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SEED GERMINATION PROBLEMS IN THE UMBELLIFERAE

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INTRODUCTION

An important problem often encountered in the culture of carrots, celery, parsley, parsnips and other economically important members of the Umbelliferae has been poor germination of seeds. Over 50 years ago Saunders (91) reported an average of only 43 per cent germination with carrot seed, no germination with celery seed, and Pieters (83) obtained germination of only 58 per cent with carrot and 53 per cent with parsley from "supposed reliable seedsmen". In 1907 Fraser, Gilmore and Clark (42) reported that as many as 80 seeds had to be sown for each carrot harvested. Tests by Brown and Goss (14, 15) and Oswald (81) during the first part of this century revealed that most of the carrot, celery, parsley and parsnip seed offered for sale did not meet the germination standards of that day. Work by later investigators has shown that poor germination is of common occurrence in the Umbelliferae and occurs despite the most diligent efforts taken by seed companies to produce high quality seed. Consequently the germination standards for the cultivated members of the Umbelliferae have been reduced and are considerably lower than for most other plants; only 55 per cent germination for carrots, celeriac and celery, and 60 per cent for parsley and parsnips is required under the Federal Seed Act (108).

Considerable research has been devoted to the factors responsible for the low percentage of germination encountered in the Umbelli-

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ferae. Investigations have revealed the occurrence of three types of seed which show reduced or delayed germination: embryoless seeds, which are non-viable; seeds with rudimentary embryos, which may germinate after a period of storage; and seeds with a dormant embryo, which require particular temperature and light conditions for germination.

In the Umbelliferae the mature fruit is dry and splits into two parts, each of which contains one seed. The seeds, plus the adherent fruit wall, are universally termed "seed" by the trade. Though this terminology is not precise, particularly where the term "seed coat" is used, it is adopted here for simplicity.

EMBRYOLESS SEEDS

The most comprehensive study of one of the reasons for poor germination in the Umbelliferae is that by Flemion and her colleagues at the Boyce Thompson Institute for Plant Research. Examination of seeds of dill revealed that many did not contain an embryo (38). The seed coat and endosperm were apparently normal, but there was an empty cavity where the small embryo normally is embedded. Embryoless seeds were found in each of the 12 lots of fresh dill seed examined, and there was a clear relation between the number of embryoless seeds and the per cent germination in each lot. Four of the lots had many embryoless seeds, ranging from 39 to 62 per cent, and had very poor germination—24 to 54 per cent. The other lots had a relatively small number of embryoless seeds (7 to 14 per cent) and had very good germination (82 to 94 per cent).

Further investigations (32, 37) revealed that poor germination due to embryoless seeds is not limited to dill alone but is common in other members of the Umbelliferae as well. Seeds from representatives of 16 genera within the family were examined, and embryoless seeds were found in all but one. The number of embryoless seeds in the samples of cultivated members ranged from two per cent for coriander to 34 per cent for Florence fennel. Durfee (28), Mann and MacGillivray (73), and Munn and Heit (77) also reported that a large proportion of seeds of Umbelliferous crops are embryoless.

It may be supposed that seeds with good germination might be obtained by separating embryoless from normal seeds during cleaning, but it is impossible to achieve the separation mechanically because embryoless seeds weigh practically the same as normal seeds. The reason for this similarity is that the embryo constitutes but a very small part of the seed. It has been calculated by J. F. Harrington (unpub.) that the embryo makes up only about one per cent of the weight of a carrot seed; 100 soaked carrot seeds weighed 0.2356 gm., and 100 embryos removed from soaked seeds weighed but 0.0024 gm. The only feasible way of obtaining seed free of embryolessness is to contol the factor or factors responsible for the condition.

Flemion and her colleagues therefore began an investigation of the possible causes. Seed grown in Holland, Denmark, North Africa, Egypt, Norway and several areas in the United States were examined (32, 38). Embryoless seeds were detected in samples from each region, so the absence of embryos could not be attributed to a factor specific to certain areas of seed production. The year in which the seed was produced was also found to have no significant effect on embryolessness (37). A study of different varieties of carrot, celery and parsnip did not reveal any significant differences due to variety (37). Spacing of the plants does not affect the number of embryoless seeds (32) or the percentage germination (48) of the seed produced. No correlation was detected between seed size and the occurrence of embryoless seeds (32), and seed size has, in general, little effect on germination, although the smallest may show reduced germination (73, 100). The seed-yield of dill plants was not correlated with the amount of embryolessness (32).

