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Long Term Effects of Gibberellin and Cytokinin on Coconut Trees

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ABSTRACT

Mature coconut (*Cocos nucifera* L.) trees were treated with a cytokinin, 6-benzyladenine (BA), or a gibberellin mixture of GA_1 + GA_7. Trunks were injected for up to six months, and each treated tree received a total of 0.2 to 1.2 g of growth substance. Trees were observed for up to 43 months after the start of treatments. BA had no visible effect. GA caused an initial precocious opening of flowers and abnormal elongation of seedless fruits. A series of elongated inflorescences and leaves followed. Inflorescences associated with the longest leaves aborted. The oldest expanding leaves at the start of treatment produced blades with undivided regions to varying degrees. The youngest or primordial leaves and inflorescences present at the start of treatment that grew out long after treatment showed no structural modification from BA or GA.

To date, coconut palms cannot be cloned, although tissue culture techniques have shown promise. The existence of rare individual trees of coconut and of other palms which produce vegetative shoots or bulbils in place of flowers or whole inflorescences (Davis 1967, 1968*b*, Padmanabhan 1976) demonstrate that various palms have the potential to change normally reproductive meristems into vegetative meristems. However, the cause of such unusual development is either unknown or presumed to be physiologically based (Henry and Schneidecker 1983). We attempted to modify the normal development of inflorescences of coconut by prolonged treatment with plant growth substances to produce vegetative structures, either side shoots or plantlets, in place of the usual flower-bearing structures. We chose two growth substances for our experiments. Gibberellins are known to affect growth of reproductive structures and leaves in other palms (Fisher 1980). Cytokinins are known to stimulate growth of lateral buds and modify meristems in general (Horgan 1984). If successful, such treatments would offer a way to vegetatively propagate desirable coconut trees by the possibility of air layering sideshoots (Davis 1968*a*, Davis et al. 1981, Sudasrip et al. 1978).

Our treatments did not induce vegetative proliferations, but the effects of the regulators on shoot development are of theoretical interest. Our findings of unusual leaf structure may also shed light on the mechanisms involved in the production of distorted leaves in palms infected by pathogens or deficient in some minerals. To our knowledge, this is the first report on the effects of prolonged treatment of mature coconut trees with either gibberellin or a cytokinin, although coconut seedlings have been previously treated with growth substances (Remison 1984, Schwabe 1976). We used a widely used synthetic cytokinin, benzyladeneine, and a mixture of two natural gibberellins, GA_4 + GA_7. Both of these growth substances are available commercially.

Materials and Methods

Experiments were carried out at the Division of Forestry, Coconut Seed Orchard located at the USDA-ARS Subtropical

Horticulture Experiment Station, Miami, Florida. Trees of *Cocos nucifera* L. var. Red Malayan Dwarf with 3–4 m of trunk were used. These were the tallest trees scattered randomly throughout the orchard. Two experiments were set up.

The first experiment used 23 trees. Injection treatments began in May 1984. For each injection a 7 cm-deep hole was drilled into the trunk 1–2 m above soil level, and the plastic tube of a Mauget Injector (J. J. Mauget Inc., Burbank, California) was driven into the hole. The injector unit was filled with 10 ml solution and pushed onto the tube. The solution was taken up within a few hours. After two days the tube was removed from the trunk, and the hole was filled with a wooden rod. Holes were drilled elsewhere in the trunk for subsequent injections. A similar injection method has been used with oxytetracycline solutions in treatment of lethal yellowing disease of coconut. Four treatment solutions were used. These were as follows:

1) High GA = 0.21 g $GA_{4/7}$ (a mixture of gibberellins 4 and 7) every 4 wk for 6 mo for a total dosage of 1.26 g per tree. This was the stock solution ABG-3035 (Lot 67-001BR) from Abbott Laboratories, North Chicago, IL 60064. Seven trees were treated.
2) Low GA = 0.021 g $GA_{4/7}$ every 2 wk for 5 mo for a total dosage of 0.21 g per tree. This was a 1:10 dilution of the stock solution with 50% ethanol. Six trees were treated.
3) High BA = 0.2 g 6-benzyladenine (=6-(benzylamino)purine) every 4 wk for 6 mo for a total dosage of 1.2 g per tree. This was the stock solution ABG-3034 (Lot 63-001BRC) from Abbott Laboratories. Five trees were treated.
4) Low BA = 0.02 g 6-benzyladenine every 2 wk for 5 mo for a total dosage of 0.2 g per tree. This was a 1:10 dilution of the stock solution with 50% ethanol. Five trees were treated.

