Branch and Inflorescence Production in Saw Palmetto (Serenoa repens)*

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The saw palmetto, *Serenoa repens* (Bartr.) Small (subfamily Coryphoideae) is widely distributed throughout the southeastern United States. It is common in pinelands, prairies and coastal sand dunes, typically with a low-growing habit. Most plants have extended underground or surface-creeping stems (Fig. 11) but sometimes it forms dense clumps. Occasional plants in sheltered or otherwise favored habitats are found with more upright, obliquely-rising or even erect stems with basal branches. Saw palmetto then approaches the habit of a typical multiple-stemmed palm.

Both saw palmetto and its associated pines are adapted to fires that are common during the dry season of winter and early spring. In an area that has been burned early in the year, *Serenoa* subsequently shows a conspicuous greening when the charred stems send up their first new leaves. Regrowth is rapid, the green of the new leaves being evident within a few days of the fire and by mid-summer, recovery of the foliage is complete. In some areas of the Everglades fires destroy hardwood hammocks, leaving only the saw palmettos at the perimeters; these form saw palmetto "rings" up to several hundred feet in diameter (Craighead, 1971: 130).

Although *Serenoa* is so widespread and so abundant in pastures that it has been considered a weed, there is lack of information about its growth habit and especially of the vegetative branching whereby it seems to spread. Even a casual examination suggests that *Serenoa* represents an exception to the general method of branching in clustering palms, in which branches arise as suckers from buds at the base of the main axis, at or below ground level. Good examples of this typical habit are provided by the native paurotis palm (*Acoelorraphe wrightii*). Many species in the genera *Bactris*, *Phoenix* and *Chamaedorea* further represent this clustering habit (Tomlinson, 1961). In all of these palms the upright seedling stem at first produces vegetative branches as suckers which originate from buds in the axils of the lower leaves. As the seedling axis develops further there is a switch from vegetative to reproductive branching. Axillary buds may at first abort, but later ones in the axils of more distal leaves grow out as inflorescences. Consequently suckering is restricted to the basal part of a stem and by repetition of this process on daughter axes, a cluster of stems is built up. Abnormal individuals in a few species produce vegetative branches at higher levels as "aerial suckers" (Davis, 1969). In *Chrysalidocarpus* species some branching normally occurs above ground level by initiation of vegetative buds in extra-axillary positions (Fisher, 1973). The normal situation in multiple-stemmed palms, however, is a clear distinction between a vegetative phase (with suckers) and a reproductive phase (with inflorescences). The two phases are sharply circumscribed.

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In contrast to this, *Serenoa* clearly produces a sequence of inflorescences and vegetative branches (suckers) along its horizontal axis, without a clear morphological distinction between vegetative and flowering phases. In the following study we have examined some details of the relative frequency of vegetative and inflorescence buds in order to provide quantitative data.

Material and Methods

Our observations are based on dissections of mature stems and seedlings of *Serenoa* collected from pinelands in several localities between Homestead and South Miami, Florida, and of four-year-old seedlings of *S. repens* growing in one-gallon cans in a nursery at Fairchild Tropical Garden. Shoot apices used for microscopic examination were fixed in FAA (formalin-acetic-alcohol), embedded in paraplast, serially sectioned at 10 μm and stained with safranin and Delafield's haematoxylin.

Regrowth of *Serenoa* was followed in an area of pineland near Fairchild Tropical Garden which was burned over in late March 1971, during a severe winter drought. The fire was sufficiently intense to kill many full-grown pines.

