Plant Architecture of Strawberry in Relation to Abiotic Stress, Nutrient Application and Type of Propagation System

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ABSTRACT

Vegetative growth of strawberry plants turns to generative growth (flower induction and differentiation) under specific thermo-photoperiods, but agronomic and nutritional factors may establish which kind of growth (vegetative or reproductive) to be strengthened. As a consequence, environmental stressing conditions assume a key function in determining plant quality during plant propagation and culture, in relation to different physiological internal factors. The result is a significant modification of plant architecture that influences the timing of forcing conditions for out of season production, the quantity of chilling to be applied and the effect of day length. Plant architecture describes the spatial distribution of vegetative and reproductive organs and their developmental phase and thus it is useful to evaluate plant quality and also to study the results of a few different propagation techniques in the nursery. Time of transplanting, regulated nutrient deficit, water application and limited substrate soil volume (smaller pot) in tray plant production are some possible stress manipulations to control plant quality. Important differences in plant architecture are also possible between cultivars, within the same cultivar grown in different environments and between farms (growers) in the same area, because growing conditions affect plant vigour, induce the formation of a very different number of lateral flower buds and modify the ability of the plant to form new lateral shoots along the main shoot. The developmental phase of the flowers is also affected. Depending on the desired production system, the plant architecture and its potential fruit production can be strongly modified, but in a predictable way, by changing and modulating the growing techniques in the nursery.

CONTENTS

INTRODUCTION

Strawberry (*Fragaria* spp.) is a herbaceous perennial plant that shows good ability to adapt to different growing conditions and environments (Darrow 1966). This behaviour is related to the epigenetic regulation (plasticity) of strawberry growth and development, and it can be heavily manipulated by agronomic practices.

Strawberry cultivars can be classified into 3 main types on the basis of photoperiod sensitivity of their flowering characters. Junebearing cultivars are widely cultivated and are considered facultative short-day (SD) plants, requiring daylengths shorter than about 11-16 h (Van den Muijzenberg 1942; Borthwick and Parker 1953; Ito and Saito 1962; Benoit 1975; Heide 1977; Konsin *et al.* 2001) or low tem-

peratures (threshold ranging between 9-21°C; Hartmann 1947; Went 1957; Ito and Saito 1962; Heide 1977) for flower initiation (Darrow 1936; Darnell and Hancock 1996). This photoperiod sensitivity leads plants to bear only one spring-summer production coming from inflorescences induced in the preceding late summer-autumn. Vegetative and reproductive developments are oppositely regulated by photoperiod and temperature.

Cultivars are classified as long-day (LD) plants if flower initiation takes place when daylength is longer than 12 h (Darrow and Waldo 1934); they bear more than one production during the year (double cropping). Cultivars are considered day-neutral (DN) (Bringhurst and Voth 1980) genotypes if flower initiation takes place irrespective of photoperiod (Durner *et al.* 1984); they are multiple (triple)
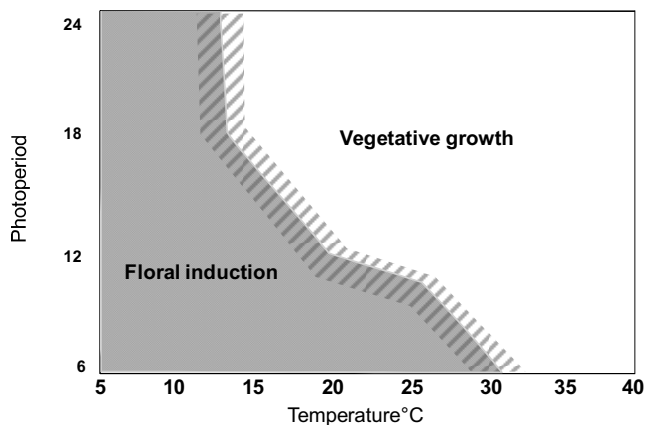
Invited Review

Fig. 1 Relation between photoperiod and temperature to induce reproductive (flower induction) or vegetative development. Modified from Ito and Saito (1962).

cropping.

Plant erratic and complex responses to daylength are also possible, thus the above mentioned classification has been described as inadequate (Durner *et al*. 1984) and cultivars should be classified in a continuum between obligate single-cropping and continuous flowering forms and the difference are only quantitative (Darrow 1966; Nicoll and Galletta 1987; Sønsteby and Nes 1998; Savini 2003). Prolonged short-day exposure of already induced plants can delay floral initiation (Moore and Hough 1962) whereas long photoperiod can hasten the development of initiated buds in SD cultivars that can be thus characterized as SD plants in relation to floral induction and LD plants regarding floral development (van der Veen and Meijer 1959; Salisbury and Ross 1991).

The photoperiod interact with the temperature and the same daylength may produce different effects according to the temperature (Ito and Saito 1962; Heide 1977; Sønsteby and Nes 1998), with cultivar dependent response (Heide 1977; Sønsteby 1997; Serçe and Hancock 2005). The longer the photoperiod, the lower the temperature needed to maximize flower bud number (**Fig. 1**; Ito and Saito 1962). Furthermore, flower buds initiation is also possible under unfavorable conditions (Takeda *et al*. 2009). Everbearing varieties show a much shorter vegetative cycle before flower formation than in Junebearing ones and form more lateral branches and inflorescences per plant.

The developmental morphology of flower initiation and differentiation in strawberry has been described using light (Ruef and Richey 1926; Waldo 1930; Scilletter and Richey 1931; Guttridge 1955; Jahn and Dana 1970) and scanning electron (Taylor *et al*. 1997; Manakasem and Goodwin 1998; Kurokura *et al*. 2005a) microscopy. Floral initiation is first evident as a raising and broadening of the apical meristem, followed by differentiation of the first bracts and of the organs of the primary flower (Jahn and Dana 1970; Taylor *et al*. 1997): sepals followed by the petals, stamens and carpels, respectively. Secondary flowers appear early in the axils of the bracts primordia. In most cultivars, a secondary flower develops terminally on each of two or three branches of the main floral axis, two tertiary flowers forming on each secondary branch, and so on (Guttridge 1985) but inflorescences vary considerably in size and branching structure (Darrow 1929; Anderson and Guttridge 1982). For the progressive stages of flower bud development, a conventional numerical scale has been proposed (Jahn and Dana 1970; Savini 2003) according to the primary flower that shows more advanced developmental stage than other flowers of the inflorescence (Waldo 1930). Also the final fruit size is bigger for primary fruits and decreases in higher order fruits.

