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The Involvement of Indoleacetic Acid in Paradormancy and Syllep-tic Shoot Development of Grafted Peach Trees and Hybrid Root-stocks

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Summary

The physiological mechanisms controlling the induction of lateral branching, which is part of the expression of growth vigour, were investigated in two hybrid rootstocks (GF 677 and Mr.S. 2/5) widely used in peach [*Prunus persica* (L.) Batsch] cultivation that were grafted to a nectarine scion (cv. 'Big Top'). As expected, field-grown rootstocks showed different degrees of vigour and also induced distinct patterns of growth on the scion. The higher the rootstock vigour, the greater the number and length of lateral shoots developed by the scion. Hence, the growth vigour affected paradormancy and we hypothesized that auxin, which is known to suppress axillary bud development following bud break when transported basipetally along the shoot, might mediate rootstock-induced branching in the top of the tree. The role of indole-3-acetic acid as a hormonal signal in lateral branching was assessed by analysing its concentration in apical and axillary buds collected from growing shoots, both intact and at different times after apex removal. Shoot pruning was used as a means to force axillary buds to overcome paradormancy, assuming that their responses would reflect their intrinsic capacity of resuming growth. The development of lateral buds of both grafted scions and intact rootstocks was positively correlated with the respective auxin concentration and following shoot apex removal the relationships became stronger. Therefore, auxin may be responsible for mediating the expression of growth vigour. The invigorating effect of a rootstock would then be dependent on its ability of inducing high auxin levels in axillary buds. The hormone would act directly within bud tissues to stimulate their growth following bud break.

Key words. Auxin – axillary bud – mass spectrometry – *Prunus persica* – syllepsis – vigour

Introduction

Most fruit trees are grown as composite plants, which are produced by grafting a scion on a rootstock. Rootstocks may markedly affect scion growth, rate of development and resistance to stresses and may also increase fruit yield and quality (Michalczuk 2002). Young peach [*Prunus persica* (L.) Batsch] and nectarine trees show a particular pattern of development, owing to their typical mode of branching, which is termed "syllepsis". This is the continuous development of a lateral (axillary) from a terminal meristem without an intervening period of rest; therefore, branching occurs simultaneously with elongation of the parent axis (Cook et al. 1999). Syllepsis varies within cultivars, but it is also influenced by rootstocks, as it was demonstrated for grapevine (*Vitis vinifera* L.; Nikolaou et al. 2000) and has practical consequences on tree training. Excessive branching is a negative feature, because more pruning and training are required, thus delaying production. Moreover, sylleptic branches often bear small and late-ripening fruits and compete for light and nutrients with the rest of the tree crown, therefore they must be removed, adding to costs of management (Loreti and Massai 2002). Syllepsis is suppressed in shoots with strong paradormancy, while lateral branching occurs when paradormancy is partially expressed or weakened (Champagnat 1978). The relationships between paradormancy, plant form and yield potential are also discussed by Martin (1987). Cline (1994) defines apical dominance (a term that is assumed to be equivalent to paradormancy) as the control exerted by the shoot apex over the outgrowth of the lateral buds. According to Lang (1990), paradormancy is a type of growth control involving a biochemical signal from another structure. Indeed, plant growth regulators play a key role in controlling this phenomenon (Blažková et al. 1999). This has been evident since the pioneering works of Thimann and Skoog (1933, 1934) and Thimann (1937), who first demonstrated the involvement of auxin in paradormancy. A great number of subsequent works confirmed these results and additional evidences have been presented. In recent years, transgenic plants overproducing the auxin indoleacetic acid (IAA) were obtained from different species and these plants have reduced shoot branching (Klee et al. 1987; Sitbon et al. 1992). Panigrahi and Audus (1966) demonstrated that the application of auxin transport in-

hibitors to the stem of intact plants can reduce or remove paradormancy. Therefore, shoot apices appear to inhibit axillary bud growth through the basipetal transport of IAA. However, this auxin flux might not act directly on lateral meristems, because the hormone does not enter axillary bud tissues (Hall and Hillman 1975; Morris 1977; Lim and Tamas 1989). Although other hormones, namely cytokinins, are clearly involved in the control of paradormancy (Klee and Estelle 1991; Emery et al. 1998), these appear not to mediate the inhibiting action of IAA. Since these studies raise questions about the role of IAA in paradormancy, we investigated the hormonal response of peach scions and rootstocks following shoot apex removal and also how rootstocks influence scion responses, by analysing the time course of IAA concentration in axillary buds. We searched for correlations between hormonal responses and pattern of development, i.e. the expression of paradormancy and syllepsis, which can markedly affect fruit yield. The experimental system of choice was representative of commercial cultivation.

