The Expression of Acrotony in Deciduous Fruit Trees: A Study of the Apple Rootstock M.9

Nigel C. Cook, Etienne Rabe, Johan Keulemans,¹ and Gerard Jacobs

Department of Horticultural Science, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa

ADDITIONAL INDEX WORDS. bud dormancy, growth habit, basitony, branching, prolepsis, syllepsis, *Malus domestica*

ABSTRACT. One-year-old shoots of apple (*Malus × domestica* Borkh.) rootstock Malling 9 (M.9 clone Nic 29), ≈60 cm long without sylleptic side shoots, were selected randomly from a commercial stoolbed in Belgium, prepared, and forced at 25 °C and 16 hours daylength to follow bud developmental rate in different positions along a 1-year-old shoot. The number of buds that reached green tip was recorded daily until 50% of shoots exhibited budburst. The evolution of dormancy of the terminal, an upper lateral, and a lower lateral bud was followed throughout the dormant period. The influence of a distal disbudded shoot piece and Promalin [3000 mg·L⁻¹ *N*-(phenylmethyl)-1*H*-purine 6-amine and 3000 mg·L⁻¹ gibberellins A₄+A₇ without a wetting agent] application on the developmental rate of these buds was evaluated. Bud developmental rate decreased during winter and increased to a maximum before budburst in spring. The distal shoot-forming ability or acrotonic branching habit in apple appears to be mediated via a greatly increased developmental rate of the terminal bud relative to the upper and lower lateral buds, respectively. The proximal budbursting tendency or basitony exhibited in early winter was weak compared to the acrotony that developed in the last month before budburst in spring. Lateral buds showed a lower developmental rate than the terminals when inhibited by a distal disbudded shoot piece, so that resultant overall growth habit within the shoot remained acrotonic throughout the dormant period. Promalin application in winter did not restore the bud developmental rate associated with spring budburst. These results are discussed with reference to observations of trees growing under conditions of insufficient winter chilling.

Branching in apple occurs predominantly via prolepsis, i.e., from dormant buds, with budburst in spring on unbranched 1-year-old shoots (for descriptions of tree architecture terminology see Hallé et al., 1978). After dormancy in winter, budburst is prolific, with the bursting of the terminal and many of the lateral buds on the axis. Not all of these buds become long extension shoots and many remain as short shoots or spurs. The most distal or apical buds, however, appear dominant and are most commonly the buds that burst and form extension shoots. It is this distal extension shoot-forming tendency that is referred to as acrotony (Rauh, 1939), as opposed to basitony, where long shoots originate from lateral buds of a more proximal origin. Trunk formation in apple is the result of acrotony (Champagnat, 1978; Crabbé, 1985).

On vigorously growing shoots, sylleptic branching occasionally occurs, i.e., lateral shoots develop concurrently with development of the central shoot axis. It appears that, after initiation, axillary meristems continue growth, apparently insufficiently inhibited by the actively growing apical meristem, i.e., poor apical dominance (Hallé et al., 1978). It is this sylleptic branching capacity that is used in the formation of feathered apple nursery trees. Apical control of the central axis is feathered in the average feathered tree as seen by a well-defined central axis (future trunk) and subordinate laterals. This contrasts with the basal dominance of the sylleptic shoots of certain nectarine varieties, whereby the central axis exhibits a poor dominance over the laterals and results in the reduced ability to form a dominant trunk (personal observation).

With the predominant proleptic branching habit of apple, overwintering and budburst in spring involves the entrance into and exit from dormancy, a process whereby the entrance and the exit appear to be promoted by low temperatures (Crabbé, 1994; Dennis, 1994).

Seasonal differences exist in the depth of dormancy between terminal and lateral buds. During dormancy, lateral buds appear less endodormant than terminal buds (Crabbé, 1987; Hauagge and Cummins, 1991). This tendency is, however, not static. It appears that, on entrance into dormancy, a distal shoot-forming or acrotonic tendency exists that shifts to a proximal shoot-forming or basitonic tendency in early winter and then becomes more acrotonic as spring approaches (Barnola and Crabbé, 1991). In intact shoots this increased growth potential of the basal buds is seldom expressed in terms of shoot growth other than under specific conditions, e.g., gravimorphisms (Crabbé, 1984; Wareing and Nasr, 1961). Bursting of basal buds is inhibited, possibly by the correlative effects of the distal shoot piece and buds (Champagnat, 1983; Suzuki and Kitano, 1989; Zieslin and Halevy, 1976).