The size of the flowers and the number and quality of floral parts vary between cultivars and depending upon the

position or rank of the flower within the inflorescence (Guttridge 1985) and also between flowers of the same position (Webb *et al*. 1978). Low quality of floral parts can lead to the production of malformed fruits (Kronenberg 1959).

Floral organs differentiation takes place with high temperature. Differentiation pace and duration determine the final number of flowers per inflorescence. A good correlation between the number of flowers inside the buds of the plants and their final fruit production has been reported (Jemmali and Boxus 1993; Savini 2003).

The inflorescence is located in the terminal position on a crown: its formation terminate the vegetative growth of the crown and is associated with a change in the rate of extension growth of the three or four uppermost axillary buds that continue the vegetative extension growth on secondary axis and become branch crowns (Guttridge 1955; Kurokura *et al*. 2005a, 2005b). Removal of flower-induced terminal apex stimulates the growth of axillary buds developing into branch crowns (Neri *et al*. 2003). The delay in differentiation of terminal flower is associated with a less lateral shoot formation because it is possible only after the arrest of main shoot growth. Under inductive conditions, terminal inflorescences initiation may occur also on branch crown, leading to further crown branching. The total number of inflorescences in a plant is dependent on the number of apical meristems. The secondary branches located underneath the last expanded leaf differentiate a very early flower before chilling and do not continue this development after of chilling, whereas those above this leaf are able to continue their differentiation (Bosc *et al*. 2010). Axillary meristems may be inactive for months and they can break out in the next growing season after a chill period.

Flower induction can be asynchronous because inductive factors are effective only on receptive organs, i.e. apex with slowing growth. It is possible to find lateral buds at same developmental stage as terminal bud in the basal portion of the crown. In this case, they grow and produce fruit at same time and they compete as nutrient sink with the main inflorescence and thus they are often referred as 'vampire buds'. Growers usually remove them manually or, if they want to maintain them appropriately, they provide higher nutrient supply to the plant.

Vegetative growth is expressed with stolon formation that is stimulated under high growth rate conditions and weak apical dominance (Neri *et al*. 2003; Sugiyama *et al*. 2004) or higher temperature under long day conditions (Darrow 1936; Heide 1977; Durner *et al*. 1984; Guttridge 1985; Le Mière *et al*. 1996). Some stolons might appear late in the season when the flower induction is already started, but this is due to a delay between formation and elongation of the stolon, therefore they appear when the flower induction is completed. Stolon differentiation begins early in the year and often first axillary meristem becomes the first stolon.

Stolons show a sylleptic behaviour (Neri *et al*. 2003) without a rest phase, starting the growth immediately after their formation as axillary meristems (Savini 2003). This capability to produce stolons is linked with the possibility to make one or several cycles during the same growing season.

Additional branch crowns are formed if conditions are favourable to increase plant size, when newly formed branch crown buds are present. This time is limited, in vigorously growing plants, to the period between the emergence of the last stolon in late summer or autumn, and the emergence of the first stolon in spring, which approximately coincides with flowering. Vegetative growth seems to be contrasted by flower differentiation and vice-versa. Plants less inclined to produce stolons usually have more lateral branches (Savini *et al*. 2005).

Plant architecture

Strawberry plant is a rosette, with a very short stem (crown); its growth is determined, with a terminal inflores-
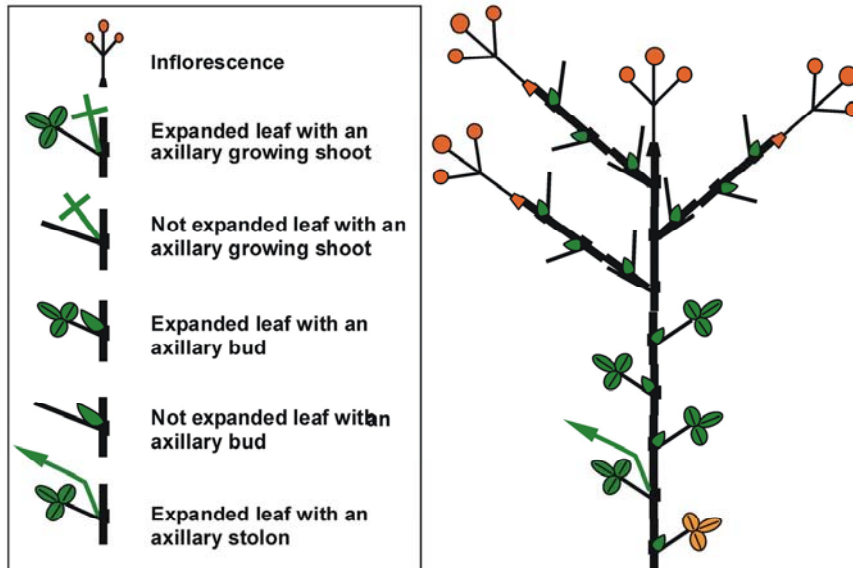
Fig. 2 Schematic drawing of strawberry plant architecture. From **Savini G, Neri D, Zucconi F, Sugiyama N** (2005) Strawberry growth and flowering. An architectural model. *International Journal of Fruit Science* **5**, 29-50, ©2005 with kind permission of Taylor & Francis, London, UK.
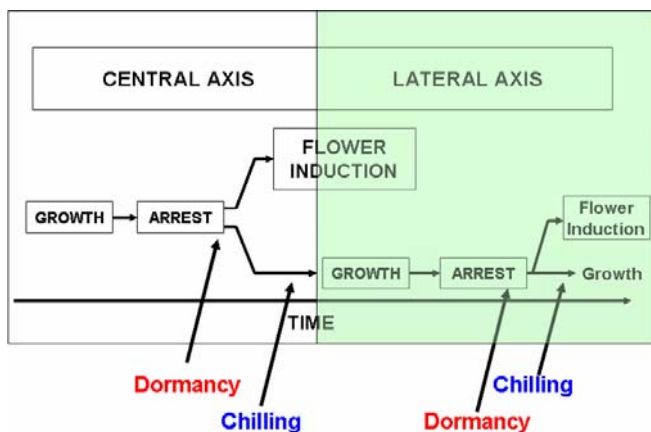

Fig. 3 Schematic representation of the physiological mechanism of flower induction. Each growing axis experiences a rapid growth and a reduction phase during which the flower differentiation can develop. Dormancy and chilling may interfere with the arrest phase resuming the growth (modified from Savini 2003). This is repeated both in the central axis or in the lateral.

