Physiological Basis of Topophysis in *Rosa* Hybrids

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Aspects of growth readiness and plant architecture are integrated into one organ, the bud. Topophysis, the positional effect of axillary buds along the shoot axis on their growth and differentiation, is an important factor as it may determine whether an axillary bud grows readily or with difficulty. Topophysis is a decisive tool for synchronizing the development and flowering in roses. Results show that growth potential, growth efficiency, and plant quality can be improved by 14% to 49% in roses by selecting proper cutting positions. Topophysis in *Rosa* is an independent phenomenon which is intrinsic to the axillary bud. At present, there is no convincing physiological explanation of the relatively stable states of behavior exerted by topophysis. We suggest that topophysic prevention of growth may be related to lack of promoters or to the presence of inhibitors of growth within the bud.

INTRODUCTION

Light dramatically affects rose plant development and growth and apical dominance is sensitive to changes in photosynthetic photon flux density (PPFD) and spectral quality. Apical dominance is weakened by high PPFD (Andersen, 1976), and red light (Vince-Prue, 1977). During apical dominance differentiation of rose leaf initials proceeds inside the apparently nongrowing axillary bud at a very low level (Marcelis-van Acker, 1994). After being released from apical dominance (correlative inhibition) by decapitation visible growth is resumed in rose axillary buds. The upper nodes of a growing rose shoot are neoformed, i.e., formed after release from inhibition, and the number of preformed nodes depends on age (Marcelis-van Acker, 1994). After a certain developmental stage axillary buds become independent of their chronological age, they all contain the same number of leaf initials, and are termed ontogenetically mature. Bud growth potential is determined by genetic and other factors including ontogenetical age, environment, and position of meristem.

Cyclophysis. This is the process of ontogenetical ageing and maturation of the meristem (Seeliger, 1924; Olesen, 1978). Ontogenetical ageing is genetically programmed, accelerated by improved growth conditions, and difficult to reverse (Fortainer and Jonkers, 1976). Cyclophysis is most advanced in the apical meristem, as this has had the biggest total growth behind it (Olesen, 1978).

Periphysis. Periphysis covers the qualities determined by environment and manifests itself as a certain aftereffect caused by previous conditions (Büsgen and Münch, 1927; Schaffalitzky de Muckadell, 1959; Olesen, 1978). It is a carry-over effect of the environment on the propagule into the progeny plant but without causing a permanent effect on the genetic nature of the plant (Hartmann et al., 1990).

Topophysis. Topophysis is the effect of axillary bud position along a shoot axis on growth and differentiation. It is a decisive tool for synchronization of development and flowering in roses. Topophysis (Ortsnatur), derived from *topos* =place and *physis* =nature/constitution, as first defined by Molisch (1916), is the persistent growth and differentiation, without genetic change, of a plant cutting, depending on the source tissue (Kenneth, 1963). Topophysis covers the effect of the position on the plant of the propagule on the type of vegetative growth subsequently shown by the vegetative progeny (Molisch, 1929; Hartmann et al., 1990). Doorenbos (1965) generalized topophysis as the phenomenon where plant parts maintain, to a certain extent, their individual characteristics when excised and grown as separate plants.

Topophysis, thus, is an important factor as it may determine whether an axillary bud grows readily or with difficulty. Results (Bredmose and Hansen, 1996) have shown that the growth potential, growth efficiency, and plant quality of roses can be improved by 49%, 14% to 34%, and 20%, respectively, by selecting proper cutting positions. Topophysis is of more than just practical interest because it cannot be adequately explained on the basis of the usual concepts of the function of chromosomes and their genes (Robbins, 1964). At present, there is no satisfactory physiological explanation of the relative stable states of behavior exerted by topophysis. We studied topophysic effects on growth and differentiation until anthesis in three rose cultivars by growing cuttings originating from seven stem positions.

MATERIALS AND METHODS

Position effects of single-node, five-leaflet-leaf cuttings on subsequent bud and shoot growth and flowering were recorded from the most apical cutting position to the most basal one in single-stemmed cut rose plants (see Fig. 1). Cuttings were excised, on mature harvestable flowering stems, 5 to 10 mm above and 40 to 50 mm below the node. Average stem diameter and fresh weight of cuttings were 5.2 mm and 2.0 g, respectively. Cuttings were dipped in a 0.15% Captan solution, and the basal part was treated with 0.3% indolebutyric acid before inserted 2 cm in rockwool cubes (7.5 cm $\times$ 7.5 cm $\times$ 6.5 cm) at 178 plants m^{-2}. Plants of *Rosa* 'Korokis' Kiss^{TM} floribunda-tea rose, 'Tanettahn' Manhattan Blue^{TM} hybrid tea rose, and 'Sweet Promise' Sonia^{TM} grandiflora rose were grown at 24.7C average air temperature in 20-h photoperiods at an average PPFD of 327 μmol m^{-2} s^{-1} from natural and supplementary light. The plants were grown on ebb-and-flood benches, irrigated with a complete nutrient solution, and supplied with carbon dioxide to a level of 1000 μl liter^{-1}. Seven cutting positions, three cultivars, and four replicates were combined in a factorial design with eight plants per treatment. Several parameters related to bud growth, shoot growth, fresh weight production, and flowering were recorded. For more details including statistics see Bredmose and Hansen (1996).