A plastic ribbon marked the fifth visible green leaf (=fourth leaf after the spear) at the start of the experiment. This ribbon was lost in most trees because the tagged leaf abscised or broke off below the tag at times between observations. Although the edges of the injection holes darkened, no internal darkening or rot was seen in the treated trunks when the trees were cut two years after the holes were made. Adjacent trees in the Coconut Seed Orchard were controls and received no treatment.

The second experiment used eight trees, all of which received a high GA treatment consisting of a short but intense dose starting in May 1985. These received injections of 0.21 g $GA_{4/7}$ every week for 3 wk for a total dosage of 0.63 g per tree. Because of tree height, leaves could not be marked at the start of this experiment.

During the two year period of these experiments there was an outbreak of lethal yellowing disease in the coconut orchard. Some controls and seven treated trees in the first experiment died. There was no apparent relationship between susceptible trees and treatment. Location within the orchard, however, was significant. One tree in the second experiment died from bud rot. Selected trees were felled, dissected, and measured in October and November 1986. Young inflorescences and apical buds were fixed in FAA and later observed and measured using a Wild M5 dissecting microscope. Final observations of surviving trees were made in November 1987, 43 months after the start of experiment 1 and 31 months after the start of experiment 2.

A representative control tree was dissected and measured (November 1986) in order to understand the pattern of leaf and inflorescence development under local growing conditions.

Results

Untreated Control.—For all the following descriptions, leaf positions (=nodes)

were numbered sequentially starting with the lowest attached leaf. Thus, the oldest leaf on a tree = 1. The spear leaf (or oldest if more than one spear) = sp. Inflorescences were numbered by their node (=number of the subtending leaf). Because the ends of many inflorescences were removed as part of the coconut breeding program, only the length of the peduncle, the lowest internode between the spathe and lowest rachilla or branch, was measured. Total leaf length and sheath length (=total − blade) were measured. Complete data for one tree is presented in Figure 1.

The control tree (Fig. 1) had 30 expanded leaves, the spear, plus two visible unexpanded leaves, and 26 leaf primordia within the bud. Leaf 31 was the spear leaf (=sp), defined by an essentially folded blade with little or no pinna separation. Leaves 32 and 33 (sp + 1 and 2 younger leaves) were also folded and visible. Leaf 29 (sp + 2 older leaves) appeared to have the youngest fully elongated sheath, and leaf 32 (sp + 1 younger leaf) had the youngest elongated blade. Leaf 30 (sp + 1 older leaf) had unfolded but still soft pinnae, and leaf 29 had a stiff blade flattened in one plane. The youngest fully elongated peduncle was number 21 or 22. Inflorescence 20 was fully exserted from the spathe. Some variation in leaf and peduncle lengths may be related to the season of their expansion, but the preceding year (1985–86) had a mild winter and thus a minimum climatic effect on growth. We have observed a noticeable shortening of leaves and inflorescences which expand after severe winter cold in other years. Plication of the blade occurs at about leaf 51 (sp + 20 younger leaves). Rachillae (=inflorescence branches) are first visible in inflorescence 36 or 37 (sp + 5 or 6 younger leaves). The bracts that subtend the first rachillae and that form after the spathe were first visible in inflorescence 40 (sp + 9 younger leaves). The youngest inflorescence bud was first visible as a meristematic ridge in the axil of leaf ca. 56 or 57 (sp + 25 or 26 younger leaves). The earliest evidence of the ridge was unclear in this specimen because the youngest four leaf primordia were damaged during dissection. However, sectioned apical buds from other coconut trees showed a clearly staining meristem in the axil of the second or third leaf primordium from the apex.