Materials and Methods

Plant material

The rootstocks selected for study were GF 677 (GF) and Mr.S. 2/5 (MrS), that were chosen because they markedly differ in vigour growth and developmental patterns, i.e. in their degree of branching. GF is a *Prunus persica*×*Prunus amygdalus* hybrid, which is known for inducing high vigour in scions (Loreti and Massai 2002). MrS is a *Prunus cerasifera*×*Prunus spinosa*, that is less invigorating than GF and has a low degree of syllepsis (Baroni et al. 1991; Massai et al. 1993). The nectarine scion used belonged to the cv. 'Big Top' (BT) and was grafted by "T-budding" in August 2000 onto 1-year-old micropropagated rootstocks that had been planted in the field in Spring 2000, thus yielding two types of grafted trees: BT grafted on GF (BT/GF) and BT grafted on MrS (BT/MrS). Consequently, 4 tree types were investigated: the rootstocks GF and MrS and the grafted plants BT/GF and BT/MrS. The experiment was located in central Italy, on a 41.7 % sand, 37.8 % silt, and 20.4 % clay soil. The distance between trees was 1 m, while rows were 2.5 m apart. Trees were arranged in three randomized blocks, each made of four replications per tree type (both grafted and not grafted), consequently there were 12 replications per tree type; each replication consisted of 10 trees, hence there were 480 plants in the field. Conventional agronomic practices were applied: superficial soil tillage between rows, one fungicide treatment in winter, fertilization with slow-releasing nutrients and drip irrigation throughout the vegetative period, which provided plants with 15 L d^{-1} of water.

Growth measurements

In May 2001, 20 plants per tree type (GF, MrS, BT/GF and BT/MrS) were randomly chosen from the three experimental blocks on the whole surface and their growth was analysed. The following data $tree^{-1}$ were calculated from biweekly measurements on the 20 trees chosen per tree type, from the end of May until the end of August: number, total length, and length $shoot^{-1}$ of flushing lateral shoots. Data from each 20-trees sample were analysed by one-way analysis of variance and mean separation was performed by Duncan's multiple range test, with the aim to search for differences in growth vigour between the rootstocks GF and MrS and between the grafted trees BT/GF and BT/MrS.

Sample collection

Apical and lateral buds were sampled from each tree type (GF, MrS, BT/GF and BT/MrS) for hormonal analysis: they were excised from developing shoots in three different periods during the growing season (May, July and August). Each sampling period started with the collection of the apical bud and of the third and fifth bud (numbering started from the apex) from shoots of the rootstocks and of the grafted scions. For each tree type 10 shoots were randomly sampled within each of its 12 replications (the trees previously chosen for growth analyses were not cut), and an individual tree was sampled only once per sampling period. Bud samples were combined to yield 12 sample types: 4 tree types (GF, MrS, BT/GF and BT/MrS) × 3 bud types (apical, third and fifth bud). At the same time, only the apices were removed from ten shoots within each of the 12 replications per tree type. These cut shoots belonged to trees that had not been sampled for buds. The same was done on a third set of plants within each replication per tree type. When 48 hours lapsed, the third and fifth bud below the apex were collected from ten of the previously decapitated shoots, and 24 hours later the same numbered buds were taken from the remaining ten cut shoots. Therefore, at each sampling period buds were collected on three different days, from intact shoots or after apex removal (T=0, intact shoots; T=48, 48 hours after apex removal; T=72, 72 hours after apex removal): May 28, 30 and 31; July 10, 12 and 13; and August 21, 23 and 24. Apical and lateral buds were quickly placed in a small, refrigerated box (at 0 °C), and then stored at –20 °C until analysis.

Hormone analysis

Samples were analysed for concentration of free IAA. Tissues were frozen with liquid N_2, homogenized with mortar and pestle and supplemented with a suitable amount of $^{13}C_6$(IAA) (99 % isotope enrichment; Cambridge Isotope Laboratories). Details of the method are given in Sorce et al. (2000). Samples were analysed by gas chromatography combined with mass spectrometry (GC-MS) and results were confirmed and refined by multiple ion monitoring (MIM) analyses. The detection threshold of the instrument was about 100 pg. Following extraction, samples were split into two subsamples, which were finally analysed three times on the GC-MS, consequently each data represents the mean of six values ± SE. The average recovery of the analyte was 78±3 %.