RESULTS AND DISCUSSION

As the three cultivars reacted similarly to the treatments average results are presented.

Developmental Time. Time from excision/planting until onset of axillary bud growth, visible flower bud, or anthesis was less in plants originating from apical bud positions than from basal positions (Table 1). In general, bud growth occurred earliest in cuttings originating from position two, which indicates the transition between sylleptic (bud growth occurs continuously) and proleptic buds (buds having

a period of inhibition) (Bredmose and Hansen, 1996). Regarding the onset of bud growth our results agree with other investigations on positional effects in roses (Jensen, 1967; Zieslin et al., 1976; Bressan et al., 1982). The plastochrone, the average number of days for a node to develop, was not significantly influenced by the position of the axillary bud (Table 1). Genotypic effects (Table 1) showed that Manhattan Blue™ hybrid tea rose developed much slower, and required 48% more time to develop a node, than the other two cultivars.

Table 1. Topophysis effects (F probability $\leq$ 0.05) on time from excision/planting until axillary bud growth, visible flower bud, and anthesis, and on plastochrone as average of three cultivars and four replicates; and cultivar effects (F pr $\leq$ 0.001) as average of seven bud positions and four replicates. Cutting positions are numbered in descending order. (After Bredmose and Hansen, 1996). Length of period between developmental phases is shown in parentheses.

	Time from planting until					
	Bud growth (days)		Visible flower bud (days)		Anthesis (days)	Plastochron (days node^{-1})
Cutting position:						
1 most apical	21.0	(13.0)	34.0	(14.4)	48.4	3.9
2	20.2	(13.5)	33.7	(14.1)	47.8	3.6
3	22.2	(13.6)	35.8	(14.1)	49.9	3.7
4	23.5	(14.5)	38.0	(13.7)	51.7	3.9
5	25.4	(14.1)	39.5	(13.5)	53.0	3.9
6	25.8	(14.1)	39.9	(13.8)	53.7	3.9
7 most basal	26.1	(15.2)	41.3	(13.9)	55.2	4.0
Lsd (p = 0.05)	1.8		1.8		1.7	(Pr<F)
Cultivar:						
Kiss™ floribunda-tea rose	19.1	(13.1)	32.2	(14.9)	47.1	3.3
Manhattan Blue™ hybrid tea rose	31.1	(15.3)	46.4	(14.1)	60.5	4.9
Sonia™ grandiflora rose	19.9	(13.6)	33.5	(12.7)	46.2	3.3
Lsd (p = 0.05)	1.2		1.2		1.2	0.2

Differentiation of root initials is dependent upon either applied or endogenous auxin, although the mode of action is unclear (Hartmann et al., 1990). Hansen and Kristensen (1990) found that the onset of bud growth in *Schefflera* and *Stephanotis* was accelerated by an increasing number of roots per cutting. In *Rosa* hybrids (Jensen, 1967; Gislerød, 1983) and *R. centifolia* (Al-Saqri and Alderson, 1996) the number of roots is also dependent on nodal position.

