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SEASONAL FLUCTUATIONS OF STARCH IN WOOD AND BARK OF TREES FROM A TROPICAL DECIDUOUS FOREST IN MEXICO

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RESUMEN

Para determinar la presencia, abundancia, forma y tamaño de los gránulos de almidón en cortezas y maderas, se estudiaron 25 especies de árboles de Chamela Jalisco, México. En la región se presentan dos períodos estacionales: uno muy seco, de aproximadamente siete meses y otro lluvioso; predomina la vegetación de bosque tropical caducifolio. Se observó una relación entre la abundancia de almidón y la estación lluviosa y la fenología de las especies que se estudiaron. Aunque no hay un patrón definido de comportamiento en cuanto a abundancia y escasez de las reservas, 61% de las especies presentaron la mayor cantidad de almidón al finalizar la primavera y en el verano, y la menor durante otoño e invierno; al iniciar las lluvias disminuye, concidiendo con el desarrollo de brotes. La forma de los gránulos es característica para cada especie, lo que puede ser útil para identificar las maderas y las cortezas. Las formas más frecuentes fueron las esféricas, elípticas, claviformes a ligeramente irregulares. Miden de 5 a 14 µm en las células axiales y 2 a 9 µm en las radiales, y son más pequeños en las cortezas.

Palabras clave: fluctuación de almidón, madera, corteza, bosque tropical caducifolio, México.

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ABSTRACT

Twenty five tree species from the region of Chamela, Jalisco, Mexico, were studied to determine presence, abundance, shape and size of starch granules in both bark and wood. The region has two well marked periods: a very dry one, lasting ca. seven months, and a rainy one; the predominant vegetation is tropical deciduous forest. A relationship between the abundance of starch granules and rain seasonality and the phenology of the species studied was observed. Although in general there is no single behavioral pattern in regard to storage and depletion of reserves, in both bark and wood, 61 % of the species possess the lowest amount of starch in late spring and summer, and the greatest during autumn and winter. The amount of starch decreases at the beginning of the rainy season, coinciding with the development of growth shoots. The shape of the starch granules is species-specific and can help in the identification of woods and barks. The most common shapes of the starch granules were spherical, elliptic, clavate, to slightly irregular, varying in size from 5 to 14 μm in axial cells, contrasting with 2 to 9 μm in radial cells, being smaller in bark.

Key words: starch fluctuation, wood, bark, tropical deciduous forest, Mexico.

The metabolic pathway of carbohydrates formed in trees is relatively well known (Kramer and Kozlowski, 1960, 1979; Ziegler, 1964; Kozlowski and Keller, 1966). These are used by trees in different ways. The largest portion is used for growth, both in length and in diameter and other portions are used in respiration, and in flower and fruit formation; the remainder is stored as starch, and is available to the tree when the demand is higher than current photosynthesis, providing the necessary energy to carry out the minimal survival functions such as respiration. When the quantity of circulating sugar produced by photosynthesis is high, the formation of starch is favored; when photosynthesis stops, the sugar concentration decreases and starch is converted into sugar. In deciduous trees of temperate regions, spring growth begins before photosynthesis resumes, and early growth is thus dependent upon the starch accumulated during the previous growing season.

Starch grains are generally made up of successive layers of amylose and amylopectin (Banks and Muir, 1980). Banks and Muir (1980) found that the size and morphology of starch grains vary between species and can be useful in species identification.

Beck and Ziegler (1989) pointed out the complexity of starch, mainly due to the great heterogeneity in the molecules and in the structure of the starch grain owed perhaps to the existence of numerous enzymes in its biosynthesis.

In a revision of about one hundred and fifty studies dealing with the synthesis and degradation of starch in seeds and leaves, Beck and Ziegler (1989) concluded that starch degradation is a combined action of both hydrolysis and phosphorolysis to metabolize or export other forms of carbohydrates, and that water stress stimulates enzymatic activity toward starch degradation, as noted earlier by Spoehr and Milner (1939).

With reference to environmental factors that influence the physiology of the formation and degradation of starch granules, the relation between temperature and starch content has been well known since long ago; Coville (1920) reported the complete disappearance of starch content in logs stored at 3°C.

