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Arrangement of vascular tissues in the peduncle of avocado (Persea americana Mill.)

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Abstract

In all three investigated cultivars, the thin part of the peduncle which originates from the inflorescence axes contained a continuous cylinder of vascular tissue interrupted only occasionally by the gaps accompanying the traces of already abscised ramifications of the inflorescence. In the cvs. Principe Negro and Fuerte, the most distal, "thick" part of the peduncle (where the tepal traces separate) contained the vascular cylinder transformed into a group of concentric or semicircular bundles. These bundles joined anew at the point where the peduncle united with the fruit, forming once more a continuous cylinder of vascular tissues. Within the fruit, the vascular cylinder divided into numerous bundles penetrating the pulp. In cv. Hass the vascular cylinder was continuous in all parts of the peduncle, and was interrupted only occasionally by gaps.

Key words: avocado cultivars, vascular tissues, peduncle anatomy, fruit nutrition, systematics

INTRODUCTION

Avocado fruit is rather large, weighing up to 1/3-1/2 kg or more. Due to high nutritive value of the fruit, this species gains much attention in many subtropical and tropical countries. Usually only one avocado fruit is formed from one inflorescence (Fig. 1.) and particular parts of the long peduncle

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originate from the axial structures of the inflorescence (Alvarez de la Peňa 1979).

The anatomical structure of the fruit peduncle is not frequently studied and is little discussed in the classical books on plant anatomy (Esau 1965, Fahn 1974). Several interesting data on peduncle structure may be found in the book by Roth (1977). The anatomical structure of the avocado pedicel was described by Arzee et al. (1970); however, he takes into consideration only the part of the pedicel where the vascular tissue forms a continuous ring. The purpose of the present paper is to investigate the arrangement of vascular tissues along the whole peduncle of the avocado, and especially in its thick part close to the fruit (a pedicel) (Fig. 1). From the point of view of nomenclature, the peduncle is the axial structure of the inflorescence, or the axial part bearing the unique flower. The pedicel or "proper peduncle" is the axial part connecting immediately the flower (or fruit) with other axes of the inflorescence (see Font Quer 1982). In the following text, we will call the whole axial part connecting the fruit with the branch the "peduncle", and we will divide it into the "thick part" which is "the pedicel" and the "thin part" which originates from other axial structures of the inflorescence (compare Fig. 1A, 1B).

MATERIAL AND METHODS

Among the three cultivars investigated, cvs. Fuerte and Hass are commonly cultivated in the world, but cv. Principe Negro is a local one not mentioned as yet in literature, and we describe it further in this paper. The fruits with their peduncles were collected periodically in three commercial orchards: two of them were situated in Atlixco (State Puebla) and the third one in Tenancingo (State México) in Mexico. In both of these places there is a long dry period between October and May (García 1981), see also Muñoz-Perez (1985). Regular irrigation was therefore applied in all of these orchards during the dry period. The trees in Tenancingo were grown in deep fertile soil.

The fruits with their peduncles and a section of the branch bearing them, were fixed in CrAF mixture, in FAA and occasionally also in 75% alcohol. Some of them, if necessary, were also cut fresh. The free-hand cross-sections were mounted in glicerol or in gelatine-glicerol. They usually were not stained and were observed in polarized light. In order to understand better the structure of the peduncle we have also observed the structure of a branch in the vicinity of the point of attachment of the peduncle using the same methods as above.

RESULTS

DESCRIPTION OF THE CV. PRINCIPE NEGRO

The chief object of the study was the cv. Principe Negro. It is believed that it originates from the seeds of cv. Fuerte. It is cultivated in Mexico in the state

of Puebla, principally near the town of Atlixco. Its small spread is due to the competition in the market from the better known cv. Fuerte. The fruit of Principe Negro has black skin at maturation which also diminishes its competitive value in the Mexican market. Nevertheless, its cultivation has not tended to decline during the recent years, probably due to the good taste of its fruit.

The tree grows monopodially, more vigorously than Fuerte, so that occasionally it is advisable to apply pruning in order to control its growth. Its foliage is dense, and the shape, color and size of the leaves is almost identical with that of Fuerte.