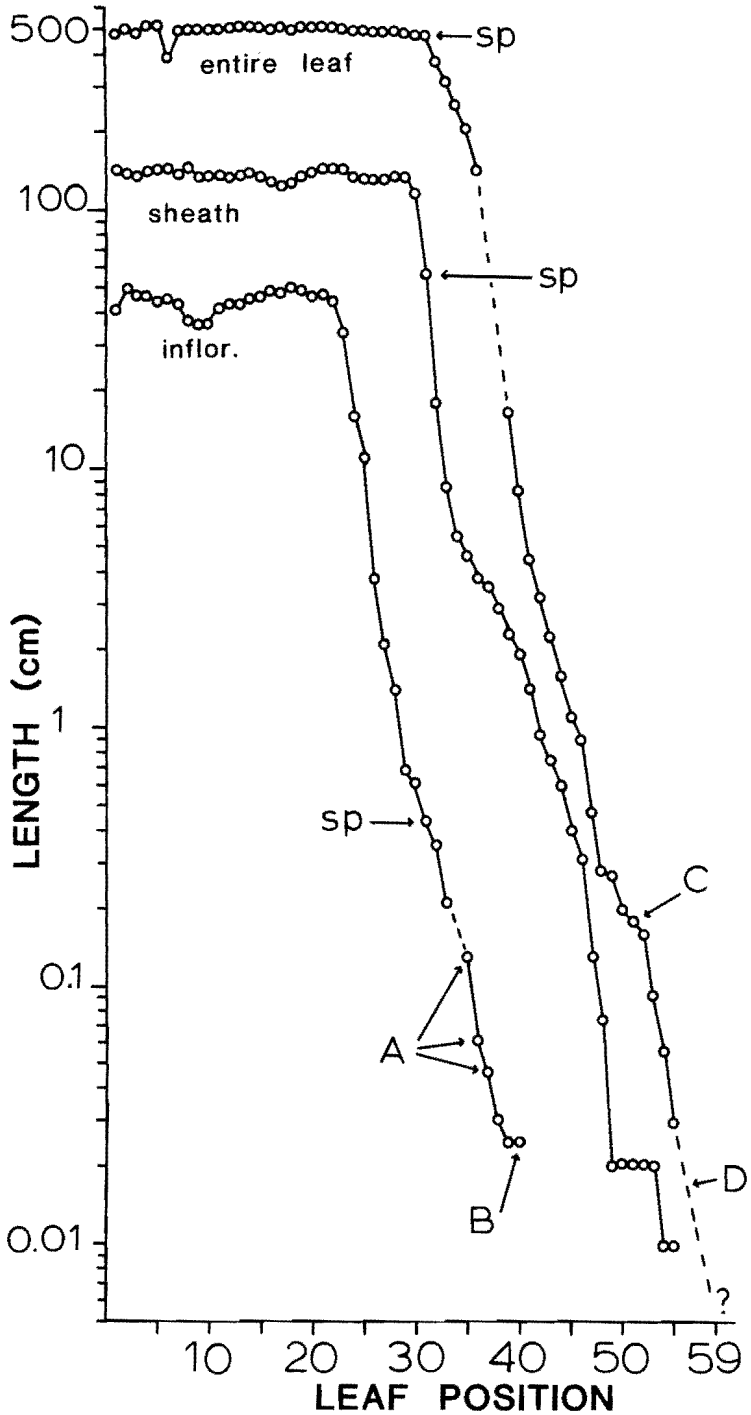
Gibberellin Treatment.—The first visible effect was a noticeable elongation of the upper inflorescences that broke through their spathes during the 6 month period of treatment, beginning 8 wk after the first injection. Both staminate and pistillate flowers prematurely opened before the peduncular bract split. Ovaries were abnormally elongated. These affected ovaries developed into small elongated fruits that lacked seeds (Fig. 2).

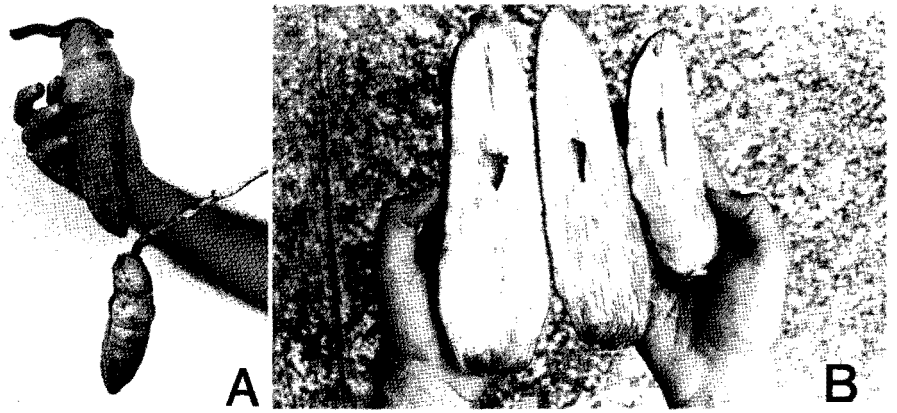
The second result of gibberellin treatment was a failure of pinnae (=leaflets) to separate. Undivided regions were seen first at the blade base of leaves several months after initial treatment (Fig. 3B).

