BRANCHING SYSTEM OF THE MEXICAN HAWTHORN “TEJOCOTE” (*CRATAEGUS* spp.)

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ABSTRACT

The architecture of the tejocote (pronunciation: tehocote) – a Mexican fruit trees is described. There is a great morphological diversity among the tejocote clones growing in Germplasm Bank of the Autonomic University of Chapingo, Mexico. The common character of all hawthorns in this bank is that the inflorescence axis dies after shedding the reproductive parts (flowers or fruits) but remains on the tree, and the growth continues from the bud situated below the dead part. The growth and ramification habit were described as long shoots showing marked apical dominance and as the complex of shoots showing weak apical dominance. The non-pruned trees of tejocote clones used as fruit trees form strong natural crown. The architecture of it is similar to the “Troll’s model” of Hallé and Oldeman (1970). Metamorphosis and reiteration are relatively frequent. The inflorescence structure was described, as well as the types of thorns in clones, which have thorns. Tejocote hawthorn may probably be an interesting fruit tree for countries with warm climate and a long dry period. It is also well adapted to shallow calcareous soils.

Key words: edible hawthorns. canopy architecture, ramification habit, inflorescence structure, morphological diversity

INTRODUCTION

There is a tendency recently to enrich the collection of cultivated plants with new species, and especially with such, which are well adapted to the local climatic and edaphic condition. For this reason, we paid close attention to the Mexican hawthorn (*Crataegus* spp.) known in Mexico under the name “tejocote”. This plant is a subject of gradual domestication. The plants are taken from the wild to home gardens where they are selected and finally small plantations are set up. This process started some centuries ago but still is carried on. The tejocote is used principally as a fruit tree because some of its genotypes produce edible fruits reaching up to 4 cm in diameter. They are tasty and rich in carotenoids and phenolic substances (Franco-Mora *et al.* 2010). The fruits are used tra-

ditionally to prepare compotes, especially during Christmas. There were also trials to use them for pectin production (Higareda-R. *et al.* 1995, Aguirre-Mandujano *et al.* 2010). The tejocote trees or shrubs are also used to form hedges around fields or as ornamental plants; for such purposes clones producing small fruits and strong thorns are preferred (Borys and Leszczyńska-Borys 1994). There are also other possible uses of tejocote hawthorns. Since the trees of some clones are very productive and their fruits have good nutritive value (Borys and Herrera-Guadarrama 1990, Borys 1996), e.g., their vitamin C content reaches 40-140 mg/100 g; they may be used as food complement for animals (Nieto-Angel and Borys 1991, García-Mateos and Nieto-Angel 2011). In several countries, for instance in Poland, the extract of flowers from native hawthorns (*C. oxyacantha* and *C. monogyna*) is

used as a medicine for heart diseases (Kaczmarek *et al.* 1973). Hawthorn fruits show strong antioxidant activity due to their content of proanthocyanidins and other phenolic substances (Froehlicher *et al.* 2009, García-Mateos and Nieto-Angel 2011).

In Mexico, tejocote has also important role in maintaining the ecological equilibrium, preventing field erosion and providing refuge for birds; their melliferous flowers serve as a source of nectar for bees and other insects (Borys 1989, Núñez-Colín 2009).

Tejocote withstands well climatic conditions of Central Mexico with winter drought lasting for 6 months and is well adapted to Mexican edaphic conditions where the soils are often shallow and calcareous (Cruz-San Pedro *et al.* 1984). For this reason, there were also attempts (rarely successful) to use tejocote as a rootstock for quince, pear or apple (Nieto-Angel *et al.* 1984).

At present time, the tejocote trees are commonly cultivated in home gardens or on small plantations in Central México (Bustamante and Borys, 1984, Flores-García *et al.* 1990). In the wild, tejocote trees or shrubs are becoming scarcer from year to year, especially in the state Chiapas (M.W. Borys, personal communication). The collection of tejocotes at the Autonomous University of Chapingo was created thanks to researchers Borys and Nieto-Angel (Nieto-Angel and Borys 1989) and is an invaluable object for taxonomic and horticultural works on Mexican hawthorn (Nieto-Angel and Borys 2008).

Other species of hawthorns are cultivated as fruit trees also in China, like for example *C. pinatifida*, which has fruits up to 16.6 g in weight and reach in vitamin C, and is resistant to fire blight and mildew (Wang-J 1998, Wang-G *et al.* 1998). In the United States of America and in several other countries various species of hawthorns are used mainly as ornamental plants but the dietetic or pharmaceutical value of their fruits and flowers are also appreciated (Picchioni and Graham 2001, Bahri-Sahloul *et al.* 2009). In the United States *C. arnoldiana* and *C. submollis* are mentioned in popular literature as having rather tasty fruits up to 2 cm in diameter that are sometimes used as fresh fruits or in pies.

The morphological aspects of tree architecture are discussed by Bell (1991). He distinguishes 23 types of tree architecture; most of them were described originally in tropical forests by Hallé and Oldeman (1970). Bell also indicates the phenomena which may modify the tree form like reiteration (when one part of tree, for instance one branch, reiterates the original model of a plant), or metamorphosis (when a group of branches start to show different behaviour than the others, for instance change their direction of growth from plagiotropic to orthotropic).

