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REGENERATION OF ROOTS FROM TRANSPLANTED COTYLEDONS OF ALFALFA, *MEDICAGO SATIVA*¹

Orville T. Wilson

THE WRITER has called attention to the readiness with which cuttings of alfalfa regenerate roots (Wilson, 1915). La Rue (1933) listed forty-two

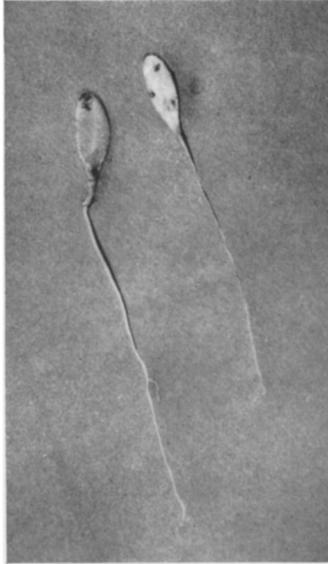


Fig. 1. Rooted cotyledons of alfalfa, *Medicago sativa* L. $\times 1.25$. Photograph by Arthur Blickle.

species of plants of which he tested the regeneration of roots from cotyledons by transferring the removed cotyledons to moist filter paper in Petri dishes and noting development. Of the forty-two

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species, *Medicago sativa* L. was the only one which failed to regenerate roots. As this result was contradictory to the writer's experience with alfalfa, additional experiments were carried out to test the regenerating capacity of the cotyledons.

In these experiments the cotyledons were removed from seedlings in the early juvenile leaf stage and set, cut end down, in moist greenhouse soil, with most of the blade exposed. A glass cover was placed over them to prevent excessive evaporation, but this was removed after the first week. After three weeks, approximately 50 per cent of the cotyledons were green and healthy (80 per cent in one experiment). When these were removed from the soil, they were found to be well rooted in a majority of cases. In one experiment sixty-seven cotyledons out of one hundred transplanted, regenerated roots. Two rooted cotyledons are shown in figure 1.

For an adequate discussion of the problem of root regeneration from cotyledons the reader is referred to La Rue's paper (1933). The present record serves only to supplement the long list of positive results there presented.

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THE FLORAL ANATOMY OF THE AVOCADO¹

Philip C. Reece

THIS STUDY of the anatomy of avocado flowers is a part of an investigation now under way on the family Lauraceae. This article is to be followed by a report on fruit bud formation of avocados and by a morphological interpretation of the apparent evolutionary tendencies in the Lauraceae, based upon comparative data.