In order to study possible genetic influence, two lots of dill seed were planted, one lot having few embryoless seeds, the other many (32). No significant difference was observed between seed produced by plants from the lot with eight per cent embryoless seeds and that produced by the plants from the lot with 38 per cent. This experiment, however, did not rule out the possibility that heredity influenced the development of embryoless seeds, because the seeds sown were a mixture of open-pollinated seed from many different plants. In corn it has been found that embryoless seeds may be caused by several recessive genes (25, 72, 90, 111), but there is no reason to believe that embryoless seeds in the Umbelliferae may be due to deleterious genes. Later tests, in which individual plants of dill and other members of the family were enclosed in separate cages and self-pollinated by flies, resulted in the production of very few embryoless seeds, indicating that the parents were not heterozygous for genes such as those in corn (31, 35, 36).

Other possible factors were also studied (32), including climate, soil type and position of the seed on the plant. The climate was found to have no significant effect on the development of embryoless seeds, agreeing with Borthwick's finding that the temperature during the time of pollination does not affect germination (11). No correlation was discovered between embryolessness and seed production on soil types ranging from light sandy loam to heavy adobe. Various fertilizers were added to the soil and found to have no apparent effect on the amount of embryolessness (32) or the germination of the seed produced (11). Flemion did note that there was a tendency for seed produced later in the season to have a higher percentage of embryoless seeds than that of the earlier seed. For Beneš (10) and Borthwick (11, 13), seed produced on the first order of carrot umbels, which is the termination of the main axis and the earliest umbel on the plant to flower, germinated better than that of later order umbels, but Flemion (32) did not detect any correlation between the amount of embryolessness and the position of the seed on the plant.

None of the factors studied by Flemion et al. in their early reports (32, 37, 38) was found to be the cause of embryolessness, but several interesting observations were made. It was noted that embryolessness is a universal problem; it seems to occur among all members of the Umbelliferae and in all areas of the world. It was also noted that approximately 90 per cent of the time both seeds of the two-seeded schizocarp were similar in that both contained embryos or both were embryoless. In only ten per cent of the 66 pairs of seeds studied was one seed with and the other without an embryo. Another interesting finding was that embryolessness seemed to be correlated with the season of the year. One lot of dill seed produced eight per cent embryoless seeds in the early planting and 20 per cent in the later planting; another lot gave nine per cent embryoless in the early and 17 per cent in the later planting (32). The most significant observation was made in an experiment with greenhouse-grown dill plants which were caged so that flies might be enclosed to ensure pollination. These plants did not produce any embryoless seeds (32).

Flemion and her co-workers were finally successful in their quest for the cause of embryoless seeds in the Umbelliferae. They enclosed various insects, known to visit umbelliferous plants, inside insect-tight cages with dill plants (31, 35, 36). Flies were kept continuously in the cages for pollination. There was an average of less than one per cent embryoless seeds in the controls (caged, no insects other than flies) and in the cages with ants, fireflies, Japanese beetles, lace wings, ladybird beetles and syrphid flies. When the tarnished plant bug (*Lygus oblineatus* Say) was introduced, however, there was a range of 33 to 85 per cent embryoless seeds. Both nymphs and adults were found to destroy the embryo at almost any stage of development. Even when only one adult *Lygus* bug was enclosed for but 48 hours, as much as 18 per cent embryoless seed resulted.

These findings provide an explanation for the observations made in previous papers. The *Lygus* bug is widely distributed throughout the world, so it is not surprising that embryoless seeds were noted in samples from all sources. The increase in embryolessness as the season advances is in accordance with the natural buildup of the *Lygus* bug population during summer. The fact that both seeds of a pair are usually similar in both being either normal or embryoles can be explained by the tendency of the *Lygus* bugs to feed on both seeds of a given pair during one feeding period. The dill plants that were grown in insect-free cages did not produce any embryoless seeds because *Lygus* bugs were excluded.

