Induction of Foliar Buds by Morphactin Treatment of Flower Bud of Pineapple (*Ananas comosus* MERR.)

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In order to improve the efficiency of the asexual reproduction of pineapple plant (*Ananas comosus* MERR.), morphactins, known as plant regulator-like chemicals, were applied to the flower bud. Prior to the morphactin application, the apices of plant materials were pre-treated with ethrel to enforce the synchronous induction of compound flower buds. The flower buds thus induced were subsequently treated with various concentrations of morphactin solution, at different developmental stages, and different replications of treatment. Following the morphactin treatments, a number of foliar buds was developed from the fruitlets of a syncarp. This foliar bud development is not observed in natural pineapple plant and also had not been reported in the other plants treated with morphactin. These foliar buds were tentatively called "buds-from-fruit" in the present paper. When morphactin at concentrations of 80 and 100ppm was applied to the materials in 6 to 12 days after ethrel pre-treatment, more than 80% of the plants produced "buds-from-fruit", and the average number of "buds-from-fruit" of single plant, i.e. single syncarp, obtained ranged between 8.8 to 15.7. The maximum number of "buds-from-fruit" obtained on a syncarp was 32. There was a certain stage in the development of the flower bud which was found to be critical as regards the effect of morphactin activity. This stage preceded the differentiation of the syncarp into flower primordium. In addition, morphactin treatment also gave rise to an increase in the number of natural foliar buds such as slips and suckers, a retardation in the emergence of the compound flower bud, and a tendency for the apical leaves of the treated plant to roll up which is a typical function of morphactin activity.

Introduction

Morphactins, derivatives of *Hydroxyfluorene-9-carboxylic acid*, are known to exert plant-regulating effects on many higher plants (HARADA 1967, HEIDE 1968, KHAN 1967, KRELLE and LIBBERT 1968, SANFORD and RAVOOF 1971, SANIEWSKI et al. 1968). In a review of the biological activities by SCHNEIDER in 1970, modification of mitotic polarity, disturbance of apical dominance systems and branching stimulation of tillers are shown to be related to reproductive organogenesis. SANFORD and RAVOOF (1971) investigating pineapple plant reported an increase in slip number by morphactin treatment of flower buds at an early stage of differentiation, and attributed the result to excessive induction of slips through activation of the dormant buds on the peduncle.

The cultivated pineapple plant does not produce seeds due to its strong self-incompatibility, and is possible to be only propagated vegetatively. A mature pineapple plant

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develops one crown on a syncarp, a few slips on the neck of syncarp, one to three suckers from a stem base, and a small number of ratoons. Although all of the above natural shoots are utilized in cultivation for multiplication, their restricted number becomes a disadvantage in pineapple improvement work because it suppresses the speedy development of the clones needed for evaluating the individuals selected or introduced and the speedy multiplication of evaluated clones. Moreover, the restriction in pineapple reproductivity becomes a barrier to general cultivation of a large number of planting materials required. These conditions are even more evident in promising cultivars such as Taikoku-kei used as experimental material, because the number of slips, which are primarily utilized for multiplication, shows generally a negative correlation with fruit yield.

Under such circumstances, the authors treated the flower buds of pineapple plant with morphactin. As a result, foliar buds could be induced from fruitlets, contributing to the improvement of the reproduction ability of the pineapple plant.

Materials and Methods

Taikoku-kei, a Thailand clone belonging to the smoothcayenne group, was used as material. It is characterized by scarce development of slips and excellent fruit quality. The plant materials used were planted in April 1975 in the field of Yaeyama Branch of Okinawa Prefectural Agricultural Experiment Station. In June of 1976, the plant materials reached to the stage just before the differentiation into compound flower bud primordia.

They were pre-treated with ethrel solution in order to enforce the synchronous induction of compound flower buds. Ethrel is an ethylene-releasing chemical which is known to exert flower-inducing effect in pineapple plant (COOKE and RANDALL 1968). The chemical used is a product of Nissan Kagaku Kogyo. Twenty ml ethrel solution at a concentration of 500 ppm was poured twice on the apex of each plant on June 9th and 10th.