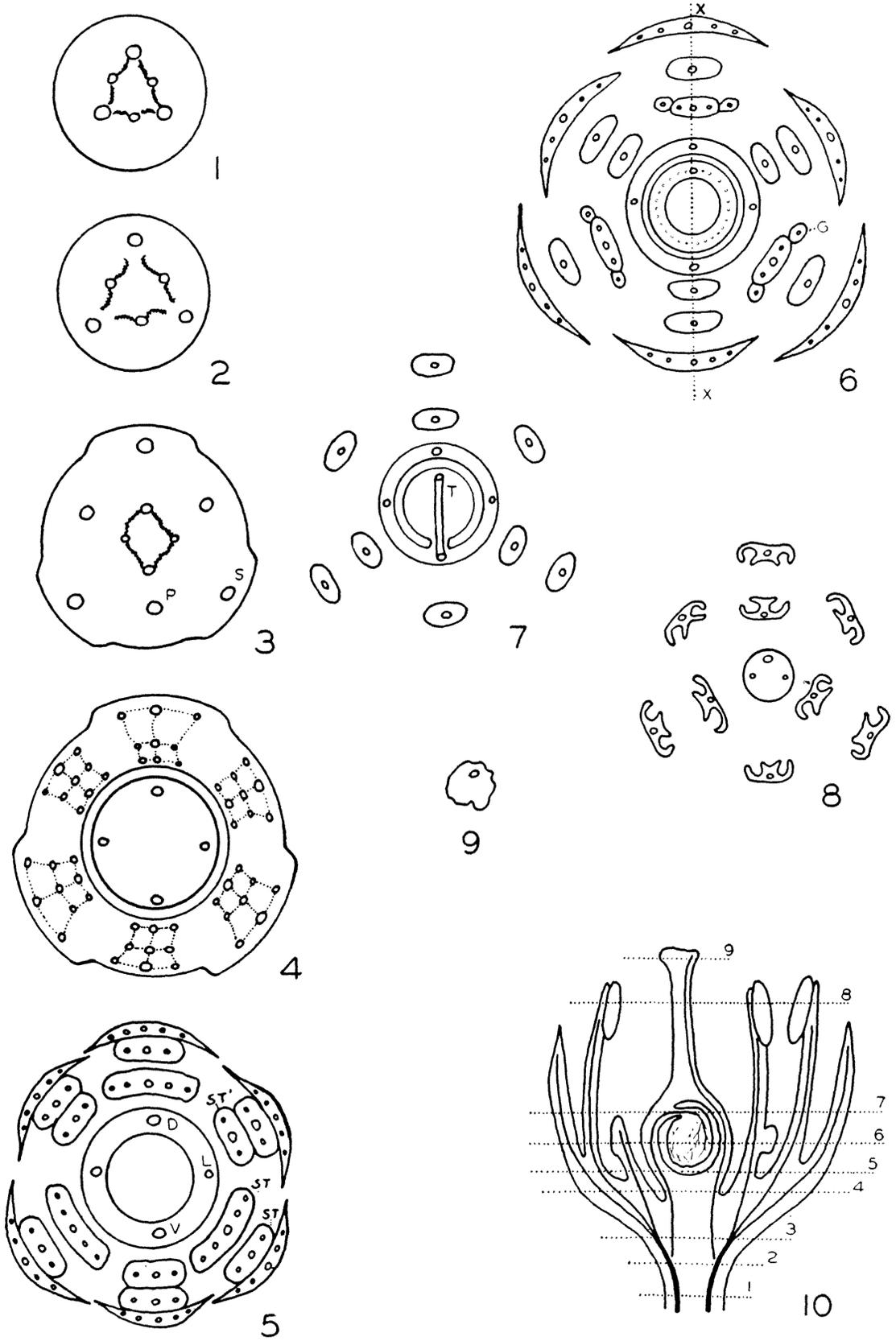
The family inhabits the tropical regions of the Americas, Asia, Australia, and Polynesia. The avocado is native to Central America and Mexico. Its culture has now become a thriving industry in the relatively frost-free areas of California and Florida.

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The writer wishes to express his appreciation to Dr. A. J. Eames, who, by his advice and criticism, aided in the development of this manuscript. Part of the research here reported was carried on in the laboratory of the Department of Botany, Cornell University, Ithaca, New York.

All the cultivated varieties of avocados belong to the single species, *Persea americana* Mill. (*Persea gratissima* Gaertn.)

The regular, bisexual, trimerous flowers of *Persea* are borne in cymose panicles. The floral plan of three, so conspicuous in this species, is popularly associated with monocotyledonous angiosperms. However, this fundamental plan of three is more prevalent among dicotyledons than is generally realized. The yellow or greenish six-parted perianth consists of two whorls upon which are inserted four stamen whorls of three members each. The anthers of the two outer whorls are introrse. Those of the third whorl are extrorse and bear glands on each side of the filament near the point of attachment on the perianth. The fourth whorl has been reduced to gland-like staminodes. The uni-



locular ovary is superior. The simple style is terminated by a small obtuse stigma. The solitary, pendulous, anatropous ovule ripens to produce a very large seed which is devoid of endosperm. The seed coat is membranous.

Examination of sections of the pedicel reveals the vascular tissue arranged in a siphonostele. Six areas of primary xylem stand out sharply, with the tissue in the intervening regions in a procambial state (fig. 1). At higher levels, approaching the receptacle, these areas depart from the stele and pass through the cortex as six tepal traces. (The term tepal is used in this report to designate any perianth segment, regardless of whether it is a member of the inner or outer whorl. At this point, no attempt is made to identify the segments as sepals or petals.) Three traces advance slightly ahead of the others and supply the outer perianth whorl (fig. 2).

After the departure of the tepal traces, the gaps left in the stele quickly close. Only a limited amount of vascular tissue remains. The stele "shrinks" toward the center of the axis, as the end of the receptacle is approached (fig. 3). The carpellary traces depart near the tip of the axis as the stele "closes in." The carpellary supply consists of a dorsal trace (midrib), two or more lateral traces, and two ventral traces (marginal veins) which are united into a single, morphologically compound vascular bundle. These traces enter the ovary (fig. 4) with the dorsal trace lying along the radius of a member of the outer perianth whorl. The ventral trace stands directly opposite the dorsal or at an angle of 180° .

