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Factors affecting bud-break in hardy nursery stock: A review

Introduction

Early control of plant growth habit and flowering are key requirements of the ornamental nursery stock industry in their attempts to produce the high quality plants that are necessary to maintain a competitive advantage in the market place. For instance, the accepted standard for class 1 rose bushes requires a minimum of three strong shoots (basal or bottom breaks) originating from just above the graft union. However, at present only *ca* 60% of the 25,000,000 bushes propagated annually make this grade (Burgess, 2001). The financial return generated by increasing the numbers of class 1 bushes produced is significant, as even a 5% improvement would be worth around £2,000,000 per annum to the hardy nursery stock (HNS) industry. Consequently, there is a demand for research to provide 'technology' that will enable the manipulation of branching. Attempts have been made to increase branching by mechanical methods, such as tipping-back and de-shooting (for example see Dubois et al., 1994), although sometimes with limited success (Burgess, 2001). Several chemical sprays, either pruning agents or branch inducing chemicals, have also been tested (for example see Burgess, 2001).

Rose bush production illustrates many of the problems experienced by the HNS industry in producing consistent yields of high quality plants. Whether or not a rose bush is sold as a class-1-standard depends on many factors. For example, some rose cultivars readily produce 'basal breaks' and exceed the average 60% yield of class 1 bushes, while many, otherwise desirable cultivars are 'shy breakers' and far fewer plants are saleable as class 1 bushes. This raises questions about the genetic mechanisms that control branching and how they interact with the environment and, more importantly, whether these mechanisms can be controlled to manipulate branching.

Currently, the principal methods of manipulating branching and flowering in many species are by mechanical means such as pruning and pinching. However, these treatments often have to be tailored to individual species requirements. In addition, chemical branch inducing and pruning agents are available and these have been used extensively to induce sylleptic branching in fruit tree production. Since both chemical and mechanical treatments need to be applied frequently and at the correct timings to achieve the desired result, these are time consuming and expensive procedures for the nurseryman to apply. For this reason, it is highly desirable to develop a ‘generic’ approach to the manipulation of branching; i.e. a system of branching control that can be used on many different species successfully and consistently.

The traditional pruning, pinching and chemical treatments affect the way that buds perceive endogenous plant growth regulator signals, by interfering with the balance in the 'growth' of the root and shoot systems. This causes buds that would otherwise be held in a dormant state to begin outgrowth and thus to affect the aerial architecture of the plant. The benefits of encouraging axillary meristems to grow at the appropriate time have been demonstrated in the development of multi-branched cuttings in the HDC-funded ‘Designer Liner’ project (Cameron et al., 1999).

There are many factors that can interact to affect the way in which axillary buds are initiated, develop and break into active vegetative growth. These factors may be considered loosely in three groups, according to how the effect of the factor originates. For instance, (1) the ‘endogenous’ factors that depend directly on the plant, i.e. they are a result of the species and the cultivar; (2) the ‘exogenous’ factors that depend on the natural environment in which the plant grows, i.e. the results of temperature, light, water and nutrition etc and (3) the ‘applied’ factors, these are the manipulative treatments to the plant that modify plant growth, i.e. the pruning/pinching and chemical applications.

Quite clearly, under protected cultivation, all the factors in (2) can be considered as manipulative treatments in addition to those listed in (3), while in the field, water to some extent, and nutrition may be controlled, but light and temperature are mostly determined by the prevailing climate. There will, of course, be many interactions between factors from the different groups as well as within groups. For example, the DNA (the genes) of a plant will predetermine the natural branching patterns, by controlling the ability of the plant to form adventitious shoots and the degree of apical dominance that is expressed. However, the environment in which the plant is growing, as the plant responds to different levels of light, temperature, water and nutrient supply may also modify the branching habit. Also, pruning or pinching and chemical branching agents will release apical dominance temporarily, and thus modify the plant's branching habit.