Fig. 4 Strawberry architecture 120 days after transplanting in Mediterranean climatic conditions. (**A**) The plant shows 3 orders of inflorescences. (**B**) 4 orders of inflorescences are shown (represented in Arabic numerals 1, 2, 3 and 4). Modified from Savini *et al.* (2006b).

cence. The features of the growth habit differ between varieties or crowns, between plants of different ages or growing under differing environments. Architecture of the strawberry plant can be represented as extended axes (Guttridge 1955; Nicoll and Galletta 1987; Yanagi and Oda 1990) on which plant vegetative and reproductive organs are reported with different colors and symbols (**Fig. 2**).

Reporting the fate of all the meristems and the developmental stages of flower organs, the analysis of plant architecture is able to show the spatial relationship between organs, along a selected period of time. Thus it is possible to dynamically study the response of the plants to growing conditions in the nursery, in the field or in forcing culture (**Figs. 3, 4**) and to better understand its behaviour.

The signal response by the plant varies in relation to its physiological phase; therefore the same cultural techniques may induce a very different result depending on the plant quality from the nursery and on the interaction with environmental conditions. If the architectural analysis is properly applied it can also help for the evaluation of plant quality in the nursery according to farmer necessity (Savini and Neri 2004).

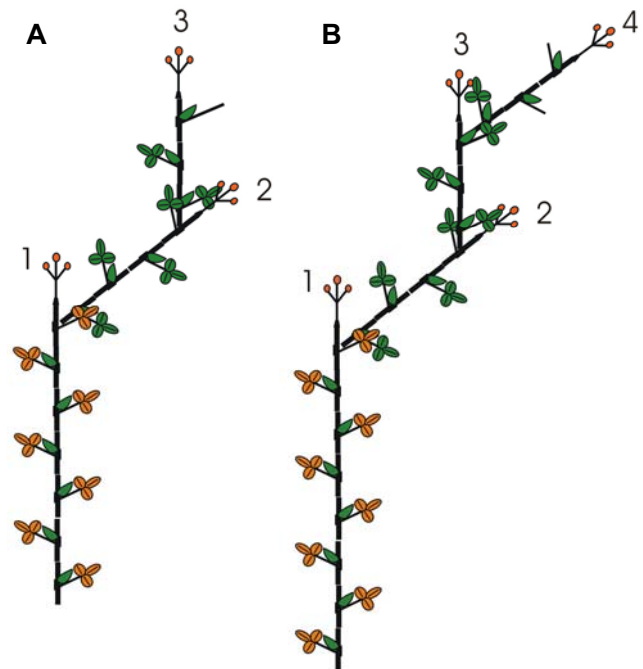Propagation techniques allow to produce many different plant types and to manage production planning. Nursery plants differ according to their dimension, initial propagation material, presence of the soil, pot type, storage technique before planting and to the presence of differentiated inflorescence. Plants propagated under different environmental and climatic conditions can differ in the number of shoots, stolons, inflorescences or flowers and require specific growing techniques. Plant quality evaluation is strictly related to the typology, but it should be even based on their crop potential. On the other hand, in the nursery stolon formation in mother plants is needed to produce new plants, and the presence of flowers is not desirable. Techniques for delaying flower induction are thus useful in this context.

Information about inflorescence number and their position along the crown are important to estimate the plant crop potential, developmental stage of floral organs is useful to estimate production earliness and synchronicity.

Numerous studies concerning the effects of photoperiod and temperature on flowering (Serçe and Hancock 2005; Verheul *et al*. 2006; Sønsteby and Heide 2006) are available, but few take into account the effects of growing conditions on the architecture of the plant (Savini and Neri 2004; Savini *et al*. 2005, 2006b; Van Delm *et al*. 2009; Bosc *et al*. 2010).

PLANT ARCHITECTURE IN RELATION TO ABIOTIC FACTORS

Abiotic stress

Abiotic stresses play an important role to control plant growth and development in the strawberry nursery tray plant production, strictly interacting with the physiological processes which lead to flower induction and differentiation. As a consequence, programmed environmental stressing conditions may assume a key function in determining plant quality in relation to different physiological internal factors of the plants. In fact, flower induction is sensitive to thermo-photoperiod but even to other several agronomic and nutritional factors, such as mineral nutrition and water supply (Guttridge 1985) then to their growth rate or to the presence of stress, but usually they are considered to play a minor role and there is little detailed information on their influence on plant architecture. Agronomic and nutritional factors may establish which kind of growth (vegetative or reproductive) to be strengthened. The knowledge of environmental and growing factors that affect the generative and vegetative behaviour of the plants is therefore strategic to improve yield and fruit quality by anticipating or delaying flower induction and determining inflorescence number and dimension.

Furthermore, it is well known that tray plants propagated under different growing conditions in the nursery, coming from different nurseries or growing systems and countries may show differences in plant vigour and fruit production. In effect, specific growing conditions induced the formation of a different number of lateral flower buds and modified the ability of the plant to form new shoots along the central axis. Developmental phases of floral buds were also affected (Van Delm *et al*. 2009).

Planned and controlled stress or balanced fertilizations can be effective means to induce and stimulate flower formation. It is interesting to understand how these factors interact with plant physiology and architecture, but we can assume that there is a main indirect effect through the whole plant vigour modification (**Fig. 3**).