The other phenomena important for understanding tree branching, like formation of sylleptic shoots (Champagnat 1965 a,b), gravimorphism and crotch angle formation are discussed by Jankiewicz (1971), Takeo and Minoru (1989), Chen *et al.* (1999), Jankiewicz and Acosta-Zamudio (2003), McSteen and Leyser (2005). The general characterization of fructification of tejocote was described by Almaguer *et al.* (1992).

The purpose of this paper is description of the type of growth and ramification of tejocote trees, which is important when one cultivates this species as fruit tree or for other purposes.

MATERIAL AND METHODS

The trees of tejocote in the Chapingo collection were 13-14 year-old during the measurements. The collection is situated at 19° 29' northern latitude and at 98° 53' western longitude and at about 2 240 m above the sea level. According to the classification of García (1981) the climate of Chapingo is defined as C(Wo)(W)b(i')g which means that it is moderate rainy, with the rains mainly during the summer. The winter rains constitute only 5-10% of the total precipitations. The summer is long with the highest monthly temperature (17.7 °C) in May. The lowest monthly temperature (11.6 °C) is in February. The annual mean temperature and precipitations in Chapingo are respectively: 15.0 °C, 645 mm, and the maximum precipitations are observed in July. The soil at the collection's site is sandy-loam and is dark brown-grey. Its layer is very shallow, frequently about 40 cm, and lays on the rather soft volcanic rock "tepetate". The slope is 3-8% and the pH is slightly over medium alka-

line. The content of the organic material is medium (Cachón-Ayora *et al.* 1976).

The trees were grafted on the tejocote rootstocks originating from the states Mexico and Chiapas (Borys and Vega-Cuen 1984; Nieto-Angel and Borys 1991).

The length and the diameter of scaffold branches as well as the distance of their base from the soil level were measured in two or three representative trees of each of chosen clones. The angles of the branches with the plumb line were measured in five points (0, 5, 20, 100 and 200 cm from the trunk) with the protractor provided with the thread ended with a weight to indicate the vertical. The leaves were measured for each tree: 10 leaves from vegetative shoots, 10 from reproductive ones and 10 from long dominant vegetative shoots. The area of leaves was calculated as for ellipse.

RESULTS

Developmental changes in tree growth.

During the first or the first and the second year after grafting, the tejocote trees were growing very vigorously, frequently more than a metre a year, but, as they start to ramify, their growth slows rapidly. This initial growth was weaker in dwarf clones.

The clones of tejocote in the collection of Chapingo may be classified into two very different types, which we have named for convenience “manzanita” and “cedar”.

The manzanita type.

The trees of this type originate mainly from the central part of Mexico, like the states Mexico, and Oaxaca. After a few years of rather vigorous growth and the formation of long shoots with marked apical dominance, they start to produce the ramifications, which do not show distinct apical dominance and form complexes of mainly short shoots. The trees are thornless and have large, elliptic, generally slightly lobular or non-lobular leaves (Fig. 5); their average dimensions for accession 100/tree 6 are: 8.65 x 4.90 cm; area 32.2 cm² and for the less vigorous accession 33/tree 58: 7.87 x 4.6 cm; area 26.8 cm². They produce relatively large, yellow fruits up to 4 cm-in-diameter and are commonly cultivated as fruit trees. The name manzanita, which we have provisionally given to this

clone, was used for tejocotes by Spaniards during the period of conquest (Núñez-Colín and Hernández-Martínez 2011).

The cedar type. The trees or shrubs of this type have shoots, which preserve strong apical dominance for a long time. They are also usually spiny, have relatively small (0.8-1.5 cm-in-diameter) red or yellow fruits. The leaves are small and lobular. In the case of the accession 8/tree 30 the dimensions of leaves are on average 3.82 x 2.68 cm, area 7.46 cm². The name, which we have adopted for this clone, refers to columnar appearance frequent among its trees. Tejocotes of cedar type are rarely used as fruit trees. More frequently are planted as ornamental plants due to their abundant flowering and brightly coloured fruits, which persist for a long time on a tree. They are frequently used for hedges. According to Núñez-Colín and Hernández-Martínez (2011) they may be classified as ornamental or medicinal plants.

We suppose that the trees showing these two types of morphology belong to two different species. The taxonomic work on hawthorns in Mexico is now progressing although it is very difficult due to occurrence of triploids and other polyploids and apomixis (Núñez-Colín *et al.* 2008, Núñez-Colín and Hernández-Martínez 2011).

Figure 1. Schemes presenting: **A.** Reiteration in the shoot: R1 – growing from the bud on the trunk, R2 – from the bud on a branch, R3 – traumatic reiteration after wounding; **B.** Metamorphosis (M) - in the apical part of the tree the branches are orthotropic and in the lower part are plagiotropic, T – transitory branches, **C** - one-year-old tejocote grafted on tejocote. Note very vigorous growth - more than 1 m during this first year of growth and plagiotropic bending occurring at the end of the season.

