

LATERAL SHOOT FORMATION IN APPLE IN THE FIRST YEAR AFTER BUDDING AS AFFECTED BY AIR HUMIDITY AND SOIL TEMPERATURE

J. Tromp
Research Station for Fruit Growing,
4475 AN Wilhelminadorp,
The Netherlands

Department of Horticulture,
Agricultural University,
Haagsteeg 3,
6708 PM Wageningen,
The Netherlands

Abstract

Under completely controlled conditions the effect of air humidity (two levels, 50% and 90%) in combination with soil temperature (12 and 22°C) on vegetative development of apple trees (cvs. 'Rode Boskoop' and 'Elstar') in the first season after budding was evaluated. Air was 20°C throughout. Irrespective of root temperature in both cultivars, shoot growth was much better at high than at low humidity. In 'Boskoop' at both humidities, growth at the soil temperature of 22°C exceeded that at 12°C, but in 'Elstar' root temperature was ineffective at low humidity. The effects on total growth were mainly in the number and length of lateral shoots; terminal growth was barely influenced by treatments. Soil temperature affected the distribution of the lateral shoots along the main axis. In both cultivars at 12°C most laterals were found in the range of 21 to 30 nodes counted from the graft union against in the 11 to 20 range at 22°C. Air humidity did not influence lateral shoot distribution. Therefore, the distance between the graft union and the most basal lateral shoot was distinctly smaller at the higher soil temperature. An attempt was made to explain these data in the scope of current hypotheses on apical dominance.

1. Introduction

In modern intensive fruit growing the economic life span of an orchard has been reduced to barely 10 to 15 years for apple and 15 to 20 years for pear. Early fruit bearing is essential, especially to balance the natural habit of vigorous growth in young trees and also to give an early return on the high financial investments that fruit-growing necessitates.

Since a clear positive relationship has been found between the number of lateral shoots (feathers) of nursery trees at planting in the orchard and total yield in the second and third years after planting (Van Oosten, 1978), feathered nursery trees are a

prerequisite for early fruit production.

The ability to form laterals, i.e., the degree of correlative inhibition mediated in some way by the growing tip of the main shoot (apical dominance), differs markedly between various cultivars of fruit trees (Wertheim, 1978). In addition, in view of strong year-to-year variations in the degree of branching it is felt that environmental factors also play an important role, but evidence from experiments where similar trees were exposed initially to different controlled climatic factors is not available. Therefore, we started a series of experiments being done in controlled-environment rooms on the effect of various climatic factors on lateral-shoot formation in apple the first year after budding. The present paper reports the results of an experiment wherein two air-humidity levels and two soil temperatures were combined.

2. Material and methods

2.1. Materials

In Jan. 1990 1-year-old apple rootstocks M.9 budded with 'Rode Boskoop' and 'Elstar' were planted into 3-liter plastic pots containing enriched pot soil. Budding height was about 20 cm; at planting the rootstocks were cut back to 1 cm above the inserted bud.

In the first week of February the trees of each cultivar were divided into four groups of 14 trees each and transferred from outdoors to four controlled-environment rooms. Initial temperature was 12°C; during February it was gradually increased to 20°C.

The four rooms were illuminated by high-pressure sodium lamps (Philips SON-T, 400 W), giving an irradiance of 90 to 95 W•m⁻¹ at plant level at the start of the experiment. To obtain the various soil temperatures the pots were placed in temperature-controlled containers filled with water.

2.2. Experimental procedure

From early March when the buds just opened in each of the rooms one of the following regimes was maintained: Low relative air humidity (RH, about 50%), soil 12°C; High humidity (about 90%), soil 12°C; Low humidity, soil 22°C; High humidity, soil 22°C. Day/night air was 20°C; daylength was 14 hr. The trees were watered as needed, and control was maintained by frequently weighing the pots. Each week the length of the main shoot and each individual lateral bud shoot length and position

(distance from graft union) were recorded.

3. Results

At both soil temperatures growth vigor of 'Boskoop' and 'Elstar' was much better at high than at low humidity (Table 1). In 'Boskoop' growth at the soil temperature of 22°C tended to exceed that of 12°C irrespective of humidity, but for 'Elstar' soil temperature had little effect at low humidity. When lateral and terminal growth are considered separately, the effect of treatments on total growth was mainly reflected in differences in lateral growth; growth of the parent shoot was influenced relatively little by treatments. Shortly after the start of the experiment in 10% to 15% of the trees in the bud range 1-5 starting from the graft union and in lesser degree in the range 6-10, one or two strong growing shoots emerged that, because there was no relationship with treatments, already may have been initiated before treatments started. Their occurrence is at least partially responsible for the variation in lateral and total growth.