After the synchronous induction of compound flower buds with ethrel, the plants were treated with morphactin (CF 125, a product of Nissan Kagaku Kogyo). The following two series of treatment were carried out to investigate the effect of different concentrations of morphactin and of treatment at different developmental stage of the plant.

Single treatment: At 4 stages of compound flower bud development, i.e., 6, 9, 12, and 15 days after ethrel pre-treatment, morphactin was applied to the plants at a concentration of 80 and 100 ppm.

Repeated treatment: 50 and 80 ppm of morphactin was applied repeatedly on the 9th and 12th day after ethrel pre-treatment, respectively.

In every morphactin application, 20 ml of the solution was poured on the apex of each plant.

At the time of morphactin application, 10 compound flower buds were collected in each treatment to examine the developmental stages of the flower buds. The collected samples were fixed in 70% ethanol and the number of horizontal rows of floret primordia developed was counted under the microscope at low magnification (X 40), as illustrated in Fig. 1-B.

Fig. 1. Explanation of terms related to pineapple fruit development used in the present paper

- A Pineapple fruit. S : Spiral row of fruitlets.
 H_n : Horizontal ring arrangement of fruitlets against fruit axis. H_1 ; first row of fruitlet arrangement, and H_2 – H_6 ; 2nd to 6th row of fruitlet arrangement.
- B Compound flower bud at early developmental stage. 1 : First floret primordium arrangement, which develops into first row of fruitlet arrangement. 2 : Second floret primordium arrangement. g : Growing point.

Five months after morphactin application, the developmental pattern of vegetative buds, which involved foliar buds developed on the fruitlets and the normal foliar buds such as crowns, slips and suckers, was assessed.

For the reason of developing on the fruit organ, the artificial foliar buds found in the present experiment were tentatively called “buds-from-fruit”.

In each treatment, 10 syncarps which gave higher number of “buds-from-fruit” were selected to examine the site of “buds-from-fruit” development on a syncarp.

Results

Compound flower bud development after ethrel pre-treatment

Compound flower bud development by ethrel pre-treatment is summarized in Table 1. No floret primordia were observed at the onset of ethrel pre-treatment. Thereafter

Table 1. Differentiation of floret bud primordia after ethrel pre-treatment

Observations	Days after ethrel pre-treatment				
	0	6	9	12	15
Number of compound flower buds observed	10	9	10	10	10
Number of rows of floret primordium arrangement per individual syncarp observed					
Average	0.0	0.8	3.7	5.7	8.4
Range	0–0	0–3	1–6	3–8	5–10

Fig. 2. "Bud-from-fruit" development following morphactin treatment on pineapple inflorescence.

Explanation of Figure 2-A~F

- A. Syncarp of control plant.
- B. Syncarp of plant treated with morphactin. Fruitlets in the apical area (*af*) are degenerated. Fruitlets show plump growth but do not develop buds-from-fruit (*nf*). Traces of detached buds-from-fruit (*tf*) on the fruitlets.
- C. Upper view of buds-from-fruit (*bf*) developed on a syncarp of treated plant. A crown (*c*) is shown in the center.
- D. Twenty nine buds-from-fruit, 2 slips and a crown developed on a single syncarp (*sy*) following morphactin treatment.
- E. Crown-like development of bud-from-fruit, abnormally plump fruitlets (*pf*) and early forms of buds-from-fruit (*ef*) on the fruitlets.
- F. Detached bud-from-fruit on aggregate of fruitlets (*ag*) developed from an original fruitlet (*of*).

floret primordia differentiated depending on the length of interval following the pre-treatment, and an average of 8.4 rows of floret primordia arrangement was counted at 15 days after the pre-treatment. The differentiation of row of floret bud primordium arrangement on the compound flower bud progressed from the base to the apex.

"Buds-from-fruit" development by morphactin

Morphactin application gave rise to "buds-from-fruit" which were the abnormal foliar buds emerged from the floret on a syncarp (Fig. 2-C). In a normal plant, the floret usually appears with a complete set of petals in a few days after emergence of the compound flower bud and develops into a fruitlet (Fig. 2-A), while the floret of morphactin-treated plant showed abnormally plump degenerated petals (Fig. 2-E) and developed into an aggregate of a small number of fruitlets resembling to the shape of a syncarp (Fig. 2-F). The green foliar bud primordia, however, appeared first on the plump fruitlets and subsequently completed their development into vegetative buds. "Buds-from-fruit" thus obtained were similar to small-sized crowns (Fig. 2-D).

