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AGGREGATED CONES IN *PINUS HALEPENSIS*

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ABSTRACT

Aggregated female cones were found in 192 *Pinus halepensis* trees growing in 54 populations in Israel, in habitats of vastly differing ecological conditions. All of these trees also carried normal (1–5 in a whorl) female cones. The number of aggregates per tree varied from one to several dozen. Some of the trees formed aggregates every year, after the first year of aggregate formation, while others formed aggregates only once, or at long intervals. Not all cones in the aggregates reached maturity. The number of cones in an aggregate ranged from six to 62, and they were usually smaller than normal. Many of the trees with aggregates showed other abnormalities, e.g., individual female cone scales, proliferated dwarf shoots, three-needled dwarf shoots, shorter cone stalks, needles on cone stalks, larger terminal cones on the main axis in cones formed during the current year, proliferated female cones, and degradation of the main axis above the aggregate. The clusters probably result from replacement of dwarf shoots by ovulate cones.

Key words: Aggregated cones, morphology, *Pinus halepensis,* proliferated cones.

INTRODUCTION

Aggregated cones (cone clusters) are one of the reproductive abnormalities of the genus *Pinus* (Doak 1935; Black 1961; Dorman 1976). Cone clusters have been reported in several pine species: *P. banksiana* Lamb. (Rudolph, Wheeler, and Dhir 1986), *P. clausa* (Chapman) Vasey (Shaw 1914; Burns and McReynolds 1966; Frankis 1980), *P. contorta* Dougl. (Black 1961; Pollack and Dancik 1979), *P. massoniana* Lamb. (Frankis 1980), *P. mugo* Turra (Frankis 1980), *P. pinaster* Ait. (den Ouden and Boom 1982), *P. ponderosa* Dougl. ex Laws. (Zobel 1952), *P. rigida* Mill. (Frankis 1980), *P. sylvestris* L. (Keslerčanek 1880; Mullins 1881; Kirchner, Loew, and Schröter 1908; Schröck 1957; Carlisle 1958; Teich and Holst 1969; Frankis 1980) and *P. thunbergii* Parl. (Frankis 1980; Lemoine-Sebastian 1982). Cones in a cluster vary from fewer than 10 to more than 100 (Carlisle 1958; Frankis 1980). Some trees forming aggregated cones display other developmental abnormalities: female and male cones formed at the same position, small mature female cones, and dwarf shoots with more needles than usual (Black 1961; Pollack and Dancik 1979; Lemoine-Sebastian 1982).

A number of suggestions have been made concerning the etiology of aggregated cones. According to Black (1961), they may result from environmental conditions. Pollack and Dancik (1979) questioned whether this is a phenotypic response to extreme environmental conditions or a distinct genotype. Others attribute aggregate cones to changes in endogenous hormone levels (Frankis 1980; Lemoine-Sebastian 1982; Rudolph et al. 1986). Only a few studies have been devoted to the genetics of cone clustering (Teich and Holst 1969; Rudolph et al. 1986). Nevertheless, several authors suggest a genetic control of cone clustering (Zobel 1952; Carlisle 1958; Frankis 1980).

Pinus halepensis, which grows naturally in the region around the Mediterranean

Sea, is the most common naturally growing and planted conifer in Israel (Zohary 1966). Most of the populations in Israel were planted by afforestation authorities, or regenerated naturally from seeds of planted populations after fires. The species produces single cones, or whorls of 2–3 female cones, each cone about 7–12 × 3–4 cm in size. The needles are formed in pairs (Zohary 1966). The species usually has many serotinous cones (Shaw 1914).

The incidence and characteristics of aggregated cones in *Pinus halepensis* are reported here.

MATERIALS AND METHODS

About 200 stands of *Pinus halepensis,* planted or naturally regenerated, were surveyed for cone clusters in 1984 and 1988. The size of the populations ranged from several dozen to several thousand trees. In populations with only scores of trees all trees were examined, and in populations with many thousands of trees, only hundreds or a few thousands of trees, but not all the trees of the population were examined. Fifty cone clusters that were formed on top of smaller trees or in the lower 5 m of higher ones, were randomly sampled. The clusters were removed, and the female cones in each cluster were counted and examined morphologically. Normal whorls of cones were also examined. Preliminary observations showed that normal whorls may sometimes consist of more than three cones. A whorl was classified as an aggregate when the whorl consisted of more than six cones, arranged in a tight compact group. When it was not clear whether a whorl of 6–10 cones was compact enough to be classified a cluster, it was regarded as normal, in order to avoid overestimating the ratio of aggregate formation.