Results

The rootstocks GF and MrS differ in growth rate and in degree of scion invigoration. These differences are particularly evident when analysing their pattern of development: syllepsis was high in vigorous GF, while in MrS few axillary buds grew out on growing shoots. Apex removal

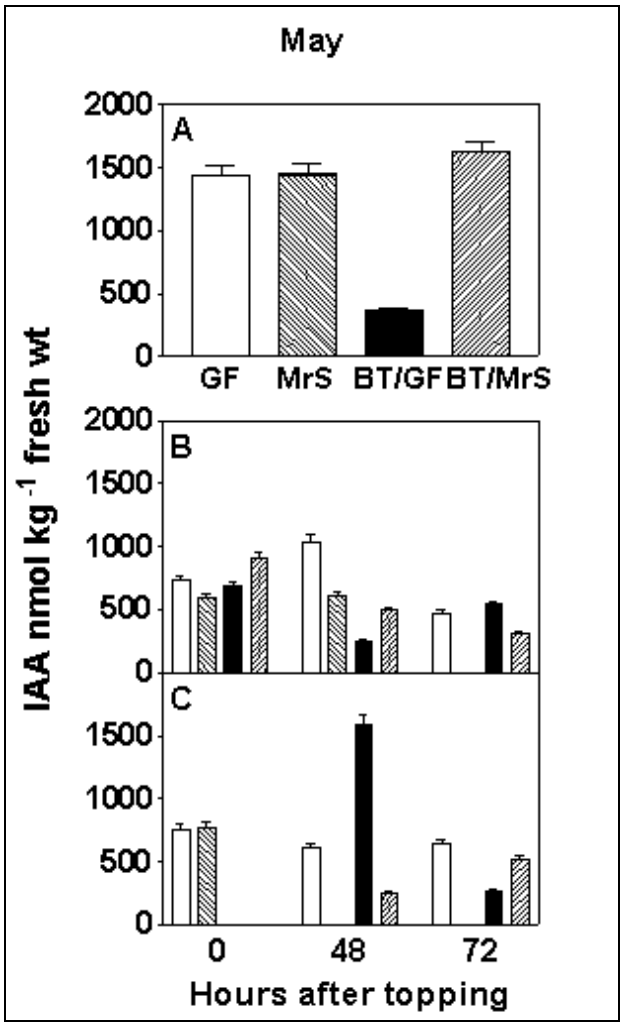


Fig. 1. Time course of IAA concentration in apical (A) buds and buds from the third (B) and fifth (C) node of growing shoots from rootstocks GF 677 and Mr.S. 2/5, both intact and grafted with *Big Top* scion. Apical buds were taken at T=0 (May 28), while axillary buds were sampled at T=0 and 48 and 72 hours after apex excision. Each data represents the mean of six values ± S.E.