Lygus bugs were enclosed with other members of the Umbelliferae, including carrot (both wild and cultivated), celery, coriander, fennel, goutweed, parsley and parsnip (35). The results of these experiments are in agreement with the findings with dill plants. Embryoless seeds were always produced when the tarnished plant bug was enclosed, ranging from 16 per cent (parsnip) to 100 per cent (parsley), while the controls—caged without *Lygus* bugs—had few or no embryoless seeds. Studies were also made with the striped cucumber beetle, the smartweed flea beetle and the stinkbug; these insects may cause some injury to dill and fennel seed but do not cause embryolessness.

By introducing *Lygus* bugs into caged dill plants in different stages of maturity it was found that the insects may cause reduced seed yield as well as embryolessness. Embryoless seeds were produced when the *Lygus* bugs were introduced during the early stages of seed development, but when they were introduced during the flowering stage, there was also a large amount of flower destruction and consequently a reduction in seed yield (35). The study made by Handford (45) is evidence of the seriousness of this reduction in seed yield. A yield of 241 pounds of seed per acre was obtained in a carrot field when the *Lygus* bug was controlled by three applications of DDT dust. When the insect was not controlled, the yield was only 101 pounds per acre.

The *Lygus* bug has been found to injure the vegetative parts of umbelliferous plants as well as to cause embryoless seeds and reduced seed yields. Flemion and MacNear (33) enclosed *Lygus* bugs with dill and fennel plants prior to the flowering stage. The terminal growing points and tips of leaves were injured in this experiment, thereby bringing about reduction of growth. Injury to leaves of celery by *Lygus* feeding has been reported by Davis (24), Hill (53), Richardson (85) and Troop (106).

Embryoless seeds have been found to occur in plants of other families, including barley (46, 69), soft chess (2), corn (25, 72, 90, 111), *Datura* (89), rice (67), rye (69) and wheat (69, 70). In none of these plants, however, have the embryoless seeds been shown to be caused by *Lygus* bugs. Usually less than one per cent of the seeds of plants other than members of the Umbelliferae will be embryoless.

Although the *Lygus* bug has not been regarded as causing embryoless seeds except in the Umbelliferae, the insect is known to damage the seed crop of other plants. Injury is done to the flowers and young fruit of many crops, including alfalfa (17, 18, 94, 95), beans (8, 9, 92), cotton (74, 76, 103), guayule (3, 87) and sugar beets (27, 54, 55, 56, 57, 58).

Investigations have been conducted on the methods by which the *Lygus* bug produces such detrimental effects. Possible causes which have been studied are: *a*) transfer of a virus or of bacteria by the insect; *b*) physical injury by insertion of the insect's stylets into the plant tissue and removal of plant sap; *c*) chemical injury by a toxic substance in the saliva of the *Lygus* bug.

It appears unlikely that the insect serves as the vector of a pathogen, because the injury is limited to the site of feeding and is nontransmissible (65). Awati (6), Taylor (103) and others have noted that the *Lygus* bug withdraws and reinserts its stylets into the same area of the host tissue repeatedly while feeding. This has been cited as evidence favoring the theory of mechanical injury (103), because repeated reinsertions in one area would lead to maceration of the tissue at that spot. Nevertheless it is not likely that the primary cause of the deleterious effects is merely mechanical injury to the tissue and removal of the plant sap during feeding. Other sucking insects seem to do similar physical damage but do not cause embryolessness or destruction of flowers and young fruit. Smith (93) attempted to cause mechanical injury to plant tissue artificially in a manner similar to that of the *Lygus* bug but was unable to duplicate the damage caused by the insect. On speculative grounds, Forbes (40) was one of the first workers to favor mechanical injury as the explanation. He criticized the theory that the injury was caused by injection of a toxic substance on the grounds that it could not be of selective advantage: " It is contrary to the order of nature that a habit of this sort should be acquired, unless it were beneficial, directly or indirectly, to the species acquiring it. It is not only impossible to show that the plant bug would be benefited by any such supposed poisoning of its own food, but it is at once evident that it would be seriously injured thereby, since this would amount to the prompt destruction of the very parts of the plant from which it was drawing its own food supply ".