Plotting the weekly records for terminal and lateral growth against time (Figs. 1 and 2, 'Boskoop') revealed that the rate of growth of the terminal shoot was fairly constant throughout, except that at low RH and soil temperature it gradually slowed by the end of the experiment. The first lateral shoots emerged a few weeks after the start of the experiment; thereafter, growth increased rapidly, especially at high humidity and soil temperature. Toward the end of the experiment the growth curve clearly flattened off. However, lateral growth at low RH at 12°C lagged behind and had not stopped by the time the experiment was terminated. It should be noted that the occurrence of lateral shoots had hardly any effect on the growth rate of the terminal shoot. 'Elstar' behaved essentially as 'Boskoop'; for reasons of space, growth curves for 'Elstar' are not given.

With respect to the distribution of the lateral shoots along the main axis, starting at the graft union for each range of five nodes the final number of emerged shoots was counted (Figs. 3 and 4), and their total length was calculated and expressed as percentage of lateral growth for the plant as a whole (Figs. 5 and 6). Soil temperature clearly affected the distribution of the lateral shoots along the parent shoot. In both cultivars at 12°C most lateral growth (number of shoots as well as proportion of total lateral growth) was found in the range of 21-30 nodes vs. the 11-20 range at 22°C. Air humidity did not influence lateral shoot distribution. Therefore, the distance between the most basal lateral shoot and the graft-union was distinctly smaller at 22 than at 12°C, but was unaffected by humidity (Table 2). Furthermore, terminal shoots when the first (always the most basal) lateral emerged were longer than at the low soil temperature but were hardly affected by humidity. It should be remarked that for the calculation of the data in Table 2 the trees that formed premature shoots below node 11 were not taken into account.

4. Discussion

Higher growth vigor at high than at low RH as found in the present experiments is consistent with data for many plant species (Hoffman, 1979), including apple (Tromp and Oele, 1972; Tromp, 1984). Similarly, the better growth at soil temperature of 22°C than at 12°C agrees with data of Nelson and Tukey (1956) and Tromp (1978, 1984) for apple and Barr and Pellett (1972) for other perennials.

With respect to the mechanism of apical dominance, two main conceptions can be distinguished (Phillips, 1975; McIntyre, 1977a, 1987; Martin, 1987). So far, the most favored one, the “hormonal” theory, assumes that the apical growing point of the parent shoot is the source of some correlative signal of hormonal nature, probably auxin, which restricts the development of lateral bud meristems. An additional role is imputed to cytokinins due to their ability to elicit outgrowth of lateral buds. The second conception, the “nutritive” theory, states that apical dominance is primarily controlled by the internal competition for water, mineral nutrients, and carbohydrates between the lateral buds and the parent shoot.

With respect to lateral branching, i.e., apical dominance as affected by environmental factors, there seems to be no information available for woody perennials, including fruit trees. Our humidity data are in good agreement with data for a number of herbaceous plants exposed to various RH values, such as *Helianthus annuus* (McIntyre, 1977b), *Cirsium arvense* (Hunter et al., 1985), and *Asclepias syriaca* (McIntyre and Hsiao, 1990), and may support the nutritive hypothesis. It may be suggested that at the high RH, due to reduced transpiration, water potential and turgor are increased, which triggers the buds from inhibition (McIntyre, 1987). In this concept the parent shoot tip is not directly involved, and the observation that lateral growth does not affect the growth rate of the main shoot (Figs. 1 and 2) is not surprising, at least if the supply of nutrients needed for continued lateral growth is not limiting. In the same line, increasing the soil temperature may have stimulated bud outgrowth via an increase of water uptake by the roots and, consequently, reduction of water stress.

Trying to fit our results with the hormone theory raises questions about the degree of lateral growth differing considerably between treatments, while the growth rate of the parent shoot, i.e., the rate of production of the correlative signal, is about the same or possibly even higher only in the treatment that induced the strongest lateral growth (high RH, root temperature 22°C). The release from inhibition of lateral buds may be controlled by some second factor as the level of cytokinins. If as is usually assumed the synthesis of cytokinins mainly occurs in root tips, the effect of soil temperature on branching becomes clear. As reviewed by Goodwin et al. (1978) root factors are involved in lateral bud growth. Skene and Kerridge (1967) found distinct qualitative differences in cytokinins between xylem sap from grapevines grown at 20 and 30°C. In xylem sap of maize the flux of cytokinins from the roots declined with

increasing soil temperature in the range 28-8°C; for some inhibitor the reverse pattern was true (Atkin et al., 1973). There is ample information that application of cytokinins to lateral buds of intact plants favors their outgrowth (Phillips, 1975; King and Van Staden, 1988).