The characteristic feature of tejocote branching system of both manzanita and cedar types is that the inflorescence axis dies after shedding flowers or fruits, so that the further growth continues from the bud(s) situated below the dead part (Fig. 2-4). Such dead inflorescence axis is not shed and persists for years. Sometimes more than one lateral bud is formed beneath the dead inflorescence. The other buds remain dormant and are even poorly visible. The growth of tejocote branches, which terminate with the inflorescence is therefore sympodial. The vegetative branches may grow monopodially.

The branches of manzanita type trees. Typical example of a manzanita long shoot, which terminates the branch, was described by us during the winter (Fig. 2).

Figure 2. Terminal part of semiplagiotropic branch in 13-year-old "manzanita" tejocote tree. The dead parts are blackened. R1 and R2 the sections of the axis formed during the first and the second year of growth, (the older parts are neglected). The ramifications 7-9 were formed during the 3rd year of growth. Scale 1:1.5.

In its axis, the older section (R1) showed the monopodial growth and the younger part (R2), terminated with an inflorescence, now dead and very small, because probably had not produced fruits. The axis produced several laterals (No. 1 to 6) on its older part and laterals (No. 7 to 9) on its younger part. Laterals No. 1 and 6 were at the time of measurements purely vegetative and each of their two yearly increments was only a few mm long. Laterals No. 2 and 5 were vegetative and monopodial during their first year of growth but they formed inflorescences during their second year of growing. Their inflorescence axes had already been dead and the bud is formed below each of them. The laterals No. 3 and 4 had been dead but at the basis of that No. 3 there was formed a collateral bud able to replace it. The laterals No. 7 to 9 were one-year-old, monopodial, and were terminated with a bud, some of those buds may be generative.

In tejocote manzanita trees, also another type of ramifications may be observed in which the apical dominance plays a little role. An example of such a branch has been presented in Fig. 3A. It was growing in the apical part of the tree (accession 33/tree 58) in full sun light. In spite of this, it showed many dead parts, which implies that in the apical part of a tree the life of branches is short and that they are relatively early replaced by the new ones. The branch R situated centrally in the picture terminates with a dead inflorescence axis (F1) and formed two short laterals No. 1 and 2. Ramification No. 1 remained vegetative and very short during its first year of growth and formed the short vegetative prolongation during the second year (1.1) which bears three ramifications. The 1.1.1 is its direct, monopodial prolongation and has a large dead segment. However, below this segment remained a bud, which was growing, flowering (F2) and forming a small prolongation alive even now (1.1.1.1.1.1). The growth of other ramifications (for instance 1.1.2) may be described in a similar way. Its characteristic feature, as already mentioned, is that the inflorescence axes die after producing flowers and fruits and growth continues from the bud(s) situated below the dead part. In each particular shoot, long internodes are intercalated with shorter ones and *vice versa*.

Figure 3. **3A.** Highly ramified branch from the apical, well illuminated part of the crown in 13-year-old manzanita tejocote tree. g – vector of gravity; F - inflorescence axes (already dead). All dead parts blackened. R – the main branch. The numeration of the consecutive branching orders: 1, 1.1, (or 1.2, or 1.3), 1.1.1 etc. scale 1:1.7. **3B.** Terminal semiplagiotropic branch, relatively well illuminated (but less than 3A) growing on the lateral side of the same tree. R1 and R2 - sections of the main axis formed during two consecutive years; other explanations as in Fig. 3A, scale 1:1.7. **3C.** The plagiotropic lateral branch growing inside the crown in a very shaded location, scale 1:1.5. Further explanation in the text.

Generally, as the system of ramification becomes more and more complicated, the yearly increments become smaller and smaller. This may be considered a symptom of aging.

The semihorizontal branch (Fig. 3B) situated laterally on the tree (accession 33/59) was relatively well illuminated, although less than the branch presented in Fig. 3A. What seems interesting, there were almost no dead branches among its

ramifications. The other phenomenon, which may be observed in this branch is a weak growth of the ramifications situated ventrally on the main axis (laterals No. 1 and no 3). Also, the lateral No. 5 situated ventrally-laterally shows weak growth and remains purely vegetative. On the other hand, the branches situated dorsally grow vigorously (No. 2, 4, 6, 7-1). The branch No. 7 is situated in the semiventral position but it is terminal one; possibly due to this it is vigorous. The dorsal, strong ramifications produced many inflorescences; however, even the ventral shoots flowered from time to time. Also on this branch (Fig. 3B) it could be observed that weak growth during one (or more years) is frequently followed by stronger growth during next year and *vice versa*. Generally, the growth increments weaken, as the branch gets older.

The branch presented in Fig. 3C was growing inside the crown in a very shaded place. In the past, it started to grow vigorously and produced an inflorescence (F_1). Probably at that time, it was better illuminated. Later on it was growing weakly and formed very few ramifications and only some, predominantly weak inflorescences. All laterals, except those, which served as prolongation of the axis, died relatively rapidly, so no one survived up to the moment of measurements. The prolongations of the axis grew as a rule from the ventral or semi ventral bud situated just below the inflorescence.