The members of each perianth whorl are coherent at the base, as well as adnate to each adjacent whorl. A cup is thus formed around the base of the ovary by the perianth with the stamens perigynously inserted upon it. In this cup, the tepal traces divide, indicating that at lower levels the bundles are morphologically compound. The branching of the bundles is in a tangential plane, so that a tepal trace and two stamen traces lie upon the same radius. This is immediately followed by branching in the radial plane. Traces apparently form a reticulate vein system with anastomosing connections between the vascular supplies of the various whorls (fig. 4).

All the stamens have three traces traversing the major portion of the filament. The lateral veins in each filament weaken and disappear below the anthers. Each stamen of the third whorl possesses a gland on each side of the filament near the base. The glands are supplied by two additional veins which arise by the radial forking of the outer veins in the filament base. Then five traces are in a row (fig. 5). The veins enter the glands above the level at which the members of all the whorls become free (fig. 6).

The single, large anatropous ovule is attached to the parietal placenta near the top of the loculus. A bundle, which has been formed by the fused ventrals, enters the funiculus of the ovule and continues down the opposite side through the raphe (fig. 7). The bundle in the ovule branches profusely, so that the integument is traversed by a network of veins. These are conspicuously developed in the seed coat when the fruit is mature.

The fourth androecium whorl consists of three staminodes, which are not as high as the ovary. The anthers of the stamens of the two outer whorls are introrse, those of the third whorl are extrorse, and are borne on long filaments which extend to about twice the height of the ovary. The dorsal and two lateral carpellary traces extend up through the simple style (fig. 8). The lateral traces disappear below the stigma. The strong dorsal trace extends into the stigma (fig. 9).

It is becoming generally recognized that imperfect or incomplete flowers have attained that condition through simplification and loss of parts. They are simple through reduction and not primitively simple. Anatomical evidence of such simplification persists long after external evidence has disappeared. Therefore anatomical investigation of the floral anatomy supplies valuable criteria for a morphological interpretation of the flower.

Considerable difference of opinion exists regarding the nature of the perianth in this genus. Small (1913) believes that the perianth consists of six deciduous sepals, in two series, united at the base. Popenoe (1914) refers to the perianth as a "calyx deeply six-parted,—the corolla wanting." Gray

Fig. 1-10. *Persea americana* Mill. In these figures: *S*, sepal (outer tepal) midrib; *P*, petal (inner tepal) midrib; *ST*, stamen bundle; *ST'*, staminode bundle; *G*, gland; *D*, dorsal carpellary trace; *V*, ventral carpellary trace; *L*, lateral carpellary trace; *T*, ovule trace.—Fig. 1-9. Cross section diagrams of the flower.—Fig. 1. Through the pedicel.—Fig. 2, 3. Successive levels showing the departure of the outer tepal (sepal) traces and the inner tepal (petal) traces. The carpel dorsal (midrib), the fused ventrals (marginal veins) and two median lateral veins are distinguishable at the level of fig. 3. The vascular tissue of the stele is fading out at the end of the axis.—Fig. 4. The perianth cup surrounds the base of the ovary. The sepal and petal traces have divided tangentially to produce the traces of four stamen whorls and radially to produce branch traces in each whorl.—Fig. 5. The perianth segments and the filaments of the third stamen whorl have become free. The locule is visible in the ovary.—Fig. 6. All floral whorls are free. The longitudinal section in fig. 10 is in the plane *X-X*. The ovule trace, derived from the fused ventrals, enters the funiculus and passes down the opposite side of the ovule near the dorsal. The integument is invested with numerous small branches of this trace.—Fig. 7. Section through the top of the ovule showing the origin of the ovule trace. The lateral stamen traces have disappeared in the upper portion of the filaments. The fourth stamen whorl reduced to staminoides has disappeared between sections indicated by fig. 6 and 7. The perianth has been omitted from this diagram.—Fig. 8. Through the anthers and style.—Fig. 9. The dorsal trace continues to the stigma.—Fig. 10. Longitudinal diagram of the flower. The levels of the cross section diagrams fig. 1 to 9 are indicated. The longitudinal diagram is in the plane *X-X* in the cross section fig. 6.

