Review paper
Прегледни рад
UDC: 581.46:634.2
DOI: 10.7251/AGREN1601001M

University of Banjaluka, Faculty of Agriculture
Agro-knowledge Journal

Morphological Characterization of Buds Being Donors of Apex for Molecular Confirmation of Differentiation of Meristem into Permanent Tissues of Stone Fruit Trees (*Prunus* sp.)

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Abstract

Molecular confirmation of the process of differentiation of meristematic tissue of plants is primarily based on histomorphological characterization of the tissues carrying these processes. For perennial plants – fruit trees, the knowledge of these processes is important to define runtime type and pomotechnical treatments but also to identify the genes responsible for determination of the apices into a generative phase of differentiation. Which apex extraction techniques will be applied depends on the structure of buds, i.e. whether an apex differentiates only into generative elements – pure flower buds, or the differentiation goes into two directions: differentiation of leaf primordium with axillar meristematic dome and differentiation of generative elements of flowers in the peak or lateral zone of an apex – mixed buds. The fruit trees of the genus *Prunus* have purely flower buds and for this purpose the whole apex is taken, between protection – cover leaves, on lateral positions of all collateral buds at shoot nodes. The moment of initiation of determination and the dynamics of differentiation of generative buds are different at different type of shoots on a tree. It is therefore necessary to know the shoots growth cessation time which is in correlation with apex determination. Fruit trees of the genus *Prunus* are ending the growth of shoots by rejection of shoot peaks, and the cast away time depends on the type, length and the position of shoots.

Key words: determination, extraction of meristem, generative buds

Introduction

Flowering in all fruit crops is of great importance because yield mostly depends on the number and quality of flower buds formed. The most important part towards fruiting is the flower initiation (Mićić et al., 1992; Benlloch et al., 2007; Hanke et al., 2007; Andreini and Bartolini, 2008; Yang and Jiao, 2016). For molecular confirmation of meristematic tissue differentiation process, which determines and differentiates into permanent tissues, it is crucial to reliably and adequately take meristematic tissue samples (buds' apices). The buds with apex that will retain undifferentiated meristematic status and the buds with apex in which the synthesis of specific proteins is initiated, which are responsible for cell determination and further differentiation have a different position on the shoot node. The bud positions at nodes and along the shoots, which enable a very reliable sampling of apices retaining vegetative status, as well as of apices entering a process of generative differentiation, were identified in stone fruit trees (Mićić, 1994; Mićić and Đurić, 1995).

The first part of this paper deals with morpho–histological analysis of the position of apices retaining vegetative character and of apices directed to a generative differentiation i.e. which differentiate into flower buds. The second part provides a morphological analysis of determining the moment when certain apices irreversibly enter the process of generative differentiation.

I. Morpho-histological analysis of the position of apices retaining vegetative character and apices directed to generative differentiation at individual nodes and along the shoots

Morpho–histological analyses of the formation of meristematic domes at nodes, i.e. in leaf axils along the shoots in stone fruit trees, show the following algorithm (Mićić and Čmelik, 1988; Mićić, 1992a, 1992b; Mićić et al., 1992; Mićić and Đurić, 1994; 1995; Đurić et al., 1999a, 1999b):

1. In winter vegetative buds, only meristematic domes – apices were differentiated, without the differentiation of primordia of other organs (Fig. 1), or with a few primordia leaves;
2. Meristematic domes of winter vegetative buds begin to differentiate leaf primordia in spring (Fig. 2) with meristematic tissue cells retained in their axils (Fig. 3);
3. Meristem in the leaf primordia axil forms primary cover leaves with meristematic tissue cells also retained in their axils (Fig. 4);
4. By the formation of primary cover leaves and retention of meristem in their axils, a meristematic basis of collateral buds is formed (Fig. 5) at all the nodes on which true shoot leaves were formed. Thus, at each node of a shoot, in the leaf axil, there are three meristematic domes (apices): central (c) and two lateral domes (b1

and b2) (further course of differentiation of these meristematic domes is determined by their nodal positions);

5. In an early stage of differentiation all of the three meristematic domes differentiate the cover leaves in a way that lateral meristematic domes always have a lower number of cover leaves compared to the central meristematic dome.
6. Differentiation of cover leaves of meristematic domes at a node, follows the formation of meristematic tissue of procambium that remains in connection with the cambium of a node in such a way that procambium of central meristematic dome has a direct connection with the cambium at shoot nodes, whereas the procambium of lateral meristematic domes has the status of lateral branching of the procambium of centrally positioned meristematic dome (Fig. 6 and 7);
7. Towards the end of vegetation, lateral meristematic domes, regardless of which node of a shoot they are at, give only generative buds or abort. The central meristematic domes, positioned at the nodes in the base part of a shoot, give generative buds, and those in the peak part of a shoot give vegetative buds, with a clear positioning border along the shoot.

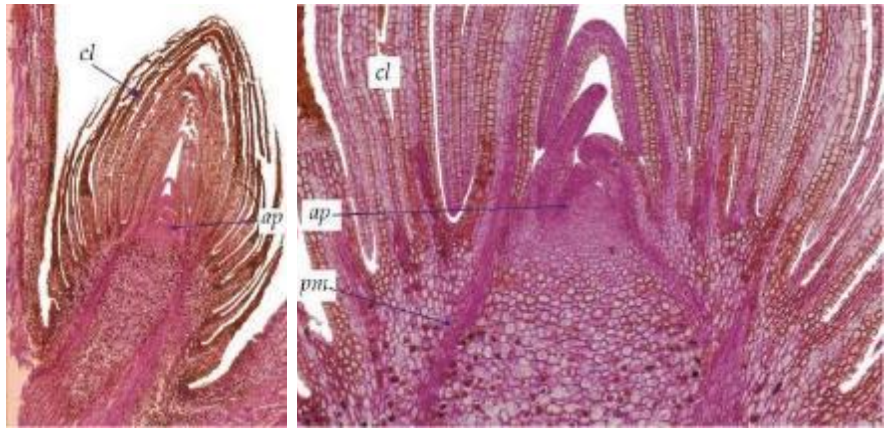

Fig. 1. Longitudinal section of plum vegetative bud when dormant: cl – covering leaves, ap – apex; pm – procambium meristem (Mićić and Čmelik, 1983).