Seedling Development

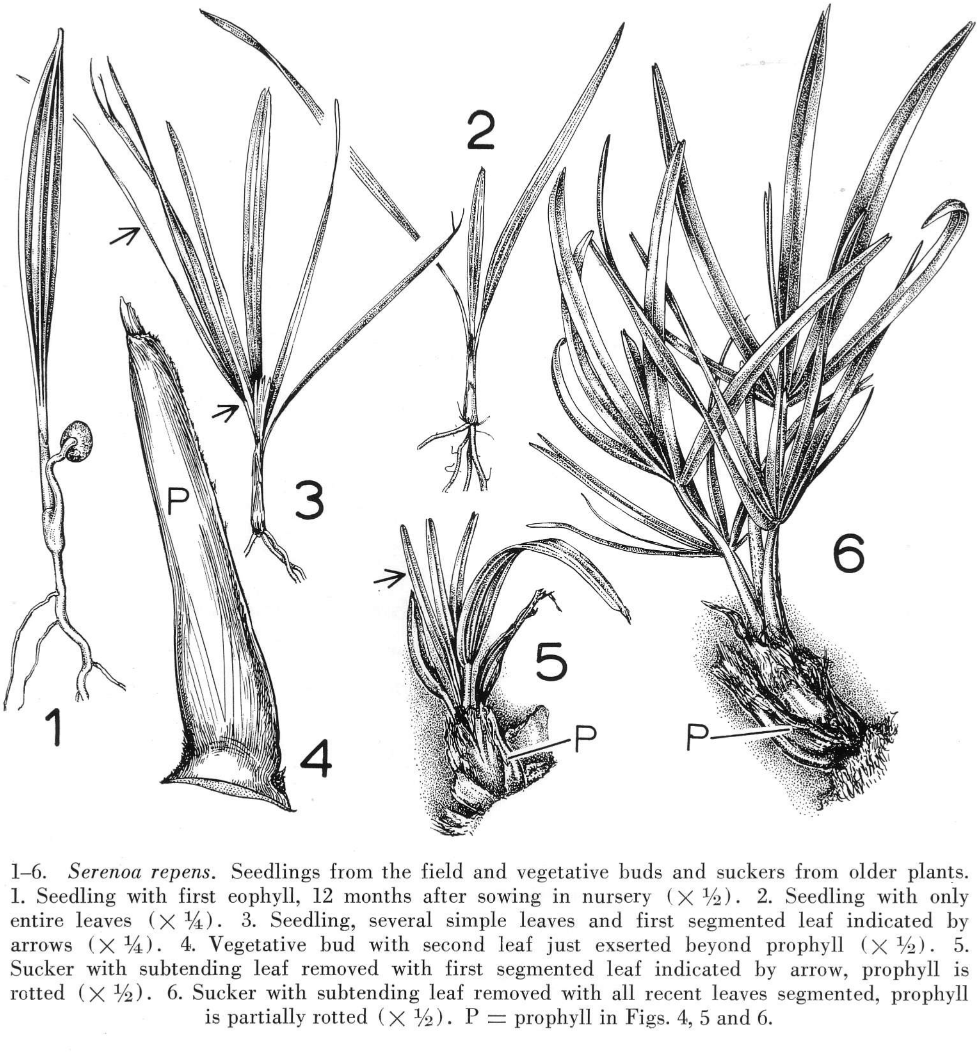
Information about early growth of *Serenoa* seedlings is provided mainly by Hilmon (1968). In a study of germination and early seedling growth he reported that 50–60% of seeds planted in greenhouse flats germinated, the first within six to eight weeks of planting. Only 19% of seeds planted in the field germinated. Removal of the endocarp increased the percentage of germination and induced earlier germination under both conditions. The first eophyll of the seedling emerged above the soil one to two months after germination (Fig. 1).

The first foliage leaves of a seedling are simple and linear (Fig. 2). Up to five of these juvenile leaves, successively wider and longer, are produced, followed by the first palmately dissected leaf (Fig. 3, arrow). Later leaves show increasing dissection. Rate of growth is slow and in field-germinated seedlings Hilmon found that seedlings 18 months after planting had an average of only 2.7 juvenile leaves and the first palmate leaf did not appear until the third year. After five and one-half years, of 30 surviving seedlings, 18 had at least one palmate leaf, 9 of these had entirely palmate leaves (with an average of 4.2 leaves per plant), and 11 still retained entirely juvenile (simple) leaves (with an average of 3.0 leaves per plant).

Branch Morphology and Development

Suckers on seedlings. In our experience, nursery-grown seedlings (Fig. 7) were more vigorous than those grown by Hilmon and within 3 years produced many suckers from axillary buds subtended by typical palmate leaves. In several seedlings the growth of the suckers equalled that of the original axis, making it difficult to distinguish parent axis from daughter sucker. We have no information as to when suckers appear in field-grown seedlings, but it is presumed to be much later than in nursery-grown seedlings.