Quiescence of axillary buds in rose plants can be released by exogenous application of benzyladenine (Ohkawa, 1984). Most likely, root-derived cytokinins transported via the xylem (Dieleman et al., 1997) into the buds are involved in the acceleration of bud growth (Qamaruddin et al., 1990). Thus, upon excision resumption of growth in an axillary rose bud may depend on its own cytokinin content and following root formation also on the supply from adventitious roots (for details see Hansen and Bredmose, 1998). After root formation an independent plant is established and this may explain the apparently lack of further position dependency in our results concerning development time, as illustrated by the almost similar figures for length of periods between developmental phases in Table 1. Thus, regarding developmental time topophysis in roses mainly affects the onset of bud growth (Bredmose and Hansen, 1996).
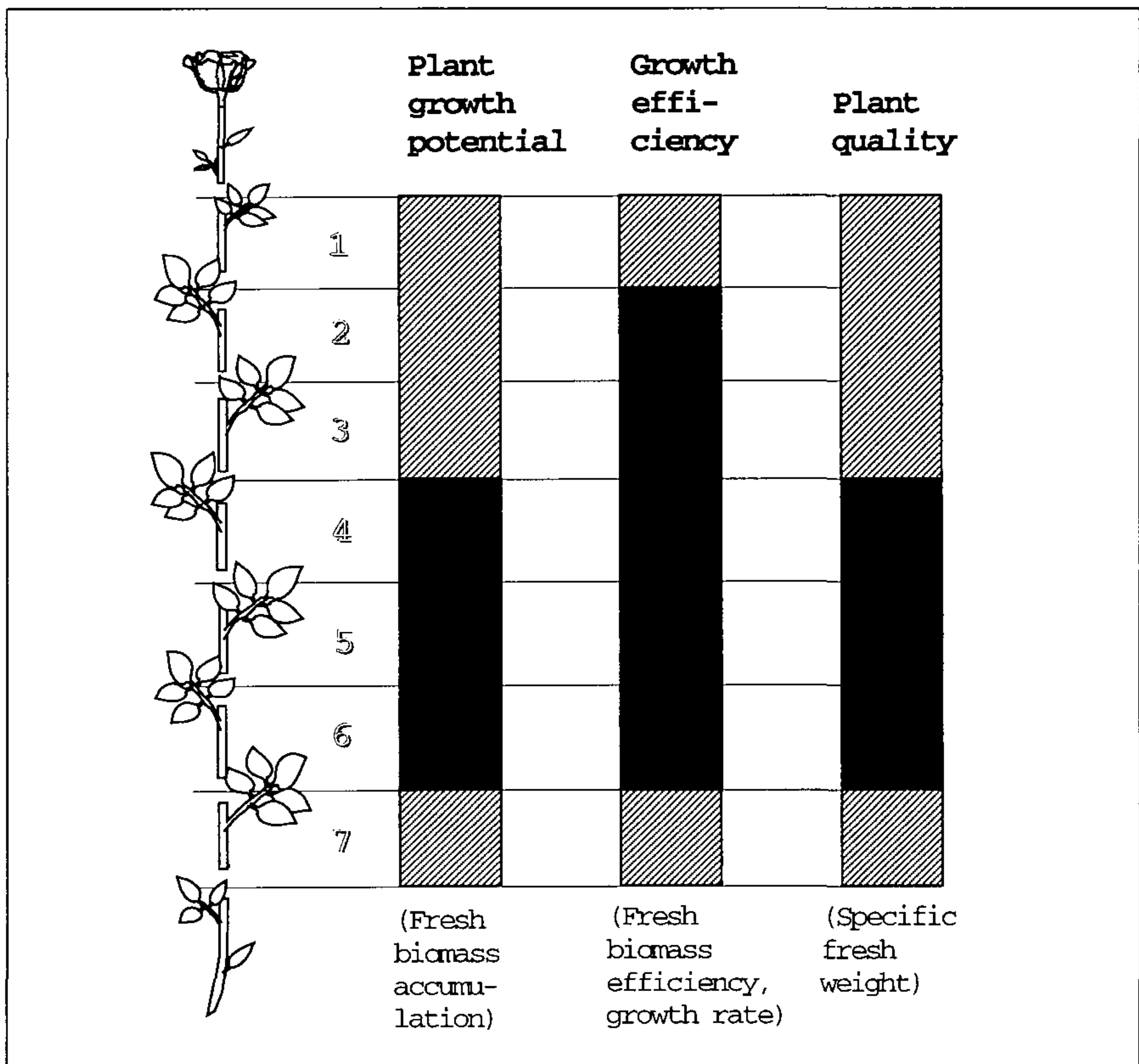

Figure 1. Influences of topophysis (after Bredmose and Hansen, 1996) on rose axillary bud growth potential (expressed by fresh biomass accumulation), plant growth efficiency (expressed by fresh biomass efficiency and by growth rate), and plant quality (expressed by specific fresh weight) of rose. The darkest area of columns show optimal cutting positions. Average of three rose cultivars ('Korokis', Kiss™ floribunda-tea rose; 'Tanettahn', Manhattan Blue™ hybrid tea rose; and 'Sweet Promise', Sonia™ grandiflora rose) grown as single-stemmed roses. The original seven cutting positions are shown schematically at left side of figure. (Graphics: Ebbe Elbrønd Andersen, Department of Ornamentals).

Growth Potential, Efficiency, and Plant Quality. Topophysic influences (Bredmose and Hansen, 1996) on bud growth potential (represented by fresh weight accumulated per bloom), plant growth efficiency (represented by fresh weight accumulation rate and by elongation rate), and plant quality (represented by fresh weight accumulated per cm of stem) in roses are illustrated in Fig. 1. Axillary buds from positions 4 to 6 possess the highest growth potential, axillary buds from positions 2 to 6 generally have the highest growth efficiency, and axillary buds from positions 4 to 6 give the best plant quality (Fig. 1). Consequently, selection of cuttings according to their position on the parent shoot reduce heterogeneity in subsequent bud and shoot growth.