The third result, visible only after all the original leaves of the crown fell more than two years after the start, was an elongation of stem tissues. This was seen in a region where leaf scars and internodes were longer than normal (Fig. 3A).

In all but two trees (Fig. 4A,B), the leaf tagged at the start of the experiment was lost during the following two years. As a consequence, only an approximate position of the leaves at the start of the experiment could be determined for most trees in the first treatment (Fig. 4C).

Figure 4A shows a tree which still had the tag on leaf 9, indicating that leaf 13 was the original spear and that a total of 20 new leaves had expanded in the 29 months since the start of treatment. From this graph (in comparison with the untreated control trees as in Figure 1) the following observations can be made with respect to the original leaf numbering *at the start* of treatment: 1) Inflorescences aborted at positions sp + 7 to 10 older; 2) Older inflorescences (sp + 11 and 12 older) were


500
100
10
1
0.1
0.01
LENGTH (cm)
entire leaf
sheath
inflor.
sp
sp
sp
A
B
C
D
?
10
20
30
40
50
59
LEAF POSITION



2. A. Intact fruits from high gibberellin-treated tree. B. Same fruits cut longitudinally.

elongated; 3) Total leaf lengths in sp + 4 older to sp + 11 younger were greater than control leaves; 4) Sheaths were elongated in sp + 11 older to sp + 1 younger; 5) Undivided regions occurred in the blades of sp to sp + 10 younger and followed a pattern described in the next paragraph; 6) Youngest leaves with undivided regions (sp to sp + 10 younger) and normally shaped new leaves (sp + 11 to 33 older) were shorter than control leaves; and 7) Internodes in the region of the undivided leaves were elongated (not shown in Fig. 4A, but similar to those in Fig. 7C).

Representative leaves with undivided regions (those indicated by solid dots in Figs. 4,7) are shown in Figures 5,6. The illustrated sequence approximates the pattern of these undivided blades which occurred in a single crown. The first elongated leaves had normal blades and elongated sheaths which frequently broke between the blade and the node. This is why so many tags were lost. The last-formed, elongated leaves had more of the lower blade region undivided (Fig. 5A–C) with less pinna separation in older leaves (Fig. 5D–F). Later leaves had both the middle and tip of the blade remaining undivided (Figs. 3B and 6A,B). The undivided regions were always plicated but varied in having the blade continuously attached to the rachis (= midrib) as in Figure 6C or having only the distal ends of the pinnae joined with separated pinna bases attached to the rachis (Fig. 5C,E) similar to normal leaf. In all the last-formed leaves with undivided regions only the blade tip had joined pinnae.

Trees treated with low GA (Fig. 4C) had fewer elongated undivided leaves and, as a consequence, had more normal leaves produced after the treatment effects showed themselves. Rate of leaf production was not obviously different between high and low GA, since total leaf production per tree varied as seen in Figure 4. The number of leaves that had expanded (after the tagged leaf) was 23 in A, 18 in B, and ca. 24 in C. However, because of the loss of

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1. Length (on logarithmic scale) of entire leaf, sheath only, and inflorescence peduncle for successive leaf positions of an untreated, control tree. Leaf positions begin with the lowest attached leaf. sp = position of spear leaf (no. 31). A = earliest indication of rachillae (nos. 36–37). B = sign of first rachilla bracts after the prophyll and peduncular bract (no. 40). C = first sign of leaf plications (no. 51). D = leaf primordia nos. 56–69 damaged during dissection. ? = position of shoot apex (no. 60). Broken connecting lines indicate intervening missing or incomplete data.

3. High gibberellin-treated tree. A. Trunk with leaves cut off to show the region of stem elongation. B. Crown of tree with pinna fusion on new leaves 16 months after start of second experiment.

tags, the number of new leaves produced per tree could not be accurately determined for each treatment.