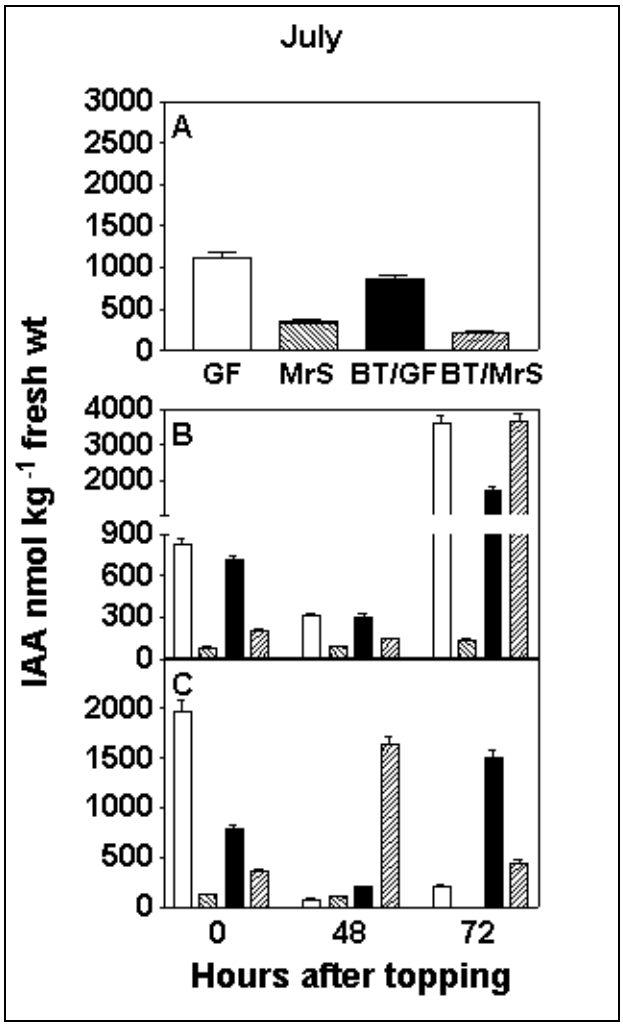


Fig. 2. Time course of IAA concentration in apical (A) buds and buds from the third (B) and fifth (C) node of growing shoots from rootstocks GF 677 and Mr.S. 2/5, both intact and grafted with *Big Top* scion. Apical buds were taken at T=0 (July 12), while axillary buds were sampled at T=0 and 48 and 72 hours after apex excision. Each data represents the mean of six values ± S.E.

was used to assess rootstock apex strength and how this may be influenced in scions. As IAA is known to be of primary importance in paradormancy control, we analysed its concentration in bud tissues from intact shoots (apical and axillary buds) and 48 and 72 hours after apex excision (axillary buds).

First sampling (May)

Results of hormone analysis on samples collected at the end of May are shown in Fig. 1. Apical buds (Fig. 1A), available only at T=0, showed similar IAA concentrations in three of the four tree types, while in BT/GF hormone concentrations were lower. There was a relation between the IAA levels and growth data of the corresponding period (Table 1). BT/GF had the highest average number of growing axillary shoots that were also more developed than in the other grafting combination. At T=0, concentrations of IAA in buds from the third node were similar in all tree types (Fig. 1B), while in the fifth bud from grafted trees the hormone was not detectable (Fig. 1C). It is worth noting that in this period the grafted plants developed more lateral shoots than did the rootstocks. Apex excision induced variable changes in IAA concentration, possibly due to tree growth potential. In GF, IAA levels had only a modest peak at T=48 in the third bud (Fig. 1B); in parallel, the growth of axillary shoots was limited (Table 1). Following apex removal, IAA concentration dropped to undetectable levels in MrS and this occurred more rapidly in the fifth (at T=48; Fig. 1C) than in the third bud (at T=72; Fig. 1B). By the same time, no lateral shoots were present. Moreover, axillary buds on cut shoots of MrS did not show any visible growth even at T=72, while in the other tree types axillary buds had begun to swell (data not shown). Hence, this rootstock was characterized by a strong paradormancy, which appeared

Table 1. Number and mean shoot length of growing axillary shoots per plant, measured on May 28, July 12 and August 21.

	Rootstocks		Grafted trees	
	GF 677	Mr.S. 2/5	BT/GF 677	BT/Mr.S. 2/5
May 28				
Axillary shoot number[z]	3.90 a[y]	0.00 b	11.91 a	6.85 b
Length/shoot (cm/shoot)	4.95	–	11.35 a	9.43 b
July 12				
Axillary shoot number[z]	37.60 a[y]	5.00 b	16.36 a	12.95 b
Length/shoot (cm/shoot)	20.00 a	16.92 a	24.67 a	18.11 b
August 21				
Axillary shoot number[z]	55.45 a[y]	5.77 b	21.54 a	15.00 b
Length/shoot (cm/shoot)	31.27 a	25.52 a	29.67 a	23.38 a

[z]Mean values for n=20.
[y]Within each row, means of rootstocks were compared separately from those of grafted trees. Values not followed by the same letter within each couple of data are significantly different at $P \leq 0.05$.

to be active, at least for the examined period, even after apex excision. The concentration of IAA sharply dropped in axillary buds from cut shoots of MrS and this may have prevented them from resuming growth, thus reflecting an intrinsic low potential for syllepsis. Grafted trees showed only limited changes of IAA concentrations in the third bud, while in the fifth bud the hormone concentration peaked at T=48 in BT/GF and slightly increased in BT/MrS (Fig. 1C). This marked rise of IAA concentration might have triggered the growth of axillary buds in grafted trees, whose buds indeed appeared swollen at T=72 (data not shown). The peak at T=48 in the fifth bud of BT/GF could account for its elevated lateral shoot production. During this period, trees differed also in the extent of growth of their axillary shoots: these had grown more in GF and BT/GF than in MrS and BT/MrS, respectively.