Уздужни пресјек вегетативног пупољка шљиве у периоду мировања: cl *–покровни листићи*, ap – *апекс*; pm – *меристем прокамбијума (Mićić and Čmelik, 1983).*

Central meristematic dome of a node in the zone of vegetative buds, at the upper part of shoot, can form a generative bud only on the nodes with early defoliation. Lateral meristematic domes of stone fruits in normal development, give only generative buds or abort at various stages of differentiation (Fig. 8O, 8P, 8R).

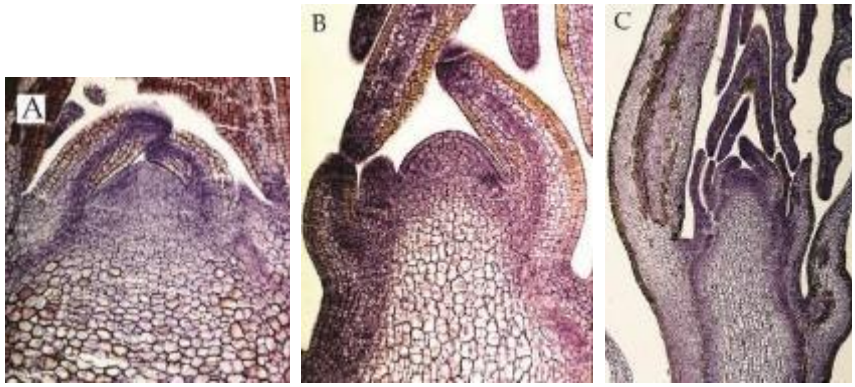

Fig. 2. Longitudinal sections of plum apex in vegetation shift. A – meristematic dome; the first morpho–histological manifestations of apex development in spring; B – elevation of meristem; C – leaf primordia differentiation (Mićić et al., 1998).

Уздужни пресјеци апекса шљиве у кретању вегетације. A – *меристематска купа*; *прве морфо-хистолошке манифестације развоја апекса у пролеће*; B – *издизање меристема*; C – *диференцијација примордија листова (Mićić et al., 1998).*

Fig. 3. Longitudinal section of leaf primordia axil with the retained meristem tissue – new meristematic domes. D – Cross section of a vegetative bud in development at the beginning of vegetation*;* E – ap – apex – meristematic dome in leaf primordium axil (Mićić et al., 1998).

Уздужни пресјек пазуха примордије листа са заосталим меристемским ткивом – ове меристематске купе. D – *Попречни пресјек вегетативног пупољка у развоју почетком вегетације;* E – ap – *апекс – меристематска купа у пазуху примордије листа (Mićić et al., 1998).*

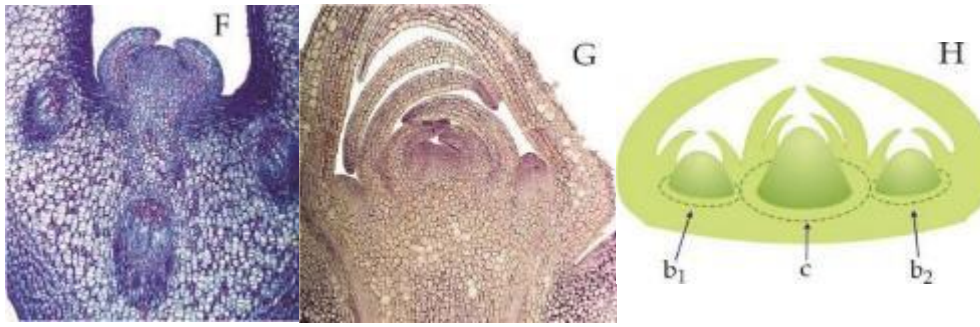

Fig. 4. Longitudinal section of meristematic dome in leaf primordia axil with primary cover leaves formed (F). Meristematic tissue, retained in the axil of primary cover leaves, gives lateral meristematic domes of a node (G). H – graphical view of collateral buds base that is characteristic for all nodes on stone fruits shoots: c – central meristematic dome, b_1 and b_2 – lateral meristematic domes (Mićić et al., 1999).

*Уздужни пресјек меристематске купе у пазуху примордије листа са формираним примарним покровним листићима (*F*). У пазуху примарних покровних листића заостаје меристематско ткиво које даје бочне меристематске купе нодуса (*G*).* H – *графички приказ основе колатералних пупољака карактеристичне за све нодусе на младарима коштичавих воћака:* c – *централна меристематска купа,* b_1 *и* b_2 *– бочне меристематске купе (Mićić et al., 1999).*

Fig. 5. Histological section of meristematic base of young collateral bud in a shoot leaf axil: I – longitudinal section, J – cross–section (Mićić, 1993). Formation of cover leaves for all three meristematic domes on a shoot node is the only morphological manifestation of growth and development before certain meristematic domes enter the process of generative differentiation.

Хистолошки пресјек меристематске основе младог колатералног пупоља у пазуху листа младара: I – уздужни пресјек, J – попречни пресјек (Mićić and Đurić, 1995). Формирање покровних листића за све три меристематске купе на нодусу младара представља једину морфолошку манифестацију раста и развоја до уласка одређених меристематских купа у процес генеративне диференцијације.