The branches of the cedar type. The branch presented in Fig. 4. (accession 8/tree 32) belongs to the tree having spiny form. Terminal section R_1 of this branch (Fig. 4 on the left) is two-year-old and bears ramifications one year old (No. 12-15). They all are terminated with dead inflorescence axes, which mean that they flowered and probably bore fruits in summer. The section R_1 is three-year-old and its ramifications are two-year-old (No. 1-11). The thorns, which have been formed on the basal part of the section R_1 (ramifications 1-7), derived from transformed shoots, which initially were green and had even very small rudimentary leaves. However, they soon have lost these leaves, became lignified, up to the apex and died (compare Esau 1965, Bell 1991). The basal part of the thorns frequently remained alive, having a bud or even ramification(s), which could supply the tissue with

hormones (Fig. 4). Collateral buds are frequently developed near the basis of the thorn. In many species of Rosaceae family each bud is accompanied with two collateral primordia, which become active when the main bud or shoot developing from it dies (Pieniążek and Jankiewicz 1966, Bell 1991). The terminal ramification of the section R_1 (No. 8-11) were thornless, relatively strong and flowered abundantly.

Figure 4. Terminal part of the lateral orthotropic long shoot from the apical part of the 13-year-old tree of the cedar type of tejocote. Dead parts are blackened. R_1 and R_2 – sections formed during two consecutive years, and C – the border between them. Scale 1:1.5

Structure of the inflorescences. An example of an inflorescence is shown on Fig. 5. The rather vigorous shoot (about 8 cm long) emerged from older section 1.5 cm long (which is terminated with dead

inflorescence axis – “din”). This vigorous shoot produced at the top the small infructescence, bearing two fruits. Sometimes there are more fruits in the infructescence. One of the fruits is growing in the axil of a small rudimentary leaf (rl). Below the inflorescence (infructescence) one may observe a bud (ab), which will form prolongation of the axis during the next year. Somewhat below, small sylleptic (precocious) shoot (ssh) appeared in the axil of a true leaf. Another bud (ab) was formed below, in the axil of the leaf, which possibly may form the lateral during the next year.

Figure 5. Example of the inflorescences of manzanita tejocote tree during vegetation., rl - rudimentary leaf, ab - axillary bud, which will renew the axis in the next year, ssh - short sylleptic shoot, din - dead inflorescence from the previous years. lt - lateral vegetative shoot. Scale 1:2.

Proposal of the classification of tejocote branches. The proposal is based on similar classifications made for apple, pear or guava trees (Calderon-Alcaraz 1983, Rey 1998). We add Spanish names to the English ones because tejocote is cultivated mainly in Mexico.

A. One-year-old branches

1. Long vegetative shoot (long shoot) – *Rama larga vegetativa* >10 cm;
2. Long floral shoot – *Rama larga floral* >10 cm;
3. Vegetative long spur – *Brindilla simple* 5.1-10 cm;
4. Long spur terminated with floral bud – *Brindilla coronada* 5.1-10 cm;

5. Short vegetative spur (dard) – *Dardo* 0.5-5 cm;
6. Short floral spur (floral dard - lamburde) – *Lamburda* 0.5-5 cm.

B. Branches older than one year (mainly complex ramifications)

Possible evolution of the point 6: the inflorescence dies after producing flowers or fruits and the growth will be continued from the bud situated directly beneath the dead part, forming for instance the dard. The resulting complex may be named “lamburde-dard”. Similar evolution may occur in other branches (No. 1-5). It seems to us that the ramifications older than one year may be named just “complex ramification”. The names lamburde and dard we adopted from Grisvard (1989).

Thorns (Fig. 6). As it has been mentioned, the thorns are transformed shoots. After being lignified, they die and serve for many years discouraging the phytophagous animals. Some clones of tejocote produce ramified thorns (Fig. 6), which originate from the ramified shoots. In such a case, the main short shoot and its small sylleptic laterals lose at about the same time their rudimentary leaves they get lignified and die. The trees of some clones have many thorns even on the trunk and on the main limbs. Such forms, if they have other values (for instance, they are ornamental or are resistant for diseases) are preferred as natural barriers for passers-by, or are used as plants for hedges. The length of the thorns vary, usually they are 3-6 cm long. Some clones produce spines only in the juvenile stage and later lose this attribute.

Figure 6. Different types of thorns of tejocote. Scale 1:1.5

Table 1. Scaffold branches of 13-year old manzanita tejocote tree (6/100). Tree height - 4.48 m. The sum of the cross-sections of the branches $S=356.61 \text{ cm}^2$.

No. of branch	Position on the trunk*	Length (m)	Cross-sectional area (cm^2)	Angle at the trunk	Angle with the plumb line***			
					5 cm	20 cm	100 cm	200 cm
1	39	4.31	66.44	21	20	24	5	10
2	40	3.20	36.73	36	45	24	8	25
3	47	3.81	44.39	35	42	34	0	0
4	62	3.48	14.92	40	43	84	99	46
5	65	3.90	19.47	35	45	15	20	42
6	69	3.25	20.57	33	31	20	70	40
7	99	1.54	3.14	50	45	50	47	-
8	144	2.99	27.32	37	35	27	45	15
9	147	2.76	42.52	35	33	44	20	10
10	150	2.98	18.68	46	43	18	35	47
11A	154	2.75	29.99	28	25	15	0	22
11B	154	2.68	32.44	34	24	15	5	50

* above the ground level (in cm), ** measured 5 cm from the trunk, ***measured at this distance from the trunk

Table 2. Scaffold branches of 13-year-old manzanita tejocote (86/1). Tree height - 4.38 m. The sum of the cross section of the branches $S=260.43 \text{ cm}^2$.