In this review, we will consider the scientific and technical literature that impinges on bud-break and the branching habit of plants, with particular reference to the control of initiation, development and outgrowth of vegetative buds. We will discuss the literature under the three groups described above, with a view to highlighting the way these factors affect or interact with pruning or other mechanical treatments to affect bud-break and branching. The first interaction we consider is with the endogenous factors that affect branching. Primarily, research in these areas involves basic science and we will report work on herbaceous ‘model’ plants such as

Arabidopsis and *Pisum* where branching mutants are available or can be created. Also, in this section we will consider work on woody plants and effects of phase change and apical dominance on branching. This leads in a natural progression to the external factors, which can influence branching and will include reports of the effects of light, water, nutrition etc. The third section will report how chemical treatments and the effect of the timing and frequency of these treatments can modify branching. Following the review, we provide a summary, that includes the conclusions that can be drawn from the literature, opportunities to exploit existing knowledge and leads that may be exploited after further research.

Pruning and pinching

Pruning and pinching are by far the most widely used techniques to control plant form and to modify branching habit, and are considered to be essential practice in the production of high quality nursery stock (Cobb et al., 1988). Pruning as a cultural technique has been practiced in China since the second century AD, initially the prime objective was to boost fruit production, while in 14th-15th centuries pruning to control plant shape became popular. However, the major use of pruning techniques is in fruit production and an extensive body of information has accumulated over the centuries, including books, (e.g. Malins, 1995; Brickell, 1992) scientific research reports (e.g. Scott 1981), reviews (e.g. Mika, 1986) and presentations at conferences (e.g. Cobb et al., 1988), as well as many internet web sites dedicated to horticulture (e.g. http://www.gardenforum.demon.co.uk). However, in spite of the numerous pruning and pinching regimes used on a multitude of plant species (for examples see Scott, 1981; Cobb, 1988; Cameron et al., 1996; Howard et al., 1996; Andrews, 1997) the basic outcome is always the same; the terminal apices are removed, apical dominance (see page 9) is released and lateral buds are able to develop and grow.

Pruning and pinching techniques are, therefore, used as mechanisms to remove or reduce apical dominance temporarily (Hillman, 1984) and in this respect, pruning is a ‘generic’ technique that is applicable to many horticultural crops. However, as many other factors interact to determine bud outgrowth, apical dominance is not a constant phenomenon and the effects of pruning may be modified in many ways. For example, Hillman (1984) lists fourteen treatments that promote the outgrowth of lateral buds held dormant by apical dominance and these also affect the outcome of pruning. In addition, the species *and* cultivar will affect the response and the desired plant form may necessitate different degrees of pruning (for examples see, Mika, 1986; Andrews, 1997; Howard et al., 1996; Cameron et al., 1999). Such varied responses may be explained by reports that the position of the bud on a shoot and it's age can influence it's ability to develop after pruning (Marcelis Van Acker, 1994; Stafstrom, 1995a; Stafstrom, 1995b; Erwin et al., 1997). Cline et al. (1999) suggests that bud position effects may result from the age of the bud, as buds may accumulate greater amounts of abscisic acid with increasing age and abscisic acid is reported to promote and/or maintain dormancy (for review see Moore, 1989). When the outgrowth of buds from specific locations on bud sticks of three cultivars of rose was monitored after budding, no differences in performance were apparent but then differences in concentrations of abscisic acid in similar buds were not significant (Burgess, 2001). However, in lupin, buds in the middle of shoots were less likely to grow than buds near to the shoot apex or shoot base (Miguel et al., 1998). Also in lupin, Emery et al. (1998) reported strong correlations between the endogenous hormone status of the buds and their potential growth rates. Buds that grew strongly, whether they were apical or basal, contained high cytokinin to auxin ratios and low concentrations of abscisic acid, while in buds that did not grow, abscisic acid concentrations were high.

The timing, relative to the physiological state of the plant, can be crucial to the outcome of pruning. For instance, it is widely recognised that dormant season pruning encourages vigorous shoot growth at the end of the dormancy, while summer pruning was reported to dwarf trees and promote flowering and improve fruit quality (Mika, 1986). However, for HNS production Cameron et al. (1999) have identified plant propagation techniques that begin to build the branch framework of the cuttings before they are excised from the mother plant. This approach to plant propagation, considers the process as a continual building of quality into the product, from stock-plant management through to sale of the new plants. This 'holistic' concept of plant propagation is being pursued and is incorporating further stock-plant and cutting management techniques, such as regulated deficit irrigation and partial root drying, to produce high quality, well branched plants (Ross Cameron, personal communication).