In both high and low GA trees, the expanded inflorescences had normal peduncle lengths and were not structurally different from those of the controls. Dissected, unexpanded inflorescence buds also appeared to be normal. In three trees treated with low GA, which were still growing 3½ years after the start of treatment, all leaves and inflorescences were normal.

The second experiment was a shorter but more frequent treatment with high GA. Since trees in the second experiment were cut and measured 17 months after the start (compared to 29 months in the first experiment), the tree crowns lost fewer original leaves and showed a more complete sequence of GA effect on leaves and

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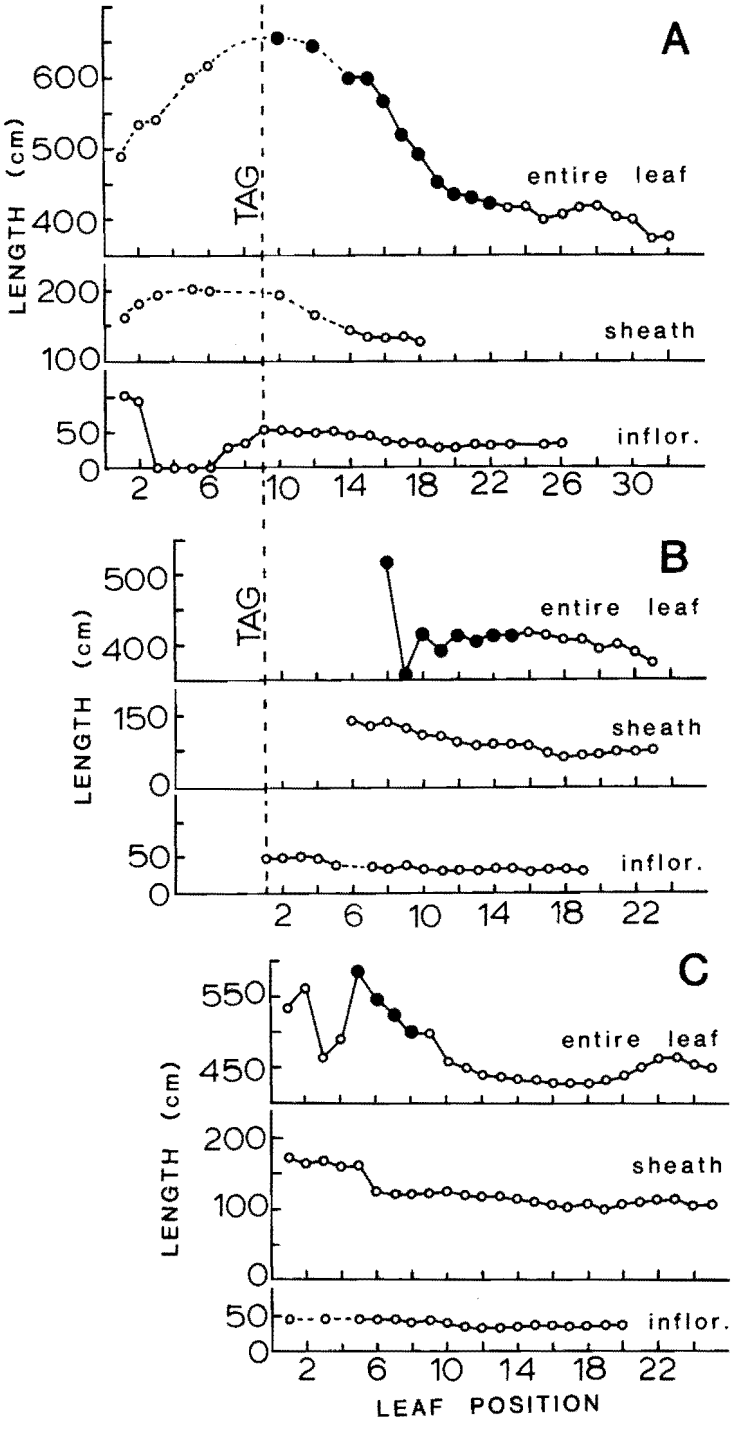
4. Length (on arithmetic scale) of entire leaf, sheath only, and inflorescence peduncle for successive leaf positions on high gibberellin-treated trees of first experiment. Trees A and B were high GA; tree C was low GA. In trees A and B the original tagged leaf was still present = vertical broken line. Thus, in tree A, leaf 13 was the spear at the start of treatment 29 months earlier. In tree B, leaf 5 was the spear but leaves 1–5 were broken off in their sheath regions. Tree C lost its tag but is shown in its estimated relationship to A and B. Open dots = normal leaves; solid dots = blades with pinna fusion. Broken connecting lines indicate intervening missing or incomplete data. Leaf position starts with the oldest and ends with the youngest expanded leaf.