Ecological and phytogeographical data were obtained from Zohary (1959), Ashbel (1963), Atlas of Israel (1970), and precipitation maps published by the Israel Meteorological Service.

RESULTS

Aggregated cones occurred on 192 trees in 54 populations (Fig. 1 and Table 1). In 32 populations, aggregates were found on more than one tree, the largest number being 20 trees in the Yeroẖam population. Aggregates were sometimes formed on trees in very small groves of only a few dozen trees, while in some stands of thousands of trees no aggregates were formed.

Aggregated cones formed only on trees that attained a height of at least 3 m, and that also produced normal cones. Normally, only one or a few aggregates occurred on each tree, although some specimens produced scores of cone clusters (Fig. 2). Some trees produced aggregates only during the last year of the study, and thus the cones were immature; other trees formed clusters several years previously and then none; still others produced cone clusters annually for the last several years.

Aggregates included 6–62 mature cones (Fig. 3). In some cases the mature clusters also contained undeveloped cones, but their number or ratio varied.

Cones in mature aggregates were usually smaller than typical mature cones. Cones in large clusters were usually smaller than those in smaller clusters, being only 5–7 cm long and 2–2.5 cm wide—significantly smaller than the normal size of 7–12 × 3–4 cm, and some were even smaller. Because *P. halepensis* has se-

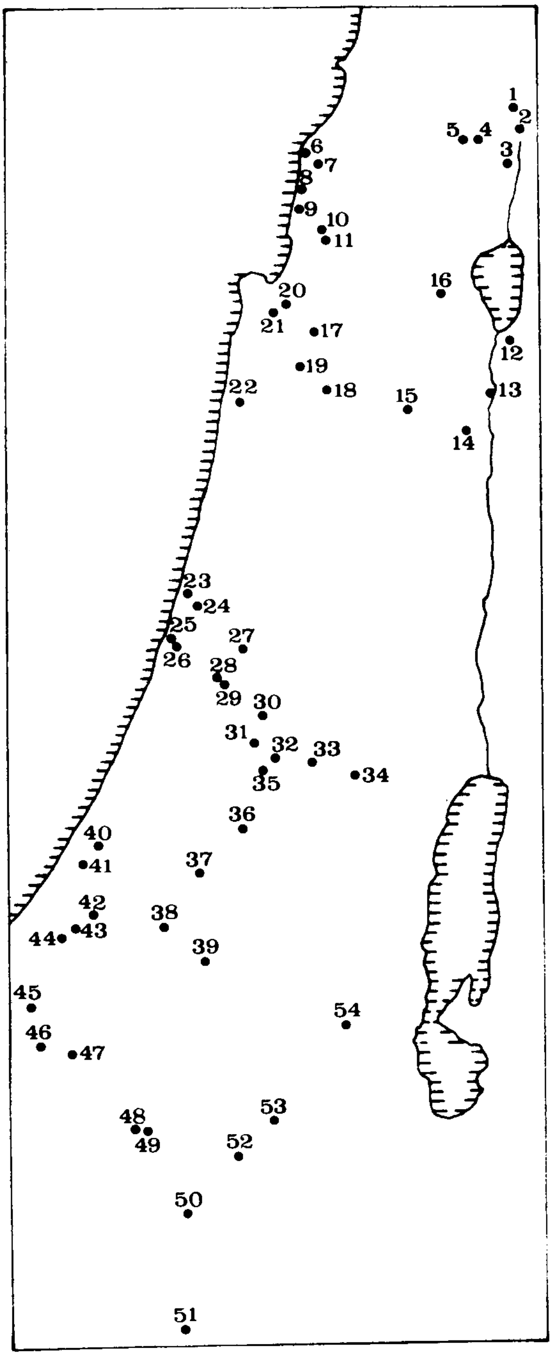

Fig. 1. Populations of *Pinus halepensis* in Israel forming cone clusters.

Table 1. Populations of *Pinus halepensis* in Israel in which aggregated cones were found.