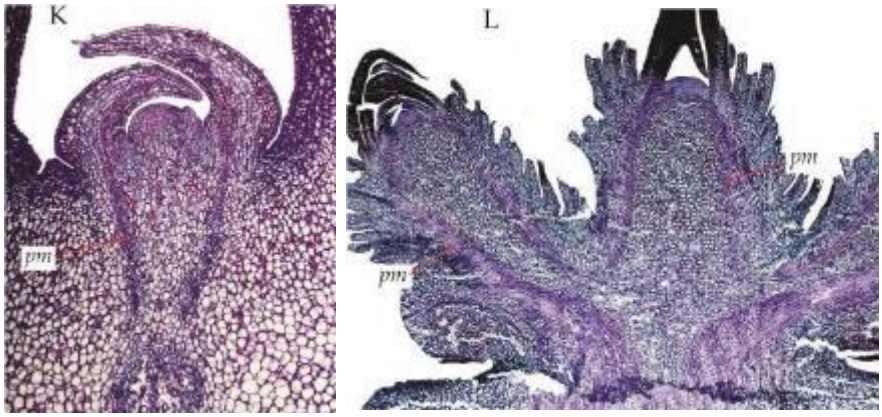

Fig. 6. With the formation of meristematic base of colateral buds, procambium meristematic tissue is formed (pm), connecting meristematic tissues of central and lateral apices with node cambium (K). Meristematic tissue of the procambium of central meristematic dome builds a direct connection with the cambium of a node, whereas meristematic tissue of the procambium of lateral meristematic domes represents a lateral branching of the procambium of central meristematic dome (L) (Đurić et al., 1999b).

*Са формирањем меристематске основе колетералних пупољака формирано је и меристематско ткиво прокамбијума (*pm*) које повезује меристематска ткива централног и бочних апекса са камбијумом нодуса (*K*). Меристематско ткиво прокамбијума централне меристематске купе гради директну везу са камбијумом нодуса, док меристематско ткиво прокамбијума бочних меристематских купа представља бочна разграњења прокамбијума централне вегетационе купе (*L*) (Đurić et al., 1999b).*

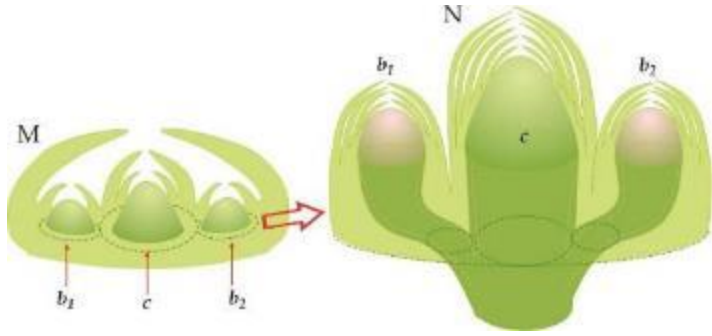

Fig. 7. Schematic diagram of the development of meristematic base collateral buds of a node (b_1, c, b_2), from their formation (M) up to entering the resting period.
Шематски приказ развоја меристематске основе колатералних пупољака нодуса (b_1, c, b_2*) од формирања до уласка у период мировања*