However, the most likely explanation of the damage caused by *Lygus* bugs is the toxic reaction of a substance in the saliva of the insect when injected into the plant tissue during feeding. This theory was alluded to by Harris in 1862 (49) and Riley in 1870 (86) who spoke of the " poisonous effect " of the insect on the host plant. It has long been believed that the *Lygus* bug injects saliva into the plant while feeding (6), and confirmatory evidence has recently been secured by Flemion, Weed and Miller (39) in a very interesting experiment. These workers obtained highly radioactive *Lygus* bugs by allowing the insects to feed on sucrose solutions to which radioactive phosphorus had been added. When the insects were allowed to feed on pods of snap bean, they imparted radioactivity to the tissue at the site of feeding, thus indicating that the insect does inject oral secretions into the host tissue while feeding. By measuring the amount of radioactivity imparted, it has even been possible to estimate the quantity of oral secretion deposited (34).

Smith (93) and others have reported that there is an exudation from the wound and swelling on the stem at the site of feeding, which would seem to indicate toxicity of a substance injected with the saliva. More positive evidence on this point was obtained when Smith found that the excised salivary glands of *Lygus pabulinus* causes a reaction in plant tissue similar to that resulting from the feeding of the insect. Therefore the available evidence supports the theory that the salivary secretions of the *Lygus* bug contain a substance toxic to plant tissue. This property is not unique to the genus *Lygus*, but is believed to occur in other members of the Miridae as well (19, 20).

It is interesting that the insects' feeding may result in destruction of the embryo in the Umbelliferae without apparent harm to the other parts of the seed. The explanation probably lies in the fact that the *Lygus* bug feeds only on succulent tender tissue. When the insect attacks the flower or very young fruit it may not have a decided preference for one certain tissue. At this stage most parts of the flower or fruit are tender and succulent, so the insect may feed on any part and cause blossom drop and reduced seed yield. In later stages of seed development, however, the embryo is still succulent, while the endosperm and seed coat have become firm (36); consequently the insect probably feeds only on the embryo.

RUDIMENTARY EMBRYOS

Another reason for poor germination in the Umbelliferae was discovered by Borthwick (11, 13). Carrot seeds were split longitudinally and examined with a binocular microscope. Many of them were found to contain a normal seed coat and endosperm, but the embryo was abnormally small in size, " sometimes so small as to be scarcely visible ". In all probability some of these were actually embryoless, but others did contain a rudimentary embryo. Flemion et al. (37, 38) have confirmed that rudimentary embryos occur in carrot and in other members of the Umbelliferae as well.

Borthwick (13) indicated that germination of carrot seed is retarded by the occurrence of rudimentary embryos. He suggested that at least some of the seeds with rudimentary embryos are viable but are dormant. A sample of carrot seed having some rudimentary embryos had a germination of 60 per cent two weeks after the beginning of the test. According to the official recommendations, carrot germination tests used to be terminated after 14 days (107), but this sample was kept in the germinator for five months; at the end of the five-month period germination had increased to 78 per cent. Other workers have also reported delayed germination of carrot seed (1, 21, 28, 29, 59, 82, 112). Recently the official recommendation for duration of carrot germination tests has been increased to 28 days (5, 108).

There is reason to believe that delayed germination of carrot seed is a serious problem to the commercial grower. Mann and MacGillivray (73) found that non-uniform germination of carrot seed contributes to the variation in root size. This is of especial importance in California because all carrots in a field are usually dug at the same time. Carrots which are delayed in their germination encounter more competition in the field than the early-germinating carrots, so that many of the roots are too small to market.

Borthwick (13) suggested that the delayed germination in carrot seed is caused by rudimentary embryos, but he did not report conclusive evidence supporting this belief. He also reported that seed from the primary umbel gave better germination than seed from later flowering umbels, but he did not state whether there were differences in per cent of rudimentary embryos in the seed from the different umbels. Flemion and Hendrickson (32) detected no correlation between the occurrence of embryolessness and of rudimentary embryos in a given lot of seeds, but it was not absolutely proven that *Lygus* bugs are not the cause of rudimentary embryos.

