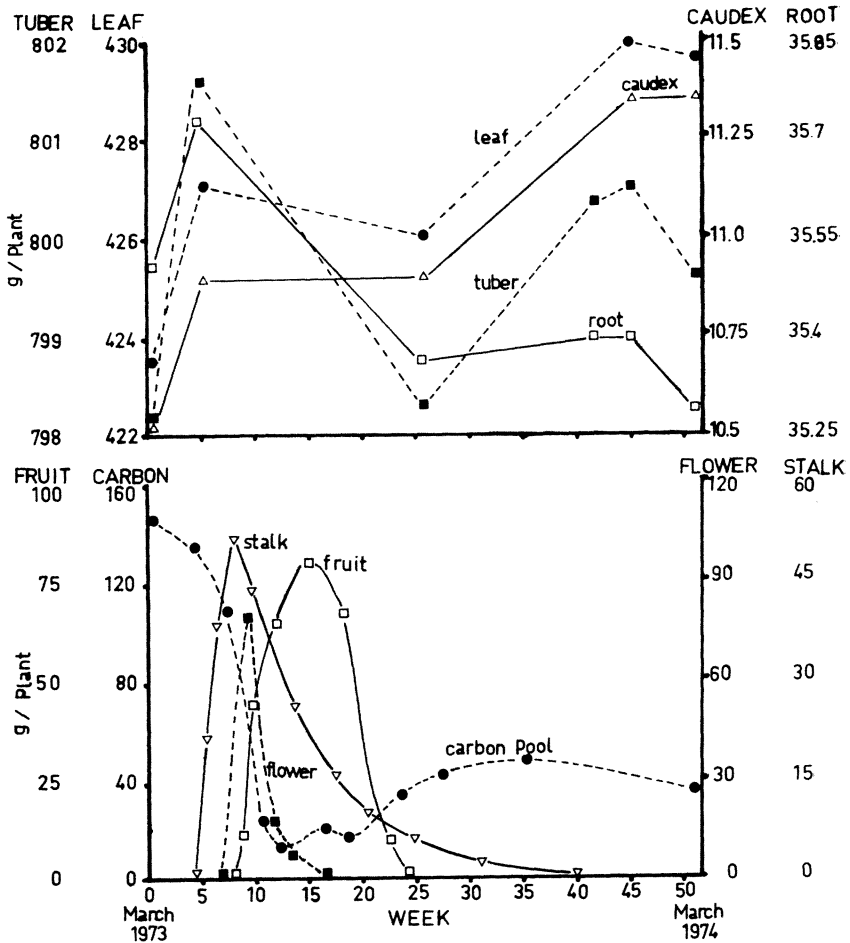
419

Fig. 4. Simulated biomasses (g per plant) for leaf, caudex, tuber, fine-roots, inflorescence stalk, flowers, fruits and carbon pool size from the *Yucca baccata* model.

ture biomass as a threshold required to initiate reproduction. *Larrea* can reproduce every year and it depends more on current photosynthate for the energy demands of reproduction than does *Y. baccata*.

420

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421