The syncarps of morphactin-treated plant were smaller in size than the control ones. In particular, the apical part of the syncarp showed reduced growth, and fruitlets at this site were degenerated. The number of fruitlets located on the lower area below the apical site developed "buds-from-fruit", but some of the fruitlets on this area, although being plump and fully grown, did not produce such structures of "buds-from-fruit" (Fig. 2-B).

The effect of different morphactin treatments is summarized in Table 2. When a single treatment with morphactin at concentrations of 80 and 100 ppm was applied in 6 to 12 days after ethrel pre-treatment, more than 80% of plants produced "buds-from-fruit", while only 50% of the plants treated with the same concentrations of morphactin developed "buds-from-fruit" in 15 days after ethrel pre-treatment. The average number of "buds-

Table 2. "Buds-from-fruit" development following morphactin treatment

Concentration of morphactin (ppm)	Interval between morphactin treatment and ethrel pre-treatment (days)	Number of plants treated	Rate of plants produced buds-from-fruit (%)	Number of buds-from-fruit produced on a syncarp	
				Average	Range
Control					
0	—	60	0	0.0	0— 0
Single treatment					
80	6	30	90	10.2	0—19
"	9	29	79	9.5	0—26
"	12	15	93	11.9	0—24
"	15	30	50	8.0	0—27
100	6	30	80	8.8	0—19
"	9	31	90	12.4	0—32
"	12	15	100	15.7	6—31
"	15	30	43	6.5	0—23
Repeated treatment					
50	9, 12	15	80	9.7	0—29
80	9, 12	15	80	7.5	0—18

"buds-from-fruit" on a syncarp of an individual plant varied between 15.7 and 6.5 when 100 ppm of morphactin was applied at 12 days and 15 days after ethrel pre-treatment, respectively. It also varied between 11.9 and 8.0, when 80 ppm of morphactin was treated at 12 and 15 days after ethrel pre-treatment, respectively. Thus, the treatment with morphactin was found to be less effective on the application at later stages of flower bud development. The maximum number of "buds-from-fruit" obtained on a syncarp was 32 when 100 ppm of morphactin was applied at 9 days after ethrel pre-treatment.

When morphactin was repeatedly applied at concentration of 80 and 50 ppm, 80% of the plants produced "buds-from-fruit" as observed in single treatment. However, the average number of "buds-from-fruit" on a syncarp was lower than those obtained in the single treatment.

The site of "buds-from-fruit" development on syncarp

The site on a syncarp where the "buds-from-fruit" induced was precisely examined as follows. In pineapple fruit, fruitlets are oriented in a regular spiral pattern, and they can be counted as first, second, third...on a spiral low, starting from the base (Fig. 1-A), namely the first fruitlets are arranged in a horizontal ring against the fruit axis, and the second ones are arranged next above to the first fruitlet arrangement. According to

Days after ethrel pre-treatment	6	9	12	15
Average fruitlet arrangement locations which induced buds-from-fruit				
100 ppm :	3.6	6.4	8.4	10.2
80 ppm :	4.4	7.2	9.1	10.7

Fig. 3. Relationship between the developmental stage of the fruit at the time of morphactin treatment and location of "bud-from-fruit"-developing site on a syncarp.

this regular pattern, the "buds-from-fruit" were counted in every horizontal arrangement of fruitlets.

As shown in Fig. 3, the area where the fruitlets induced "buds-from-fruit" on a syncarp moved from the base to the apex, according to the delay in morphactin application. This movement was found to be paralleled with the differentiation of frolet bud primordium arrangements, which increased according to the delay of morphactin application time as shown in Table 1. When morphactin was applied twice, in 9 and 12 days after ethrel pre-treatment, the range of dispersion of fruitlet arrangement location on a syncarp where "buds-from-fruit" were produced (Fig. 4) was almost the same as observed when single treatment was applied on those respective days (Fig. 3).