Under conditions in the Western Cape, South Africa (34°S), final tree form in orchards depends largely on whether whips or feathered trees are planted, i.e., if the initial branching occurs before planting via syllepsis or after planting via prolepsis. Additionally, proleptic branching after cutting the whip back after planting results in a different tree form than when proleptic branching occurs on an intact whip (personal observation). At present, whips are the predominant nursery trees sold. With prolepsis, changes in growth potential during dormancy may have relevance to final tree form as expressed differentially under varying climatic conditions. A modification of the normal budbursting pattern, known as delayed foliation, is observed with insufficient chilling during the dormant period (Jacobs et al., 1981). A further phenomenon associated with insufficient chilling and delayed foliation is a change in growth habit in terms of an increasing basitonic tendency (personal observation). This has practical and financial implications when training fruit trees in climates with insufficient chilling. We present the observations on these correlative phenomena in trees growing in a climate with sufficient chilling, making reference to phenomena observed with insufficient chilling. A better understanding of the normal growth phenomena will aid in the understanding of growth phenomena under conditions of suboptimal chilling.

Received for publication 7 Mar. 1997. Accepted for publication 8 May 1997. We are grateful to J. Crabbé for his comments regarding this manuscript. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Fruiteelcentrum, K.U.Leuven, Willem de Croylaan 42, B-3001 Leuven-Heverlee, Belgium.

Materials and Methods

One-year-old shoots of the rootstock Malling 9 (M.9 clone Nic 29), ≈ 60 cm long without sylleptic side shoots, were selected randomly in a commercial stoolbed near St-Truiden, Belgium (51°N). Rooted stoolshoots were harvested on 4 Oct. 1995, 8 Nov. 1995, and 5 Dec. 1995. The remaining rootstocks were harvested 19 Dec. 1995 and planted near Leuven, Belgium (51°N), then removed on 6 Jan. 1996, 31 Jan. 1996, and 28 Feb. 1996. Shoot termination in the stoolbed occurred in early September 1995; spring budburst started in late March 1996. Natural leaf abscission had begun on 8 Nov. 1995 and was completed by 5 Dec. 1995.

On each of the above dates, 280 rootstocks were cut to 60-cm lengths, roots were removed, and rootstocks were cut in half (Fig. 1). For observations on the terminal buds (treatments T-P and T+P), from 40 rootstocks, two groups of 20 upper shoot halves (30 cm in length) were bundled while the lower shoot halves were discarded. The uppermost buds [the terminal (T) and upper one to two lateral buds of one of the bundles] were dipped in an aqueous solution of Promalin (P) (3000 $\text{mg}\cdot\text{L}^{-1}$ *N*-(phenylmethyl)-1*H*-purine 6-amine and 3000 $\text{mg}\cdot\text{L}^{-1}$ gibberellins A_4+A_7) without a wetting agent (treatment T+P). This was the standard concentration for all Promalin treatments. For the upper lateral bud, seven groups of 20 upper shoot halves with the upper 10 cm removed were bundled (treatments U-SH-P and U-SH+P). The uppermost buds of four of these bundles were dipped in Promalin for 5 s (treatment U+SH+P). Five more groups of 20 upper shoot halves with the upper 10 cm disbudded were bundled (treatments U+SH-P and U+SH+P). The uppermost remaining buds of three of these

bundles were painted with Promalin (treatment U+SH+P). For observations on the lower lateral bud, seven groups of 20 lower shoot halves with the upper 10 cm removed were bundled (treatments L-SH-P and L-SH+P). The uppermost buds of four of these bundles were dipped in Promalin (treatment L+SH+P). Five more groups of 20 lower shoot halves with the upper 10 cm disbudded were bundled (treatments L+SH-P and L+SH+P). The uppermost remaining buds of three of these bundles were painted with Promalin (treatment L+SH+P).