Second sampling (July)

The concentrations of IAA in the buds taken in mid July are reported in Fig. 2 and show striking differences compared to the previous sampling. Although environmental factors might be involved in these changes, it may be assumed that the intrinsic growth potential of each tree type was likely responsible for the observed hormonal differences. The number of lateral shoots (Table 1) was positively related with hormone concentration in the third and fifth buds at T=0, both in rootstocks and in grafted plants. On July 10, the elongation of lateral shoots was not significantly different between rootstocks. This appears to be related to the time course of IAA in MrS lateral buds (Fig. 2B and C), whose hormone concentration did not drop to undetectable levels following apex removal, as seen in May, but instead remained constant, except for the fifth bud at T=72. Hence, the auxin content of bud tissues could allow for a greater elongation of the resulting axillary shoots, which in MrS appeared for the first time in this period. Apex excision led to sharp peaks of IAA concentration in lateral buds of the trees, although with varying patterns and except for MrS. The hormonal response was prompt and strong and could be the basis of the elevated growth of axillary shoots, whose average length had increased in this period by more than 100 % in most tree types, as compared to May. A sharp decrease in IAA concentration of the fifth bud of GF between T=0 and T=48 was observed: it is likely that at T=0 such buds had just started to develop, hence their high hormone content. Following apex removal, their growth would have been temporarily suspended, because of the hormonal imbalance induced by cutting. The resumption of growth might have undergone a lag period exceeding 72 hours, thus escaping detection.

Third sampling (August)

The results of the last period examined are illustrated in Fig. 3. At T=0 the hormonal status was similar to July for apical buds only (Fig. 3A), whereas marked differences were found in axillary buds, both before and after shoot apex removal (Fig. 3B and C). Although third buds still showed IAA peaks, these were lower than in July and were unevenly distributed in time. Concerning fifth buds, similarities with July results were found only in BT/MrS, whose IAA concentration peaked at T=48. In the MrS rootstock the hormone levels increased slightly following apex excision, therefore the response of this tree type was reversed in comparison to the previous sampling periods. It was difficult to find a relationship between hormonal responses to shoot pruning and bud development, since the pattern of IAA changes became less clear and axillary shoot growth slowed down in general (Table 1). The increase of both number and length of lateral shoots between July 12 and August 21 was lower than in the previous period. Shoot elongation appeared to be particularly affected, as its values did not differ significantly between rootstocks and between grafted trees. By this time of the growing season, paradormancy might have lost its primary role in controlling branching, while the action of environmental factors might have become more important.

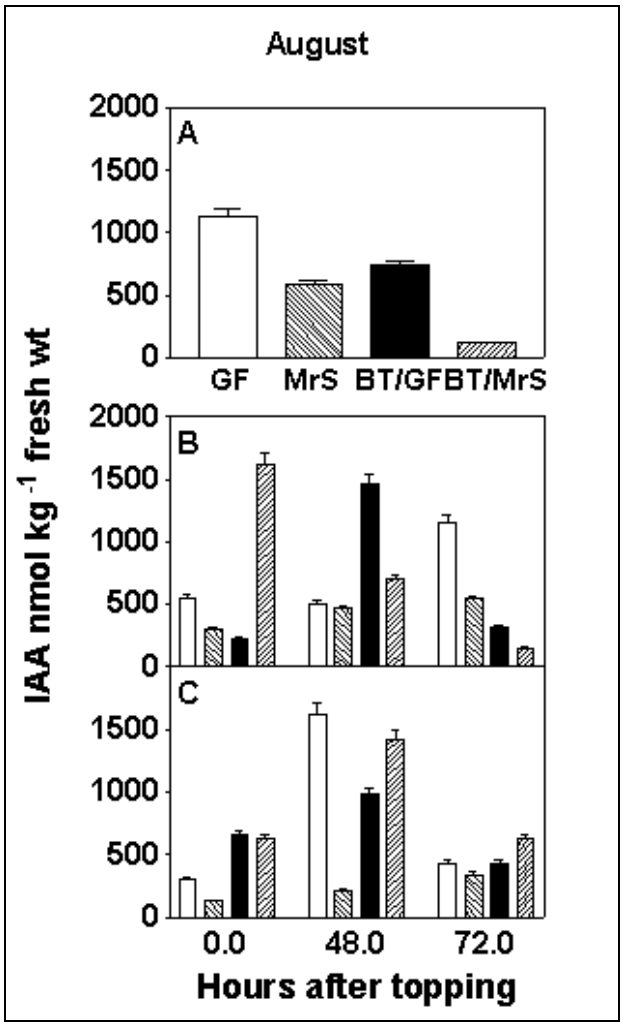


Fig. 3. Time course of IAA concentration in apical (A) buds and buds from the third (B) and fifth (C) node of growing shoots from rootstocks GF 677 and Mr.S. 2/5, both intact and grafted with *Big Top* scion. Apical buds were taken at T=0 (August 21), while axillary buds were sampled at T=0 and 48 and 72 hours after apex excision. Each data represents the mean of six values ± S.E.