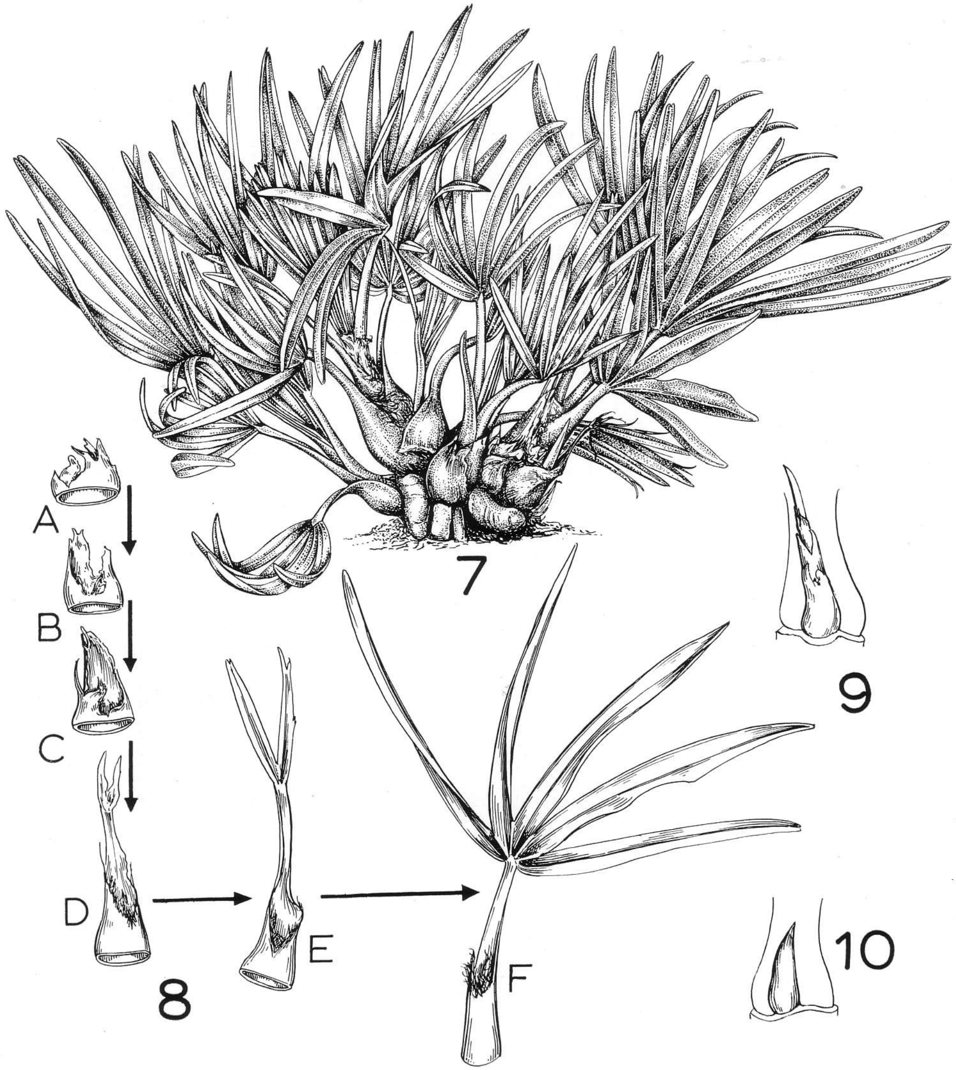
The vegetative sucker bud is covered initially by its first leaf, a scalelike prophyll (Fig. 10) but this is ruptured by growth of subsequent leaves (Fig. 9). These successive leaves (e.g. Fig. 8) are larger but still scalelike (Fig. 8,B–C) followed by leaves with reduced blades (Fig. 8,D–E) until the adult leaf, still with few segments, is formed (Fig. 8,F). This is usually the sixth leaf on the axis of the sucker.



1–6. *Serenoa repens.* Seedlings from the field and vegetative buds and suckers from older plants. 1. Seedling with first eophyll, 12 months after sowing in nursery (× ½). 2. Seedling with only entire leaves (× ¼). 3. Seedling, several simple leaves and first segmented leaf indicated by arrows (× ¼). 4. Vegetative bud with second leaf just exserted beyond prophyll (× ½). 5. Sucker with subtending leaf removed with first segmented leaf indicated by arrow, prophyll is rotted (× ½). 6. Sucker with subtending leaf removed with all recent leaves segmented, prophyll is partially rotted (× ½). P = prophyll in Figs. 4, 5 and 6.