No.	Position on the trunk*	Length (m)	Cross sectional area (cm^2)	Angle at the trunk	Angle with the plum line***			
					5 cm	20 cm	100 cm	200 cm
1	0.21	0.91	2.04	45	35	20	-	-
2	0.28	1.25	3.64	52	17	0	52	-
3	0.63	2.72	38.25	45	37	27	80	52
4	0.69	2.52	18.84	67	64	60	50	85
5	0.72	2.90	25.50	62	37	12	15	50
6	1.17	3.03	40.57	23	17	0	0	45
7	1.20	3.18	96.37	20	25	20	40	45
8	1.22	2.56	35.23	25	0	0	54	85

*, *** explanation as in Table 1

Table 3. Scaffold branches of the 13-year-old cedar tejocote tree (8/32). Tree height - 2.75 m. The sum of the cross-sections of the branches $S=102.58 \text{ cm}^2$. Length of all branches between 1-2 m.

Branch No.	Insertion above the soil level (cm)	Cross sectional area (cm^2)	The angle with the vector of gravity*			
			0	5	20	100
1	3	6.59	65	19	45	20
2A	47	9.61	70	42	30	70
2B	42	15.20	48	36	50	75
3	45	20.41	36	17	25	72
4	51	9.07	32	18	30	20
5	58	3.14	28	22	32	30
6	72	17.33	25	6	25	10
7	75	21.23	20	10	37	15

*measured at this distance from the trunk

Trunk and scaffold limbs. The tejocote trees of manzanita type form usually very regular main scaffold and hardly need any correction with pruning. They have usually 5-9 limbs (sometimes up to 12) rather regularly spaced on the trunk, situated separately or in groups of two (in such a case the two branches are situated on nearly opposite sides of the trunk). Such disposition of the branches on a strong leader prevents breakage of the crown (Jankiewicz and Acosta-Zamudio 2003). The tree 6/100 of manzanita type (Table 1), very vigorous, having 12 scaffold branches may be the example. Some of its branches like No. 1 and 3 are strong, orthotropic and tend to form another trunk (reiteration). Also the branch 9 and 11 A, situated at the top of the tree, show orthotropism and they tend to play a role of extension of the leader. Other branches are growing all the time plagiotropically (branches 4 and 7), or become plagiotropic at larger distance from the trunk (1-2 m), for instance the branches 5, 6, 10, 11B. There are also branches whose behaviour combines these two tendencies, like for instance the branches 2 or 8. In another vigorous tree of manzanita type, clone No. 86/1 (Table 2), the three branches situated near the top (No. 6-8) are strong and their crotch angles are narrow (20-25°) so they replace partly the leader which at this age of the tree, as a rule, is not distinct. Nevertheless, they are all inclined plagiotropically in their distal parts (1-2 m from the trunk). The branches situated lower on the trunk (No. 2-5), with rather moderate growth, form relatively large angles with the trunk and all of them show plagiotropic inclination at the distance 1-2 m from the trunk. In the tree 33/59 belonging to the same manzanita type but growing not very vigorously there are six main limbs 2-3 m long, which show plagiotropic inclination in their distal parts except for the two lowest limbs, which are more orthotropic and show the tendency of reiteration.

In the cedar type tree 8/32 (Table 3) whose growth is medium to weak, the branches are relatively thin (diameter: 2.0-5.2 cm) and their length is 1-2 m. The lower branches (1, 2A, 2B) form large angles with the trunk; however, the branches situated higher on the tree (branches 3-7) show the angles with the trunk more and more narrow

(metamorphosis). The angles with the vertical, measured 5 cm from the trunk, in all branches are narrower than those measured at their juncture with the trunk. However, at the distance of 1 m from the trunk the lower branches (2 A, 2 B and 3) became distinctly plagiotropic. The uppermost four branches show narrow angles with the plumb line at all distances from the trunk. Therefore, the tree in its higher part has columnar form. The branch 1 is curved upward and possibly tends to form "the additional trunk" (reiteration).

Figure 7. Example of the angles of the branches with the plumb line. They were measured in 5 points: at the trunk, and at 5, 20, 100, and 200 cm from the trunk. The angle at the distance 5 cm is not shown at the picture (it was 52°).

As we have mentioned the trees of the cedar type are very diverse in their form. The columnar form described here is relatively common. More examples of the scaffold of tejocote trees are presented by Perez Ortega and Mendez Santiago (2001).

DISCUSSION

Since the detailed description of tejocote branching system was almost lacking we tried to provide it in the present paper. We are aware that many details in this area deserve further investigation and we have indicated several problems of this kind.