Photoperiod

Photoperiod is a primary environmental factor controlling the transition from vegetative to reproductive growth in strawberry. The application of LD conditions on SD plants delayed flower induction and then the blooming ability was delayed too (Bosc *et al*. 2010). Artificial light or light-proof covering can be used to alter the flower differentiation degree and the plant architecture: plants under SD conditions or SD followed by LD conditions showed similar plant architecture, with advanced flower development for the terminal flower and some flower buds in the top portion of the plant; under LD or LD followed by SD conditions plants showed less developed terminal inflorescence and less flower buds and differentiated secondary branch (Bosc *et al*. 2010). Short induction period resulted in less-developed inflorescences than the long induction period (Bosc and Demené 2009).

Propagation, location (altitude and latitude) and transplanting time are main factors in modulating environmental conditions. Plants can be propagated under favorable conditions for floral induction in northern areas and then transplanted in southern areas to stimulate floral organs formation. Temperature is considered as important as photoperiod for flowering at high latitudes where long photoperiods

Table 1 Effect of red light-emitting diode lamps on flowering in strawberry 'Festival' (Takeda *et al*. 2008).

	Flowered plants (%)			
	3 October	**24 October**	**27 November**	**17 December**
Control	70.3	83.0	95.7	95.7
Red Light	37.3	45.7	58.3	62.3

prevail (Heide 1977). The place of cultivation modify notably the ability of the plant to form new crowns along the principal axis, for instance more in the Center and North Italy and less in the South which have a warmer winter. On the contrary, the total number of the inflorescences per plant increased going to South. In South Italy, the later plantation under conditions of cooler temperature and short photoperiod, which are favorable to the flower differentiation determines lower vegetative growth and the formation of only one extension crown per plant.

Light intensity and quality

Flower initiation in SD strawberries may be regulated by light quality (Collins 1966; Vince-Prue and Guttridge 1973) and intensity. Increasing light intensity (e.g. from 25 or 150 to 650 µmol m^{-2} s^{-1}), the number of flowers per plant is significantly higher both in the wild strawberry *Fragaria vesca* (Chabot 1978) and in a DN cultivated strawberry (Dennis *et al*. 1970). Increasing the percentage of shading on the plant, a reduction in crown (Wright and Sandrang 1995) leaves and inflorescence number (Awang and Atherton 1995) can be observed. Kumakura and Shishido (1985) found that light intensity reduction (85% shading) along with lower temperature increased flower induction, but affected it during reducing day-length period.

Spectral composition of the irradiation appears to quantitatively affect flower bud initiation (**Table 1**; Takeda 2010). Photoperiod extension on SD plants does not delay floral initiation when using red light, whereas using far red light it retards floral initiation and using red along with far red light decreases floral initiation only when the red/far red ratio is low (Vince-Prue and Guttridge 1973; Kadman-Zahavi and Ephrat 1974; Guttridge 1985). Red light from Light Emitting Diode lamps at 662 nm can delay flower bud initiation (Takeda 2010). But Jonkers (1965) found no marked differences in the number of flowering plants or in days to flower bud development under either incandescent (rich in far-red) or fluorescent (rich in red) light. The use of photo-selective nets over the plants may select the light signal that stimulates flower initiation, in particular red and blue nets prevent flower initiation (Takeda 2010).

Temperature

Temperature affects the response of flower induction to photoperiod in both SD and DN cultivars. Temperature affects also the rate of flower initiation and the number of flowers within the inflorescences without significant control of photoperiod. Flower bud formation can be totally (Ito and Saito 1962; Chabot 1978) or partially (Okimura and Igarashi 1997; Verheul *et al*. 2006) inhibited at prolonged high temperatures, in the range of 26°C (Durner *et al*. 1984; Oda and Yanagi 1993) to 30°C (Ito and Saito 1962; Chabot 1978; Durner and Poling 1988; Okimura and Igarashi 1997) whereas flower number is lower in plants at 24°C, compared to 18°C (Heide 1977). In warm areas, such as at tropical to equatorial latitudes, strawberry can be commercially grown only in the highlands, where temperatures are lower.

Natural daily fluctuation of temperatures (26.7°/15.6°C day/night), induce earlier flower formation compared to a constant temperature of 21°C (Hartmann 1947), and earlier flower initiation than at higher (35°/25°C) day/night temperature (Bish *et al*. 1996). No similar effects of fluctuating temperatures are reported in DN cultivar under a 16 h
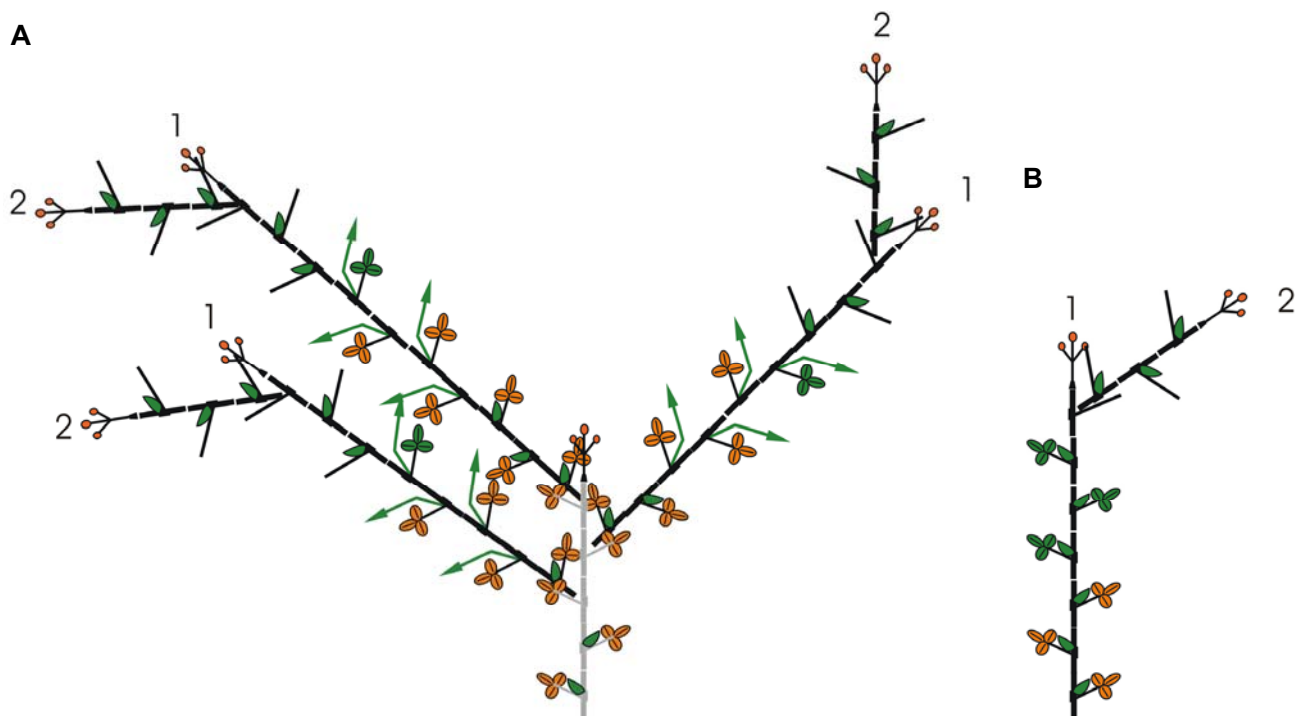
Fig. 5 Strawberry architecture of different plant types. (**A**) Frigo plant planted in July, (**B**) fresh plant planted in September (modified from Savini *et al.* 2005). The plants were dissected before winter rest. Arabic numerals represent the orders of inflorescences.