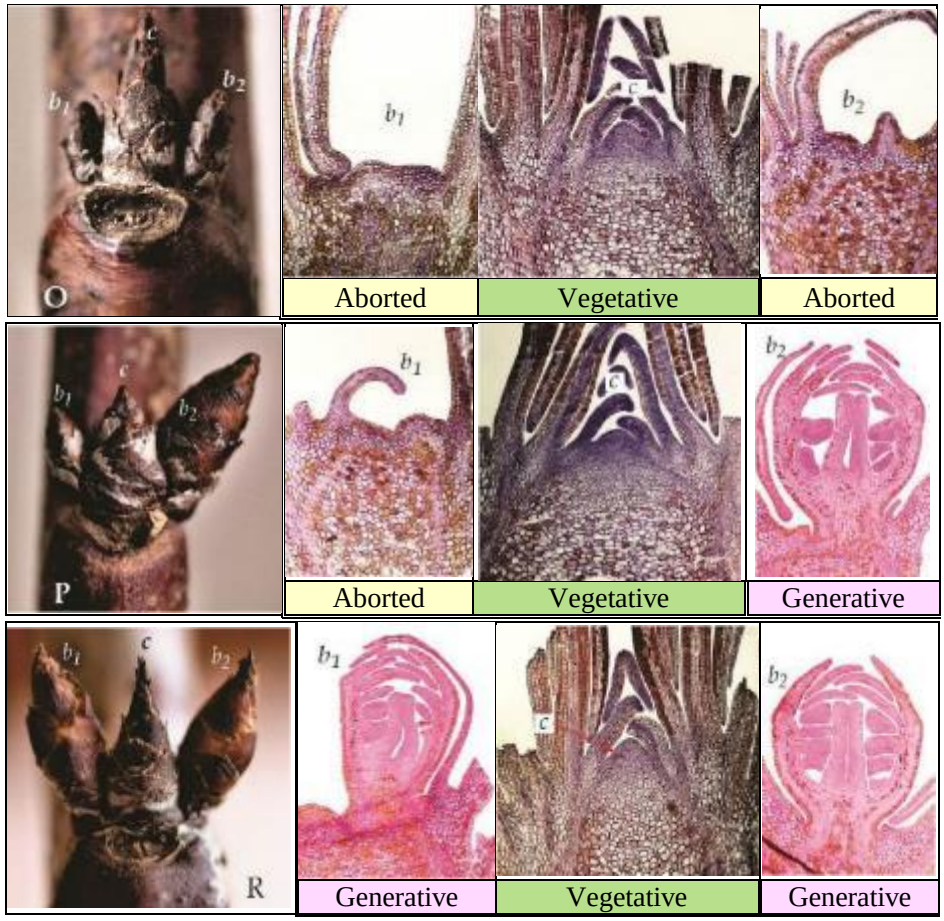

Fig. 8. Combinations of representation of lateral and the central bud in a collateral arrangement on the upper nodes a plum annual growths (*Prunus domestica* L.) during rest period: O – Central meristematic dome (c) formed a vegetative bud and lateral meristematic domes atrophied (b_1, b_2); P – Central meristematic dome formed a vegetative bud (c) while one lateral meristematic dome atrophied (b_1), and the other lateral meristematic dome differentiated into a generative bud (b_2); R – Central meristematic dome formed a vegetative bud (c) and both lateral meristematic domes differentiated into generative buds (b_1, b_2), (Mićić et al., 2015)

*Комбинације заступљености бочних и централног пупољка у колатералном распореду на горњим нодусима једногодишњих прираста шљиве (*Prunus domestica *L.) у периоду мировања:* O *– централна меристематска купа (*c*) је формирала вегетативни пупољак, бочне меристематске купе су атрофирале;* P *– централна меристематска купа је формирала вегетативни пупољак (*c*) док је једна бочна меристематска купа атрофирала (*b_1*), а друга бочна меристематска купа је диференцирала у генеративни пупољак (*b_2*);* R *– централна меристематска купа је формирала вегетативни пупољак (*c*), а обе бочне меристематске купе су диференцирале у генеративне пупољке (*b_1, b_2*) (Mićić et al., 2015).*

Depending on the moment of dying – atrophy of these meristematic domes, different morphological traces can be observed on the nodes. If atrophy occurs very early, observed from the centrally positioned bud of a shoot node, one can see covering leaves' wrinkles on lateral meristematic dome. If the abortion of lateral meristematic dome occurred in later stages of differentiation, smaller lateral buds, with atrophied meristem, can be found on the node until the beginning of the next growing season, owing to the living activities of their cover leaves (Fig. 8O, 8P).

Different types of stone fruit trees on different growth categories have different lengths of zone with generative buds at central meristematic domes at the base and vegetative buds at the top of shoot, with a clear line between these two zones (Figs. 9, 10).

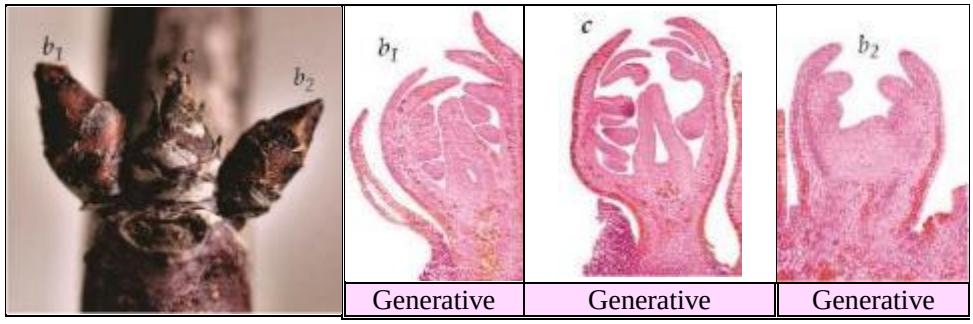

Fig. 9. On the base nodes of plum one–year–old growth all the three meristematic domes (b_1, c, b_2) of a node differentiate into generative buds (Mićić et al., 2015).

На базним нодусима једногодишњих прираста шљиве све три меристематске купе нодуса (b_1, c, b_2*) диференцирају у генеративне пупољке (Mićić et al., 2015).*

II. Morphological characterization of the moment of change of meristem character

In plums, as a species belonging to the genus *Prunus*, growth of shoots ends by rejection of apical meristem (Fig. 11), which is a basic characteristic of sympodial branching (Mićić and Đurić, 1995). A consequence of shoot apex rejection, is morphologically identified at all shoots apices showing rejected leaf scars by the side of terminal buds and a scar of abscission zone of the rejected shoot apex (Figs. 12, 13, 14). Our research (Mićić and Đurić, 1995) shows that the growth of shoots in other species of genus *Prunus* ends the same way, while Kostes et al. (2014) reported that sour cherry, peach and almond have monopodial, whereas apricot has simpodial branching.