The effect of soil temperature on the height of lateral shoot development (Figs. 3-6, Table 2) must be due to some factor originating in the roots. It may be reasoned that the ability of lateral shoots to grow out is at least partly controlled by the balance between, on the one hand, the degree of rest increasing with bud age, and on the other hand the level of cytokinins coming from the roots that stimulate growth activity. Then, under conditions of reduced cytokinin supply at the lower soil temperature, the time required to turn the balance in favor of shoot outgrowth will be extended. As a consequence, bud outgrowth is delayed and will only occur in later-formed, i.e., lesser-inhibited and higher-inserted, buds.

An intriguing question is the reason growth of the parent shoot is so little affected by the various treatments and does not benefit from the obviously favorable growing conditions at high humidity and soil temperature. Some limiting factor may be suggested, such as the rate of nutrient translocation in the vascular system to the growing point or, alternatively, air temperature.

In conclusion, air humidity and soil temperature are important controlling factors in lateral bud growth in nursery apple trees.

Acknowledgment

Thanks are due to Mr. C.A.R. Romer for extensive technical assistance.

References

- Atkin, R.K., Barton, G.E., and Robinson, G.E. 1973. Effect of root-growing temperature on growth substances in xylem exudate of *Zea mays*. J. Expt. Bot. 24:475-487.
- Barr, W. and Pellett, H. 1972. Effect of soil temperature on growth and development of some woody plants. J. Amer. Soc. Hort. Sci. 97:632-635.
- Goodwin, P.B., Gollnow, B.I., and Letham, B.I. 1978. Phytohormones and growth correlations, p. 215-249. In: D.S Letham, P.B. Goodwin, and T.J.V. Higgins (eds.). Phytohormones and related compounds: A comprehensive treatise II. Elsevier, North Holland Biomedical Press, Amsterdam, Oxford, New York.
- Hoffman, G.J. 1979. Humidity, p.141-171. In: T.W. Tibbitts and T.T.

- Kozłowski. Controlled environment guidelines for plant research. Academic Press, New York, London
- Hunter, J.H., Hsiao, A.I., and McIntyre, G.I. 1985. Some effects of humidity on the growth and development of *Cirsium arvense*. Bot. Gaz. 146:483-488.
- King, R.A. and Van Staden, J. 1988. Differential responses of buds along the shoot of *Pisum sativum* to isopentenyladenine and zeatin application. Plant Physiol. Biochem. 26:253-259.
- Martin, G.C. 1987. Apical dominance. HortScience 22:824-833.
- McIntyre, G.I. 1977a. The role of nutrition in apical dominance, p. 251-273. In: D.H. Jennings (ed.). Integration of activity in the higher plant. Symp. Soc. Expt. Biol. 31.
- McIntyre, G.I. 1977b. Environmental control of lateral bud growth in the sunflower (*Helianthus annuus*). Can. J. Bot. 55:2673-2678.
- McIntyre, G.I. 1987. The role of water in the regulation of plant development. Can. J. Bot. 65:1287-1298.
- McIntyre, G.I. and Hsiao, A.I. 1990. The role of expanded leaves in the correlative inhibition of axillary buds in milkweed (*Asclepias syriaca*). Can. J. Bot. 68:1280-1285.
- Nelson, S.H. and Tukey, H.B. 1956. Effect of controlled root temperatures on the growth of East Malling rootstocks in water culture. J. Hort. Sci. 31:55-63.
- Phillips, I.J.D. 1975. Apical dominance. Annu. Rev. Plant Physiol. 26:341-367.
- Skene, K.G.M. and Kerridge, G.H. 1967. Effect of root temperature on cytokinin activity in root exudate of *Vitis vinifera* L. Plant Physiol. 42:1131-1139.
- Tromp, J. 1978. The effect of root temperature on the absorption and distribution of K, Ca and Mg in three rootstock clones of apple budded with Cox's Orange Pippin. Gartenbauwiss. 43:49-54.
- Tromp, J. 1984. Flower-bud formation in apple as affected by air and root temperature, light intensity and day length. Acta Hort. 149:39-47.
- Tromp, J. and Oele, J. 1972. Shoot growth and mineral composition of leaves and fruits of apple as affected by relative air humidity. Physiol. Plant. 27:253-258.
- Van Oosten, H.J. 1978. Effect of initial tree quality on yield. Acta Hort. 65:123-127.
- Wertheim, S.J. 1978. Manual and chemical induction of side-shoot formation in apple trees in the nursery. Scientia Hort. 9:337-345.