Site name and number in Figure 1.	Phytogeographical territory	Altitude in m	Rainfall in mm and irrigation	No. of trees examined in population	No. of trees with aggregated cones
Amir	M[1]	–60	520	S[2]	2
Gonén	M	–50	500	S	1
Yeshud haMa'ala	M	–60	450	S	1
Yesha Junction	M	400	600	H	5
Malkiyya	M	660	700	H	1
Rosh haNiqra	M	50	640	S	1
Bez̲et	M	30	650	S	1
Nahariyya	M	15	620	S	1
Loẖamé haGeta'ot	M	15	600	S	1
Aẖihud	M	50	620	T	8
Yas'ur	M	20	610	S	2
Sh'ar haGolan	I	–190	390(+ir)	S	8
Newé Ur	I	–220	400(+ir)	S	2
Bet She'an	I	–120	380	S	1
Nurit	M	100	440	H	3
Lavi	M	250	580	T	2
Qiryat Tiv'on	M	100	620	S	1
Megiddo	M	150	600	H	1
Yoqne'am	M	120	700	T	1
Nesher	M	80	680	S	2
Mt. Karmel	M	600	700	T	1
Zikhron Ya'aqov	M	60	580	S	1
Herzliyya	M	50	550	H	8
Ramat haSharon	M	50	550	H	7
Tel Aviv	M	50	550	H	2
Ramat Gan	M	50	550	H	4
Giv'at Koaẖ	M	120	550	T	4
Yagél	M	50	560	S	1
Zetan	M	50	560	S	1
Modi'im	M	180	540	H	4
Canada Park	M	230	540	H	13
Sha'ar haGay	M	300	550	T	1
Bet Neqofa	M	650	660	H	1
Jerusalem	M	750	550	T	9
Eshta'ol	M	350	560	T	1
Giv'at Yesha'yahu	M	340	470	S	1
Lakhish	M	220	400	H	2
Beit Qama	I	250	310	S	1
Lahav	I	450	300	H	2
Bet Shiqma	I	70	460	S	3
Yad Mordekhay	I	40	450	H	5
Mefallesim	I	100	390	S	1
Sa'ad	I	110	370	S	2
Alumim	I	100	360	H	6
Magén	I	100	240	H	5
Gevulot	S	130	180(+ir)	H	9
Z̲e'elim	S	150	180(+ir)	S	1
Retamim	S	300	130(+ir)	H	9
Revivim	S	300	130(+ir)	S	3
Sedé Boqér	S	450	100(+ir)	H	3
Miz̲pe Ramon	I	840	90(+ir)	H	2
Yeroẖam	I	480	120(+ir)	H	20

Table 1. Continued.

Site name and number in Figure 1.	Phytogeo-graphical territory	Altitude in m	Rainfall in mm and irrigation	No. of trees examined in population	No. of trees with aggregated cones
Dimona	I	560	130	H	9
'Arad	I	500	170	H	5

[1] M= Mediterranean district; I = Irano-Turanian district; S = Saharo-Arabian district.

[2] S = scores; H = hundreds; T = thousands.

rotinous cones, some aggregates included both opened and closed cones, although most were closed (Fig. 3).

Several morphological abnormalities occurred in 37 of the 50 cone clusters examined, and several of these carried more than one type of abnormality. The abnormalities included: (1) Proliferated dwarf shoots on the branch below the cluster (Fig. 4). These shoots continued to grow, forming long normal shoots that emerged between the pairs of needles. (2) Needle pairs formed in four clusters on some of the cone stalks, which normally carry no needles. (3) Thirteen branches that carried cone clusters had abnormal 3-needled dwarf shoots intermingled with normal 2-needled ones above, inside, or below the aggregate (Fig. 5). (4) In some aggregates that were formed in the year of study and were still immature, cone stalks were much shorter than normal ones; in some aggregates, both short and normal length stalks were found (Fig. 6). (5) Individual female cone scales were formed in 14 clusters. Three of these clusters had a zone, several centimeters long, of individual female cone scales on the main axis of the cluster (Fig. 7, arrow). Such scales were found only in trees that formed aggregates. Another cluster had a similar zone of individual female cone scales only on one side of the cluster. Individual female cone scales occasionally occurred on branches that carried no cluster. (6) Similar individual cone scales were found at the bases of the branches that emerged from the upper part of 15 aggregates. These scales were compact, with a gradient between a zone of individual female cone scales and a cone which proliferated and formed a branch (Fig. 8). The solitary female cone scales, as well as the scales at the base of the upper branch, appeared at the site of normal dwarf shoots. Proliferated female cones sometimes formed in normal cone whorls in the trees that formed aggregates. (7) In eight immature clusters, at the time of pollination, or 2–3 months later, the apical cone of the cluster was larger than the others (Fig. 9). This cone either terminated the cluster, or proliferated and formed from one to four branches. Six of the terminal cones were very large (4 cm long and 2 cm wide) 2–3 months after pollination when normal cones are usually only 1–2 cm long. The apex of three of these huge terminal cones was flat, instead of the normal pointed shape. On the other hand, three other mature clusters terminated with dwarf terminal cones (Fig. 10). (8) In many instances, the branch that carried the cluster failed to grow soon after the formation of the cluster, and the segment above the cluster was thin, short, and dead.