Dormancy due to immature embryos can often be overcome by after-ripening (84); that is, seeds stored for a period before planting germinate better than do freshly harvested seeds. When Rose (88) classified the reasons for delayed germination of seeds in general into five categories—hard-coatedness, frosted seeds, need of after-ripening, exclusion of oxygen by the seed coat, and cause of delay not determined—he included seeds of celery, dill, parsley and parsnip in the last category. Odland (80) also obtained negative results, since one-week-old carrot seed showed 94 per cent germination, while seed 13 to 20 weeks old germinated 93 per cent. Franck and Wieringa (41) found that after-ripening did increase the rate and amount of germination of dill seed but appeared to have a detrimental effect on germination of carrot and parsley seed. Old celery seed was found to germinate better than new seed by Hopkins (60). Gardner (43) also obtained positive results with after-ripening; one-year-old carrot seed germinated much better than fresh seed. The cause of delayed germination in the Umbelliferae is still in doubt and is worthy of further investigation.

Dormancy due to immature embryos can sometimes be overcome by exposing the seed to moderately high temperatures (23), but germination of carrot seed was not increased by soaking the seed in hot water (73). Other attempts to increase germination include scarification (43, 73), presoaking (59), increasing the oxygen supply (43), and treatment with thiourea (73) and other chemicals, but none of these improved the germination. It is interesting that exposure of carrot seeds to very high radio frequency irradiations seems to increase their germination (4, 44, 63), but there is no evidence of this being related to the problem of rudimentary embryos.

DORMANCY IN CELERY

An important reason for the poor germination sometimes encountered in celery seed lies in its dormancy when temperature and light are not suitable. The first important report on this problem was by Hicks and Key (51) in 1897. They found that celery seed planted in the dark, with the temperature kept constantly at 20° C., remained dormant but would germinate if exposed to light or to alternating temperature (30° C. six hours, 20° C. 18 hours).

There have been no further major discoveries on the problem of dormancy in celery, but their findings on the beneficial effect of light and of alternating temperature have been fully confirmed by later investigators. In 1908 Kinzel (66) reported no germination in celery seed kept in the dark for five months at 20° C., but prompt germination occurred when it was exposed to the light. This was contrary to the earlier belief that celery seed would finally germinate in the dark if kept there for several months. Hopkins (61) has stated that light has "but little influence" on germination of celery seed, but this disagrees with the findings of other workers. She found that germination of new seed was 64.1 per cent in the light and 67.3 in the dark, while that of old seed was 85.6 per cent in the light and 86.8 per cent in the dark. Possibly the reason the seeds germinated in the dark was that they were sown in a greenhouse where they received the stimulating effect of diurnal alterations in temperature, but it is still surprising that the germination was practically identical in the dark and in the light. Niethammer-Prag (78) found that celery seed germinated in the light but not in the dark when the temperature alternation was 15–35° C. Taylor (102) found celery seed did not germinate in the dark when the temperature was constantly warm but did if the temperature was constantly cool or alternatingly cool and warm. Nutile and Canfield (79) planted celery seed in both light and darkness at constant temperatures of 20° C. and 30° C. and at alternating temperatures of 20° C. for 16 hours followed by 30° C. for eight hours, and of 10° C. for 16 hours followed by 20° C. for eight hours. Germination did occur in the dark, except when the temperature was kept constantly at 30° C., but in every case there was higher germination in the light than in the dark. Toole and Toole (105) also found that celery seeds will germinate in the dark if given alternations in temperature.

It has long been known that germination of many light-sensitive seeds is stimulated by alternations in temperature (22). Harrington (47) found that a temperature of 20° C. for 16 to 18 hours, alternating with 30° C. for six to eight hours, gave good germination, while the celery seed at constant temperature germinated well only when temperature was low (15–20° C.). Moringa (75) also obtained good germination when the temperature was alternating cool and warm or constantly cool. Hopkins (61) found celery seed was dormant when the temperature was constantly warm (30° C.) but germinated at constantly cool (15° C.) or alternating temperatures (10° and 25° C.). Taylor (102) obtained only four per cent germination at a constant temperature of 70° F., and none at 80° F. in the dark. This inhibition of germination by continuously warm temperature was overcome by a temperature period of 50° F. for two or more hours daily. Nutile and Canfield (79) obtained but 1.3 per cent germination at 30° C. in the light and none in the dark. When alternating temperatures of 20°–30° and 10°–20° C. were used, germination was 61.5 and 69.9 per cent in the light and 28.9 and 37.0 per cent in the dark, respectively. Toole and Toole (105) discovered that an alternation of 15° and 25° C. gave better results than the 20°–30° C. alternation used in official germination tests.