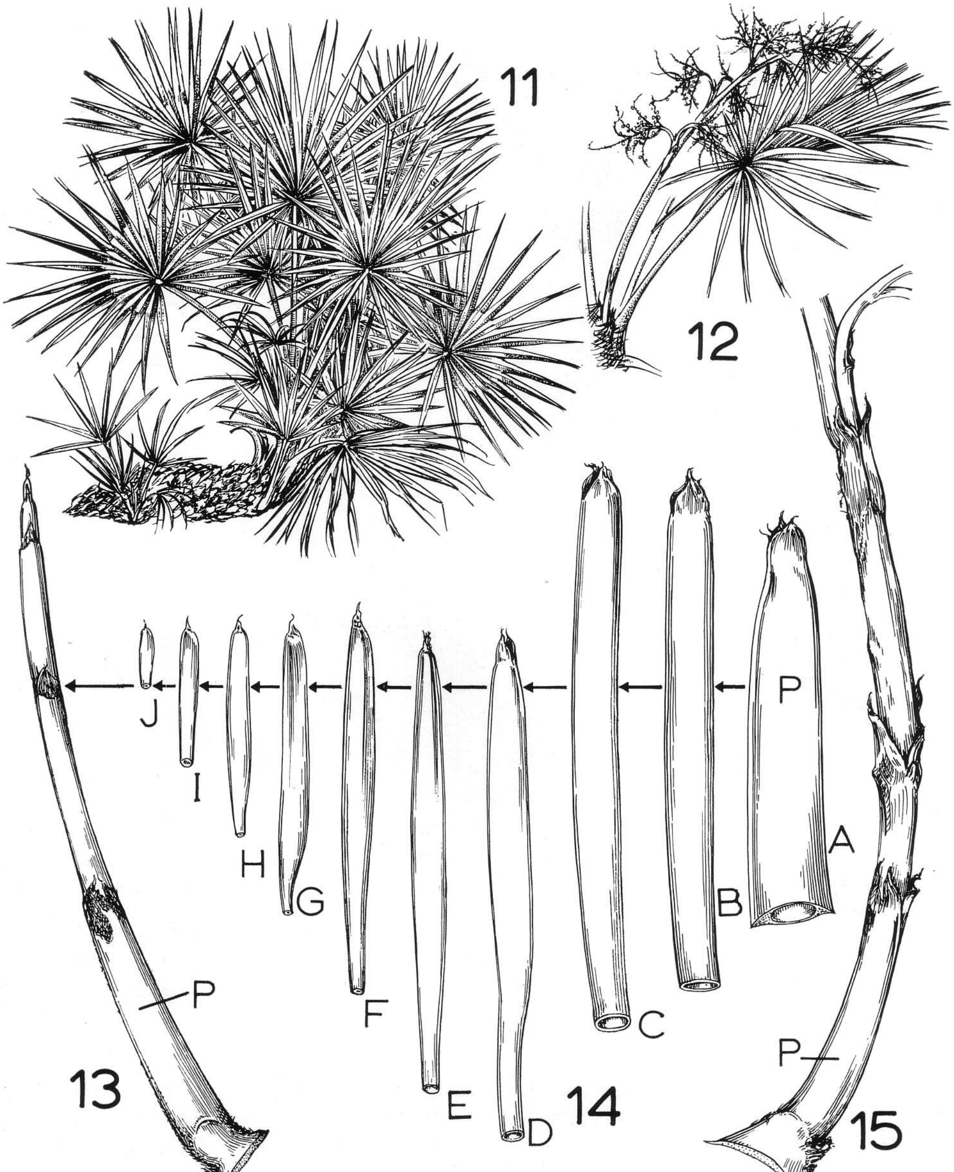
Axillary buds of the seedling always become suckers and never inflorescences.

Microscopic examination of serial sections of seedling apices show that in the axil of every leaf primordium except the three youngest there is a single bud (Figs. 19 and 20). Interpretation of serial sections is made difficult because the crown is not conical but bowl-shaped, with the apical meristem at the base of a shallow depression. Consequently older leaves are attached to the stem in a higher plane than younger leaves. We can indicate the relative positions of leaf primordia by referring to the youngest as P_1 (Figs. 21 and 24) and successively older ones as P_2 . . . etc. The first visible evidence of an axillary bud is in the axil of the fourth youngest primordium (P_4) as a small mound of tissue enclosed by the tubular leaf base (Figs. 23 and 26). The bud in the axil of a