(1908) and Hutchinson (1926) also speak of the six-parted calyx and imply the lack of a corolla. This viewpoint may be attributed to a lack of anatomical evidence and to hesitancy in interpreting the perianth of a dicotyledon as consisting of a three-parted calyx and a three-parted corolla. However, Van Tieghem (1891) considered the floral formula to be "(3 S + 3 P + 3 E + 3 E' + 3 E'' + 3 E''') + C" and said that "the calyx and the corolla, composed each of a single whorl, are sepaloïd or petaloïd, but like each other and concrescent in a tube. The median sepal is posterior."

The floral anatomy supports the view of Van Tieghem. There is no evidence that the corolla is absent. The concrescence of the perianth into a tube and the resemblance of one whorl to the other may not be accepted as valid criteria for considering that the perianth consists of a calyx only. If such reasons were to be considered valid, they should be applied in the interpretation of the perianth in liliaceous forms, in which the morphological conditions of the calyx and corolla are exactly the equivalent of those found in the perianth of the avocado. However, the fact that the perianth traces arise at two levels is in itself sufficient evidence that the perianth does not consist of a calyx alone.

Comparative studies of present plant forms as well as paleobotanical studies indicate that the fundamental type of architecture in pteropsid vascular plants is dichotomy. Working upon this theory, Hunt (1937) investigated the vascular anatomy of the style and stigma in certain groups. A study of the gross and anatomical structure of these organs convinced him that evidence still exists in the modern flower indicating that the carpel has been ultimately derived by reduction from a dichotomous branch system through the intermediate stage of an unspecialized palmately three-lobed appendage. The simple stamen commonly found in angiosperms may also have been similarly derived by reduction from a sporophyll which, in the ancestors of the angiosperms, was probably a fertile branch system.

The condition in which the vascular supply to a number of stamens arises as the result of the division of a single bundle has been investigated in a number of forms by Wilson (1937), who believes that such stamens have been derived from a primitive branch system, the ultimate branchlets of which were terminated by sporangia.

Reduction in most angiosperms has progressed so far in the stamen that only a single trace passes through the filament to the anther which consists of two bi-sporangiate synangia brought into close conjunction. It may therefore be assumed that the additional traces in an avocado stamen probably indicate a retention of a primitive condition. The various whorls exhibit various degrees of reduction. Members of the third whorl are the most primitive. Although each trace is fused with a tepal trace through part of its course, the trace later branches to produce three bundles, a median which extends to the anther and two laterals which pass some dis-

tance through the parenchyma of the somewhat fleshy stamen. The lateral bundles branch dichotomously near the base of the filament to supply the glands. Reduction of a primitive fertile branch system has probably proceeded in many directions to produce the stamen. The avocado stamen may have been derived from a much branched structure through some intermediate three-branched stage, forming a series similar to the series postulated by Hunt for the carpel.

The gynoeceium consists of a single carpel. The existing carpel usually lies in the plane of a sepal (outer tepal) and is alternate with the members of the fourth androecium whorl (staminodes). However, the carpel frequently lies on the radius of a petal (inner tepal) and opposite a staminode. The writer believes that this is evidence of reduction from a multi-carpellate ancestor.

The great increase in size which comes with the ripening of the ovary is accompanied by the formation of many additional cells in the pericarp. In the mature fruit, although the main vascular system remains fundamentally the same, it is complicated by branches which are differentiated in the new tissue. These branches consist chiefly of protoxylem cells accompanied by a few elongated parenchyma cells.

The presence of a single seed with its very large embryo and no endosperm indicates a high degree of specialization. Indeed, the gynoeceium has become so specialized that in so far as this species is concerned all evidence indicating the presence of more than one ovule in ancestral forms is lost. The profuse vascular supply in the integument may be regarded as the retention of a primitive characteristic. This condition has been retained coincident with the development of the large seed.

Hutchinson (1926) states that the members of the Lauraceae represent the extreme limits of reduction in the Magnolian alliance and that valvular dehiscence in this group and in the Berberidaceae is probably due to parallel evolution and is not a sign of affinity. He places them in the Apetalae but upon a different line from that giving rise to the Amentiferae.