Germination of the members of the Umbelliferae other than celery has not been found to be inhibited by both darkness and constantly warm temperatures. The presence of light has been reported to improve the germination of carrot (43, 78) and other members of the family, but, at least in the case of carrots, alternation of temperature does not increase germination (41, 47, 50, 68).

In addition to the necessity of light and correct temperature, a high moisture content is also necessary for germination of celery seed. Bailey (7) found that "sparingly watered" celery seeds germinated better than those "profusely watered", but more precise investigations by Doneen and MacGillivray (26) reveal that a high soil moisture content is a prerequisite for germination. Most seeds will germinate when the moisture content is near the permanent wilting percentage, but maximum germination of celery seeds is not realized unless the moisture content is near field capacity. Since the germination period is so critical, because of the requirements for correct moisture content and temperature, presprouting of seeds in an ideal environment has been proposed (102, 104). Taylor has suggested a method in which the seed is moistened and kept in a germinating chamber with high humidity and controlled temperature alternations of 48° F. for 16 hours and 70° F. for eight hours daily; the seed is planted in the field about eight days later when it is beginning to sprout. This procedure brought about good germination, reduction in the preemergence period (and consequently less competition from weeds) and very uniform stands at relatively low costs (102).

DORMANCY IN *Heracleum*

Extremely interesting work on the problem of dormancy in another member of the Umbelliferae, *Heracleum sphondylium* (cowparsnip), has recently been reported by Stokes (96–99). Seeds of this plant require exposure to low temperature for germination. Seeds kept at 15° C. were dormant but those kept at 2° C. for two to three months germinated.

This requirement for after-ripening at low temperature did not appear to be affected by oxygen or carbohydrate supply, but it did appear to be related to the supply of soluble nitrogenous compounds. Chemical analyses indicated that the low temperature promotes the hydrolysis of endosperm proteins to amino acids. Seeds kept at 20° C. for eight weeks had only 0.44 mg. amino nitrogen per gm. dry weight, while those kept at 2° C. had 0.53 mg. There was also a difference in the proportions of the different amino acids. The endosperm of the seeds kept at 2° C. had an increased amount of arginine and glycine and a reduced alanine content as compared to that of the seeds kept at 20° C. It was therefore suggested by Stokes that low temperature is necessary for germination because it brings about the formation of the particular amino acids which are required for nutrition of the embryo during germination. Additional evidence in favor of this theory was obtained by culture of excised embryos. Vigorous seedlings developed from the embryos in cultures containing glycine and arginine as the only sources of nitrogen, but development was poor when alanine and other amino acids were used in place of glycine and arginine. It was also noted in the embryo culture experiments that growth of the embryo was favored by the presence of light.

DISCUSSION

The most important seed problem in the Umbelliferae may be considered largely solved from a practical standpoint. Embryoless seeds and reduction in seed yield have been shown to be caused by the *Lygus* bug. Control of the insect during the period of flowering and seed development will improve the quality of the seed. During the last century the best means of controlling the insect was by a formidable mixture of " strong tobacco-water, quassia-water, vinegar, and cresylic soap " (86). Harris (49) in 1862 was able to recommend only such ineffective control measures as thorough irrigations so the plants would be able to " withstand the attacks of these little bugs ". Breeding varieties resistant to attack by the *Lygus* bug has been suggested (103), but this is unlikely as there is no known source of resistance in the Umbelliferae. Fortunately an efficient and economical method of control has been discovered. Application of DDT at the correct time will greatly increase the amount of seed produced and its rate of germination. In 1949 the Department of Vegetable Crops of the University of California recommended dusting of all carrot seed fields in the State with DDT. The resulting seed crop had the highest rate of germination in history (62). Handford (45) reported increasing the seed yield of carrots one and one-half times by DDT applications. The ability to control the *Lygus* bug with DDT is of especial importance now that the use of pelleted seed (16, 113) and F_1 hybrid seed of carrots (109, 110) has been proposed, since these expensive procedures would not be practicable if the germination of the seed were low.

Aside from the practical considerations, the problem of embryoless seeds in the Umbelliferae is also interesting from an academic standpoint. It seems astonishing that this small insect could cause a plant to produce seeds without an embryo, but the research of Flemion, Smith and others has demonstrated that one of the components of the saliva injected into the plant by the insect while feeding is apparently a toxic substance which causes disintegration of the embryo.