All clusters formed during the last year, when their morphological position could still be safely determined, were produced in the usual position of normal female cones (Fig. 11). This was true both for clusters in which an apical cone terminated growth, and those in which a branch was formed above the cluster.

The populations forming cone clusters range over a broad geographical area in

Fig. 2–6. Aggregated cones in *Pinus halepensis.*—2. A part of the crown of a tree growing in Ramat Gan that formed numerous cone aggregates. Six cone aggregates are seen (arrows).—3. A large aggregate with 62 cones from Sha'ar haGolan. This tree formed cone aggregates regularly every year from 1982 to 1988 (and an unknown number of years before 1982). Most of the cones in the aggregate were closed. June, 1984.—4. A proliferated dwarf shoot (arrow) on a branch from Canada Park which formed an aggregate at its apex.—5. Dwarf shoots with three needles instead of two on the base of a branch from Jerusalem with an aggregate. All normal needle pairs were removed before photographing.—6. Short and long cone stalks in an aggregate from Aḫihud. July, 1988.

Israel (Fig. 1), from the desert to humid areas, and from elevations of 840 m above sea level in Mizpe Ramon to 220 m below sea level in the Jordan Valley. Annual rainfall ranged from about 100 to 700 mm (Precipitation Map). The phytogeographical districts where these trees were found were Mediterranean—the humid district of Israel, naturally covered with forest and maquis, and the arid Irano-Turanian and Saharo-Arabian districts, naturally covered by annuals and small shrubs (Table 1).