Each of these 26 bundles was placed in a glass jar, with its base in water containing 5 $\text{ml}\cdot\text{L}^{-1}$ household bleach (5% sodium hypochlorite), and then directly placed in a Phytotron. The Phytotron maintained a constant 25°C at $\approx 40\%$ relative humidity and 16 h of daylength. The water (containing bleach) in the jar was replaced daily. The number of shoots in each bundle with buds that reached green tip was recorded daily until a minimum of 10 shoots per bundle had burst. The mean is presented where more than one bundle per treatment was observed.

Results and Discussion

These results report on data collected from biological tests to calculate the depth of dormancy during fall and winter, measured as the number of days until 50% of the shoots for each observation had burst under forcing conditions. Cannell (1989) refers to the rate of bud development, expressed as the inverse of the time to budburst. We present these data in this form: (days to 50% budburst) $^{-1}$. This measurement of bud developmental rate indicates the growth potential of a bud.

Whenever budburst occurred, it was always in the uppermost buds. In all treatments the developmental rate decreased to a minimum associated with the deepest dormancy in November and December, followed by an increase towards a maximum in late February (Fig. 2). Developmental rate of all buds in fall (October), ≈ 6 weeks after shoot growth termination, was never greater than in spring (late February), irrespective of how the shoots were manipulated. In the period of the lowest developmental rate, neither Promalin nor removal of an inhibitory shoot piece enhanced the developmental rate so that it was comparable with the developmental rate in late February.

In the beginning of the dormant period we observed a basitonic tendency, i.e., the lower lateral bud (≈ 40 cm from the apex) without a distal disbudded shoot piece exhibited a greater developmental rate than the upper lateral bud (≈ 10 cm from the apex) without a distal disbudded shoot piece, which in turn exhibited a greater developmental rate than the terminal bud (Fig. 2A). After the deepest dormancy the developmental rate of the terminal bud increased exponentially compared to the linear increase in developmental rate of the upper lateral and sigmoidal increase of the lower lateral buds. By late February an acrotonic tendency was observed, whereby the developmental rate was greatest in the terminal bud and then lower in the upper and the lower laterals, respectively. These results agree with the observation common to many woody species in which this shift occurs over the dormant period from acrotonic to basitonic and then to acrotonic as spring approaches (Barnola and Crabbé, 1991).

While a basitonic tendency was observed in early and deep dormancy, this basitony was associated with a low developmental rate. By contrast, the acrotonic tendency observed in late February is associated with a high developmental rate. Furthermore, the differences between buds in terms of developmental rate were much smaller in early dormancy and deep dormancy than near budburst in spring, an indication that the acrotonic gradient in

Fig. 1. A diagrammatic representation of the manipulations to the rootstocks. T = terminal bud; U = upper lateral bud; L = lower lateral bud; SH = 10-cm distal disbudded shoot piece; P = Promalin; (+) and (-) represent the presence or absence, respectively, of a distal disbudded shoot piece and/or Promalin application; black bud indicates Promalin application; arrow indicates bud observed for sprouting. The number of observed bundles, each consisting of 20 shoots, is indicated in parentheses.

Fig. 2. The change over time in developmental rate of buds in different positions along a 1-year-old shoot. Treatments according to Fig. 1. T = terminal bud; U = upper lateral bud; L = lower lateral bud; SH = 10-cm distal disbudded shoot piece; P = Promalin; (+) and (-) represent the presence or absence, respectively, of a distal disbudded shoot piece and/or Promalin application.

spring is more defined than the basitonic gradient of early and deep dormancy.

Buds treated with Promalin generally exhibited an increased developmental rate. The terminal buds were more responsive than the upper and lower laterals, respectively (Fig. 2 B-D). In the terminal buds, Promalin had the greatest effect during the deepest dormancy (October to December). Closer to spring budburst, Promalin was less effective and even reduced the developmental rate when applied on 28 Feb. 1996. In lateral buds, Promalin was more effective after the deepest dormancy and remained effective until late February (Fig. 2 C and D). In all cases, Promalin did not sufficiently restore the developmental rate observed during early and deepest dormancy to that observed in late February; i.e., the developmental rate after adequate chilling could not be mimicked by bud treatment with Promalin.