On the other hand, in the last thirty years, the subject of reserve substances has been dealt with abundantly and diversely, especially in food plants, as shown by Priestley (1970). There is also some knowledge about the distribution and retranslocation of stored carbohydrates in trees of temperate regions (Kramer and Kozlowski, 1960). In a study on the relationship between translocation of substances and tree growth, Zimmermann (1964) indicates three important possibilities: a) material translocated from active leaves to growth sinks; b) material retranslocated from places of storage to places of growth; and c) material stored very near the place of growth, mobilization thus involving a minimum of long distance transport. He also mentions various general aspects on the behavior and pathways of reserve substances during dormancy and phloem reactivation (Zimmermann, 1964). However, studies of trees from tropical regions are scarce. Fink (1982) studied the distribution of starch and acid phosphatases in ten tree species from an evergreen tropical forest of Venezuela. He found that the starch content decreases during the growth of apical buds, increasing later, and that acid phosphatases (required for the synthesis of starch granules) show activity the whole year, to which he attributed the continuous growth of tropical trees. In this regard, Essiamah and Eschrich (1985) studied the changes in starch content of six temperate tree species from Europe and found four phases: a) maximum starch content in the autumn; b) starch dissolution into sucrose during winter latency; c) resynthesis from sucrose in early spring; and d) starch dissolution in late spring during bud swelling and breaking.

However, no information is available regarding starch accumulated in the vascular tissue of trees from dry, semidry or seasonally dry regions, and the influence and importance of the reserves' metabolism in the survival of the plants of these regions. In view of the dearth of information on reserves in trees of those regions, the main objectives of this work are:

-To study the general morphologic characteristics such as shape and size of the starch granules for a number of species, since those features could aid in the identification of woods and barks.

-To know the abundance of starch both in wood and bark throughout the year in order to find out the general trend of storage of reserve substances in a tropical deciduous forest or deciduous seasonal forest.

-To compare our results with those obtained for trees of temperate and cold zones.

-To correlate the presence of starch with phenological and reproductive aspects of the species studied.

MATERIALS AND METHODS

Study site. The study was conducted at UNAM's Biological Station in Chamela, Jalisco, situated at 19°30'N latitude, 105°03'W longitude, 35-50 m altitude, less than 2 km from the Pacific coast of Mexico.

The climate, following Köppen's system modified by García (1981) is classified as warm subhumid, with a mean annual precipitation of 748 mm. Approximately 80% of the rain falls between July and October, with a seasonal drought from November through May. The annual mean temperature is 24.5°C (Fig. 1). This climate approaches the driest of those characteristic of tropical forests in Mexico (García, 1981; Bullock, 1986).

The vegetation at Chamela consists of two main types: the more prevalent is tropical deciduous forest on the slopes, with trees up to 15 m tall and abundant shrubs; and a taller semideciduous forest restricted to streams, with trees up to 20 m tall, and an abundance of epiphytes and lianas. The families with the greatest number of species of the deciduous forest are Leguminosae, Euphorbiaceae, Rubiaceae and Bignoniaceae; some of the dominant species are *Caesalpinia eriostachys, Cordia alliodora, Bursera* spp. and *Lonchocarpus* spp. (Pérez, 1982; Lott *et al.*, 1987). Almost all of the trees drop their leaves during the dry season.

Sampling. Thirty-one trees belonging to 25 of the most frequent species were studied (Table 1). Sometimes two trees of the same species were included, in order to find out their similarity in behavior. By means of a cylindrical hollow punch, wood and bark samples, 15 mm diameter and at least 1 cm of wood tissue, were taken from the trunk at between 1 and 1.5 m height. The trees were tagged and sampled quarterly in the following dates: May 25 (spring), July 23 (summer), November 23 (autumn), February 15 (winter) (Fig. 1). Sampling was done in spring, almost at the end of the season when the temperature increases slightly; in summer during the rainiest period; in autumn when the rains have totally ceased and some trees start dropping their leaves; and in winter at the end of the coldest month.