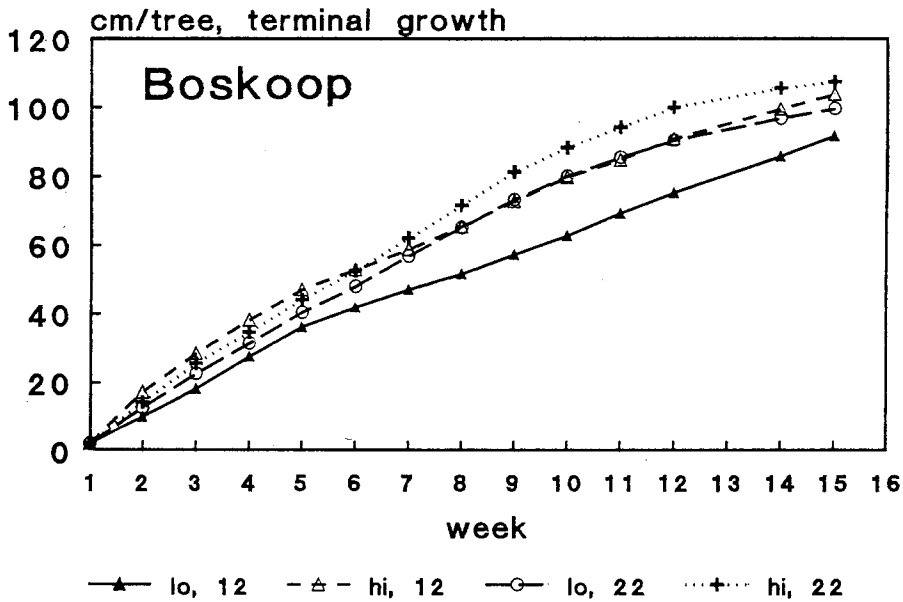


Fig. 1. Growth pattern of the terminal shoot of 'Rode Boskoop' apple at two air humidities (RH lo = 50%, hi = 90%) and two soil temperatures (12 and 22C).

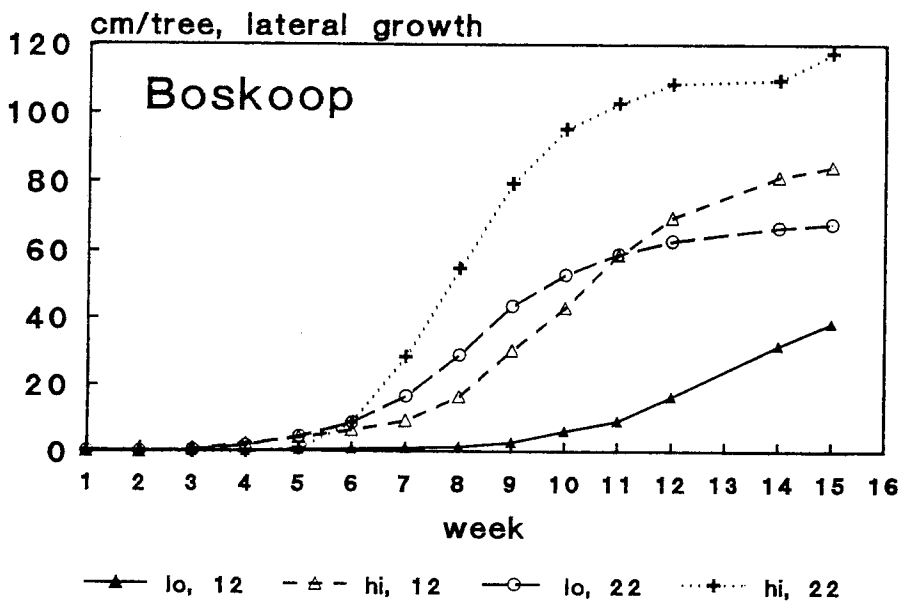


Fig. 2. Pattern of lateral shoot growth of 'Rode Boskoop' apple at two air humidities (RH lo = 50%, hi = 90%) and two soil temperatures (12 and 22C).