The inflorescence is of panicle type and may be axilar or terminal. There are on average about 200 flowers in the panicle. The flowers are about 1 cm in diameter and are composed of 2 verticiles with 3 tepals in each. The androceum is composed of 12 stamens of which 9 are functional. The gineceum has one pistil. The ovary is superior, unilocular in which only one ovule develops. The dichogamic group, to which cv. Principe Negro belongs, is characterized by the fact that its flowers open for the first time at noontime as female, they close before evening, and during the next morning they open as male, terminating their cycle in the afternoon. In the region of Atlixco blooming occurs in October and November and the harvest takes place in August and September.

The fruit is a drupe with a thick exocarp easily separable, somewhat crispy and lightly wrinkled. The mesocarp is fleshy, without fibers, with the taste similar to that of Fuerte. At maturity the color of the skin is black-violet with light brown lenticels.

ANATOMICAL INVESTIGATIONS

Avocado peduncle is a complex structure and one may discern in it usually three parts which descend from different axial parts of the inflorescence (Fig. 1). Several cross-sections of the branch and the peduncle of cv. Principe Negro were made as shown in Fig. 1B and C. Some of them are shown in more detail in Fig. 2. The cross-section of the branch near the point of attachment of the peduncle (Fig. 2-BR₁) shows the cylinder of vascular tissue with a rather thick stratum of the phloem, (much thicker than in peduncle). The cylinder of the vascular tissue is occasionally interrupted by a gap accompanying a leaf or bud trace. The pith contains some sclerified cells. The vascular cylinder is surrounded by phloem fibers and by a cortex with numerous sclereids.

The swollen peduncle base near the junction with the branch (Fig. 2-P₁) shows some features characteristic of the abscission zones: the xylem ring is very wide but it is composed mostly of xylem parenchyma. The ring of the phloem is thin, as in other parts of the peduncle. Instead of groups of phloem fibers, there are in this zone groups of sclereids, some of which are elongated perpendiculary to the long axis of the organ. The sclerification of the pith is not very marked.

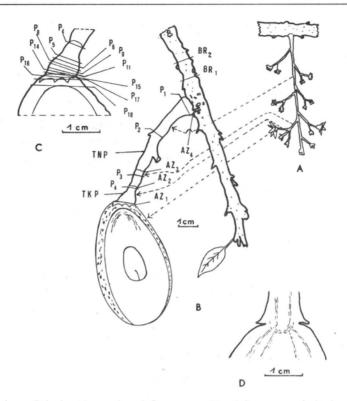
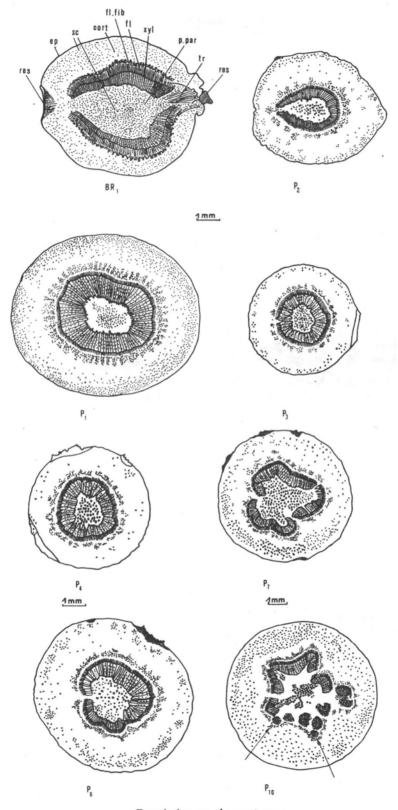


Fig. 1. Avocado cv. Principe Negro: A – inflorescence, B and C – young fruit about half-grown with its peduncle and a section of a branch, D – longitudinal section of a fruit showing spreading of vascular bundles in the pulp. BR₁, BR₂, P₁ etc. – places where the cross-sections were taken from the branch and from the peduncle, AZ₁, etc. – abscission zones, TKP – thick part of the peduncle, TNP – thin part of the peduncle

In the thin part of the peduncle (Fig. 2-P_{2,3}) the xylem forms a continous ring and contains few axial parenchyma. The cylinder of the pith has a very small diameter. The stratum of the phloem is thin. Some gaps may occur in the vascular cylinder accompanying the traces leading to the already shed branchlets of the inflorescence. The phloem fibers are well developed. There are few sclereids in the cortex. Generally the anatomical structure of the thin part of a peduncle shows great similarity to that of the branch, with the exception that in the peduncle the diameter of the pith is small and the layer of phloem is thin.