A distal 10-cm disbudded shoot piece reduced the developmental rate observed under forcing conditions. The inhibition caused by the upper distal disbudded shoot piece (0 to 10 cm from the

apex) was greater in the beginning of dormancy than at any other time (Fig. 2E). After deepest dormancy, a distal disbudded shoot piece reduced the developmental rate by a value that remained roughly constant (Fig. 2 E and F). When Promalin was applied to a bud with a distal disbudded shoot piece, the developmental rate was increased, more so in an upper than a lower lateral. A 10-cm disbudded distal shoot piece reduced the developmental rate of lateral buds so that they exhibited a comparable and often lower developmental rate than terminal buds. In intact shoots this inhibition, caused by a distal disbudded shoot piece, increased with increasing length (Champagnat, 1978). More proximally positioned buds are increasingly inhibited. This inhibition observed under forcing could play a role in preventing the expression of this basitonic tendency during dormancy.

The duration of budburst was greatest when the developmental rate was at a minimum in October, November, and December. As spring budburst was approached, the duration of budburst decreased (Table 1). Promalin tended to reduce the duration of budburst, while a distal disbudded shoot piece increased the duration of budburst. At a lower developmental rate, buds in a comparable position on different shoots tended to burst over a longer period. There were, therefore, greater differences between buds in terms of developmental rate before and during deep dormancy than after deep dormancy. Cold and Promalin had a normalizing effect on the duration of budburst. A distal disbudded shoot piece accentuated these differences in developmental rate between buds. However, as chilling was accumulated, distally inhibited buds became more

uniform. Cold accumulation appears to play a role in the normalization of bud growth potential.

These data imply that total dormancy, as measured by the rate of bud development under forcing conditions, has more than one component. The observed improvement of developmental rate via the application of unnaturally high concentrations of cytokinin and gibberellins confirms the results of Arias and Crabbé (1975). This direct application of cytokinin and gibberellins to the buds implicates a possible lack of endogenous hormonal substrate within the bud. This may be due to an inaccessibility of the bud (Crabbé, 1994; Faust et al., 1991), as an abundant supply of cytokinin has been observed at bud sprouting in spring (Cutting et al., 1991). Closer to natural sprouting, as acrotony strengthens, the terminal bud loses its sensitivity to Promalin. It would appear that by this time the terminal bud has become self-sufficient in terms of hormonal requirement. In contrast, in lateral buds, Promalin application maintains a promotive influence. It seems that with the strengthening of acrotony in late February the terminal bud exerts a primigenic dominance (Bangerth, 1989) due to the increased growth rate, whereby the dominant terminal bud receives sufficient growth hormone. Throughout dormancy a distal disbudded shoot piece maintains a paradormant inhibitory ability under forcing conditions. Champagnat (1983) states that this inhibition can be removed by girdling, indicating an involvement of the auxin

Table 1. The duration of budburst calculated from when the first shoot in each bundle burst until 50% of the shoots had burst as observed during Winter 1995 and 1996 (Northern Hemisphere).

Treatment	Duration of budburst (d)					
	4 Oct.	8 Nov.	5 Dec.	6 Jan.	31 Jan.	28 Feb.
Terminal – Promalin	5.00	7.70	6.30	3.30	1.30	0.50
Terminal + Promalin	2.00	0.60	2.25	1.10	0.40	1.10
Upper lateral – shoot piece – Promalin	0.43	5.57	4.37	1.80	0.90	0.40
Upper lateral – shoot piece + Promalin	4.16	1.18	2.45	0	0.10	0
Upper lateral + shoot piece – Promalin	15.00	6.33	5.43	1.47	0.77	1.20
Upper lateral + shoot piece + Promalin	3.73	5.50	1.75	0.30	0.30	0.15
Lower lateral – shoot piece – Promalin	0	2.10	1.80	1.63	1.60	1.43
Lower lateral – shoot piece + Promalin	0	1.18	2.38	0.55	1.10	0.35
Lower lateral + shoot piece – Promalin	3.17	10.23	6.20	0.67	0.77	2.67
Lower lateral + shoot piece + Promalin	0.83	6.35	3.15	2.20	1.80	0.70

transport system. As a result of a positional advantage, the terminal bud, in the absence of distal inhibitory influences, can establish primigenic dominance and, thus, a well-defined acrotony.