Morphactin effect on compound flower bud emergence

Morphactin treatment affected also the emergence of the compound flower bud (Table 3). In application of 100 ppm of morphactin in 6 days after ethrel pre-treatment, compound flower bud emerged at 37.8 days after ethrel pre-treatment, while control compound flower bud emerged at 32.9 days after the pre-treatment. The difference between the above two emergent times, that is retardation in compound flower bud emergence through morphactin application, was about 5 days. This retardation was decreased according to increase of duration between morphactin application and ethrel pre-treatment. Final application of morphactin in 15 days after ethrel pre-treatment almost eliminated the retardation. The same inclination was also observed in 80 ppm morphactin application. Such findings indicate that the effect of morphactin was stronger in the earlier stages of the development of the compound flower bud.

Morphactin effects on the other pineapple development

In addition, morphactin treatment also gave rise to an increase in the number of natural foliar buds (Table 4). While control plants produced one crown, 0.8 suckers but no slips on average, the treated plants produced an average number of 0.9 to 2.1 suckers, 0 to 2.1 slips with a slight reduction in the number of crowns.

On the other hand, a tendency for the leaves to roll up, one of the characteristics of morphactin activity which had been reported in various plants (SCHNEIDER 1970), was also observed in the pineapple plant. This rolling-up tendency of leaves was noted in some of the treated plants which did not produce the compound flower bud. At the time when morphactin was applied, the apical leaves did not emerged yet, and remained at the stage of leaf primordia. These apical leaves elongated after morphactin treatment without expanding and they tended to roll up. This phenomenon was also found in the

Fig. 4. Dispersion of fruitlet arrangement locations which induced "bud-from-fruit" in duplicated morphactin treatment 9 and 12 days after ethrel pre-treatment.

Table 3. Delay in compound flower bud emergence following morphactin treatment

Interval between morphactin treatment and ethrel pre-treatment (days)	Number of days needed from ethrel pre-treatment time to compound flower bud emergence		
	morphactin 100 ppm	80 ppm	0 ppm
Control			32.9
6	37.8	36.7	
9	35.5	36.1	
12	34.4	34.1	
15	33.3	33.3	

Table 4. Effect of morphactin treatment on development of normal foliar buds

Concentration of morphactin (ppm)	Interval between morphactin treatment and ethrel pre-treatment (days)	Number of plant treated	Number of foliar buds produced on a plant			
			slips	crowns	suckers	total
Control						
0	—	60	0.0	1.0	0.8	1.8
Single treatment						
80	6	30	2.1	0.8	1.3	4.2
"	9	29	0.7	0.9	0.9	2.5
"	12	15	0.1	0.9	1.0	2.0
"	15	30	0.2	0.5	1.8	2.5
100	6	30	1.8	0.9	1.3	4.0
"	9	31	1.3	0.9	0.9	3.1
"	12	15	0.0	1.1	1.2	2.3
"	15	30	0.03	0.3	2.1	2.4
Repeated treatment						
50	9, 12	15	0.9	0.8	1.6	3.3
80	9, 12	15	0.5	0.7	1.5	2.7

"buds-from-fruit" in a few cases. Some of the "buds-from-fruit" at early developmental stages showed an elongation of the thickened and rolled-up leaflets with production of anthocyan, but they did not develop further.

Discussion and conclusion

"Buds-from-fruit" induction

As stated in the introduction of the present paper, the cultivated pineapple plant does not produce seeds and is propagated vegetatively by a limited number of crowns, slips, suckers and ratoons. This becomes an obstacle to the speedy multiplication of clones in the field of breeding work and general cultivation. The author's aim was to remove the obstacle by increasing artificially vegetative buds by using morphactin according to SANFORD's investigation (SANFORD and RAVOOF 1971). The morphactin application was performed in the young flower buds induced synchronously by ethrel pre-treatment, and resulted in the induction of foliar buds from fruitlets, i.e. "buds-from-fruit", as tentatively called. Such findings had not been reported previously in the other plants treated with morphactins.