photoperiod (Okimura and Igarashi 1997). The fluctuating temperatures can be artificially applied to reproduce natural environment or to manipulate flower induction (Reichart 1973; Chabot 1978; Durner *et al.* 1984; Bish *et al.* 1997). Regardless of temperature level, a temperature gradient from root to shoot stimulates vegetative growth in comparison to a gradient in the opposite direction and to lack of such gradient (Leshem and Koller 1965).

Temperatures below 15.6°C delay flower differentiation (Darrow 1966). Low temperature is also related to chilling. Exposure to cold temperatures (below 7-10°C) applied to overcome dormancy may induce strong vegetative growth in strawberry (Guttridge 1958; Voth and Bringhurst 1958; Pringer and Scott 1964; Wahdan and Waister 1984; Theranifar *et al.* 1998). Under favorable climatic conditions plants may balance reproductive responses (Darnell and Hancock 1996), and for greenhouse strawberry production cold treatments can avoid the yield decreasing due to a reduction of vegetative vigour. Chilling reduces flower induction and stimulates floral differentiation (Durner and Poling 1987) along with leaf number and runner formation (Bringhurst *et al.* 1960; Porlingis and Boynton 1961; Piringer and Scott 1964; Bailey and Rossi 1965; Guttridge 1969; Braun and Kender 1985; Rice 1990; Kahangi *et al.* 1992; Lieten 1997; Tehranifar and Battey 1997). In warm regions, chilling preceding the optimum digging date in the nursery may be advantageous for early fruit production, while extra chilling after the optimum digging date may reduce flowering (Durner and Polling 1988). Flower production is possible in non-chilled plants (Lieten 1997) but trusses are shorter and produce smaller berries (Hamann and Poling 1997). A lack of cold can be compensated by artificial lighting (Van Delm *et al.* 2010).

Cold temperatures are usually applied to store the plants before planting for programmed cropping (Blommers 1965; Rosati 1971; Dijkstra and Van Oosten 1972; Benoit 1973; Dammann 1974; Anderson and Guttridge 1975). During prolonged cold storage, sugars and starch content can decline and this is correlated with a decrease of number of emerging inflorescences and flowers (Molot and Leroux 1973; Kinet *et al.* 1993; Dradi *et al.* 1996; Sønsteby and Hytonen 2005). The stress related to the duration of cold storage may result in earlier flowering (Lieten *et al.* 1995).

Altitude

The location of the nursery affects the flower induction that takes place earlier at higher altitude (Savini *et al.* 2006b) whereas environments with long photoperiod and relatively high temperature minimize flower induction and promote vegetative growth. Then the differentiation proceeds and all the flowers reach the same development degree, but the number of flowers is different (Savini *et al.* 2006b). At low altitude (higher temperature) plants show reduced vegetative growth and develop lower number of leaves compared to higher altitude (Riyaphan *et al.* 2005). Fresh plants from the Spanish highlands nurseries (800-1200 m) give good fruit productions, beginning in February, when dug up within first ten days of October and transplanted in Southern Italy, after few days of storage and transport (Savini 2003). Transplanting at low altitude allows longer flower induction and differentiation period with the production of more flowers and earlier fruits (Savini *et al.* 2006b). In Southern Italy, the major part of the flower differentiation take place in the buds of 2nd and 3rd order on the extension crown because the mild weather during the fall allow a prolonged favorable period to differentiation (**Fig. 4**). In this condition, vegetative growth may be easily resumed using flashlight or gibberellins application (Aspuria and Fujime 1995; Robert *et al.* 1999). Moreover in the Northern Italy the inflorescence in the primary bud has a higher number of flowers (13-14) in comparison to the South (10). This behavior could be due to the prolonged positive conditions for the differentiation that are common in the north during the growth of the primary buds at the beginning of the fall season. This favorable time is drastically shorter during secondary buds differentiation because of the early arrival of the autumn cold. While in the south, the useful time for the differentiation has the tendency to sustain a constant differentiation for the whole warm autumn and both orders of inflorescence have a similar number of flowers (Savini 2003).

Plant propagation

Nursery plant productions undergo continuous development. In the past, when the cultivation was polyennial, fresh

Fig. 6 Tray plants production in Belgium. (**A**) In the field during September. (**B**) Root system of tray plant.

Fig. 7 Tray plants in the green house in Belgium. (**A**) Plants after transplanting, (**B**) fruit production after 40 days of transplanting.

plants were transplanted in autumn or in spring depending on winter climate. Subsequently the use of frigo stored plants for Junebearing annual systems with summer planting became popular to increase fruit size and shorten production period in the next spring. The frigo plants, before the plantation, have only one terminal bud with an inflorescence, differentiated in the preceding year before the cold storage period. While after transplanting, the period of growth at the end of the summer induces the development of a different number of lateral buds during the autumn (**Fig. 5**; Savini *et al.* 2005).