Discussion

In the present work, tree growth vigour was evaluated on the basis of the extent of axillary bud development. The two rootstocks were characterized by marked differences in growth vigour. As expected, GF was far more vigorous than MrS, in terms of total number of axillary shoots developed from May to August, while the elongation of such shoots did not have significant differences. Rootstocks also influenced the growth of the BT scion by expressing their different invigorating effects in the aerial part of the grafted trees, whose pattern of development was strictly dependent on rootstock genotype. The latter may upset paradormancy in the scion, thus changing its degree of branching, potentially by altering hormone metabolism and/or transport. It is well known that axillary bud growth is under the control of the basipetal IAA flux originating from the shoot apex. Apex-derived hormone signals inhibit lateral buds, although they apparently do not enter bud tissues (Hall and Hillman 1975; Morris 1977; Lim and Tamas 1989; Leyser 2003). Some experimental evidence raises some questions about this classic theory and suggests that IAA might stimulate axillary bud outgrowth, as reported by studies on *Phaseolus vulgaris* L. (Hillman et al. 1977; Gocal et al. 1991), *Elytrigia repens* (L.) Desv. (Pearce et al. 1995) and pea (Beveridge et al. 1994). These studies demonstrated that auxin levels in the bud actually increase as lateral buds begin to enlarge and grow. Moreover, dormancy release in potato tubers is accompanied by a rise of IAA concentration in buds (Sorce et al. 2000). Our results agree with these data on non-woody plants, and therefore infer that IAA plays a positive role in axillary bud growth in *Prunus* sp. The development of lateral buds of both grafted scions and intact rootstocks was positively related with the respective IAA concentrations and following the shoot apex removal, such a relationship still appeared to be valid. Auxins might then mediate the expression of growth vigour via the hypothesis that the stronger the invigorating potential of the rootstock, the higher the hormone concentration rises in axillary buds, thus leading to extensive syllepsis. Following apex removal, the reduction of auxin basipetal transport may enhance cytokinin biosynthesis in the roots. The increased cytokinin flux from the roots to the shoot is thought to be a primary signal for the resumption of growth in lateral buds, which would be enhanced by the consequent rise of IAA concentration in bud tissues (Bangerth et al. 2000). The IAA content in buds depends on biosynthesis, transport, catabolism, conjugation and compartmentation activities (Bartel 1997) that undergo genetic control, and therefore represent unique characters of a rootstock. However, it must be borne in mind that a large number of different factors may affect syllepsis. The discrepancies observed in August might be attributable to the action of these non-hormonal factors, which could have attained a high degree of control on bud development in this period, thus overcoming paradormancy (Champagnat 1989). The role of such factors appears to be relevant, because our experiments were carried out on field-grown trees, instead of using model systems (i.e. herbaceous plants grown under strictly controlled conditions). The inhibitory role of the apex-derived auxin in paradormancy is widely accepted and does not seem to be questionable, therefore it must be concluded that IAA apparently displays contrasting behaviours. The reason why auxin is able to elicit opposite responses in buds may reside in the site of action of the hormone. Apex-derived IAA is thought to inhibit lateral bud growth by acting in the stem tissues (Shimizu-Sato and Mori 2001) and specifically in the xylem and interfascicular schlerenchyma (Booker et al. 2003). Conversely, the hormone would positively affect axillary bud development when operating directly inside bud tissues, where it can stimulate cell growth and promote xylem vessel differentiation (Berleth et al. 2000; Aloni 2001). Our results suggest that IAA may mediate the expression of syllepsis and therefore the degree of growth induced by rootstocks on the aerial part of grafted plants. The precise origin of this IAA is yet to be determined, but it may be from both root-derived auxin, which is acropetally transported in the xylem, and bud-synthesized auxin, which could increase following a rise of cytokinins exported from roots.

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