Developmental analysis of morphactin-activating stage

The fruitlet arrangement location on a syncarp where the "buds-from-fruit" were induced moved from the base to the apex, according to the delay in morphactin application (Fig. 3). This change paralleled the differentiation of floret primordium arrangement locations which increased in number according to the delay in morphactin application time (Table 1). On the basis of these results, it was thought that there was a certain stage in the development of the flower bud which was found to be critical as far as the effect of morphactin was concerned.

The compound flower buds which had reached the stage of an average of 0.8 floret primordia arrangements in 6 days after ethrel pre-treatment (Table 1) developed "buds-from-fruit" on 3.6 fruitlet arrangement locations in average, following the application of a 100 ppm dose of morphactin (Fig. 3). The difference between the above two locations amounted to 2.8. When morphactin was applied at the same concentration at 9, 12, and 15 days after the pre-treatment, the differences in locations were 2.7, 2.7 and 1.8, respectively. In the same way, morphactin application at a concentration of 80 ppm resulted the differences of 3.6, 3.5, 3.4 and 2.3 arrangement locations, respectively. Roughly speaking, the differences between fruitlet arrangement locations developed "buds-from-fruit" by morphactin application and number of floret primordium arrangements differentiated at the time of morphactin application were two to four locations. This means that the initial cells of floret primordia which located potentially two to four arrangement locations apex side to the primordia visible under microscope (X 40) at the time of morphactin application, would be critically stimulated by morphactin. Thereafter, those stimulated cells would developed to fruitlets shooted "buds-from-fruit".

When morphactin was applied twice in 9 and 12 days after ethrel pre-treatment, the range of dispersion of fruitlet arrangement locations where the "buds-from-fruit" were induced (Fig. 4) almost involved that of a single application on these respective days (Fig. 3). Such findings suggest the existence of two different activated sites on the compound flower bud by treatment of morphactin at two different developmental stages, and also support the existence of a critical stage in the development of flower bud following morphactin treatment.

Morphological analysis of "buds-from-fruit" development

"Buds-from-fruit" thus obtained were similar to a small-sized crown (Fig. 2-D). At the base of the buds, a small number of fruitlets developed and formed a small-sized aggregate simillar to the shape of a syncarp (Fig. 2-F). Therefore, it was thought that instead of developing into a fruitlet, the floret developed into a syncarp following morphactin treatment, and consequently a secondary apical foliar bud, i.e. a "bud-from-fruit", was developed.

Although further research is needed to understand the meachanism of effect of morphactin on the development of flower organs, the developmental pattern of "buds-from-fruit" could be related to the controlling system of apical dominance or dormancy and to the proliferating nature of pineapple itself.

Morphactin effects on the other pineapple development

In addition to the above modifications in flower bud development, morphactin treatment also resulted in a delay in compound flower bud emergence and rolling-up tendency of apical leaves. This would tend to indicate that morphactin exerted both a modification effect on the morphological development and a suppression effect on the growth of pineapple inflorescence. The rolling-up tendency of apical leaves could be considered as an antagonistic result of the above effects. Thus, morphactin could also exert various effects on different organs with different patterns in the pineapple plant, as reported by SCHNEIDER (1970) in other plant species such as temporary increase in tillering in *Gramineous sp.*, increase in emerging lateral bud and extension growth of lateral shoots in *Pisum sativum*, delay in emergence of bud of storage organs of *Solanum tuberosum*, inhibition of shoot growth and branching stimulation in *Solanum tuberosum*, delay in bolting in *Lactuca sativa* and *Apium graveolens*, transformation of inflorescence in *Helianthus annuus*, and retardation of flowering, fruiting and ripening in *Oenothera biennis*, *Pisum sativum* and *Phaseolus vulgaris*.