The structure of the thick part of the peduncle is rather complicated and changes greatly as one investigates it approaching the fruit. In its proximal part, the vascular cylinder is complete and relatively wide (Fig. 2-P₄). In this region the peduncle is not yet swollen (Fig. 1C). A little further toward the fruit the swelling of the peduncle is already evident (Fig. 2-P₆) and the pith has a much larger diameter. The shape of the vascular ring becomes irregular (Fig.



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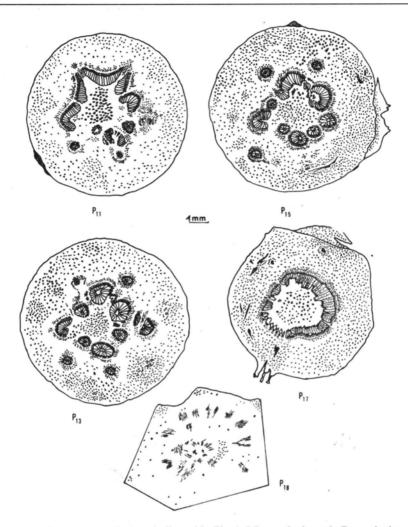


Fig. 2. Some of the cross-sections as indicated in Fig. 1. BR₁ – the branch, P₁ – the basal part of the peduncle, P_{2, 3} – thin part of the peduncle, P₄ to P₁₅ – the thick part of the peduncle, P₁₇ – peduncle at the junction with the fruit, P₁₈ – peduncle below the surface of the fruit (compare Fig. 1D). ep – epidermis; sc – sclereids; cort – cortex; fl. fib – phloem fibers or sclereids; fl – phloem; xyl – xylem; p. par – pith parenchyma; tr – trace of a bud, a leaf or an inflorescence; res – rests of an abscised leaf or ramification of an inflorescence. The arrows in P₁₀ indicate where the traces toward the tepals separate from the central vascular cylinder

 $2-P_7$). Furthemore, toward the fruit, the fractionation of the vascular system becomes more evident (Fig. $2-P_{10}$). Concomitantly, the vascular bundles of tepals start to separate from the central vascular system (Fig. $2-P_{10,11}$) and they displace gradually toward the margins of the cross-section, as one approaches the fruit (Fig. $2-P_{13,15}$). Finally they divide into particular strands and disappear (Fig. $2-P_{15,17}$). Meanwhile the fragments of vascular cylinder roll

up, forming concentric bundles (Fig. 2-P₁₃). But further on, just at the closest proximity to the fruit, they unroll (Fig. 2-P₁₅), and join again to form a continuous vascular ring at the junction with the fruit (Fig. 2-P₁₇). Furthermore, already in the fruit, this vascular ring becomes dispersed, forming numerous vascular strands (Fig. 2-P₁₈) penetrating the pulp of the fruit.

In the peduncle of cv. Fuerte (Fig. 3) the structure of the vascular tissue is similar to that of Principe Negro. The vascular tissue forms a closed cylinder in the cross-sections of the thin part of the peduncle (Fig. 4- F_2) and in the proximal part of its thick part (Fig. 4- F_4). A few milimeters further, however, the vascular cylinder becomes very irregular (Fig. 4- F_6) and fragmented (Fig. 4- F_8) in the region where the vascular bundles of the tepals separate. Finally, the vascular cylinder is transformed into a ring of separate concentric bundles (Fig. 4- F_{10} and F_{12}). Similarly, as in Principe Negro, these bundles join again (Fig. 4- F_{13}) to form a closed ring in the region of the junction of the peduncle with a fruit (Fig. 4- F_{14}). Finally, the vascular tissue disperses in the pulp of the fruit into numerous small strands (Figs. 4- F_{15} and F_{16}).