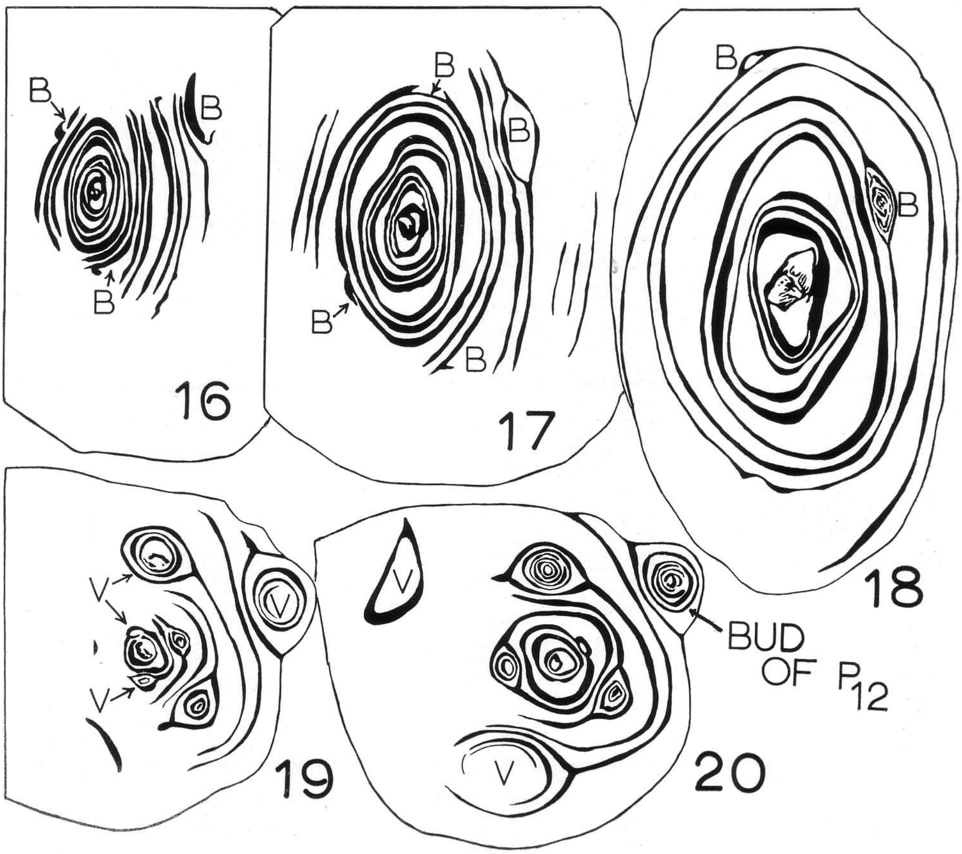


7–10. *Serenoa repens.* 7. Seedling four years old grown under nursery conditions, many buds grown out as suckers and equalling or exceeding main axis (× 7⁄16). 8A–F. Sequence of leaves removed from a single sucker, starting with the prophyll (A) and ending with the first segmented leaf form (F) (× ½). 9. Expanding vegetative bud, in axil of second youngest visible leaf in the plant shown in Fig. 7. (× ½). 10. Unexpanded vegetative bud, in axil of youngest visible leaf in the plant shown in Fig. 7. (× ½).

leaf when it is in position P_5 is well-defined and elliptical in transverse section, but occupying only a narrow section of the stem circumference. The prophyll of the branch first becomes distinguishable on the bud in the axil of the leaf in position P_5 or P_6, i.e. about the second or third youngest bud. Older buds develop an increasing number of leaf primordia (Figs. 19 and 20), e.g.



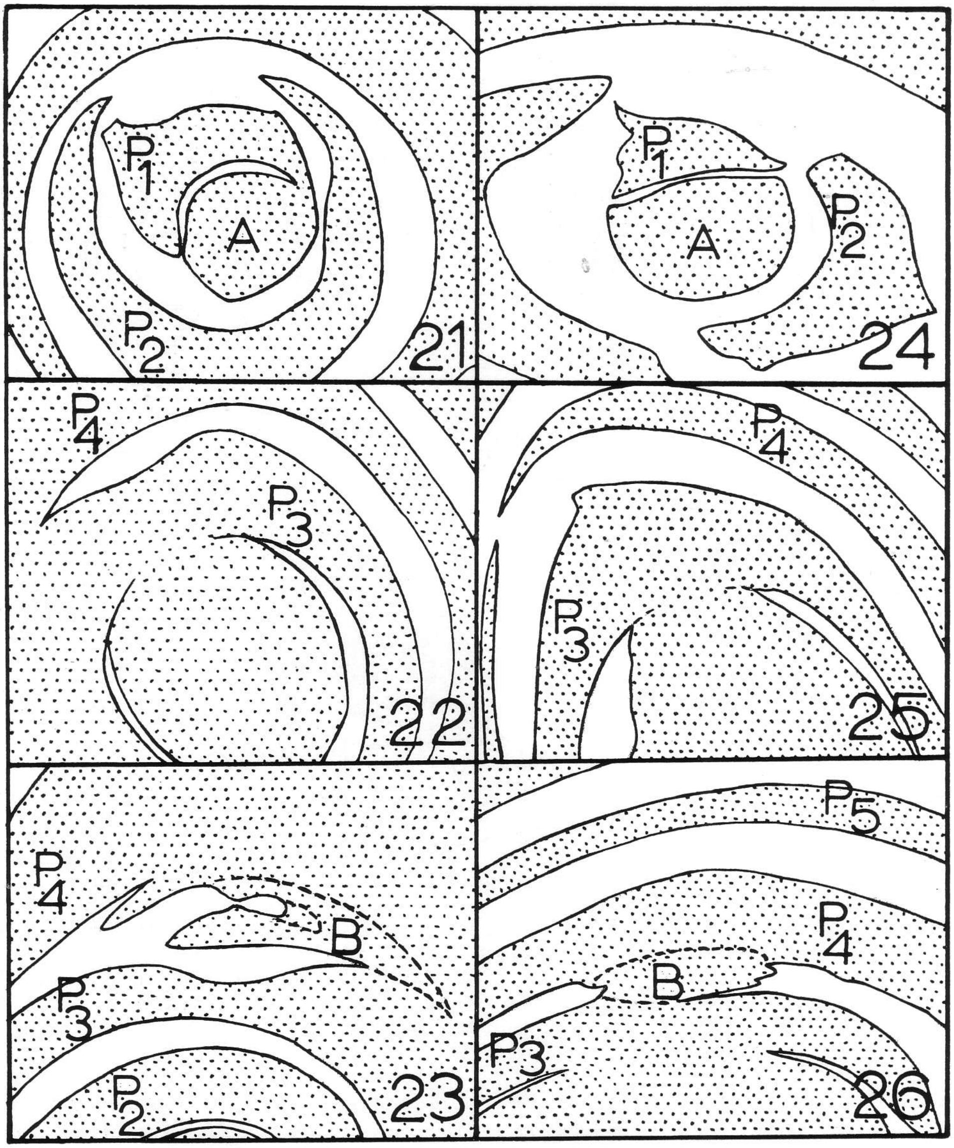
11–15. *Serenoa repens.* 11. Adult plant in field with suckers (× 1/22). 12. Detail of adult plant showing an inflorescence and its subtending leaf (× 1/22). 13. Expanding inflorescence bud (× 1/3). 14. A–J. Sequence of bracts dissected from axis shown in Fig. 13, starting with prophyll (A), first branch of inflorescence is subtended by bract C (× 1/2). 15. Base of a fully expanded inflorescence (× 1/3). P = prophyll in Figs. 13, 14 and 15.