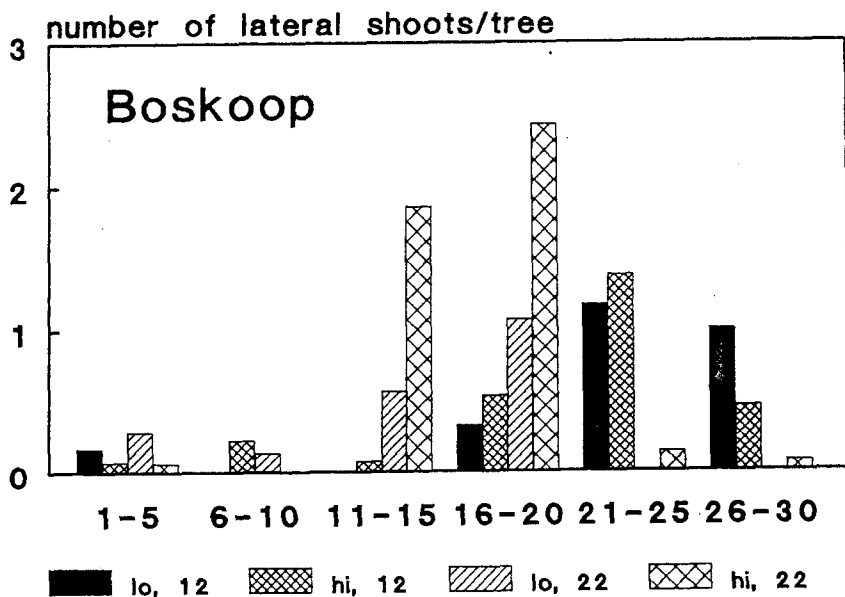


Fig. 3. Final number of lateral shoots per five-node range counted from the graft union of 'Rode Boskoop' apple at two air humidities (lo = 50%, hi = 90%) and two soil temperatures (12 and 22C).

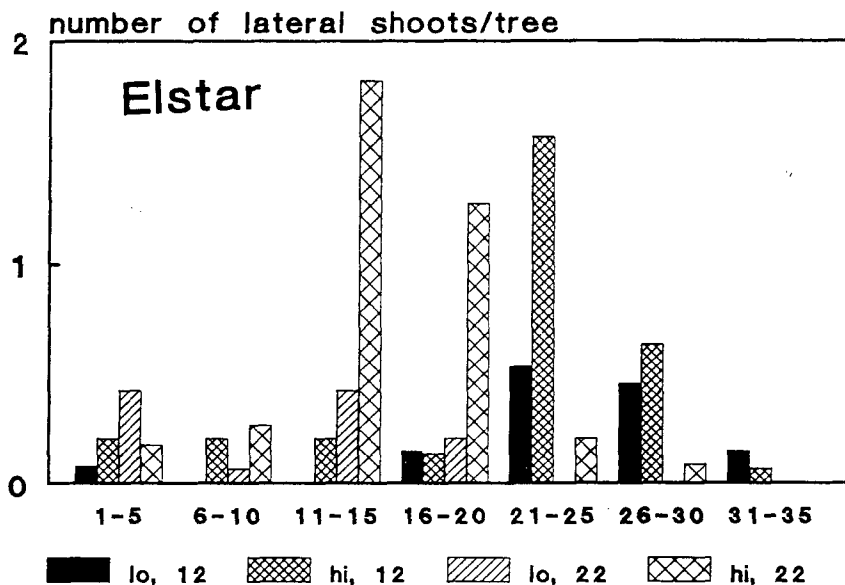


Fig. 4. Final number of lateral shoots per five-node range counted from the graft union of 'Elstar' apple at two air humidities (lo = 50%, hi = 90%) and two soil temperatures (12 and 22C).