One unsolved problem is the cause of the embryoless seeds occasionally found by Flemion when the plants were grown in insect-free cages. The number of embryoless seeds was small in these control plants—less than one per cent—but it suggests that some factor other than the tarnished plant bug may also cause embryoless seeds. It is quite possible, of course, that eggs or undetected insects were on the plants at the time they were enclosed in cages or that the *Lygus* bug, especially nymphs, could have gotten into the cages in some way and caused the damage.

If it be true that embryoless seed is produced when *Lygus* bugs are excluded, it would be of interest to study how they occur. Embryoless seeds are known to occur occasionally by single fertilization (46, 71). Double fertilization normally occurs in the Umbelliferae (12, 64), but if triple fusion occurred without accompanying syngamy, embryoless seeds might result. This explanation seems unlikely, however, for it does not account for the cavity where the embryo normally is embedded. It seems quite evident that an embryo started to develop in these seeds, but it later degenerated. Another possibility is that of deleterious genes, as in corn, but genetic studies have not been made.

Still another unsolved problem is that of the cause of rudimentary embryos in carrots. It has been suggested (32) that the occurrence of rudimentary embryos might be the result of harvesting techniques, climatic conditions, genetical influence, toxic feeding of *Lygus* bugs or other factors. There is reason to believe that rudimentary embryos are responsible for delayed germination, so this problem is of practical interest.

It has been proven that celery seed may be dormant when kept in the dark at warm temperatures, but the dormancy can be broken by cool or alternating warm and cool temperatures or by light. Crocker (22) has written: "There is need of a very thorough and detailed chemical, microchemical and physiological study of the effect of light upon the coats and living portions of several light-favored and light-inhibited seeds and fruits. There is also need of a similar study of the changes brought about in seeds and fruits by agents and conditions which substitute for light ".

Many theories have been offered to explain the effect of light on light-sensitive seed (22), but none has been conclusively proven. One possible explanation is that of an " inhibition of inhibitors ". It has been suggested that light of a certain wave-length will destroy an inhibitor of germination (30). Extracts from celery seeds have been reported to inhibit the germination of celery and other seeds (52, 101, 102), but much more evidence will be necessary to prove that the beneficial effects of light and of low and alternating temperatures on celery germination is due to inactivation of an inhibitor.

Another theory is that the beneficial effect is attributable to stimulation by light and low temperatures of the formation of metabolites required during germination. There is no conclusive evidence for celery with regard to this theory, but the research of Stokes has provided information for another member of the family, *Heracleum sphondylium.* Germination of *Heracleum,* like that of celery, is favored by low temperature and light, but *Heracleum* differs from celery in that the seeds must be treated for several months at low temperature. The results indicate that the low temperature stratification is necessary because it promotes the hydrolysis of the reserve proteins in the endosperm to the particular amino acids which are required for growth of the embryo. The explanation for the dormancy of celery seed when sown in the dark at a continuously warm temperature may be analogous to that for *Heracleum,* but there has been no report of evidence supporting or contradicting this theory.

SUMMARY

Poor germination of seeds is of common occurrence in the Umbelliferae. Probably the most important of several causes is the presence of non-viable seeds which have no embryo. Embryoless seeds have been found to result from the feeding of the *Lygus* bug on the developing seed. The insect seems to inject a toxic component of its oral secretions while feeding; this causes degeneration of the embryo. Control of the *Lygus* bug by use of insect-tight cages or

by application of insecticide greatly reduced the number of embryoless seeds and also increased the seed yield.

Rudimentary embryos have also been found in seed of the Umbelliferae, but the cause is not definitely known. It has been suggested that the seeds with rudimentary embryos are the cause of the delayed germination often encountered in carrots.

Dormancy occurs in celery seed when temperature and light are unfavorable. This dormancy can be overcome by exposing the seed to light and cool or alternating cool and warm temperatures during the germination period. Seeds of *Heracleum sphondylium* are also dormant when the temperature is warm, but several months at low temperature will break the dormancy. Low temperature seems to favor germination by promoting the breakdown of reserve proteins in the seed to the particular amino acids which are necessary for growth of the embryo.

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