Clearly pruning and pinching will be essential tools in the production of HNS for the foreseeable future. However, it is likely that the ways in which they are used will change as more integrated systems of plant production are developed and greater emphasis is placed on stock-plant management to provide pre-branched liners, (Cameron et al., 1999) or perhaps cuttings preconditioned to develop the desired branching habit.

Genetics

It can be expected that plants of different species will exhibit a variety of branching patterns. However, provenances of a single species may also display different growth habits. For instance, when *Quercus robur* seedlings were raised from acorns collected from two sites in Holland and compared for growth and branching habit, there were marked differences in the phenotypes observed (Harmer, 2000). Selections from plant breeding programmes may also show different branching habits, for instance apple seedlings resulting from controlled crosses involving 'Mcintosh Wijcik' segregated reliably for normal and compact growth types, compact trees exhibited strong apical dominance and showed a strong upright, non-branching habit (Lee et al., 1977). In a comparison of rose seedlings it was demonstrated that batches of seedlings contained some plants that produced high numbers of basal-breaks, when they were grown on their own roots, while others produced few basal-breaks (De Vries et al., 1983). However, those that yielded most basal-breaks on their own roots produced fewer basal-breaks when they were grafted on to *Rosa laxa* 'Inermis' rootstocks, while those that yielded low numbers of basal-breaks on their own roots, produced more basal-breaks when grafted.

The degree of expression of particular genes can affect branching habit during lateral meristem formation and the imposition of apical dominance. A mutant-based approach towards understanding branching habit in plants has been developed for a number of species, including *Arabidopsis*, tomato (*Lycopersicon esculentum*), petunia (*Petunia hybrida*) and garden pea (*Pisum sativum*). Mutations affecting branching include the *axr* (Leyser, 1997) and *supershoot* genes (Tantikanjana et al., 2001) from *Arabidopsis*; *bu*, *ls* and *to-2* from tomato (Brenner et al., 1987; Schmitz et al. 1999), the *dad* series from petunia (Napoli et al., 1999) and *bushy* (Symons et al., 1999) and the *ramosus* (Latin = many branches) series of garden pea (Napoli et al., 1999). However, at present the *ramosus* (*rms*) mutants of garden pea represent the largest range of phenotypically and physiologically described branching mutants.

Several genes have been identified that promote the formation of lateral and adventitious shoot meristems including the 'supershoot' (*sps*) gene of *Arabidopsis* (Tantikanjana et al., 2001) and the 'bushy' (*bsh*) gene of garden pea (Symons et al., 1999). Both of these genes induced massive over-production of lateral shoot meristems and suppression of apical dominance. The five *rms* mutants of garden pea show increased branching at aerial and basal nodes as a result of outgrowth of lateral buds, i.e. apical dominance is compromised. Christine Beveridge and co-workers at the University of Queensland have used the garden pea *rms* mutants extensively to investigate the genetic regulation of bud outgrowth. Results from these studies have been published in several research papers (Apisitwanich et al., 1992; Arumingtyas et al., 1992; Beveridge et al., 1994; Beveridge et al., 1996; Beveridge et al., 1997a; Beveridge et al., 1997b; Beveridge et al., 2000; Napoli et al., 1999; Rameau et al., 1997; Stafstrom, 1995a; Symons et al., 1997; Morris et al., 2001) and a review (Beveridge, 2000).

The *rms* genes appear to be closely associated with the control of apical dominance (see next section), and consequently the outgrowth of lateral buds. The reports indicate that the pea mutants *rms1* through *rms5* are not deficient in auxin (indole-3-acetic acid, IAA) or in the basipetal transport of this hormone, but, four of the five mutants *rms1*, *rms2*, *rms4* and *rms5* exhibit a very reduced cytokinin concentration in xylem sap. However, this reduction in sap cytokinin concentration appears to be caused by a property of the shoot and may be part of a feedback mechanism induced by an aspect of bud outgrowth, i.e. it is a result of, rather than a cause of increased branching. The shoot-to-root feedback signal is unlikely to be auxin itself, as auxin levels and transport do not correlate with xylem sap cytokinin concentrations in various intact and grafted mutant and wild-type plants. The genes, *Rms1* and *Rms2* act in both the shoot and the rootstock to regulate the level or transport of a graft-transmissable signal. Several grafting studies and double mutant analyses have linked the gene *Rms2* with regulation of the shoot-to-root feedback signal. *Rms1* and *Rms5* are associated with a second unknown graft-transmissable signal that is postulated to move in the direction of root-to-shoot. Exogenous auxin appears to interact with both of the signals regulated by *Rms1* and *Rms2* in the inhibition of branching after decapitation. So far the modes of action of the genes *Rms3* and *Rms4* are not apparent, although both appear to operate largely in the shoot.