A
B
C
TAG
entire leaf
sheath
inflor.
LENGTH (cm)
LEAF POSITION
600
500
400
200
100
50
0
150
550
450
2
6
10
14
18
22
26
30


A
B
D

6. Leaves of high gibberellin-treated trees showing increasing amount of pinna fusion. A. Upper half of blade with pinna fusion. B. Most pinnae of blade fused to various degrees. C. Close view of fused pinnae in lower third of blade.

inflorescences before and after treatment (Fig. 7). Following the leaf positions from the base of the crown, there was an increase in leaf length due initially to sheath elongation and then both sheath and blade elongation. Undivided blade regions appeared after the longest leaves and continued for 9–10 leaves. These leaves showed the same trend in the position of the undivided regions as in the first experiment (Figs. 5,6): first the base, then the middle, and lastly the tip of blade. The last-formed leaves are equal in length to or shorter than leaves produced before the start of treatment.

Inflorescences axillary to the first elongated leaves (and also after the longest leaves in Fig. 7A) aborted. All those inflorescences expanding later were normal in structure. Dissected, unexpanded inflorescence buds had normal structure. Inflorescences opening shortly after the start of treatment produced abnormal, elongated fruits (as in Fig. 2) which did not mature. Four trees which were still growing 30 months after the start of treatment had normal leaves above the fused leaves and 10–12 normal inflorescences expanded above the last of the fused leaves.

Internodes and leaf insertions were elongated in positions of elongated leaves (Fig. 7C) as in the first experiment.

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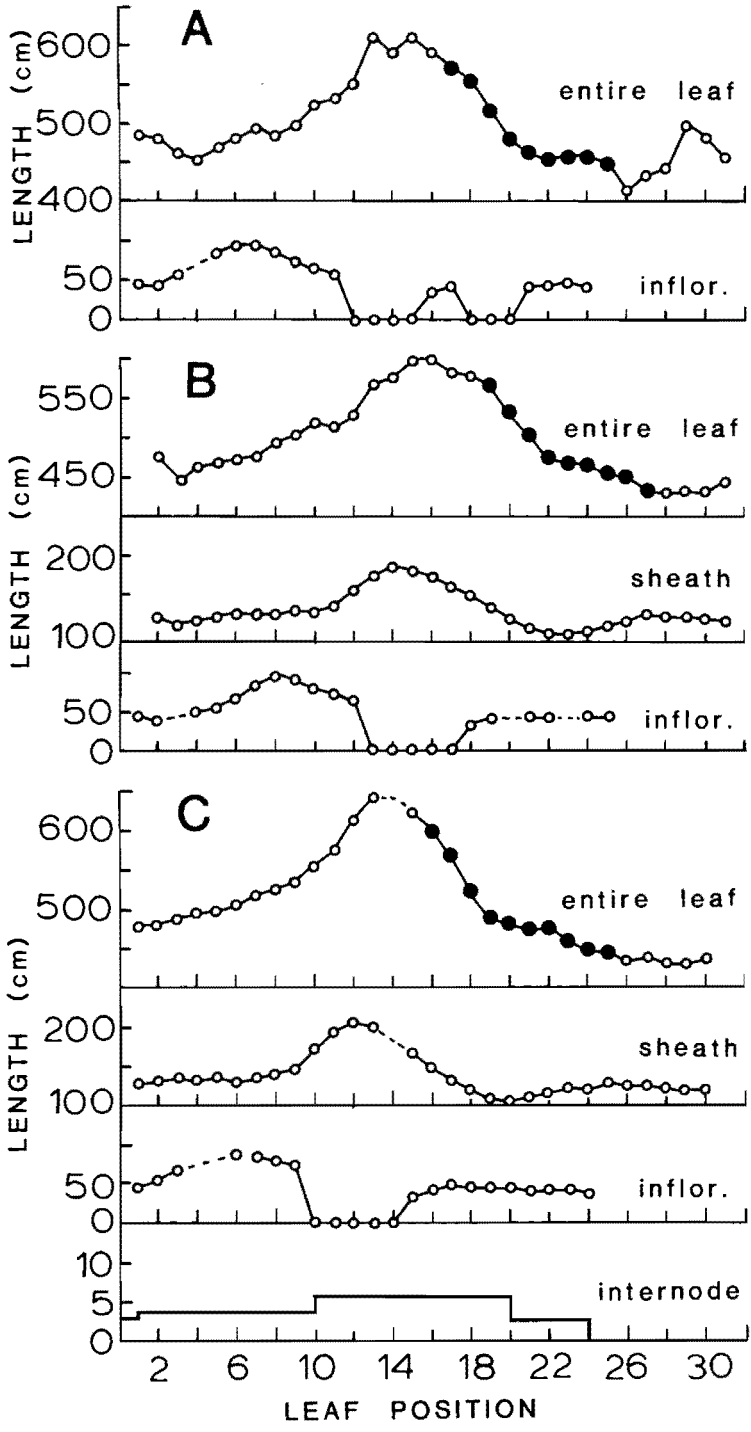
5. Leaves of high gibberellin-treated trees showing increasing amount of pinna fusion. A. Only lower-most pinnae fused and region very elongated. B. Only lower pinnae fused and little elongation. C. More lower pinnae fused. D. Pinnae fused in lower fourth of blade. E. Lower half of blade fused with some free basal pinnae. F. Lower two-thirds and tip of blade fused.