16–20. *Serenoa repens.* Transverse sections of apical buds at different levels. 16–18. Sections from adult stem at (16) level of apex, (17) 200 μm above apex, (18) 520 μm above apex respectively; the outermost leaf = P_{21}. This stem had 8 green leaves, with the youngest visible leaf = P_{23}. 19–20. Sections from sucker on a seedling: (19) at level of apex, (20) 200 μm above apex respectively. The outermost bud is in the axil of P_{12} which itself was the fourth leaf of the sucker; all buds will become suckers (all × 6⅓). B = bud of adult axis (either sucker or inflorescence); V = vegetative bud of seedling.

in Fig. 20, the bud in the axil of leaf P_8 has two leaves while that in the axil of P_{12} has six leaves.

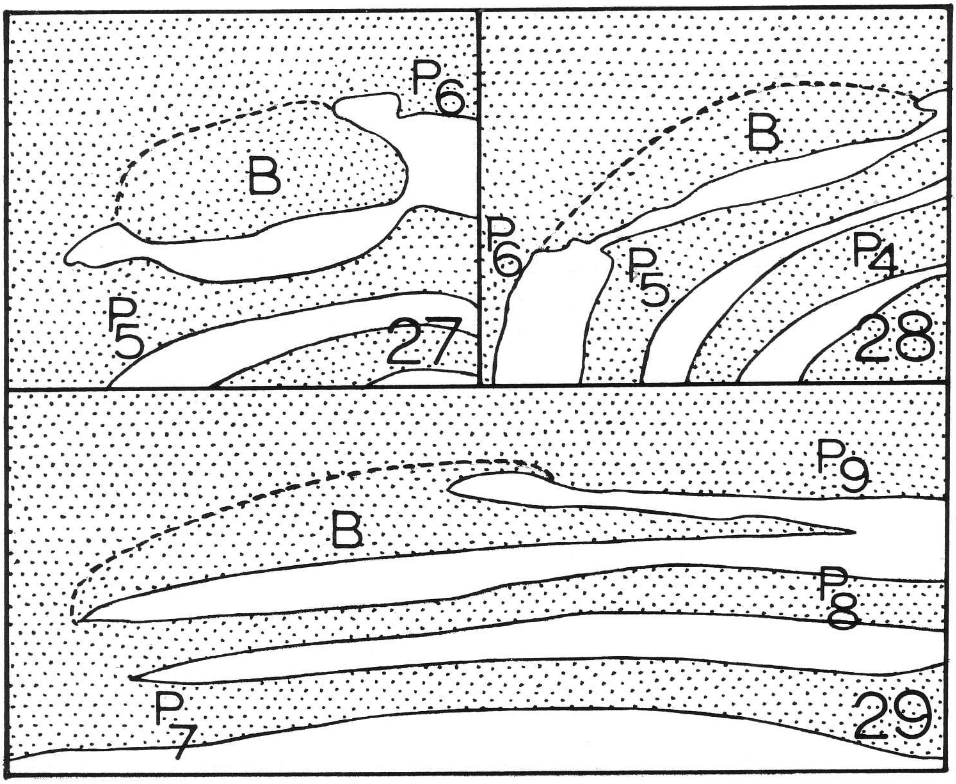
Initiation of axillary buds on adult shoots. The youngest axillary bud of the adult apex is first evident in the axil of P_3 or P_4 (Fig. 26) and all leaves older than this primordium subtend single buds (Figs. 16 and 18). Early stages of bud development are similar to those of the seedling axis. However, at position P_6, i.e. when a bud is the third youngest, it clearly undergoes more encircling growth than a seedling bud (Fig. 27) and so occupies a greater sector of the parent stem (Fig. 28). At position P_9 (when the bud is the sixth youngest) its sheathing base is striking (Fig. 29). The prophyll first appears at position P_{19} to P_{22} (when the bud is the 16th to 19th youngest) although at this stage bud size is no longer proportional to bud age, i.e. younger buds can be larger than older buds. This suggests that some