If the frigo plants are stored too long, they suffer the transplanting in September-October and they are not able to well grow and differentiate so to give a production starting from December or January in mild climate (South Italy and in general in Mediterranean conditions). In this condition, the frigo plants are actually substituted by the use of fresh dug plants with naked root from the altitude nursery or the north regions with early cold in the autumn.

Nowadays to programme the out-of-season production, tray plants are increasingly used as they are less susceptible to problems associated with adverse winter conditions and able to preserve a vegetative-reproductive equilibrium, with particularly high flower differentiation and starch reserves in the crown. To produce this type of plant, stolons are planted in August in trays with peat substrate (Lieten 2000). Tray plant cultural techniques in autumn must provide adequate conditions for floral induction to obtain an optimal fruit production and quality during winter and spring (**Fig. 6**). The plants are characterised by very rapid growth in late summer and early autumn. Then after the growth ceases due to low temperatures, plants are moved into the climate control chambers at low temperature (-2°C) for cold storage until the time of forcing in the greenhouse for programmed

production. Refrigerated plants are ready for planting in different seasons because they are already flower induced under appropriate thermo-photoperiodic conditions (**Fig. 7**).

To increase the number of flowers per plant, the stolons prepared in the summer can last for longer in the nursery fields with favourable conditions (Waiting Bed - WB) to grow so much to have more than one differentiated crown per plant and a potential production of 500-800 g fruit (**Fig. 8**). They are stored with bare roots at the same refrigerated condition of the tray plants. An intermediate situation between frigo (bare root cold stored) plants and WB plants results when selected big plants from the nursery (commercial class A++) are cold stored after flower differentiation in the same refrigerated condition. A++ plants have a good potential to give a production after transplanting, but generally less than 400 g per plant.

Planning strategies and techniques with fresh plants allow as well as to control the vegetative and generative behaviour of the plants. Remarkable thermal excursion between day and night and low summer temperatures (high altitude) are favourable conditions in the strawberry nursery, interesting for fresh plants production: flower induction takes place early and leads to higher inflorescence number than in the low land. These conditions in tray plants stimulate vegetative growth too (Savini *et al.* 2006a).

Plant architecture shows significant modification changing the date of forcing. The plants respond to low temperatures in different ways depending on the physiological phase of particular organs and their relative positions.

Axillary meristems at maximum level of dormancy (middle of September in France) do not develop secondary shoots after placing the plants in the greenhouse. As the chilling requirement is increasingly satisfied, the axillary meristems initiate new secondary shoots, but when the

Fig. 8 Waiting Bed (WB) plants in Belgium. (**A**) Plants after transplanting in the field in July, (**B**) good production obtained in September.

temperature is too cold (delayed placing in the greenhouse after the end of October) lateral growth is damaged (Savini *et al*. 2006a).

In bare rooted plants, root system mainly serves for overcoming the transplantation crisis and subsequently degenerates. Removal of part of the leaves stimulate compensative growth of the plant (Hansen 1996) and shoot formation in the basal part of the crown, coming out from existing meristems; plant vigour and fruiting increase (Guttridge *et al.* 1960). Small cold stored plants transplanted without leaves have small vegetative growth compared to larger tray, waiting-bed or frigo plants transplanted with initial leaves (Palha *et al.* 2010). Plant defoliation after repotting produces low nutrition conditions that can reduce numbers of flowers and then inflorescence size, apparently because of initiation failures (Anderson and Guttridge 1982).

Plant deblossoming increase leaves (Daugaard 1999) and runner production in some cultivars (Scott and Marth 1953; Robertson and Wood 1954; Moors and Scott 1965), in some other cultivars runner increasing is reported only with defoliation combined treatment, whereas in other genotypes flower removal does not promote runner production (Waithaka 1985). Removal of runners stimulates and hastens branch crown development (Hancock 1999).

Early transplanting stimulates shoot formation and flower differentiation, whereas late transplanting reduce crop load. Advancing the plugging date of SD plants to early July can induce the plants to flower early (Takeda and Newell 2007) instead of growing transplants in artificial, SD and low temperature conditions in late summer (Verheul *et al*. 2006, 2007). Planting date does not affect vegetative growth whereas flowers and inflorescence number increase with later planting dates in autumn production systems

(Palha *et al*. 2010).

When the formation of shoots stimulate prolonged and no contemporary fruit production, delayed planting is necessary. When transplanting delay is needed, plants must be already differentiated from the nursery. Small planting distance (high density) affect lateral shoots growth with advantage for uppermost buds.

Nutrients

The nutrient level and type of substrate strongly influence the growth and architecture of the plant (Savini 2003; Savini and Neri 2003). The relative ratio between nitrogen and phosphorous controls the vegetative equilibrium in many plant species. High nitrogen availability can stimulate both stolon and shoot formation, depending upon the supply time and plant growth rate (Savini 2003; Savini and Neri 2004). When apex growth is fast, stolons formation is induced. Excess nitrogen in fertilization can affect flower induction (Fujimoto 1972; Furuya *et al*. 1988; Matsumoto 1991; Yamasaki *et al*. 2002) determining a delay in flower differentiation and stimulating stolon or vampire buds formation. Increasing nitrogen can increase stolon number and affect their length, with genotype dependent response (Silberbush and Lips 1988; Moon *et al*. 1990; Tworkoski *et al*. 2001). If high nutrient supply stimulates vigour after apex growth is stopped, axillary latent meristems are reactivated to growth and generate shoots in the basal part of the crown increasing the total number of possible inflorescences, but not stolons. When fertilization is made later on, it can stimulate shoot formation in the upper portion of the plant. These shoots show less developed flowers compared to terminal primary inflorescence. Very high nitrogen levels (50 mg/plant) may totally prevent flower buds formation, even under extended inducing treatment (Yamasaki *et al*. 2002). The reduction in availability of soil nutrients, especially nitrogen deficiency, seems to increase plant sensitivity to inductive conditions (Strik 1985; Battey *et al*. 1998; Lieten 2002). Nevertheless, during inductive period, nitrogen, potassium, phosphorus and manganese content in shoot apex and leaves of induced plants is higher compared to non induced plants (Yamasaki *et al*. 2000; Eshghi and Tafazoli 2007). However, the rates of uptake are lower in autumn than in spring for all nutrients (Tagliavini *et al*. 2005). Reduced nutritional level depress vegetative growth and can promote flower induction (Guttridge 1985) and production of more flowers. Plants under low nitrogen availability start to initiate flower buds after few days of inducing treatment, but after flower bud initiation, the differentiation of the floral organs requires more nitrogen (Yamasaki *et al*. 2002). If low nutrient supply persists during flower induction and differentiation it could revert the meristem from reproductive to vegetative growth (van den Muijzenberg 1942) or affect the regular formation (Strik 1985; Battey *et al*. 1998; Lieten 2002) and reduce the numbers of flowers and the inflorescence size, apparently because of initiation failures (Anderson and Guttridge 1982).