A
B
C
entire leaf
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LENGTH (cm)
600
500
400
50
0
550
450
200
100
10
5
2
6
10
14
18
22
26
30
LEAF POSITION

Cytokinin Treatment.—There was no visible effect of either high or low BA on leaf length, blade shape, and inflorescence length or structure from the beginning of treatment until 42 months later. All were similar to those of the untreated controls. Fruits developed normally, and no obvious inflorescence abortion occurred.

Discussion

The mixture of gibberellins 4 and 7 promoted elongation growth of the trunk, leaves, inflorescence axis, and fruit. In all of these organs only those at the end of their growth were affected. Thus, newly exposed ovaries produced elongated but seedless fruits; inflorescences that were already expanding or about to push out of their enclosing bracts developed elongated peduncles; leaves near the spear stage and those most recently fully elongated became stretched; and internodes associated with the elongated leaves were themselves elongated. Many elongated leaves were up to 12–13 nodes below the spear at the start of treatment (Fig. 4A). This indicates that GA caused fully expanded leaves yet presumably not fully matured leaves, which were located below the tagged leaf (the third or fourth leaf below the spear) to elongate abnormally. Only the sheath was elongated in the oldest leaves. In younger leaves most elongation occurred in the blade, as evidenced in the shift of curves for sheath and entire lengths in Figure 7.

The undivided blade regions in sequential leaves generally follows a pattern starting at the base of the blade of early leaves and ending at the tip of the blade in later leaves. This is opposite to the general pattern of tissue elongation and maturation, which starts at the tip of the blade and moves down to the sheath as the leaf expands (Fig. 1 and Fisher 1978). Thus, GA blocks pinna separation only in those parts of the blade which are still enlarging at the time of treatment. All parts of the blade, including undivided regions, still have plications or foldings. Those leaves just initiating plication (sp-20 at the start of treatment) or increasing the numbers of plications showed no blockage of pinna separation when they finally emerged from the bud 20 plastochrons or about 30 months later. Thus, GA appears to act only on later stages of leaf development after all plications have been formed (Dengler and Dengler 1984, Dengler et al. 1982, Kaplan et al. 1982). Similar undivided blades (called "pinnae fusion") caused by GA was noted in other species of palms with pinnate and palmate leaves (Fisher 1980).

The earliest stage of leaf development, e.g. initiation of plications (Fig. 1C), and of inflorescence development, e.g. rachilla initiation (Fig. 1A) or bud initiation (Fig. 1D), were all unaffected by GA or BA in our experiments. Leaves and inflorescences which were at these early stages at the time of treatment finally grew out some 19–20 plastochrons or 28–30 months later and were quite normal. Both high and low GA treatments had an obvious effect on later developmental events. It is unclear if the ineffectiveness at earlier stages was due to an inability of these stages to alter development or because the level of GA in the young leaf and inflorescence primordia was too low.