Topophysis is Intrinsic to the Axillary Bud. Our results indicate that topophysis in *Rosa* is an independent phenomenon determined by factors intrinsic to the bud (Bredmose and Hansen, 1996), as also reported for *Citrus* (Halim et al., 1988; Jones et al., 1976), and noticed in *Populus* (Rohde et al., 1997). This suggestion is based on four reasons:

1) Halim et al. (1988) generally found no anatomical differences in the vascular system between buds and stem of differently positioned *Citrus* buds; and similar observations were done in roses by Zamski et al. (1985).

2) Isolated nodes grown on nutrient medium should all sprout equally if only nutrient gradients are responsible, however, Zieslin et al. (1976) found that rose axillary buds grew faster *in vitro* if they originated from upper rather than from basal positions.

3) For ontogenetically mature axillary buds of rose, like those in the present experiment, Marcelis-van Acker (1994) found that the chronological age of the bud did not clearly affect the subsequent shoot growth.

4) Finally, Halim et al. (1988) reported that inhibition of *Citrus* bud growth is intrinsic to the axillary bud because the inhibition was found in situ as well as in vitro. Also research by Jones et al. (1976) suggested that the state of inhibition in *Citrus* is related to inhibitors within the bud. In addition Rohde et al. (1997) noticed that at least the two most basal axillary buds on *Populus* shoots were prevented from growth by a mechanism other than apical dominance, and suggested that they are endodormant, i.e., the prevention is caused by factors intrinsic to the bud.

Though our buds carried stem tissue, we suggest that the prevention observed in *Rosa* also is caused by factors intrinsic to the bud. Because comparative studies, by Marcelis-van Acker and Scholten (1995), with axillary rose buds, revealed that the developmental process is very similar in vitro and in situ. Therefore, we suggest that topophysis in *Rosa* is an independent phenomenon which is intrinsic to the axillary bud rather than being controlled by correlative influences (apical dominance) at the time of bud development.

Influence of Inhibitors and Promoters. Gradients in inhibition due to position of buds, like those reported here, have been correlated with an accumulation of especially abscisic acid (Jones et al., 1976; Zieslin et al., 1978). Positive correlations between axillary bud growth and adventitious root formation in cuttings of *Schefflera arboricola* and *Stephanotis floribunda* have been attributed to root-produced cytokinin transported to the buds (Hansen and Kristensen, 1990). It could be interesting to investigate if inadequate levels of cytokinin in the buds (Ohkawa, 1984; Hansen and Kristensen, 1990; Qamaruddin et al., 1990; Dieleman et al., 1997) could cause the prevention of growth observed.

Buds forming the basal shoots on roses derive their cytokinin from the roots (Dieleman et al., 1997). Maybe a rose cutting is capable of de novo synthesis of cytokinins, as Dieleman et al. (1997) mention as a possibility, in addition to import from the phloem. However, most likely a balance between cytokinins and abscisic acid is involved, as has been proposed for regulation of basal rose bud growth (Zieslin and Khayat, 1983), possibly in interaction with other growth regulators. The addition of cytokinin appeared necessary for pea buds to develop when isolated from the intact plant (Gould et al., 1987).

In the concept of Positional Information (Wolpert, 1971; as cited by Greyson, 1994) developing and differentiating systems contain molecules (morphogens) that influence cell differentiation, and the pattern of morphogen distribution reflects sites of synthesis and the direction of their transport. Patterning in plant meristems could be based on intercellular, mechanical stimuli, or morphogens could be plant growth regulators (Greyson, 1994).

Aspects of growth readiness and plant architecture are integrated into the organogenic capacity of one organ, the bud. In many cases the influences of various endogenous and exogenous factors on the growth processes in buds are unsolved. Concerning the endogenous regulation this is largely due to the lack of early monitorable components in early stages (Rohde et al., 1997). In genetically transformed *Populus* Rohde et al. (1997) found the expression of two chimeric cell cycle genes to reflect the growth activity of the buds, and this occurred prior to visible changes in bud morphology. As for roses, in *Populus* axillary bud growth inhibition increased basipetally. Application of such molecular indicators may allow refinement of knowledge about bud growth and perhaps, topophysis.

Hormone Gradient Model of Stafstrom. Generally auxins are synthesized in the shoot apex and transported basipetally, and cytokinins are synthesized in root apices and transported to the shoots. At any point along the plant axis a relative and absolute level of each hormone exists. If buds grow when the level of cytokinin to auxin is high, and if the sensitivity of buds to these growth regulators vary according to their position, then the hormone gradient model (Stafstrom, 1993) might account for the observed positional effects on the time necessary for onset of bud growth (topophysis). But not necessarily for all other topophysic effects. Further, auxin may promote synthesis of a secondary inhibitor (Stafstrom, 1993), which could be abscisic acid.

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