The botanical identity of plant material in Chapingo germplasm collection of tejocote was a problem for us because of its great variability. To omit this we have chosen two very distinct types and named them “manzanita” used as fruit tree and “cedar” of rather ornamental type, hoping that their true botanical names will soon be found due to a work in this field done recently (Núñez-Colin *et al.* 2011 and the literature cited there). The characteristic mark of all tejocote types growing in the Autonomous University of Chapingo collection is the death of the inflorescence axis after flowering or fruiting. The apple or pear trees behave differently: the inflorescence axis remains alive after shedding flowers or fruits and leaves. What is the cause of such peculiar behaviour of tejocotes? Analysing in detail the structure of the tejocote inflorescence it may be seen that almost each flower or fruit is growing in an axil of a true or rudimentary leaf. It is well known that the tissues of almost all plants need the constant supply of auxin. Without the auxin they die. The auxin is transported mainly basipetally, so generally the given leaf, bud, or fruit keeps alive only the tissues situated below it (proximal) (Jankiewicz and Acosta-Zamudio 2003). The flowers and fruits supply the auxin to the inflorescence axis when they are attached to it. When flowers or ripening fruits and the rudimentary leaves are shed, the inflorescence (infructescence) axis dies because there is no source of auxin left.

Analysing the type of ramification in manzanita tejocotes one may observe that among the uppermost ramifications in the apical part of the canopy (Fig. 3A) there are many dying shoots whereas among the terminal branches in the lateral parts of the canopy there are very few dead shoots (no one in the branch presented in Fig. 3B). How common this phenomenon is must be investigated in the future. The frequent death of branches situated at the top of the tree may be evoked by the damage caused by excessive solar radiation (Li *et al.* 2009) and especially due to its UV-B component (Jenkins 2009). The lateral branches are partly shaded so they are less exposed to this unfavourable factor. Since the orchard is situated at the altitude of 2.240 m above sea level and in the sub-

tropical conditions, the supposition that excessive light and UV-B radiation may damage the uppermost branches may be put forward. Heavily shaded branches like that presented in Fig. 3C develop weakly, probably due to scarce photosynthetically active radiation reaching it.

The lack of spines in manzanita tejocotes is their taxonomic character, which otherwise is very advantageous in the plant which is cultivated for its fruits. The cedar type clones are usually spiny but to a very different degree. In dicotyledonous plants different parts like leaves, stipules, etc. may be transformed into thorns (Esau 1965). In tejocote, as it was mentioned, the lateral short shoots are transformed into thorns. In several clones of cedar type tejocote, the thorns are formed only during the juvenile phase of the tree or shortly later. Such phenomenon occurs also in other species of Rosaceae family, for instance, in apple and pear trees.

Stronger growth of the laterals situated on the dorsal side of horizontally oriented shoots is one of the symptoms of gravimorphism, (Jankiewicz 1971; Jankiewicz and Stecki 1976, Jankiewicz and Acosta-Zamudio 2003). Unequal illumination of the dorsal and ventral sides of the lateral shoot may additionally strengthen this phenomenon. In the vigorous thorny shoots frequently one or two collateral buds develop aside of the thorn. Probably their development is stimulated by the death of the large part of the lignified thorn.

A system of classification of the crown architecture of different species of trees was proposed by Hallé and Oldeman (1970), and Bell (1991). It seems that the tejocote crown architecture fits to the “Troll’s model” of these authors. In this model, the main axis is monopodial and orthotropic but becomes plagiotropic with the age and is losing its dominance. This frequently is observed in manzanita tejocotes. The lateral branches only for some time are purely monopodial; they become alternatively sympodial and monopodial and frequently more or less plagiotropic.

Reiteration could be observed sometimes when a very strong water sprouts appeared on the trunk or on the horizontal limb. Sometimes also the lateral branch becomes orthotropic and tends to form an additional trunk. It is possible that this

phenomenon will appear more frequently as the trees become older. Metamorphosis is common in tejocote trees and the branches frequently have larger angles in the lower than in the upper part of the crown.

According to what is known about apple trees, the crown is resistant to breaking when the main limbs are collocated on the trunk singularly or in groups of two (rarely three), but in this case the limbs of the pair should be situated on the opposite sides of the trunk. The branch insertion is strong when the basis of a branch is covered at least from one side with the tissues of the leader (Jankiewicz and Acosta-Zamudio 2003). The not pruned trees of manzanita tejocote tend to form naturally such a type of the crown with a marked leader when a tree is young. This may help the tree to support the heavy crop. In manzanita tejocote trees the scaffold branches in the lower part of the trunk have usually medium to large crotch angles, however somewhat in a distance from the trunk (5-20 cm) the branches bend slightly upward what is connected probably with the vigorous growth of the trees in their early years. More distal parts of the branches usually tend to be more plagiotropic except those, which show the tendency to reiterate. Such phenomenon occurs frequently also in several other species of trees of temperate zone (Bell 1991). The fact that tejocote trees form naturally very resistant and well-balanced crown is fortunate for fruit growers. Due to the resistance to long winter droughts and ability to grow on calcareous soils tejocote trees may be tried as potential fruit trees in countries, where such conditions are common.