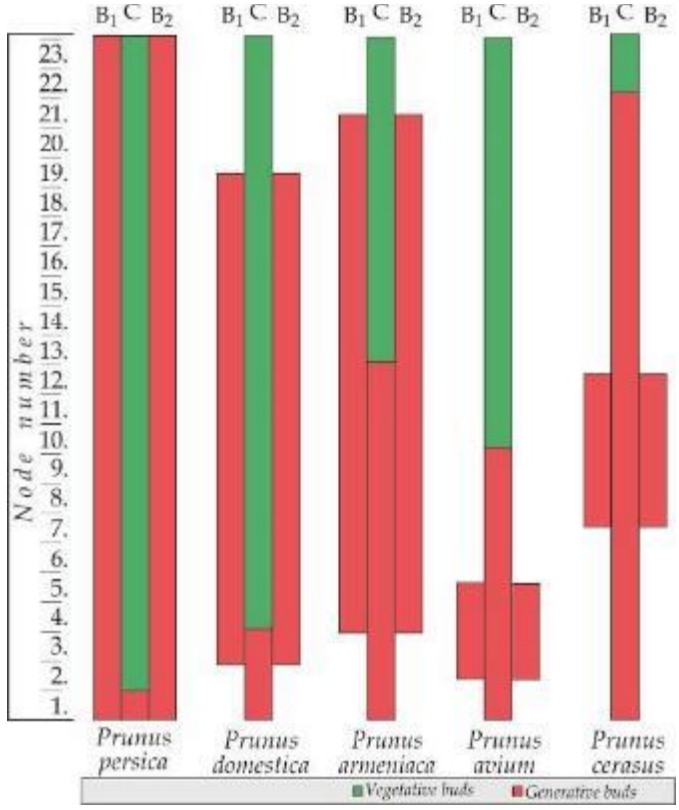

Fig. 10. Zones of dominant representation of vegetative and generative buds on the nodes of certain species of stone fruit trees (C – central position on a node; B_1 and B_2 – lateral positions on a node). Exclusively generative buds are formed in all species of stone fruit trees on node lateral positions. Generative buds are formed in the central position of a node in growth base, whereas vegetative buds are formed in the upper zone. The border between the two of them is always clearly expressed (adapted from: Mićić and Đurić, 1995).

*Зоне доминантне заступљености вегетативних и генеративних пупољака на нодусима појединих врста коштичавих воћака (*C *– централна позиција на нодусу;* B_1 *и* B_2 *– бочне позиције на нодусу). Код свих врста коштичавих воћака на бочним позицијама нодуса формирају се искључиво генеративни пупољци. На централним позицијама на нодусу у бази прираста формирају се генеративни пупољци, а у вршном дијелу вегетативни пупољци. Граница између њих увијек је јасно изражена (адаптирано према Mićić and Đurić, 1995).*

Fig. 11. Morphological indicators of plum shoot apex growth: S – Shoots apex in a vigorous growth – the ratio of the size of leaves is in correlation with growth dynamics; T – The first symptoms of the beginning of shoot growth braking – evident is a difference in the size of leaves at the shoot apex compared to those directly below the apex.

Морфолошки показатељи раста врха младара шљиве: S – *врх младара у интензивном порасту – однос величине листова је у корелацији са динамиком пораста;* T – *први симптоми почетка кочења раста младара – изражена је разлика у величини листова на врху и листова непосредно испод врха младара.*

A relation between morphological indicators of growth braking i.e. rejection of apical meristem and determination of buds at nodes, was determined by a dynamic cutting of the upper part of shoots (Mićić and Đurić, 1995; Mićić et al., 1998), i.e. making apical dominance of those nodes that have previously been found to be giving exclusively generative buds in their normal growth and development (Fig. 15). By bringing these nodes into apical dominance, it was found out that meristematic domes at these nodes maintain their vegetative character until the moment of occurrence of growth braking symptoms and apical meristem rejection (Figs. 16, 17, 19AD and 19AE).

By bringing meristematic domes of the same positions in apical dominance after rejection of apical meristem, they shall differentiate into generative buds (Figs. 18, 19AF) the same way as it happens in a normal growth of shoots. This means that meristematic domes of these nodes had already been irrevocably directed into the program of generative differentiation.

Fig. 12. Morphological indicators of plum shoot apex growth: U - shoot growth stopped (shoot apical leaf – sal reached normal size), in course is formation of abscission zone for rejection of a shoot apex; V - appearance of shoot apex after the rejection of apical meristem, rsa – a scar of rejected shoot apex (Mićić and Đurić, 1995).

Морфолошки показатељи раста врха младара шљиве: U *– раст младара заустављен (вршни лист младара –* sal*, достигао нормалну величину), у току је формирање апсцисне зоне за одбацивање врха младара;* V *– изглед врха младара послије одбацивања апикалног меристема,* rsa *– ожиљак од одбаченог врха младара (Mićić and Đurić, 1995).*

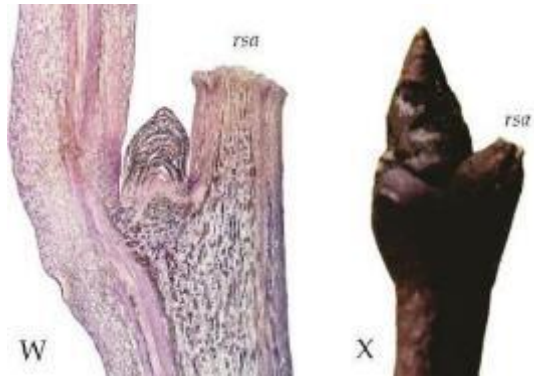

Fig. 13. Morphological characterization of shoot apex rejection: W – longitudinal histological section of shoot apex immediately after rejection of the apical meristem. X – on the apices of all annual growth in the rest period, near the apical buds, one can observe rejected leaves scars and rejected apical meristem scars (rsa –scar of rejected shoot apex) (Mićić et al., 1998).

Морфолошка карактеризација одбацивања врха младара: W *– уздужни хистолошки пресјек врха младара непосредно по одбацивању апикалног меристема.* X *– на врховима свих једногодишњих прираста у периоду мировања поред вршних пупољака уочавају се ожиљци од одбаченог листа и ожиљци од одбаченог апикалног меристема (*rsa *– остатак од одбаченог врха младара)(Mićić et al., 1998).*