The anatomical structure of cv. Hass peduncle (Figs. 5 and 6) differs markedly from that of Principe Negro and Fuerte. In Hass the thick part of the peduncle is not markedly swollen (Fig. 5) and the vascular cylinder does not undergo fragmentation. Even in the region where the vascular strands leading toward the tepals separate, the vascular ring is continuous showing only the gaps accompanying the tepal traces (Figs. 6-H₁ to 6-H₅).

DISCUSSION

As we have already mentioned, the anatomical structure of the avocado peduncle has been little investigated and we know of only one paper dealing with this problem in detail (Arzee et al. 1970). Our results concerning the anatomical structure of the thin part of the peduncle (Fig. 1) coincide well with the description given by Arzee et al. (1970). However, these authors do not mention the phenomena which we have observed in the thick part of the peduncle of Principe Negro and Fuerte, namely, the fragmentation of the vascular cylinder, succeeded by the formation of separate concentric bundles and more distally their junction to regenerate the complete vascular cylinder.

Fragmentation of the vascular cylinder in the peduncles, and its transformation into a group of separate bundles is mentioned by Boone (1928, cit. Roth 1977) for the family Rosaceae. Roth also describes his studies with Anacardium occidentale. The peduncle of this species is markedly swollen and constitutes one of the edible parts of the fruit (the other being the achene). In the proximal part of the Anacardium peduncle the vascular tissue forms a closed cylinder. However, in the thickened part of the peduncle the vascular cylinder divides into separate concentric bundles dispersed in the parenchyma.

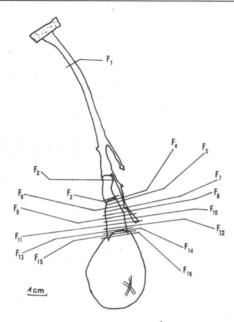
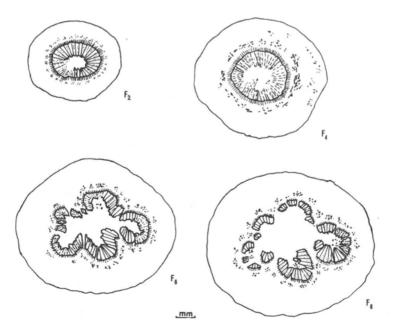


Fig. 3. The young fruit of cv. Fuerte with its peduncle. The places where the cross-sections were taken are marked as F_1 to F_{16}



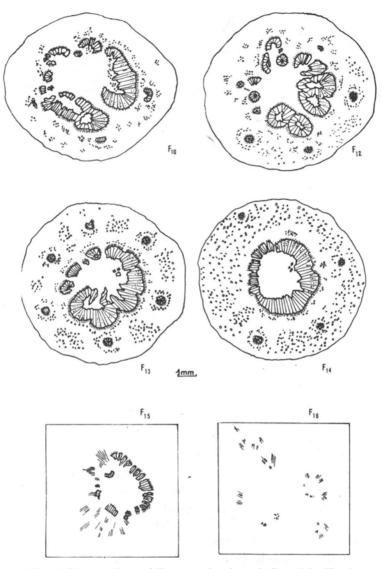


Fig. 4. Cross-sections of Fuerte peduncle as indicated in Fig. 3

Nevertheless, these bundles unroll and join together at the point where the peduncle contacts the fruit. This type of structure closely resembles, therefore, that which we have found in Principe Negro and Fuerte.

The physiological meaning of the vascular cylinder fractionation is, according to Boone (cit. Roth 1977), to augment the mechanical resistance of the peduncle against the tension caused by the weight of the fruit. We suggest other possibility which does not exclude that proposed by Boone: the surface of the contact between the parenchyma and the phloem is augmented about

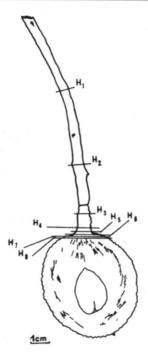


Fig. 5. The fruit and the peduncle of cv. Hass. The cross-sections shown in Fig. 6 are marked as H_1 to H_8

twice (Table 1) in the region where the vascular cylinder is fragmented (in comparison with the thin part of the peduncle). It seems therefore possible that vascular cylinder fragmentation may favor the exchange of metabolites between the parenchyma and vascular system of the peduncle in the close vicinity of the fruit. This may be important for the nutrition of the fruit. In apple and pear trees the swollen part of the short shoot known as a bourse may have a similar function — it swells shortly after flowering which suggests a connection of this phenomenon with fruit development. However, we have not found papers in literature dealing with the problem of a special type of metabolism in the peduncle or in the short shoot which would serve as a preparatory step to fruit nutrition.