The wood and bark samples were fixed in a solution of FAA (Saas, 1958) for further analysis in the laboratory. Free hand sections as well as microtome sections were made and treated with a 2% solution of Iodine-Potassium (IKI) to stain the starch granules. The abundance of starch was estimated in sections of bark and wood (axial and radial parenchyma) as follows: 1, scarce = 25% of the tissue occupied by starch; 2, regular = 50% of the tissue occupied by starch; 3, abundant = 75% of the tissue occupied by starch; 4, very abundant = 100% of the tissue occupied by starch. Five granules were measured for each individual under a light microscope with a calibrated eyepiece scale.

The specimens for observation under the scanning electron microscope (JEOL JSM-35) were cubes of 5 mm by side, air-dried and covered with gold.

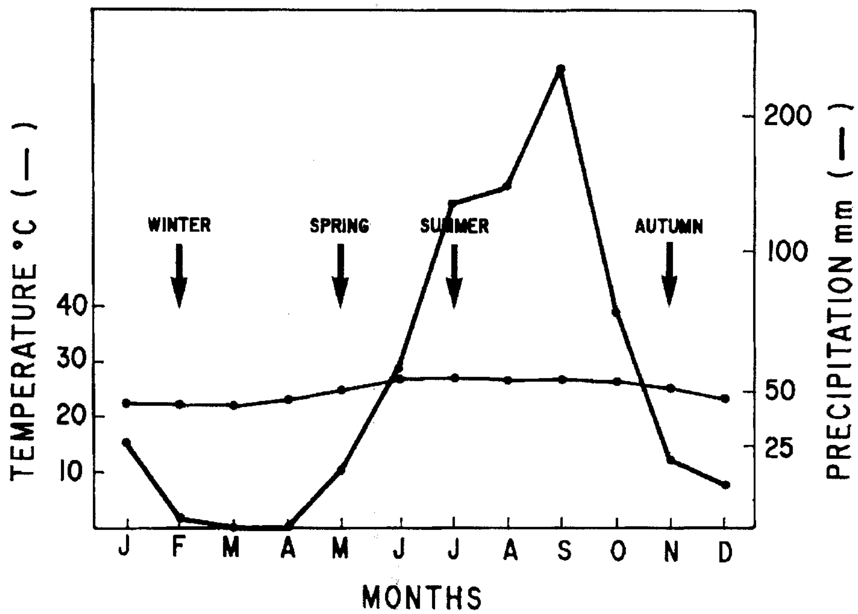

Fig. 1. Climogram for Estación de Biología Chamela (taken from Bullock, 1986). Arrows show when samples were collected.

RESULTS AND DISCUSSION

All species studied present starch as a reserve substance, the shapes of the starch granules were spherical, elliptic, clavate, to slightly irregular (*Jatropha standleyi*), and elongated (*Pithecellobium mangense*) (Fig. 2, Table 1). The shapes were clearly species-specific, and varied between different species of a genus; for example, *Caesalpinia coriaria* with spherical granules, and *Caesalpinia sclerocarpa* with elongated granules (Fig. 2). Granule size was very variable between species, but typically in the axial parenchyma cells of the wood was 5-9 µm, as a rule; in bark, the size of starch granules was smaller, the most frequent being 2-5 µm. (Table 1).

In most species, abundance was greater in wood than in bark (Figs. 3 and 4). In wood, starch abundance in axial parenchyma was often greater than in ray parenchyma, while no such trend was obvious in bark.

In general, both in wood and in bark, the periods with the highest starch content are autumn and winter, and the beginning of spring (May), decreasing slightly before the rainy season (end of May), decreasing sharply (sometimes totally) a short time before the rainy season reaches its peak.

Summarizing briefly, 61.2% of the individuals present decreased starch and, in some cases, total loss during the summer; only 16.1% show total loss or decrease in spring; 9.6% in autumn, and 12.9% in winter.