Efficiency of "buds-from-fruit" induction by morphactin

The 32 "buds-from-fruit" obtained on a syncarp by morphactin treatment at a 100 ppm dose at 9 days after ethrel pre-treatment (Table 2), are the maximum number of "buds-from-fruit" in the present experiment. On the other hand, the range of dispersion of horizontal fruitlet arrangement locations on the syncarp where the "buds-from-fruit" are induced following single morphactin treatment at various concentrations varied 5 to 9 as seen in Fig. 3. These numbers are very low when compared with those of the normal syncarp of Taikoku-kei, used in the present experiment, which generally bears about 150 fruitlets on about 18 fruitlet arrangement locations. This low rate resulted partly from the decrease in growth of the syncarp consecutive to the degeneration of the fruitlets at the apical zone of the syncarp following morphactin treatment. It was also caused by an incomplete activation by morphactin to induce "buds-from-fruit" from the developed fruitlets (Fig. 2-B).

From the above analysis, although it is assumed that it would be difficult to activate a full number of fruitlets on control syncarp to induce the "buds-from-fruit", the number of "buds-from-fruit" could be increased by activation of all the fruitlets developed on a morphactin-treated syncarp. This could be achieved by improving the treatment method and conditions. The repeated morphactin treatment at 9 and 12 days after pre-treatment, by which the range of dispersion of activated sites to induce "buds-from-fruit" on a syncarp was extended beyond those in the respective single treatments (Fig. 3, 1), would be one of the possible methods, although the total number of "buds-from-fruit" did not increase in the present experiment.

The increase of normal foliar buds by morphactin

Morphactin treatment also gave rise to an increase in the number of natural foliar buds, such as slips and suckers (Table 4) which was thought to be due to germination of dormant buds on the stem as a result of morphactin's property of breaking dormancy,

as reported by SANFORD *et al.* (1971). The effects on activation of normal dormant vegetative buds by morphactin are especially evident in slip development (Fig. 2-F), because the present material used, Taikoku-kei, is characterized by scarce development of slips. This was also demonstrated in the present experiment in which the control plant did not produce slips (Table 4).

The morphactin treatment described above was shown to actively promote the multiplication of pineapple seedlings, primarily by the induction of "buds-from-fruit" and also by increasing the induction of normal foliar buds such as slips and suckers.

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モルファクチン処理によるパイナップルの花芽からの栄養芽の誘発

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パイナップルは自家不和合性植物であり、増殖は果実頂部に発生する冠芽（1本）、果実首部に発生する裔芽（2~3本）、主茎上に発生する吸芽（1~2本）および塊茎芽（0~2本）を利用しているが、増殖率が低く栽培、育種上問題である。本報ではパイナップルの急速増殖を目的として、花芽のモルファクチン処理による栄養芽誘発効果を検討した。供試品種は裔芽発生が少ないタイ国系優良系統であり、モルファクチンは植物の形態形成に強い調節的作用で知られている。処理はまず材料が花芽分化の直前の状態に達した時期に、エスレル 500ppm 水溶液を個体あたり 20cc ずつ 2 日連続して茎頂部に冠注し、花芽の同調分化を強制したのち、4 時期の花芽発達段階に 80 および 100ppm のモルファクチン水溶液を茎頂部に冠注処理した。その結果、処理

した花芽から発達した果実上に、自然には発生しない栄養芽が多数発生した。この栄養芽は、1個の小果上に2次的に数個の異常小果が形成され、これが集合して小形の果実様体となり、その頂部に発生した。ここではこの栄養芽を便宜上果実芽 (buds-from-fruit) とよぶ。いずれのモルファクチン濃度区においても、エスレル前処理後 6~12 日目の発達段階の花芽に対するモルファクチン処理が高い果実芽誘導効果を示し、処理個体の 80% 以上が果実芽を着生した。1果あたり平均果実芽数は 6.5~15.7 で最高数は 32 であった。モルファクチン処理によって果実芽を誘発した小果の果実上の位置は処理時の花芽分化段階と平行して移動し、モルファクチンが作用する花芽の適発達段階の存在を示唆した。この適発達段階は解剖顕微鏡下で認められる花芽原基分化期以前にあると推定された。モルファクチンは、果実芽誘導効果の他に、裔芽および吸芽の増発効果、花芽の抽出遅延および巻葉化作用も示した。以上、モルファクチンによりパイナップルの果実上に栄養芽を誘発することを明らかにしたが、増殖技術の実用化のためにはなお検討すべき点が残されている。

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