The dormancy of a bud can be seen as the sum of inhibitions. This agrees with the “French school” (Dennis, 1994; Crabbé, 1994), which implies that dormancy is the combination of a multiple of influences. During dormancy, Promalin application and the removal of a distal inhibitory shoot piece only partially restore the developmental rate; an additional inhibition of growth or endodormancy remains that is characteristic to the bud. The total dormancy, as measured as a low developmental rate in a bud, can, therefore, be seen as the sum of this endodormant component plus the paradormant components (outside the bud) of hormonal substrate inaccessibility and distal shoot inhibition.

The phenomenon of increased basal dominance is observed more in areas with mild winters, even with the use of rest-breaking chemicals (personal observation). Basal dominance involves an increased vigor of the basal shoots or branches relative to the central axis (leader) so that, over time, the development of a dominant trunk is hindered. When apple and plum varieties are trained to central leaders from unbranched whips without cutting back of the leader, it is necessary, under Western Cape conditions, to promote lateral branching by notching or scoring. These released basal shoots often exhibit an increased autonomy or dominance, i.e., a growth habit more common to uninhibited shoots. Heading the whip shortly after planting is a common alternative to promote lateral branching and reduce transplant shock when training central leaders. Heading promotes excessive basal dominance, more so in areas with less winter chilling, requiring extensive manipulation (summer pruning and bending) to reestablish dominance of the central leader. After heading, acrotony is maintained (Crabbé, 1985). However, it would appear that with milder winters the hierarchy between upper and lower shoots is less clearly defined, indicative of weaker acrotony. These shoots exhibit an increased autonomy and appear less sensitive to epinastic influences. Manipulations that release lateral buds from the otherwise normal acrotonic growth habit (unmanipulated situation) allow a greater expression of basitonic tendencies and, thus, greater autonomy of the basal shoots. It is possible that with mild winters the lack of an extended chilling period and the accompanied ecodormant situation prevents the reinstatement of the well-defined acrotony that is seen in the data of late February. Research on this issue continues.

Lespinasse and Lauri (1996) mention basal dominance of lateral shoots as a problem in certain apple varieties and ascribe the problem to proximity to the roots. Root influences, which also play

a role in gravimorphic responses (Smith and Wareing, 1964), may play a role in the basal dominance observed with insufficient chilling. Lespinasse and Lauri (1996), however, report on observations of feathered nursery trees. As previously mentioned, extreme basal dominance in some nectarine cultivars is observed when branching occurs via syllepsis. When trees of these nectarines are trained from whips as opposed to feathered trees, basal dominance can be almost entirely eliminated (personal observation). Tree architecture thus differs when branch formation is the result of prolepsis or syllepsis. When basal dominance is established during the growing season on sylleptic lateral shoots, the acrotony that is established in the following spring develops on individual, more autonomous basal shoots. Within the branched complex basal dominance is, therefore, accentuated further. However, where acrotony is established on the unbranched whip a definite change in growth habit from basal dominant to a well-defined acrotony is observed. Basal shoot autonomy is reduced considerably. Sylleptic branching circumvents the intervention of a dormant period and associated correlative phenomena necessary for trunk development via acrotony in basal dominant nectarines. In agreement with Lespinasse and Lauri (1996), the acrotonic form is more desirable from a tree-training perspective due to the increased trunk-forming capacity. Practices that promote shoot autonomy and resultant basal dominance should be avoided.

In conclusion, under conditions of sufficient chilling, the basitonic tendencies observed in early and deep dormancy are poorly defined, as seen by the small differences between buds in different positions, and are associated with a generally low growth potential. The possible inhibitory influences of the shoot combined with a low growth rate may be responsible for the lack of expression of basitony and a continual expression of acrotony in apple. Additionally, the acrotonic tendency expressed in spring is mediated via a greater general growth potential accumulated in late February (Northern Hemisphere) and expressed via an exponential increase in developmental rate of the terminal buds relative to the weaker increase in developmental rate of the lateral buds. The acrotonic growth habit in apple is, therefore, due to the greater developmental rate or primigenic dominance of the terminal and upper lateral buds combined with the positional advantage associated with progressively less distal inhibition.