Nutrient application effect is therefore dependent on the timing of the application: if applied at the beginning of inductive thermo-photoperiod conditions, nitrogen, phosphate and potassium fertilizer delays flower bud initiation more than delayed application (Yamasaki and Yano 2009). Temporary suspension of fertigation, during the flower induction of tray plants, allows to anticipate the differentiation of terminal flower bud with positive effects on inflorescence development and flower number (**Fig. 9**; Savini 2003); while continuous high nutrition delays flower initiation and may induce some defect in primary berries (Yoshida 1992; Lieten 2002). Malformed fruits are reduced, if high nitrogen supply is delayed after sepal differentiation. With continuous supply of nutrients, lateral shoots outgrowth take place from the apical part and continue downward, whereas, if the fertigation is suspended, shoots formation occur exclusively from apical buds (Savini 2003). With
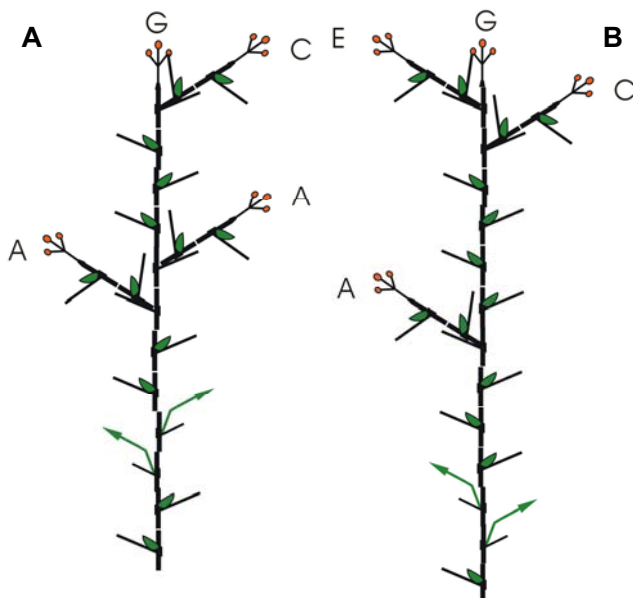
Fig. 9 Plant architecture in relation to nutrient supply technique. (A) Under continuous fertigation and **(B)** with suspension of nutrition. The plants were dissected 45 days after the treatment (modified from Savini 2003). Capital letters represent progressive stages of flower bud development, according to the primary flower, from A: Primary flower primordium to H: formed primary flower with yellow anthers.

reduced nutrition at the end of summer until mid–September, crowns do not became bigger, but floral initiation is favored and fruit number can increase, with more quarternary and quinary flowers on first and second truss and more secondary and tertiary flowers on second and third truss (Lieten 2002). Starting nutrient application after September can strongly reduce crown size. During nursery, reduced nitrogen application (7.5 kg N/ha) at the beginning, followed by increased supply (15 kg N/ha) at the end of August or in September and decreased nitrogen application (7.5 kg N/ha) in October may advance flower initiation in comparison to low or high constant supply from the beginning of August (Desmet *et al*. 2009). Low nutrient supply during flower differentiation until mid October prevents the further development of initiated flowers that cannot produce fruits, even with high nutrient conditions during the other growth phases of the plant. Reduction after mid October does not affect the fruit production.

The lack of manganese does not have any effect on the flower characteristics, and fruit number (Lieten 2004). About the source of nutritional factors, the addition of organic matter (cattle, poultry, sheep or manure) stimulate production of leaves and accelerate flowering date compared to conventional fertilizer (Abu-Zahra and Tahboub 2008).

In relation to interaction with plant architecture and growth, nutritional protocol should be managed in different ways during propagation in the nursery and during plant growing.

Water

Mild water deficits (-0.03, -0.05 and -0.07 Mpa) can reduce fruit production because of decreased mean fruit weight and diminished fruit number (**Table 2**; Davies and Albrigo 1983; Gehrmann 1985; Peñuelas *et al*. 1992; Serrano *et al*. 1992). This can be related to the fact that branch crowns development is dependent on water supply and they do not develop under strongly reduced water supply (25% of daily water consumption) while few shoots develop under mild water stress (Gehrmann 1985). Moreover, even mild water stress determines rapid reduction of photosynthesis (Lenz 1975). Different water regimes have no effects on the duration of fruit production (Dwyer *et al*. 1987; Serrano *et al*.

Table 2 Number of branch crowns and flowers of strawberry plants cultivar 'Korona' as influenced by different levels of water supply (Gehrmann 1985).

	Water supply (% of daily water consumption)			
	100	**75**	**50**	**25**
Crowns on 19 February	5	3	3	2
Crowns on 19 September	6	3	3	2
Crowns on 7 May	19	8	4	3
Flowers	25	23	20	21

1992).

Stolon production and growth are sensitive to moisture stress (van Der Zanden and Cameron 1996; Tworkoski 2001). A sufficient water supply is essential for an acceptable yield, but water stress after the beginning of the flowering may allow flower induction even under unfavorable environmental conditions (Naumann 1961). This is particularly important during bud differentiation, flower and fruit development. Naumann (1964) obtained higher yield providing water in autumn as compared to spring irrigation, because of a better supply during flower bud initiation and differentiation.