Table 1. List of species studied, size and shape of starch granules

Species	Wood µm	Bark µm	Shape	Family
Astronium graveolens	9	5	clavate	Anacardiaceae
Sciadodendron excelsum	10	5	spherical	Araliaceae
Ceiba aesculifolia	12	7	spherical	Bombacaceae
Bourreria purpusii	5	3	irregular	Boraginaceae
Cordia alliodora	3	2	spherical	Boraginaceae
C. alliodora	5	4	spherical	Boraginaceae
Cordia elaeagnoides	5	3	spherical	Boraginaceae
Cochlospermum vitifolium	9	5	irregular	Cochlospermaceae
Ipomoea wolcottiana	7	3	irregular	Convolvulaceae
Celaenodendron mexicanum	14	3	elliptic	Euphorbiaceae
C. mexicanum	12	4	elliptic	Euphorbiaceae
Jatropha standleyi	11	5	irregular	Euphorbiaceae
Gyrocarpus jatrophifolius	9	5	spherical	Hernandiaceae
Apoplanesia paniculata	6	2	irregular	Leguminosae
Caesalpinia coriaria	9	4	spherical	Leguminosae
C. coriaria	10	3	spherical	Leguminosae
Caesalpinia eriostachys	12	5	irregular	Leguminosae
C. eriostachys	14	5	irregular	Leguminosae
Caesalpinia platyloba	11	4	elliptic	Leguminosae

Table 1, continued

Species	Wood µm	Bark µm	Shape	Family
Caesalpinia sclerocarpa	16	2	elongated	Leguminosae
C. sclerocarpa	12	4	elongated	Leguminosae
Cynometra oaxacana	9	4	irregular	Leguminosae
Erythrina lanata	10	3	irregular	Leguminosae
Lonchocarpus eriocarinalis	9	3	spherical	Leguminosae
Lysiloma microphylla	14	7	clavate	Leguminosae
Pithecellobium mangense	14	3	elongated	Leguminosae
P. mangense	10	3	elongated	Leguminosae
Platymiscium lasiocarpum	7	3	spherical	Leguminosae
Ficus cotinifolia	9	6	spherical	Moraceae
Trophis mollis	7	5	spherical	Moraceae
Jacquinia pungens	9	6	spherical	Theophrastaceae

In both wood and bark, *Jacquinia pungens* behaved in direct contrast to the rest of the species, which is in complete accord with its phenology, since as a heliophyte it sheds its leaves during the rainy season and puts forth new leaves during the dry season (i. e., during fall and winter). Thus, mobilization of reserves is mainly in fall and winter in agreement with Janzen's (1970) and Janzen and Wilson's (1974) results in Costa Rica.

In all bark cases, an increase and decrease of starch content was observed, which could point out to a greater translocation of the reserve in bark, slightly different from its behavior in wood where smaller fluctuations are present (Figs. 3 and 4). Apparently the starch first utilized is the one more accessible or closer to the phloem zone in the bark and, when this reserve is depleted, starch from more distant zones is employed, in agreement with Kozlowski and Keller (1966), and Ziegler (1964). Furthermore, the starch stored in the rays is more rapidly utilized than that of the axial elements.

Correlating the starch fluctuation with the phenology of the species and with the climate of the study area, we observed the next facts in every season of the year.