Literature Cited

- Arias, O. and J. Crabbé. 1975. Les gradients morphogénétiques du rameau d'un an des végétaux ligneux, en repos apparent. Données complémentaires fournies par l'étude de *Prunus avium* L. *Physiol. Vég.* 13:69–81.

- Barnola, P. and J. Crabbé. 1991. La basitonie chez les végétaux ligneux. Déterminismes et variabilité d'expression, p. 381–396. In: C. Edelin (ed.). *L'Arbre, Biologie et développement*, Naturalia Monspeliensia.
- Bangerth, F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiol. Plant.* 76:608–614.
- Cannell, M.G.R. 1989. Chilling, thermal time, and the date of flowering of trees, p. 99–113. In: C.J. Wright (ed.). *Manipulation of fruiting*. Butterworths, London.
- Champagnat, P. 1978. Formation of the trunk in woody plants, p. 401–422. In: P.B. Tomlinson and M.H. Zimmermann (eds.). *Tropical trees as living systems*. Cambridge Univ. Press, Cambridge.
- Champagnat, P. 1983. Bud dormancy, correlation between organs, and morphogenesis in woody plants. *Soviet Plant Physiol.* 30:458–471.
- Crabbé, J.J. 1984. Correlative effects modifying the course of bud dormancy in woody plants. *Z. Pflanzenphysiol.* 113:465–469.
- Crabbé, J.J. 1985. Aspects of the apical control on branching in one-year-old caulinary axes of woody plants. *Acta Universitatis Agriculturae* 33:555–560.
- Crabbé, J. 1987. Aspects particuliers de la morphogenèse caulinaire des végétaux ligneux et introduction à leur étude quantitative. Centre d'Etude de la Reproduction Végétale, Brussels.
- Crabbé, J. 1994. Dormancy, p. 597–611. In: C.J. Arntzen and E.M. Ritter (eds.). *Encyclopedia of agricultural science*, vol. 1. Academic Press, New York.
- Cutting, J.G.M., D.K. Strydom, G. Jacobs, D.U. Bellstedt, K.J. Van Der Merwe, and E.W. Weiler. 1991. Changes in xylem constituents in response to rest-breaking agents applied to apple before budbreak. *J. Amer. Soc. Hort. Sci.* 116:680–683.
- Dennis, Jr., F.G. 1994. Dormancy—What we know (and don't know). *HortScience* 29:1249–1255.
- Faust, M., D. Liu, M.M. Millard, and G.W. Stutte. 1991. Bound versus free water in dormant apple buds—A theory for endodormancy. *HortScience* 26:887–890.
- Hallé, F., R.A.A. Oldeman, and P.B. Tomlinson. 1978. *Tropical trees and forests. An architectural analysis*. Springer-Verlag, Berlin.
- Hauagge, R. and J.N. Cummins. 1991. Seasonal variation in intensity of bud dormancy in apple cultivars and related *Malus* species. *J. Amer. Soc. Hort. Sci.* 116:107–115.
- Jacobs, G., P.J. Watermeyer, and D.K. Strydom. 1981. Aspects of winter rest of apple trees. *Crop Production* 10:103–104.
- Lespinasse, J.M. and P.E. Lauri. 1996. Influence of fruiting habit on the pruning and training of apple trees. *Compact Fruit Tree* 29:75–82.
- Rauh, W. 1939. Über Gesetzmäßigkeit der Verzweigung und deren Bedeutung für die Wuchsformen der Pflanzen. *Mitt. Dtsch. Dendr. Ges.* 52:86–111.
- Smith, H. and P.F. Wareing. 1964. Gravimorphism in trees. III. The possible implication of a root factor in the growth and dominance relationships of the shoots. *Ann. Bot.* 28:297–309.
- Suzuki, T. and M. Kitano. 1989. Dormancy and spring development of lateral buds in mulberry (*Morus alba*). *Physiol. Plant.* 75:188–194.
- Wareing, P.F. and T.A.A. Nasr. 1961. Gravimorphism in trees. I. Effects of gravity on growth and apical dominance in fruit trees. *Ann. Bot.* 25:321–340.
- Zieslin, N. and A.H. Halevy. 1976. Components of axillary bud inhibition in rose plants. I. The effect of different plant parts (correlative inhibition). *Bot. Gaz.* 137:291–296.