The stress due to the excess of salt in irrigation water can significantly reduce the production of inflorescences, flowers (Khayyat *et al*. 2009) but even of leaves and crowns (Awang and Atherton 1995). As a consequence there is a loss of fruit setting (Saied *et al*. 2005) even in absence of visible plant injury (Brown and Voth 1955). Furthermore, high salt concentration has inhibitory effects on stolon outgrowth (Ondrašek *et al*. 2006).

Growing substrate

The substrate is one of the fundamental factors to modulate the plant development. Because sensitivity of the plant to flower induction is greater when the growth is reduced, substrate can affect the plant response inducing different levels of vegetative vigour and number of nodes per shoot in relation to the cultivar. Production potential changes in relation to the type of substrate and it is possible to make SD cultivars produce similarly to Everbearing cultivars using appropriate substrate. Even shoot location and number along the crown is affected by the substrate (**Fig. 10**; Savini 2003).

Fine peat is an optimal substrate for propagation of large runner (Kehoe *et al*. 2009). With organic substrate (peat and compost) plants of DN cultivar showed lower flower differentiation in the second flower flush compared to inert substrate (Savini 2003) and earlier fruit production. Organic substrate led to lower development of the plant with a lower number of inflorescences per plant and consequent low production. The low fruit load resulted in an increase of vegetative growth and this probably led to the formation of a greater number of stolons (Savini 2003) in the following growth. When grown with an inert substrate, plants produce many high order inflorescences, leading to asynchronous production (Savini 2003). In substrate containing peat, 'Camarosa', 'Gaviota' (SD) and 'Selva' (DN) cultivar produce the highest number of crowns and leaves compared to sand or perlite without peat (Tehranifar *et al*. 2007). Plants grown in sand 100% produce flowers earlier but lowest number of fruit than in other growing media (peat, perlite, cocopeat or combined media) (Tehranifar *et al*. 2007). Without nutrition adjustment, rockwool substrate determines less vegetative growth, lower yield and earlier harvest in comparison to peat (Jansen 1997).

Small pot volumes increase plant sensitivity to inducing conditions (Fujishighe 1994) and stimulate early flower induction during plant root system formation, but if the growing period in the tray is too prolonged, root occupies the whole substrate volume and it is under stress condition, resulting in lower flower quality. At low plant density (33-
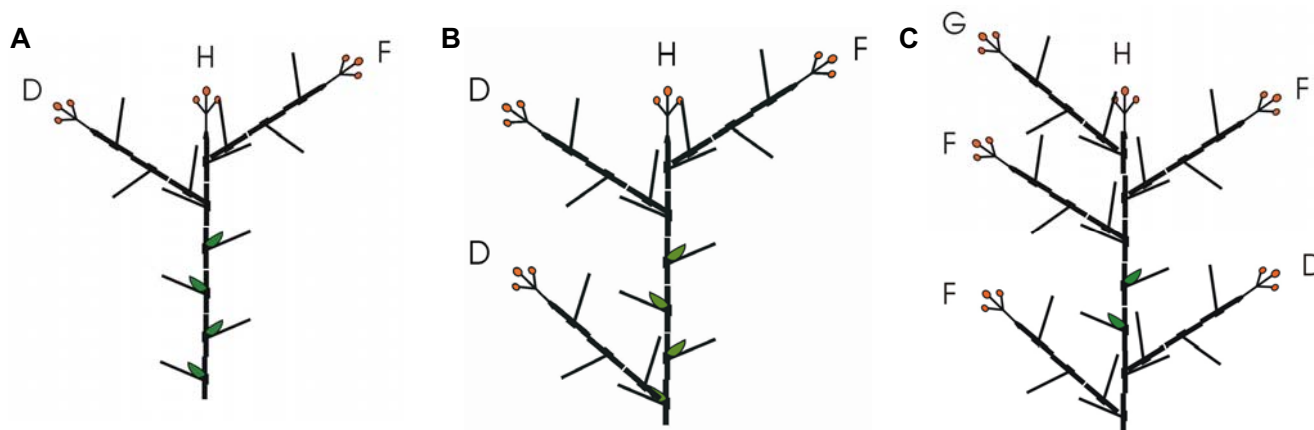
Fig. 10 Architecture of 'Darselect' plants grown with different substrates. (**A**) Blonde peat/pine bark/coco fibre, (**B**) Blonde peat /brown peat /perlite, (**C**) commercial mould. Modified from Savini (2003).

43 plants/m^2) during the autumn, more inflorescences and flowers form and higher yield is possible in the following spring than at higher density (66-87 plants/m^2) (Jansen 1997).

CONCLUSIONS

Reproductive and vegetative behaviour of strawberry plants are known to be sensitive not only to temperature and photoperiod but also to several agronomic and nutritional factors. Plant propagation systems and growing techniques can modulate many abiotic factors to modify environmental conditions. Knowledge about the effect of abiotic factors on the production of flowers, shoots or runners in strawberries, provide management tools to program the plants and the yield.

Even mild and controlled abiotic stressing conditions can be powerful means to modify strawberry plant architecture. They play an important role to control plant growth and development, through the control of the intrinsic vigour during plant propagation in the nursery, and thus strictly interacting with the physiological processes which lead to stolon formation, branching and flower induction/differentiation. Therefore, the control of growth and development of the plant in the nursery can strongly modify the entity and the time of fruit production in the field after transplanting.

Plant architecture that describes the spatial distribution of vegetative and reproductive organs and their developmental phase is therefore useful to evaluate plant quality. This will have an impact on the possibility to predict the production (time and quantity) by analysing the real architecture of plants at the moment in which the plants are forced or chilled. The plant dimension, amount of chilling and growing degree hours are the other basic information to manage the production potential and timing. The genetic differences have a high hierarchic rank in the control of flowering but the interaction with the type of propagation and cultural techniques, such as planting date and forcing condition, make impossible to generalize and to predict any results without an empirical approach. Even though, it can be argued that, knowing the plant architecture, the potential fruit production can be modified in a predictable way by changing and modulating the growing techniques in the nursery and after transplanting, according to the desired production system and the specific genetic material.

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