REFERENCES

- Aguirre-Mandujano E., Nieto-Angel R., Hernández-Rodríguez L., Sánchez-Guzman M., Pérez-Alonzo C., Cuevas-Bernardino J.C. 2010. Caracterización de pectinas de tejocote (*Crataegus* spp.). Universidad Autónoma Chapingo, Chapingo, Méx., México. 69 p.
- Almaguer-Vargas G., Vidal-Lezama E., Borys M.W. 1992. Caracterización de la frutificación de tejocote (*Crataegus pubescens* H.B.K. (Steud)). Revista Chapingo 16 (77): 131-133. [in Spanish with English abstract]
- Bahri-Sahloul R., Ammar S., Grec S., Harzallah-Skhiri F. 2009. Chemical characterization of *Crataegus azarolus* L. fruit from 14 genotypes found in Tunisia. J. Hort. Sci. Biotech. 84: 23-28.
- Bell A.D. 1991. Plant form. An illustrated guide to flowering plant morphology. Oxford University Press, Oxford.
- Borys M.W. 1989. Valor ecológico del tejocote (*Crataegus* spp.). Congreso de Ecología 'La Era Ecológica' Puebla, Pue, pp. 111-124.
- Borys M.W. 1996. Valores del tejocote (*Crataegus* spp.): diversificación de caracteres. Revista Chapingo, Ser. Horticultura 5: 51-84. [in Spanish with English abstract]
- Borys M.W., Herrera-Guadarrama A.J. 1990. Fruit size components and organic composition of cultivated Mexican hawthorns (*Crataegus pubescens* H.B.K.) grafted onto a common stock. Acta Hort. 274: 93-102.
- Borys M.W., Leszczyńska-Borys H. 1994. Tejocote (*Crataegus* spp.): planta para solares, macetas e interiores. Revista Chapingo, Ser. Horticultura 1: 95-107. [in Spanish with English abstract]
- Borys M.W., Vega-Cuen A. 1984. Selección de tipos de tejocote (*Crataegus pubescens* H.B.K.) en el Estado de Chiapas, Puebla y México. Revista Chapingo 1(9): 193-199. [in Spanish with English abstract]
- Bustamante-O, F., Borys M.W. 1984. Preliminary evaluation of yields in two plantations of improved *Crataegus pubescens* H.B.K. Revista Di Agricultura Subtropical e Tropical 78: 741-749.
- Cachón-Ayora L.E., Nery G., Canalao de la C. H.E. 1976. Los suelos del área de influencia de Chapingo. Folleto Misceláneo. Colegio de Posgraduados. Montecillos, México.
- Calderon-Alcaraz E. 1983. La poda de árboles frutales. Editorial Limusa, México.
- Champagnat P. 1965 a. Physiologie de la croissance at de l'inhibition des bourgeons: dominance apicale et phenomene analogue. Encycl. Plant Physiol. 15(1): 1106-1164.
- Champagnat P. 1965 b. Rameaux court et rameaux long: problemes physiologiques. Encycl. Plant Physiol. 15(1): 1165-1171.