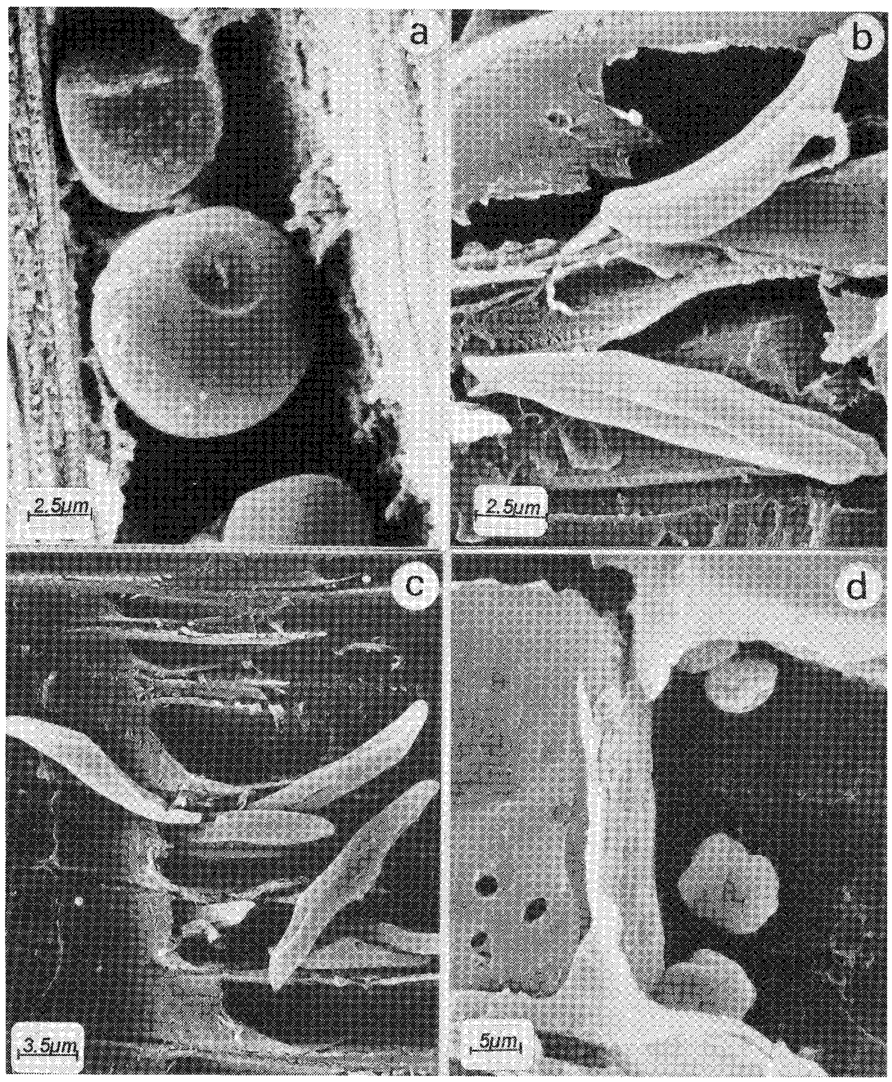

Fig. 2. Starch granule shapes in wood of different species: a. *Caesalpinia coriaria*, spheric granules. b. *Pithecellobium mangense*, elongated granules; c. *Caesalpinia sclerocarpa*, elongated granules; d. *Jatropha standleyi*, irregular granules.

Spring. The temperature has increased 1-2°C reaching an average of 25°C and average maximum of up to 30°C (Bullock, 1986). Trees begin growing apical buds and, although most are still leafless, several (about ten) species are flowering and fruiting. The forest is predominantly gray with some individuals still presenting flowers (Pérez, 1982).

According to Ziegler (1964) the total exhaustion of reserves happens only when there is a massive fructification; the absence or decrease of starch in most of the species (Figs 3 and 4) seems to be totally due to their flowering or fruiting.

On the other hand, it is evident that no species showed a maximum starch content in bark in the spring (Fig. 4), which clearly indicates that starch has begun to be hydrolized and its resulting products are translocated to be used in the formation of apical buds. Therefore, it seems to be in the bark, especially in the phloem, where the translocation of the reserves begins, in agreement with the ideas of Zimmermann (1964), who observed that when the buds open, the reserve material moves upward via the reactivated phloem until reserves are exhausted.

Summer. By mid-June the temperature reaches an average of 27°C monthly and rains fluctuate from 56.4 mm in June to 234.6 in September (Bullock, 1986). As water becomes available, all the species rapidly begin bud sprouting; the species that started their buds since March develop their leaves completely.

The decrease in starch content at the beginning of summer, when rains start, is very noticeable in wood (Fig. 3), and even more so in the bark (Fig. 4) of most of the species of the deciduous seasonal forest. This agrees with the findings of several authors (Ziegler, 1964; Zimmermann, 1964) with species of temperate or cold forests in which the initiation of the growth buds demands high starch utilization, the reserves thus being noticeably depleted.

Autumn. The rainy season ends at the beginning of November. Approximately 50% of the species remain leafy for a short time, while the rest of the species are actively shedding their leaves. The forest appears still moderately green. An increase of starch in wood could be observed, and no species lacked starch in wood (Fig. 3). In bark (Fig. 4), the starch content also increased in most of the species although *Jacquinia* lost totally its starch.