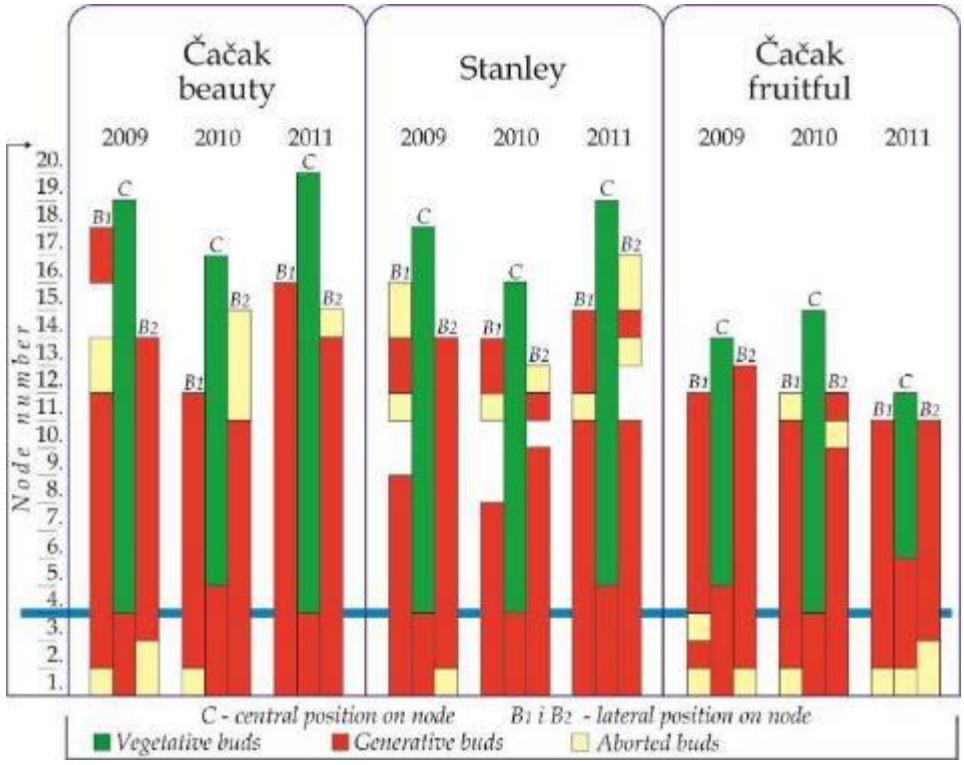

Fig. 14. The structure of buds on the nodes of mixed fruit bearing shoots of plum tree (adapted from Mićić et al., 2015). To prove the moment of irreversible entering of meristematic domes into generative differentiation program, important consideration relates to the representation of the buds at the base nodes of growth. The graph illustrates that in all the years of testing, in all three varieties tested, the central meristematic domes (C) of three base nodes differentiated into generative buds (marked by blue line). By a dynamic bringing of these meristematic domes into apical dominance by shoots pruning, one can determine the moment when these meristematic domes will not maintain their vegetative character, i.e. when the effect of apical dominance will have no influence on the course of differentiation of meristematic domes at these nodes.

Структура пупољака на нодусима мјешовитих родних гранчица шљиве (адаптирано према Мићић et al., 2015). За доказивање момента неповратног уласка меристематских купа у генеративни програм диференцијације битна констатација односи се на заступљеност пупољака на базним нодусима прираста. На графичком приказу види се да су у свим испитиваним годинама код све три испитиване сорте централне меристематске купе (C) *на три базна нодуса диференцирале у генеративне пупољке (означено плавом линијом). Динамичким довођењем ових меристеамтких купа у апикалну доминацију прикраћивањем младара, може се утврдити моменат када ове меристематске купе неће задржати вегетативни карактер, односно, када ефекат апикалне доминације неће имати утицај на ток диференцијације меристематских купа ових нодуса.*

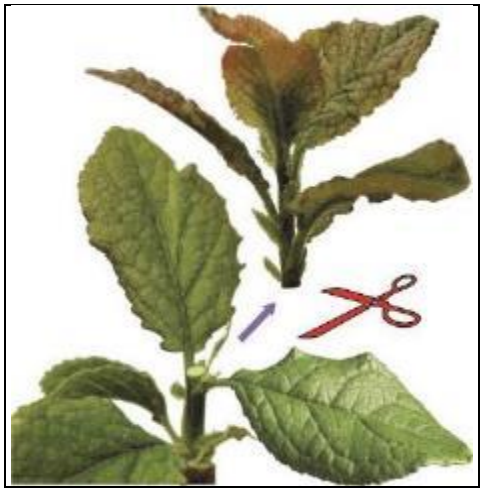

Fig. 15 and 16. By pruning of shoots to three basic leaves, these nodes are brought to apical dominance. The effect of apical dominance is that meristematic domes, by their nodal position, in the spontaneous growth and development, are irreversibly directed to generative program of differentiation, retain their vegetative character, i.e. do not enter the program of generative differentiation (Mićić, 1993).

**a, b, c, d: before cutting; a', b', c', d': after cutting*

By successive bringing of meristematic domes into the apical dominance, with their nodal positions, in their spontaneous growth and development, inevitably directed to generative program of differentiation, it is possible to precisely determine the moment when the apices of these buds are irreversibly directed from vegetative phase into generative program of differentiation. Namely, the shoots pruning during vegetative differentiation of meristem of lateral buds (a, b, c), results in the formation of vegetative buds, whereas shoots pruning after their entering the generative program of differentiation (d) will not affect a further course of differentiation and generative buds will be normally formed (see Fig. 19), (Mićić, 1993).