21–26. *Serenoa repens.* Serial transverse sections of shoot apices (all × 130). 21–23. Seedling apex at three different levels. (21) Apex and axil of P_1 without a bud. (22) Axil of P_3 without a bud. (23) Axil of P_4 subtending youngest bud. 24–26. Adult stem apex at three different levels. (24) Apex and axil of P_1 without a bud. (25) Axil of P_3 without a bud. (26) Axil of P_4 subtending youngest bud. B = bud; A = apex.

buds are subjected to an inhibiting influence.

Since there were very few vegetative (sucker) buds compared with either inflorescence or aborted buds, we have insufficient information to be able to decide when reproductive and vegetative buds diverge in their individual develop-

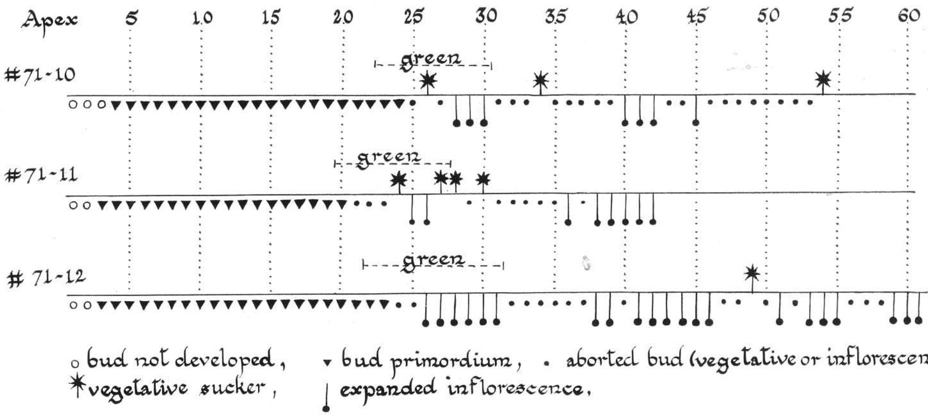


27–29. *Serenoa repens.* Serial transverse sections of shoot apices. 27. Sucker from seedling as in 21–23; axil of P_6, third bud (× 130). 28. Adult stem as in 24–26; axil of P_6, third bud (× 130). 29. Adult stem as in 28; axil of P_9, sixth bud. B = bud.

ment. At later stages a distinction is possible because the vegetative sucker has a wider insertion, i.e. is more elliptical in transverse section, whereas the inflorescence is narrower, i.e. more crescent-shaped in section.

Morphology of the young inflorescence. The inflorescence bud has a narrow sheathing base (Figs. 13 and 15). The first leaf (prophyll) is tubular and its mouth splits as younger parts grow through it (Figs. 13 and 14A). Subsequent bracts are distichously arranged, scalelike and without a developed blade. They also encircle the main axis of the inflorescence (Figs. 13 and the sequence of leaves B–J shown in 14). After fruits mature the inflorescence axis disintegrates gradually, rather than abscising as a unit.