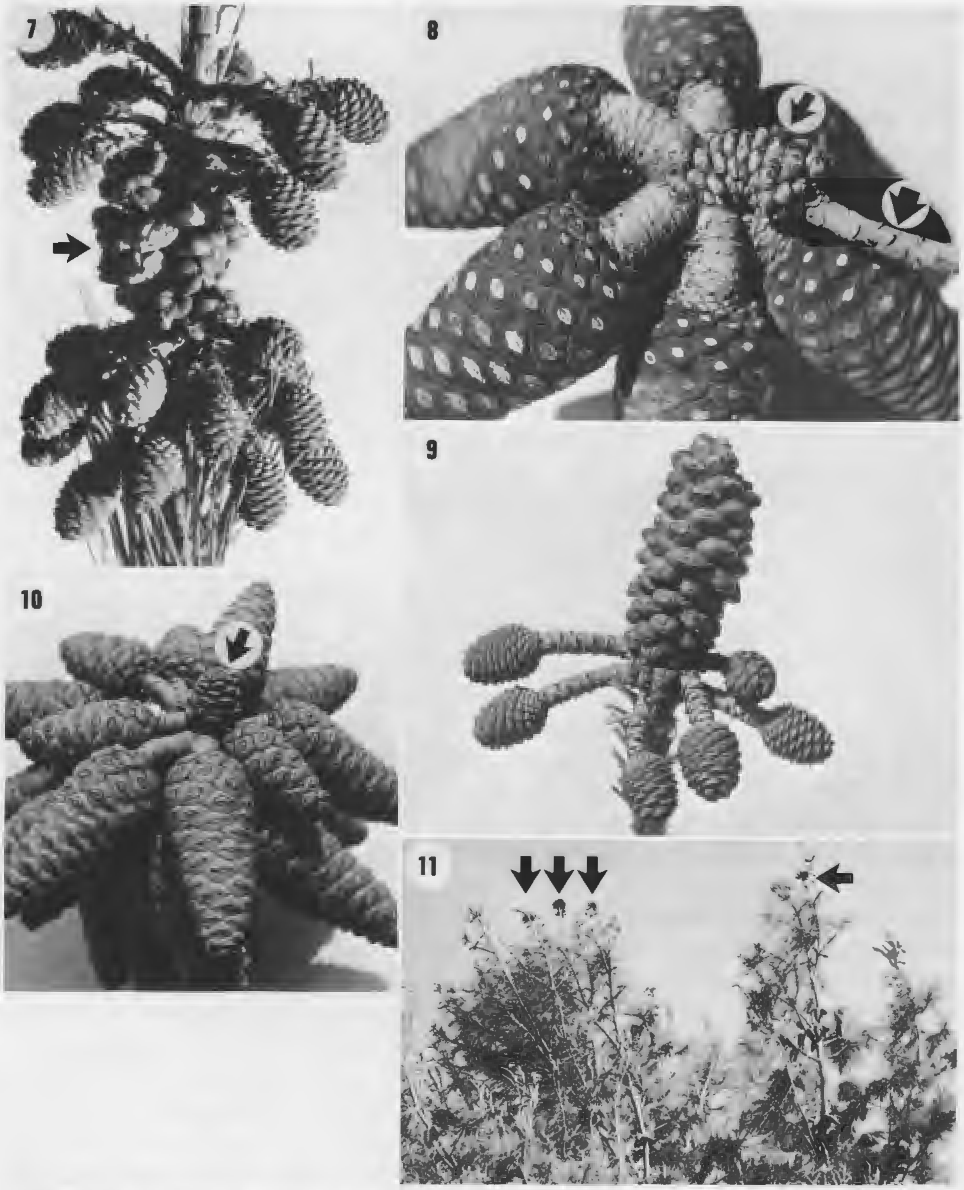

Fig. 7–11. Aggregated cones in *Pinus halepensis*.—7. A zone of 4 cm of individual female cone scales (arrow) in the middle of an aggregate from Jerusalem. One needle pair was formed on a cone stalk in this aggregate. A few 3-needled dwarf shoots were formed on lower parts of the branch. July, 1988.—8. A small cone aggregate from Magén. The upper part of the aggregate displays female cone scales (small arrow), and a thin branch proliferates (larger arrow).—9. A huge terminal cone from Jerusalem with a flat end four months after pollination. July, 1988.—10. A dwarf terminal cone (arrow) in a second year aggregate from Herzliyya. Size differences are prominent. July, 1988.—11. Initiation of four cone aggregates (arrows) in a tree growing in Canada Park. The aggregated were formed in the normal position for female cone initiations. May, 1988.

DISCUSSION

Aggregated cones of *Pinus halepensis* occur in a low ratio: one tree carrying such cones to several hundred trees without such cones. This proportion is lower than in *P. clausa, P. massoniana, P. rigida,* and *P. thunbergii* (Frankis 1980), but higher than in other species in which only a single tree or a few trees are known with such cones (Zobel 1952; Burns and McReynolds 1966; Rudolph et al. 1986). *Pinus halepensis* has serotinous cones (Shaw 1914); thus, aggregated cones accumulated during many years are found. In pine species that do not have serotinous cones, old aggregates may be shed, and the actual ratio may be higher than reported. The number of cones in an aggregate of *P. halepensis* was similar to that reported for other pines, i.e., from less than 10 to several dozen (Zobel 1952; Carlisle 1958; Black 1961; Dorman 1976; Pollack and Dancik 1979; Rudolph et al. 1986). Rare cases have been reported of much larger cone clusters: more than 100 in a cluster in *P. sylvestris* (Mullins 1881; Carlisle 1958), and several hundred in *P. massoniana* (Frankis 1980).

Cone clusters in the upper buds of the crown of *P. halepensis* appear in the normal location of female cones in this species. The original position of cones cannot always be safely determined after several years. Thus, their position was considered only in clusters formed during the current year. The position in *P. halepensis* is the same as in *P. sylvestris* (Teich and Holst 1969; Frankis 1980), and in some instances in *P. ponderosa,* in which clusters of female cones either replace dwarf shoots, or are formed in the position of male cones at branch bases (Zobel 1952). Cone clusters also appear in the position of male cones in *P. contorta* (Black 1961), *P. clausa, P. massoniana, P. mugo, P. rigida,* and *P. thunbergii* (Frankis 1980), and *P. banksiana* (Rudolph et al. 1986).