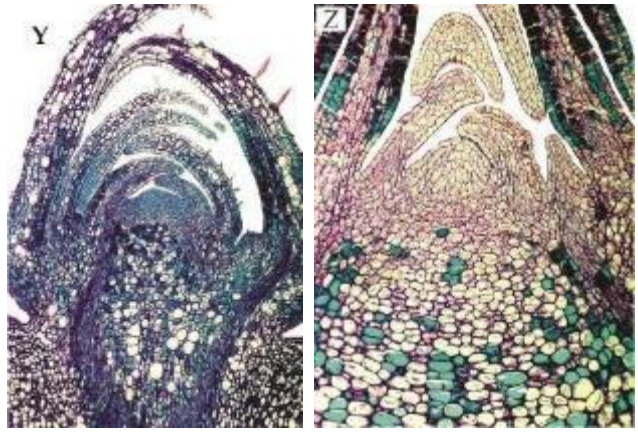

Fig. 17. Longitudinal histological sections of buds in leaf axils at nodes that, by pruning of shoots, were successively brought into apical dominance and retained their vegetative character: Y – apex in the middle of vegetation; Z – apex in the rest period.

Уздужни хистолошки пресјеци пупољака у пазуху листа на нодусима који су сукцесивним прикраћивањем младара довођени у апикалну доминацију и који су задржали вегетативни карактер: Y *– апекс средином вегетације;* Z *– апекс у периоду мировања*

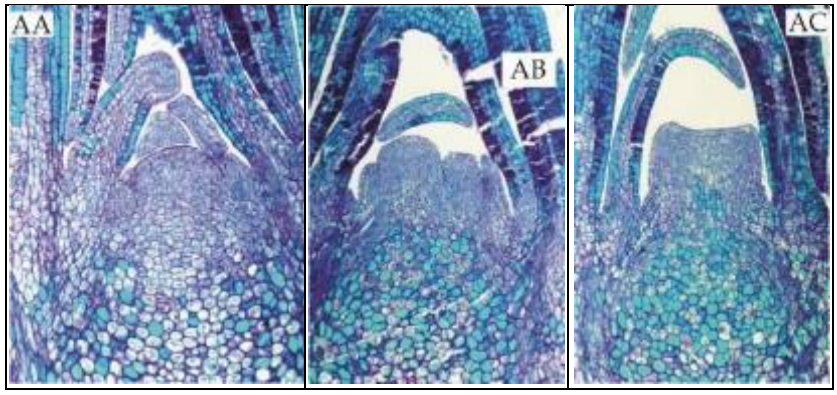

Fig. 18. Longitudinal histological sections of buds in leaf axils at nodes that, by pruning of shoots, were successively brought into apical dominance from the moment of stopping of growth and rejection of shoot apex: AA) expansion and elevation of apex; AB) occurrence of the first primordial elements of flower axis; AC) initial.

Уздужни хистолошки пресјеци пупољака у пазуху листа на нодусима који су сукцесивним прикраћивањем младара довођени у апикалну доминацију од момента престанка раста и одбацивања врха младара: AA*) ширење и издизање апекса;* AB*) појава првих примордијалних елемената осовине цвијета;* AC*) иницијална диференцијација набора који дају чашичне листиће и зид чашичног удубљења на примордији цвјетног пупољка.*

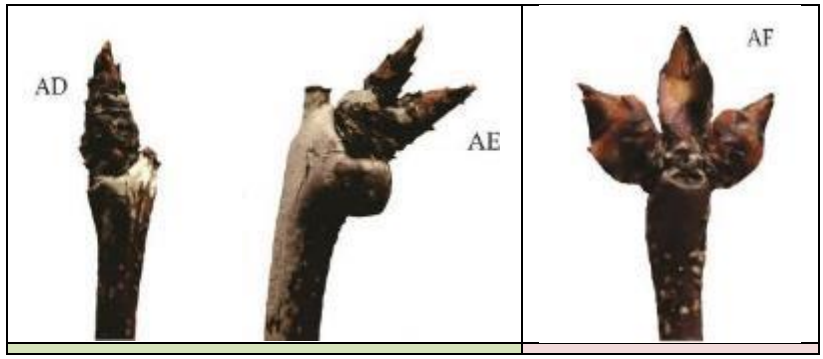

Fig. 19. The buds formed on top of pruned shoots (see Fig. 16): AD and AE – buds that retained vegetative character (pruning conducted before rejection of shoot apex); AF – buds that differentiated in generative buds after being brought into apical dominance after rejection of shoot apices, (Mićić 1993).

Пупољци формирани на врху прикраћених младара (видјети Сл. 16.): AD *и* AE *– пупољци који су задржали вегетативни карактер (прикраћивање изведено прије одбацивања врха младара);* AF *– пупољци који су диференцирали у генеративне пупољке послије довођења у апикалну доминацију по одбацивању врха младара.*

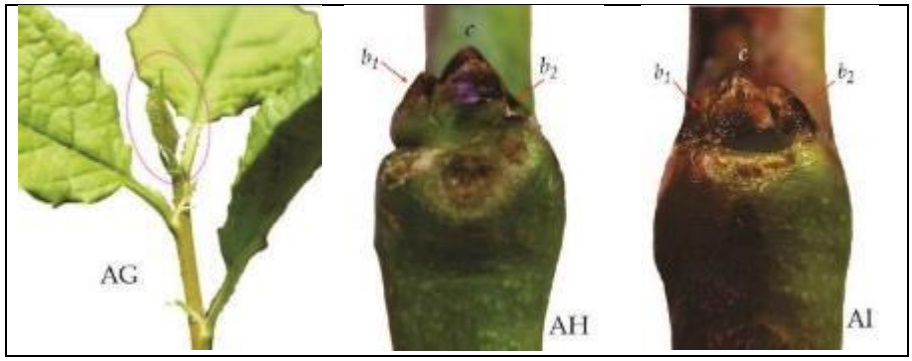

Fig. 20. The appearance of shoot tip just before the rejection of shoot apex (AG). Morphological appearance of lateral buds in the middle part of shoot in which the process of initial differentiation of flower primordia was determined at the histo–morphological level (AH, AI), (Mićić et al., 2015).