Winter. The average mean temperature goes from 22.3 to 23.8°C, and there are occasional rains, with monthly averages ranging from 16.4 to 3.6 mm. The forest is very dry, trees and shrubs are leafless with an overall general grayish appearance although there are some species blooming and fruiting. In the wood of all individuals studied abundant starch was found, except in *Jacquinia*, that lacks starch but has abundant foliage.

The results regarding content of starch in bark and wood of species from the seasonal deciduous forest is remarkably different from the results obtained by Essiamah and Eschrich (1985) for temperate species. They report four phases of change (synthesis, dissolution, resynthesis and dissolution) not found in the species of the deciduous seasonal forest, where the phase of winter dissolution is lacking. Our results coincide more, though not completely, with those of Fink

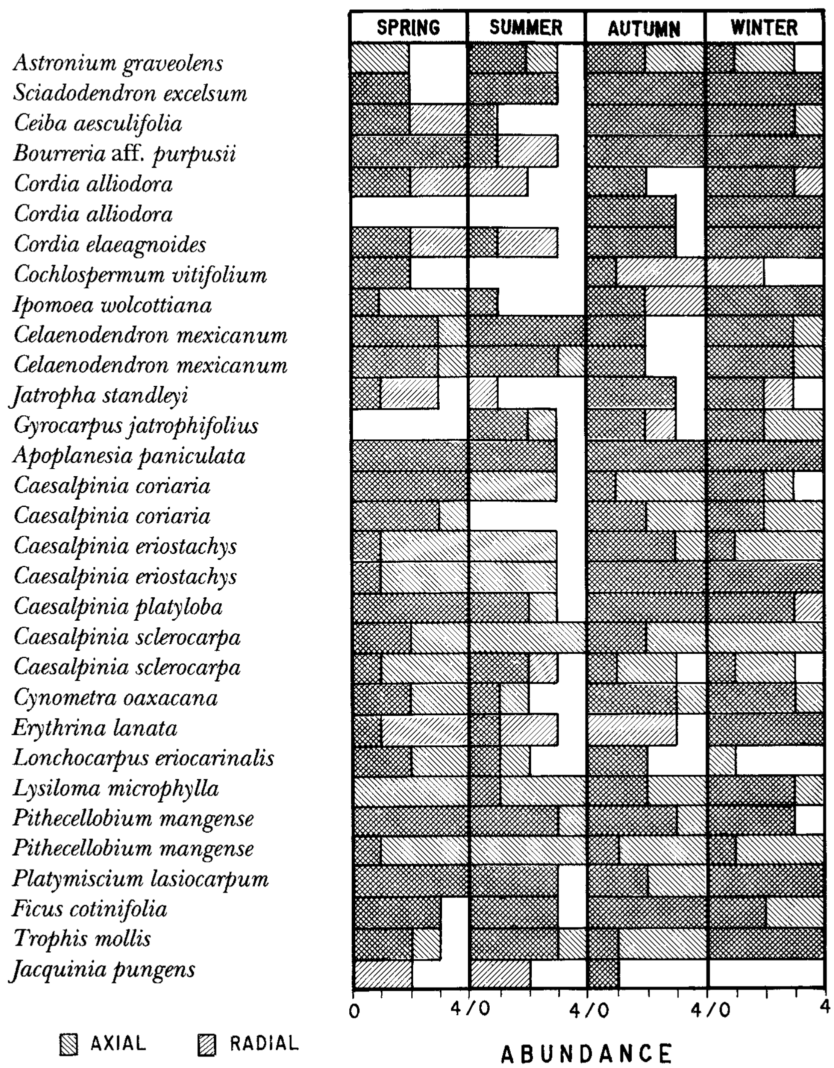

Fig. 3. Starch content in wood of trees from Chamela. The content was estimated as follows: 1, scarce= 25% of the tissue occupied by starch; 2, regular= 50% of the tissue occupied by starch: 3, abundant= 75% of the tissue occupied by starch; 4, very abundant= 100% of the tissue occupied by starch.