The writer has investigated the floral anatomy of the Fagaceae (1938) and finds striking similarities of floral and inflorescence characters. Both groups are mainly tropical and display a trimerous floral plan with a six-parted perianth and twelve perigynously inserted stamens. The gynoeceium in each case has apparently been reduced from a six-carpellate ancestor. A network of veins in the membranous seed coat surrounds the large fleshy embryo. The ament of the Fagaceae is also fundamentally a cymose panicle but is much more specialized than that of the Lauraceae.

The possibility of a common origin of the Lauraceae and Fagaceae in the early differentiation of Angiosperms is suggested by these similarities of floral and inflorescence characters. However, these similarities are the result of parallel evolution and do not indicate close relationship.

SUMMARY

This study of the floral anatomy of *Persea americana* reveals that this species is clearly a specialized form derived from a primitive angiosperm stock and that the perianth consists of a three-parted calyx and a three-parted corolla. The anatomy does not support the interpretation that the perianth consists of a six-parted calyx or that the corolla is absent.

The vascular anatomy of the stamen indicates that it has been derived by reduction from a branch system. Vertical compression has resulted in the fusion of the vascular supply of the main limb or rachis of this branch system to the bundles supplying the perianth.

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MORPHOLOGY OF TINOSPORA CORDIFOLIA, WITH SOME OBSERVATIONS
ON THE ORIGIN OF THE SINGLE INTEGUMENT, NATURE
OF SYNERGIDAE, AND AFFINITIES OF THE
MENISPERMACEAE¹

A. C. Joshi

AS LITTLE work had been done on the embryology and cytology of the family Menispermaceae prior to 1933, an investigation of some members of this group was started by the writer in that year. During the course of this work an account of the development of pollen was published (Joshi and Rao, 1935), and in 1937 the writer described the structure of the gynoecium and development of the ovule and embryo-sac in *Cocculus villosus*. In the present paper a similar study has been made of *Tinospora cordifolia* Miers.

The earlier work on the family was fully summarized in the paper on *Cocculus villosus* (Joshi, 1937). There is therefore no necessity to recapitulate it here. It is necessary only to mention that since then the writer has come across a small embryological work on *Tinospora cordifolia* by Abraham (1935), but this is not very critical, and in it several features have been left unobserved by the author.

THE DEVELOPMENT AND STRUCTURE OF THE OVULE.—The gynoecium of *Tinospora cordifolia* consists of 3-6 free carpels. The most common number is three. Gynoecia with four, five, or six carpels are increasingly rare. These carpels arise from the floral axis in a spiral order, and when the number is more than three, the last carpel is frequently abortive just as in *Cocculus villosus* (Joshi, 1937).

The mature carpels are always uni-ovulate (fig. 3), but, as in *Cocculus*, two ovules are present in each carpel in the early stages (fig. 1). One ovule

arises from each of the two margins of the carpels. As the carpellary margins come close together and fuse, the two ovules come to lie nearly in one line, and one of them takes up a position slightly above the other. Both continue to develop equally until the megaspore-mother cell stage (fig. 1). Generally after this, growth suddenly stops in the lower ovule, which is then gradually crushed into an insignificant scaly structure by the developing upper ovule (fig. 2, 3). One can see the beginning of this gradual degeneration of the lower ovule as the tetrad is formed in the upper. By the time the latter reaches the 4-nucleate embryo-sac stage (fig. 2), the lower has completely lost its shape.

This behavior of the ovules in *Tinospora*, however, is not so constant as in *Cocculus*. While examining the latter (Joshi, 1937), I found no exception to this condition. In *Tinospora*, exceptional cases are frequently seen. Figure 5 shows a carpel in which both the ovules have reached the 4-nucleate embryo-sac stage simultaneously. Figure 4 shows a carpel in which the lower ovule has reached the 4-nucleate embryo-sac stage, while the upper is still at the one-nucleate embryo-sac stage. But such variations are of no importance in the end. By the time the mature embryo-sac is formed in the upper ovule, the lower ovule always ceases to grow and is crushed in every case. The general form and structure of the carpel at this stage is shown by figure 3, and no exception to this condition has been observed.

Both ovules after their differentiation from the carpellary margins continue to grow straight till

¹ Received for publication March 22, 1939.