Inflorescence abortion occurred at the four to five nodes associated with the longest sheaths and at nodes distal to the long-

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7. Length (on arithmetic scale) of entire leaf, sheath only, and inflorescence peduncle for successive leaf positions on high gibberellin-treated trees of second experiment. In tree C the average lengths of internodes are also presented. Open dots = normal leaves; solid dots = blades with pinna fusion. Broken connecting lines indicate intervening missing or incomplete data. Leaf position starts with the oldest and ends with the youngest expanded leaf. Measurements taken 17 months after start of treatment.

est inflorescences. These positions were the seventh to tenth nodes below the original spear leaf. This is the region of stem elongation that has been documented in other palms (Fisher 1978).

A basic difficulty of interpreting our observations is the long plastochron interval, the time between expansion, and presumably initiation, of successive leaves. In treated trees the average plastochron interval was about 1.5 months during more than two years for treatment 1 and about 1.1 months for treatment 2. Control trees have an average interval of about one month, longer in the winter and a little shorter in the summer. Therefore, periodic treatments over a three-week (experiment 2) or six-month (experiment 1) period encompased either part of one or about four plastochrons, respectively. For interpreting developmental effects, the short burst of experiment 2 is more useful. For inducing major changes in development, i.e., the original goal of modifying inflorescences, the long term treatment 1 is preferable. However, we have no information on how long GA remains at effective concentrations in the tree after the last injection.

Two methods for applying growth substances to small palms have been used: periodic foliar sprays and feeding trough cut leaf tips. Neither GA nor BA had an effect on plant height, number of suckers, or "flower number" (presumably number of inflorescences was meant) in seedlings of *Chamaedorea* after a year of monthly spray treatments (Broschat and Donselman 1986). Spraying leaves of small coconut seedlings with GA_3 or the cytokinin kinetin had no effect of leaf length when measured a year after treatment, although these growth substances affected the dry weight of roots, stem, and leaves at some concentrations (Remison 1984). Leaf tip feeding with different gibberellins on several palm species (*Caryota, Chamaedorea, Chrysalidocarpus, Elaeis, Phoenix,* and *Rhapis*) showed that GA_3 and GA_4 + GA_7 were equally effective, while GA_{13} had little effect on promoting elongation of leaves and fusion of pinnae. Only *Rhapis* was old enough to flower, and GA inhibited flowering, although the basis for this response (bud abortion or lack of bud initiation) was not determined (Fisher 1980). Leaf feeding of seedling coconut with GA_3 resulted in similar pinna fusion (Schwabe 1976).

The application of GA_3 to flowers of *Phoenix* caused seedless fruits to develop (reviewed by Mohammed 1985), similar to the earliest effect of $GA_{4/7}$ in coconut—the production of elongated, seedless fruits on those inflorescences having newly exposed pistillate flowers at the start of treatment.

Partially undivided blades were reported and illustrated in coconut trees attached by leaf-eating beetles (*Plesispa* sp.) by Davis et al. (1985: 104). These abnormal leaves look similar to those in GA-treated trees (Figs. 5,6). Thus, raised gibberrellin levels might be present in the infected trees, although Davis et al. (1986) suggested injury-induced drying of tissues caused leaflet margins to remain attached to each other. Undivided blades have also been seen by T. A. Davis (personal communication) in adult trees after rhinoceros beetle damage and in seedlings after drought.

Small abnormal leaves with only partly divided leaves occur in rare coconut trees in South India (Patel 1938). Such leaves are produced continuously over many years after the seedling stage (T. A. Davis, personal communication). They may be genetically based and related to disturbed endogenous levels of gibberellin. Undivided and distorted leaves also are symptomatic of boron deficiency again suggesting giberellin involvement.

Since high and low BA concentrations had no visible effect, we do not know if the cytokinin was even present in the regions of growth at elevated or effective concentrations. Broschat and Donselman (1986) found no effect of foliar sprays of BA on *Chamaedorea* seedlings.

We conclude that the trunk injection

method can be used to introduce effective doses of GA into coconut palms. Repeated injections can maintain GA levels that modify shoot growth over long periods. Although no significant changes occurred in inflorescences following our six-month treatment with high GA, a longer treatment period might still be successful in modifying the youngest buds.

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