*Изглед пупољака на нодусу непосредно прије одбацивања врха младара (*AG*). Морфолошки изглед бочних пупољака у којима је на хисто-морфолошком нивоу утврђен процес иницијалне диференцијације примордија цвијета (*AH, AI*), (Mićić et al., 2015).*

Stopping of the growth of a shoot apex (Fig. 20. AG) is a reliable morphological indicator of the apices of node lateral buds entering irreversible into a generative program of differentiation (Fig. 20. AH, AI).

From this morphological indicator to the initial changes at the histological level that confirm processes of differentiation of initial structures of the flower axis, it is available for the study of molecular characterization of reprogramming of vegetative meristem into generative apex.

Algorithm of these processes makes it clear that extraction of the apex, for the purpose of molecular characterization of meristematic domes which were determined or entered into a process of generative differentiation, should be performed from lateral buds of a node (b1, b2). For molecular confirmation of retention of vegetative character, meristematic domes should be taken from central buds of a node at the upper part very of a shoot, as it is illustrated at Fig. 21 (see also Figs. 10 and 14).

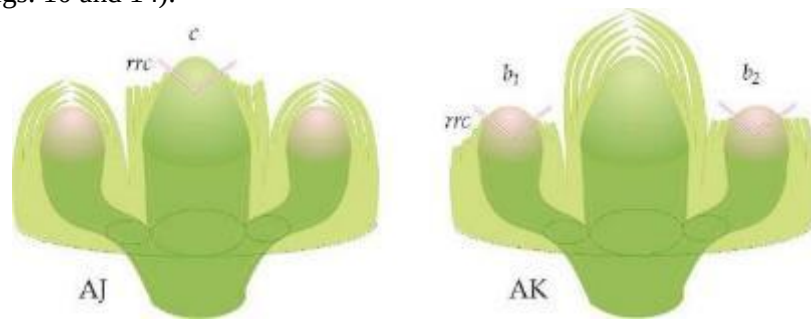

Fig. 21. Schematic view of method for extraction of apices for molecular characterization of meristem transformation from vegetative to generative meristem: AJ – apex of vegetative character (c – apex of a bud centrally positioned at a node at the upper part of a shoot; rrc – remnants of removed cover leaves (See Fig.10 and 14); AK – apex in which there is a process of determination of meristem of generative character: b_1, b_2 – apices of buds laterally positioned at nodes; rrc – remnants of removed cover leaves, but this can not be confirmed on histological level.

Шематски приказ методе екстракције апекса за молекуларну карактеризацију трансформације меристема из вегетативног у генеративни меристем: AJ – *апекс вегетативног карактера (*c – *апекс пупољка централног положаја на нодусу,* rrc – *остаци отклоњених покровних листића) (видјети Сл. 10 і 14);* AK – *апекс у коме се одвија процес детерминације меристема генеративног карактера и остале секвенце диференцијације генеративних пупољака (*b_1, b_2 – *апекс пупољака бочно позиционираних на нодусима),* rrc – *остатци отклоњених покровних листића, али ово не може бити потврђено на хистолошком нивоу.*

Conclusion

Differentiation of generative buds and blooming are a prerequisite for fruiting of plants. Fruit trees are perennial policarpic plants and differentiation of generative buds is preceding the year of fruiting. Knowing the moment of transition from the vegetative to generative phase of differentiation, as well factors that affect this process, are crucial for the implementation of pomotechnical measures aimed at regular fruiting. In the pree-molecular markers era, the basic method of determining the transition to generative differentiation were histological analysis of buds and meristematic domes.

Molecular techniques now allow the determination of the moment of transition to the generative differentiation but also the determination of flowering genes.

The extraction of the apex, for the purpose of molecular characterization of meristematic domes which were determined or entered into a process of generative differentiation, should be performed from lateral buds of a node, while for molecular confirmation of retention of vegetative character, meristematic domes should be taken from central buds of a node at the upper part very of a shoot.

Acknowledgements: This study was a part of the project (grant No. 19/6-020/961-141/12) co-financed by the Ministry of Science and Technology of the Republic of Srpska.

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Морфолошка карактеризација пупољака донора апекса за молекуларно потврђивање диференцијације меристема у трајна ткива код коштичавих воћака (*Prunus* sp.)

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Сажетак

Молекуларна потврда процеса диференцијације меристемских ткива биљака првенствено се заснива на хисто-морфолошкој карактеризацији ткива у којима се ови процеси дешавају. Код вишегодишњих биљака - воћака, познавање ових процеса је важно да би се дефинисали динамика и помотехнички третмани, али и да се идентификују гени одговорни за детерминацију апекса и њихово усмјеравање у генеративну фазу диференцијације. Која техника екстракције апекса ће бити примјењена зависи од структуре пупољака, односно да ли апекс диференцира само у генеративне елементе – чисто цвјетни пупољци, или диференцијација иде у два правца: диференцијација лисних примордија са бочним меристемским купама и диференцијација генеративних елемената цвијета на врху или бочно на апексу - мјешовити пупољци. Воћке рода *Prunus* имају чисто цвјетне пупољке и за ову сврху се узима цијели апекс, између покровних листића, са бочних позиција свих колатералних пупољака нодуса. Моменат покретања детерминације и динамика диференцијације генеративних пупољака су различити на различитим типовима прираста. Због тога је неопходно да се зна вријеме престанка раста младара који је у корелацији са детерминацијом апекса. Воћке рода *Prunus* завршавају раст младара одбацивањем врха, а вријеме одбацивања зависи од типа, дужине и положаја младара.

Кључне ријечи: детерминација, екстракција меристема, генеративни пупољци

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Received: September 13, 2016
Accepted: November 09, 2016