Table 1

The length of the contact line between the phloem and the parenchyma in the cross-sections of peduncles of avocado. About half grown fruits

Cultivar	The thin part of the peduncle	The thick part of the peduncle	
		main vessel bundles	the traces of tepals
Principe Negro Fuerte	12.0* 7.1*	21.9 22.3	7.4 8.4

^{*} Averages of 3 peduncles (in mm).

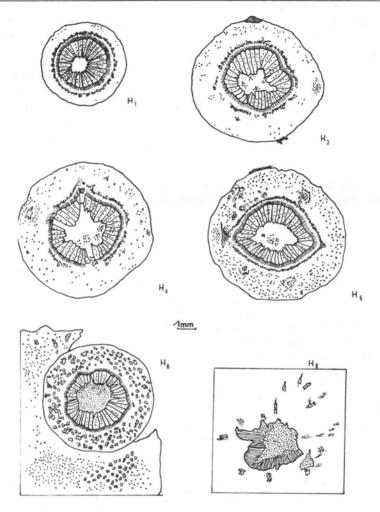


Fig. 6. Cross-sections of the peduncle of cv. Hass cut as indicated in Fig. 5

In cv. Hass, peduncle swelling near the fruit is not pronounced and the vascular cylinder is not divided into separate bundles. This means that the fragmentation of the peduncle vascular cylinder is not necessarily needed for cv. Hass fruit nutrition.

The phenomenon whereby the vascular cylinder fragmentation occurs in some cultivars and not in others may be utilized in systematics of wild and cultivated avocado forms. The fragmentation of the vascular cylinder in Principe Negro and Fuerte occurs always in the peduncle region where the tepal traces separate. It is possible therefore that these two phenomena are closely connected. Some mechanisms leading to vascular ring fragmentation are discussed by Phillipson et al. (1971). These problems will be discussed in more detail in our next paper.

We have investigated peduncles of Fuerte and Hass cultivars in many orchards in Mexico and Puebla states and never have we found exceptions from the tissue pattern described in this paper.

We hope that the description presented in this paper will help in understanding the nature of the disease of a rather physiological character named "ring neck of avocado peduncle", which is of economic importance in Mexico and other countries (Vazquez and Acevedo 1970).

Acknowledgements

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Układ tkanek waskularnych w szypułce awokado (Persea americana Mill.)

Streszczenie

Badano układ tkanek waskularnych w szypułce 3 odmian awokado: Principe Negro, Fuerte i Hass. U wszystkich 3 odmian cienka część szypułki, powstała z osi kwiatostanu, ma zamknięty walec tkanki waskularnej przerywany gdzieniegdzie przez luki towarzyszące śladom po opadłych już odgałęzieniach kwiatostanu. W grubej części szypułki związanej bezpośrednio z owocem oddzielają się od centralnego walca tkanek waskularnych wiązki prowadzące do działek okwiatu. W tym samym miejscu u odmian Principe Negro i Fuerte walec tkanek waskularnych rozdziela się na szereg pasm, które tworzą osobne, koncentryczne lub półksiężycowate wiązki. Dzięki temu

powierzchnia kontaktu między floemem a miękiszem w tym rejonie znacznie się zwiększa, co może mieć znaczenie dla odżywiania owocu. Wymienione wiązki, na które podzielił się system waskularny szypułki łączą się znowu w pierścień w miejscu gdzie szypułka styka się z owocem. W głębi owocu pierścień ów dzieli się jeszcze raz na liczne wiązki, które rozpraszają się w miękiszu owocu. W szypułce odmiany Hass wymienione zjawiska nie zachodzą i cylinder waskularny zarówno w części grubej szypułki, jak i w cienkiej pozostaje niepodzielny.