- Chen R., Rosen E., Masson P.H. 1999. Gravitropism in higher plants. *Plant Physiol.* 120: 343-350.
- Cruz-San Pedro E.A., Nieto-Angel R., Borys M.W. 1984. Comportamiento de plantulas de tejocote (*Crataegus pubescens* H.B.K.) a los suelos calcáreos. *Revista Chapingo* 9(45/46): 206-207. [in Spanish with English abstract]
- Esau K. 1965. *Plant Anatomy*. 2nd edition. J. Wiley, New York.
- Flores-García A., Pérez-Jiménez G., Carrizal-Ávila E. 1990. Evaluación de la producción de tejocote mejorado (*Crataegus pubescens* H.B.K.) en Tetela del Volcan, Morelos. Tesis Profesional. Depto de Fitotecnia. Universidad Autónoma Chapingo; Chapingo, México.
- Franco-Mora O., Aguirre-Ortega S., Morales-Rosales E.J., Gonzales-Huerta A., Gutierrez-Rodríguez F. 2010. Caracterización morfológica y bioquímica de frutos de tejocote (*Crataegus mexicana* DC.) de Lerma y Ocoyoacac, México. *Ciencia (Toluca)* 17: 61-66.
- Froehlichter T., Hennebelle T., Martin-Nizard F., Cleenewerck P., Hilbert J.L., Tortin F., Grec S. 2009. Phenolic profiles and antioxidative effect of hawthorn cell suspensions, fresh fruit and medicinal dried parts. *Food Chem.* 115: 897 - 903.
- García E. 1981. Modificaciones al sistema de Clasificación Climática de Köppen para adaptarlo a las condiciones de la República Mexicana. Instituto de Geografía. Universidad Nacional Autónoma de México. Mexico D.F.
- García-Mateos M. del R., Nieto-Angel R. 2011. Valor nutracéutico del tejocote (*Crataegus* spp.) en Mexico. Universidad Autónoma Chapingo, Chapingo, Méx., México 63 p.
- Grisvard G. 1989. La poda de los árboles frutales, peral y manzano. Mundi-Prensa, Madrid.
- Hallé F., Oldeman R.A.A. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson et Cie Editeurs, Paris. [in French with English abstract]
- Higareda-R. A., Prado E.A., Salazar-Montoya J.A., Ramos-Ramírez G.E., Rosales D.M. 1995. El contenido comercial de pectina de la pulpa de tejocote. *Revista Chapingo Ser. Horticultura* 1: 155-157. [in Spanish with English abstract]
- Jankiewicz L.S. 1971. Gravitropism in higher plants. In: Gordon M.J., Cohen M.J. (eds), *Gravity and the Organism*. University of Chicago Press. Chicago, USA pp. 317-331.
- Jankiewicz L.S., Acosta-Zamudio C. 2003. Auxinas. In: Jankiewicz L.S. (ed.), *Reguladores del Crecimiento, Desarrollo y Resistencia en Plantas*. vol. 1. Propiedades y acción. Universidad Autónoma Chapingo, México; Ediciones Mundi-Prensa, Madrid.
- Jankiewicz L.S., Stecki Z.J. 1976. Some mechanisms responsible for differences in tree form. In: Cannel M.G.R., Last F.T. (eds.), *Tree physiology and yield improvement*. Academic Press, London.
- Jenkins G.I. 2009. Signal transduction in response to UV-B radiation. *Annu. Rev. Plant Biol.* 60: 407-431.
- Kaczmarek F., Mrugasiewicz K., Wrociński T. 1973. Isolation of hyperoside and vitexin rhamnoside from inflorescences of *Crataegus* and investigation on their effect on coronary blood flow. *Herba Polonica* 19: 138-143.
- Li Z., Wakao S., Fischer B.B., Niyogi K.K. 2009. Sensing and responding to excess light. *Annu. Rev. Plant Biol.* 60: 239-260.
- McSteen P., Leyser O. 2005. Shoot branching. *Annu. Rev. Plant Biol.* 56: 353-74.
- Nieto-Angel R., Borys M.W. 1989. Banco de Germoplasma de Tejocote (*Crataegus* spp.) de la República Mexicana. *Revista Chapingo, Ser. Horticultura* 1: 95-107. [in Spanish with English abstract]
- Nieto-Angel R., Borys M.W. 1991. El tejocote (*Crataegus* spp.) en México. In: Palomino-H. P.R.G., Castillo F., Gonzalez-H. V.A., Livera-M. M. (eds), *Avances en el estudio de los recursos fitogenéticos de México*. Sociedad Mexicana de Fitogenética. Chapingo, México.
- Nieto-Angel R., Borys M.W. 2008. Germoplasma y usos del tejocote en México. In: Cruz-C. J.G., Torrez-L. P.A. (eds), *Enfoques tecnológicos en la fruticultura. Un tributo a Raúl Mosqueda*. UACH, México.
- Nieto-Angel R., Borys M.W., Barrera-Guerra J.L. 1984. Tercer año de comportamiento vegetativo de 4 cultivares de manzana (*Malus pumila* Mill) injertados en tejocote (*Crataegus pubescens*

- H.B.K.). X Congreso Nacional de Fitogenética. Aguascalientes Ags., México.
- Núñez-Colín C.A. 2009. The tejocote (*Crataegus* sp.) a Mexican plant, genetic resource that is wasted. A review. Proc. Intern. Symposium on Underutilized Plants for Food Security, Nutrition, Income and Sustainability Development. Arusha, Tanzania. 3-6.03.2008. Acta Hort. 806: 339-346.
- Núñez-Colín, C.A., Hernández-Martínez M.Á. 2011. La problemática en la taxonomía de los recursos genéticos de tejocote (*Crataegus* sp.) en México. Rev. Mex. Ciencias Agr. 2: 141-153. [in Spanish with English abstract]
- Núñez-Colín C.A., Nieto-Angel R., Barrientos-Priego A.F., Segura S., Sahagun-Castellanos J., Gonzáles-Andrés F. 2008. Distribución y caracterización eco-climática del género *Crataegus* (Rosaceae subfam. Maloideae) en México. Revista Chapingo. Ser. Horticultura 14: 177-184. [In Spanish with English abstract]
- Picchioni G.A., Graham C.J. 2001. Salinity, growth and ion selectivity of container-grown *Crataegus opaca*. Sci. Hortic. 90: 151-166.
- Pérez-Ortega S.A., Méndez-Santiago A.H. 2001. Descripción de la arquitectura de árboles de tejocote (*Crataegus* spp.) del banco de germoplasma de la Universidad Autónoma Chapingo. Tesis - ingeniero agrónomo. Depto de Fitotecnia UACH. Chapingo, México.
- Pieniążek J., Jankiewicz L.S. 1966. Development of collateral buds due to benzylaminopurine in dormant apple shoots. Bull. Acad. Polon. Sci. Ser. Biol. 14: 185-187.
- Rey J.Y. 1998. L'étude architecturale du goyavier. II. Expérimentations. Fruits 53: 251-255. [in French with English abstract]
- Takeo S., Minoru K. 1989. Lateral bud development and shoot growth in low-pruned *Morus alba* as affected by stem orientation. Physiol. Plant. 76: 493-499.
- Wang GuangQuan, Meng QingJie, Li ZongLan, Wang GuanZhen 1998. FuHong Zi, an early, fine hawthorn germplasm. Crop Genetic Resources 1: 48 (Hort. Abstr.)
- Wang JinGuang 1998. Wulenghong a new hawthorn variety. China Fruits 2: 55. (Hort. Abstr.)