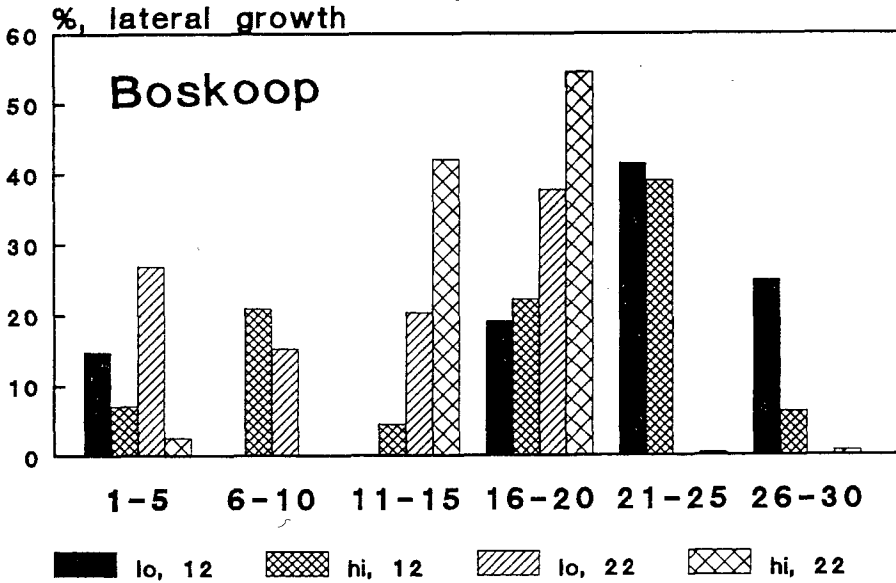


Fig. 5. Final lateral shoot growth per five-node range counted from the graft union of 'Rode Boskoop' apple expressed as percentage of total lateral growth at two air humidities (lo = 50%, hi = 90%) and two soil temperatures (12 and 22C).

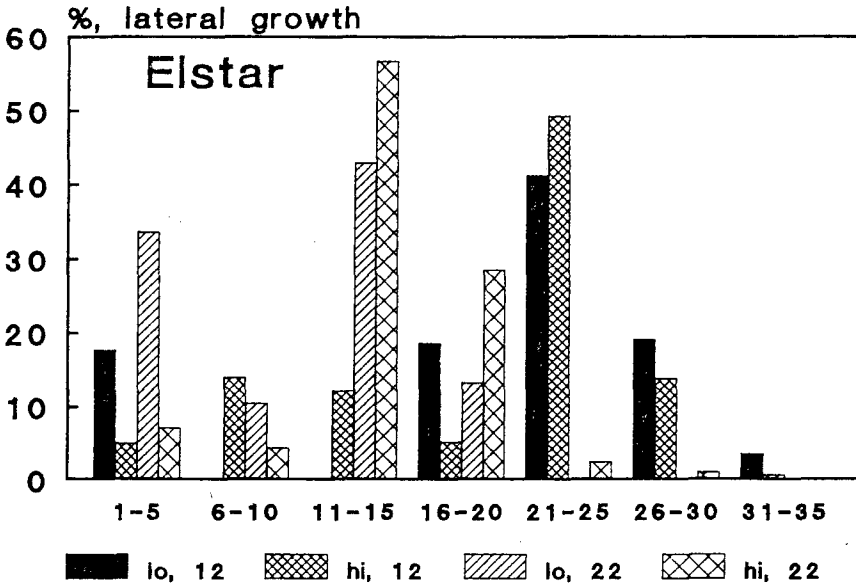


Fig. 6. Final lateral shoot growth per five-node range counted from the graft union of 'Elstar' apple expressed as percentage of total lateral growth at two air humidities (lo = 50%, hi = 90%) and two soil temperatures (12 and 22C).

Table 1 - Terminal, lateral and total shoot growth (cm/tree) of cvs 'Rode Boskoop' and 'Elstar' at the end of the experiment at 2 air humidities and 2 soil temperatures. Between brackets the number of lateral shoots per tree.

RH	°C	Rode Boskoop			Elstar		
		Terminal	Lateral	Total	Terminal	Lateral	Total
low	12	91.7	38.5	130.2	79.8	19.7	99.5
			(2.7)			(1.4)	
high	12	103.8	84.5	188.2	89.4	51.7	141.1
			(2.8)			(3.1)	
low	22	99.6	67.8	167.4	83.9	28.0	111.9
			(2.1)			(1.1)	
high	22	107.4	110.4	217.8	91.1	88.4	179.5
			(4.5)			(3.9)	
LSD 0.05		8.1	33.6	37.4	10.5	43.3	51.3

Table 2 - Height of insertion from graft union (cm/tree) of the first lateral shoot and length of the terminal shoot at the time of its emergence (cm/tree) of cvs 'Rode Boskoop' and 'Elstar' at 2 air humidities and 2 soil temperatures.

RH	°C	Rode Boskoop		Elstar	
		From union	Terminal	From union	Terminal
low	12	51.4	68.8	48.1	62.7
high	12	48.1	65.1	42.7	54.8
low	22	33.3	52.4	22.0	34.8
high	22	33.2	51.1	27.5	47.0
LSD 0.05		6.6	8.0	12.0	12.0