Morphology of vegetative suckers. Suckers are found at intervals on older parts of the stem (Fig. 11). They typically develop after the subtending leaf has rotted. The base of the vegetative bud partially encircles the stem axis and is swollen just above its attachment, unlike the base of the inflorescence (cf. the base of Figs. 4 and 13). In early stages of development of suckers on the adult axis the first few leaves are entire and resemble the first leaves on a seedling (cf. Figs. 2 and 3). Subsequently segmented leaves are developed, transitional to the adult type (e.g. arrow, Fig. 5). The prophyll and the base of the first



30. Diagrammatic representation of distribution of buds along three different shoots of *Serenoa repens.*

leaves of the sucker are split by the development of younger leaves (Figs. 5 and 6). Continued development of the sucker depends on its production of roots which penetrate into the soil through the rotted remains of leaf bases. It seems that normally suckers remain small and partially inhibited, their further enlargement being stimulated either by damage to the main apex or possibly by continued growth of the main apex a sufficient distance away so that apical dominance is no longer effective.

Morphology of aborted buds. A large proportion of buds commonly remain small and inactive, eventually drying up but persisting simply as a brown flap of axillary tissue.

Branch Periodicity

Seasonality of flowering. We have thus shown that every leaf of the adult plant subtends a single axillary bud. These buds have three possible courses of development. They may either abort, or grow out as inflorescences, or least frequently, develop as suckers. The age of first flowering after seedling development has not been determined.

The unfolding of inflorescences on mature plants is striking and evidently seasonal. In South Florida inflorescences first emerge from within the crown of foliage during February and new inflorescences continue to appear from mid-March to mid-April (Hilmon, 1968). Flowering starts about the end of April and continues until June. Fruits develop during the summer and ripen blue during September and October. Fruit productivity is highly variable (Smith, 1972).

The expansion of new leaves is least active during January to March, at the time of rapid inflorescence emergence. Most new leaves expand during the period June to September (84% of the annual production according to Hilmon). Hilmon's data also indicate that an expanded leaf is alive for about 18 to 26 months.

Sequence of bud types. Three adult axes were examined carefully for the distribution and kinds of buds along them. The individual results are presented separately in the diagrams which form Fig. 30. In the dissection of these shoots the oldest recognizeable bud or its remains was noted and successively younger leaf bases were removed as far as the youngest expanded green leaf, with records taken of the type of branch in each leaf axil. Microscopic examination was needed to observe buds subtended by younger leaves and leaf primordia (i.e. those younger than those labelled "green" in Fig. 30). As described earlier the youngest bud is in the axil of leaf P_3 or P_4 (younger leaves represented by open circles in Fig. 30). Vegetative (sucker) buds and inflorescence buds are indistinguishable until about P_{20}. In buds associated with older leaves the distinction between abortive (solid unstalked circles in Fig. 30) and non-abortive buds becomes apparent. Of the non-abortive buds, after about P_{20} vegetative buds (stars in Fig. 30) can be distinguished from inflorescence buds (stalked circles in Fig. 30) because they are shorter and thicker. Both types of buds occupy precisely the same position within a leaf axil.

Summary and Conclusions

These observations show that in *Serenoa repens* both the reproductive branches (inflorescences) and vegetative branches (suckers) arise from buds identical in their position in a leaf axil and indistinguishable in their early development. Later, buds that develop into suckers on the adult axis tend to have a thicker but less crescent-shaped attachment. This feature is especially noticeable in vegetative buds of the seedling in which all axillary buds develop into suckers.

In the adult plant, a high proportion (about 50%) of all axillary buds abort; of the remainder, the great majority (80%) become inflorescences and the minority (20%) become vegetative suckers. Inflorescences grow out within the crown of existing (i.e. green) leaves but suckers grow out much later, after the subtending leaves have died. These vegetative buds are partially inhibited. There is no regular sequence in the production of these two kinds of branch, and this irregular alternation of reproductive and vegetative buds along the adult axis represents a notable exception to the general pattern of branching in palms. Furthermore, inflorescence expansion is seasonal with several inflorescences of different ages flowering within a short period.

On this basis vegetative and reproductive branch buds are homologous, their differences being determined by a relatively late change in growth pattern.

Acknowledgements

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Literature Cited

Craighead, F. C. 1971. The trees of South Florida. Vol. 1. The natural environments and their succession. Univ. of Miami Press, Coral Gables.

Davis, T. A. 1969. Ramifying and twisting stems of palmyra palm (*Borassus flabellifer*). Principes 13: 47–66.

Fisher, J. B. 1973. Unusual branch development in the palm, *Chrysalidocarpus*. Bot. J. Linn. Soc. 66: 83–95.

Hilmon, J. B. 1968. Autecology of saw palmetto, *Serenoa repens* (Bartr.) Small. Ph.D. Dissertation, Duke Univ. [Univ. Microfilms Order #69-22063].

Smith, D. 1972. Fruiting in the saw palmetto. Principes 16: 30–33.

Tomlinson, P. B. 1961. Essays on the morphology of palms. V. The habit of palms. Principes 5: 83–89.