The great variation in the number of cones in clusters of *P. halepensis*—6–62 cones—is related to two factors: the number of cones initiated in the cluster, and subsequent development. The number of cone initiations probably is controlled by the amount of hormonal signals, which may determine the fate of apices (Owens 1969; Allen and Owens 1972; Ross and Pharis 1987). The development of first-year cones to maturity, or the abortion or premature death of a young cone, may be attributed to several factors. Female cones abort when pollination is insufficient (Sarvas 1962), and this probably holds true for some cones in the aggregates as well. Competition among developing cones for resources may also contribute to the failure of some cones. The role of resource limitation is clearly reflected in the smaller-than-normal size of cones in the clusters of *P. halepensis,* as well as in other pines (Black 1961; Burns and McReynolds 1966; Frankis 1980; Rudolph et al. 1986). Resource limitation may also cause the death of the part of the branch above the cluster, which I saw in many instances. Reproductive effort is known to limit vegetative growth (Rohmeder 1967; Lysova and Khizhnyak 1975; Hoffmann and Alliende 1984), as well as the development of the vascular system (Wilton and Roberts 1936; Wilton 1938). These phenomena probably also reflect hormonal effects.

The abnormalities accompanying the formation of cone aggregates in *P. halepensis* also occur in other pines, whether having or lacking cone clusters (Chamberlain 1935; Doak 1935; Black 1961; Dorman 1976; Lanner 1969; Pollack and Dancik 1979). These abnormalities included many changes in position, and relations between reproductive and vegetative organs. This vast morphological variability raises several questions. Normal development of the shoot in *Pinus* follows a sequence of production of sterile bracts, male cones, dwarf shoots, and later, branch buds or female cones (Doak 1935). Often, one or more of these features are missing from the sequence. The development of normal and abnormal shoots probably depends on the signals for scales, dwarf shoots with needles, male cones, female cones, branches, individual female cone scales, proliferated female cones, and proliferated dwarf shoots. Normal development means not only the development of normal organs, but also their appearance in the right position and spacing. That so many types of leaves and shoots exist does not mean that as many types of developmental signals exist, since a small number of signals may control several developmental patterns (Sachs 1988). Nevertheless, the number of signals and their relationships is still open to study.

Homeosis is the development of an organ in the position of another organ (Sattler 1988). Two types of homeosis are associated with cone clusters in *Pinus halepensis*: (1) Needle pairs formed in some of the cone stalks, which normally carry no needles. (2) Individual female cone scales formed at the site of normal dwarf shoots on the main axis of the cluster, on branches that carried no cluster, and at the bases of the branches that emerged from the upper part of aggregates. Homeosis was also demonstrated in other types of abnormal flowering in conifers, e.g., bisexual cones, where male cones were formed in the position of female cone scales in *Pinus "maritima"* (Goebel 1905) and *Cupressus sempervirens* L. (Lev-Yadun 1992). In addition, Chamberlain (1935) described a female cone of *Pinus* sp. in which spur shoots that carried somewhat stunted needles replaced the cone scales on one side. This is the opposite of the situation in *Pinus halepensis,* where individual female cone scales occurred at the site of normal dwarf shoots on the main axis of the cluster, and on branches that carried no cluster. The identification and characterization of the homeotic genes that are involved in the development of such cases might illuminate the developmental processes and evolution of the female cone.

Three factors may be involved in the formation of aggregated cones: (1) genetic, (2) environmental, and (3) pathological. All these factors can change the regulation of the differentiation of the shoot apex. The suggested effects of environment on aggregate formation (Black 1961; Pollack and Dancik 1979) are probably indirect, with environmental conditions affecting regulatory (probably hormonal) interactions in the shoot apex, or in the signal (hormonal?) sources. The indirect effects of environmental conditions on cone cluster formation probably resemble similar effects on cambial activity following changes in hormonal interactions (Larson 1962, 1963, 1964). In *P. halepensis,* aggregates formed in various and sometimes contrasting environmental conditions; therefore, I suggest that in this species, environmental conditions have no effect on the induction of aggregated cones. The possibility that a pathological agent is involved remains open. I suggest that the seed collection procedures of the afforestation authorities in Israel—collection of seeds from a limited number of trees that bear many cones—may result in the spread of such a mutation all over the country.

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