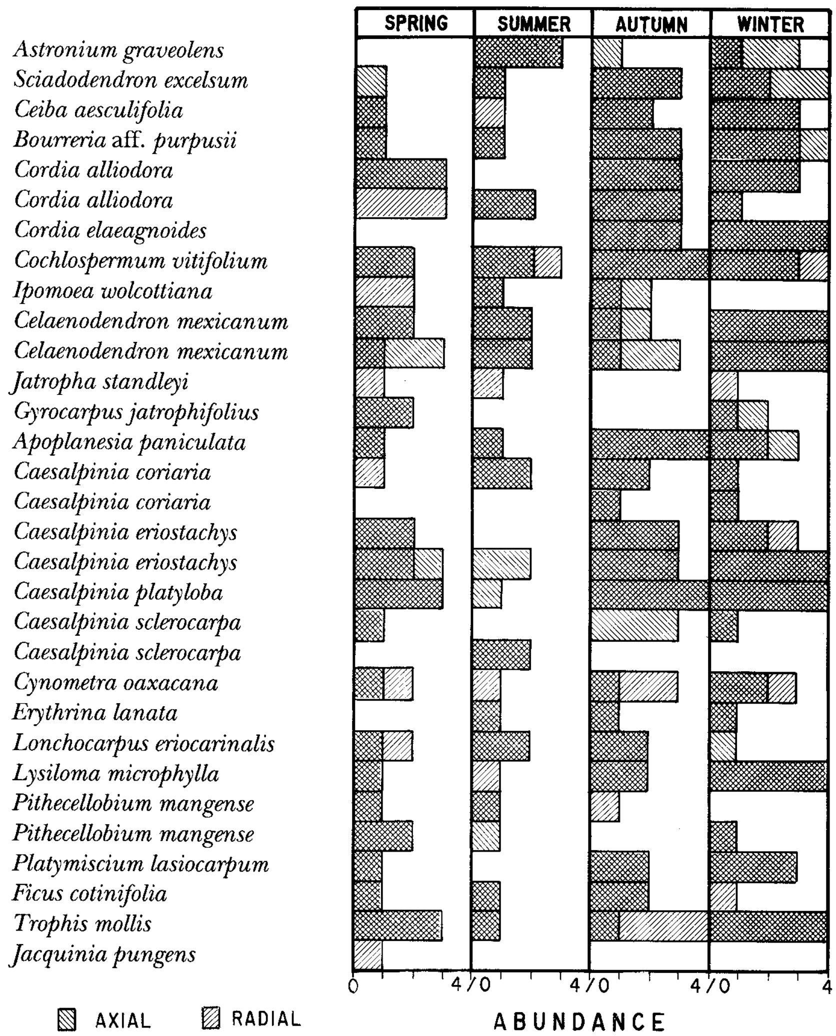

Fig.4. Starch content in bark of trees from Chamela. The content was estimated as follows. 1, scarce= 25% of the tissue occupied by starch; 2, regular= 50% of the tissue occupied by starch: 3, abundant= 75% of the tissue occupied by starch; 4, very abundant= 100% of the tissue occupied by starch.

(1982) for several tropical species from Venezuela, that present a decreased starch content before bud growth, but seem to be active all year round, as expected of species from a tropical evergreen forest.

Bullock (1992) worked with *Jacaratia mexicana* and *Spondias purpurea* from the same region of study as ours, evaluating, through chemical methods, the seasonal changes in the content of nonstructural carbohydrates. He found that both species show a decrease in carbohydrate content in the summer, though one species showed the decrease in the trunk, whereas the other showed it in the branches. These results are similar to those found by us for 61% of the species studied. We consider this to be the most general trend concerning storage and consumption of carbohydrates in the trees of this region.

In the species of the tropical deciduous forest the decrease in starch content is noticeable; there is no constant activity since, during almost 6 months of drought, almost all the species lose their leaves.

Starch storage seems to be closely related to water availability, i.e., to the rainfall pattern in the region, although each species has its own particular adaptations, depending on its phenology; however, it is necessary to sample more intensively in order to confirm the general trends stated herein for the reserve substances in the tropical deciduous forest.

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