Insertion of the *rolC* gene from *Agrobacterium rhizogenes* into *Lotus corniculatus* and petunia has resulted in striking alterations to plant habit. *Lotus* plants were dwarfed, with shorter internodes, increased shoot and root branching and apical dominance appeared to have been reduced (Pozarkova et al., 1995). Similarly, in petunia there were reductions in plant height, leaf and flower size and a break in apical dominance leading to increased branching, however, male and female fertility was reduced (Winefield et al., 1999). Insertion of the agrobacterial isopentenyltransferase gene into tobacco, resulted in plants that produced three times more zeatin riboside than non-transformed plants (Alekseeva et al., 2000). Several morphological changes were apparent in transformed plants including dwarfism, excessive shoot branching and reduced root growth.

Ultimately, a thorough understanding of the genetics of bud-break and branching will enable the production of new cultivars with the desired branching habit (as well as other desirable attributes). These new cultivars may arise through conventional breeding or by genetic manipulation programmes. The products of such programmes may be used either directly as new genotypes or as rootstocks to promote branching and other desirable characteristics in existing cultivars (c.f. the range of rootstocks available for apple trees). A clonal rootstock that promoted basal branching in rose scions would be highly desirable.

Apical Dominance

Apical dominance, also referred to as 'correlative inhibition' (Hillman, 1984), may be defined as the control exerted by the shoot apex over the outgrowth of the lateral buds (Cline, 1994). Apical dominance is generally considered to be a classical example of a developmental correlation, where one organ of a plant affects another organ. This refers to the inhibition of growth of subtending lateral (axillary) buds by a growing shoot apex. While the mechanism of apical dominance is incompletely understood at present, work has shown that the basipetal transport (i.e. from apex to base) of the plant hormone auxin is one 'inhibitor' of lateral bud outgrowth. It is also believed that bud-break in spring is in response to increasing levels of the cytokinin group of plant hormones (for review see More, 1989). Studies have shown that auxin transport inhibitors applied to the dominant shoots release lateral buds from inhibition and that lateral buds may be released from inhibition by local applications of cytokinin (Hillman, 1984).

According to Cline (1997), apical dominance and its release follows four separate developmental stages: (I) lateral bud formation, (II) imposition of inhibition of lateral bud outgrowth, (III) release of lateral bud from apical dominance by loss of apex, i.e. by decapitation or flowering etc., (IV) shoot and branch development. Stage (I) is primarily under genetic control and the numbers of lateral buds formed will depend on the nature of the growth habit of the plant and interactions with the environment. However, according to Evans et al. (1997) the genetic regulation of lateral shoot meristems is only one step in the control of branching and many mutations that affect the number of visible branches, do not affect the formation of the lateral shoot meristem. Evans et al. (1997), also suggested that plants can change the number of branches by regulating bud outgrowth or by replacing a vegetative meristem with a floral meristem or *vice versa*. One factor that appears to be important in the formation of lateral meristems is cytokinin, for instance in *Stellaria media*, which frequently lacks axillary buds, benzylaminopurine treatment resulted in axillary buds forming in most leaf axils (Tepper, 1992). Also, axillary shoots were stimulated in cotyledonary nodes of mung beans following preconditioning with benzylaminopurine (Avenido et al., 2001).

The degree of imposition of inhibition of lateral bud outgrowth (stage II) is variable. For example, it is negligible in *Arabidopsis* or glasshouse-grown *Coleus* (Cline, 1996), and lateral buds continue to develop virtually unimpeded through to stage (IV). Cline (1996) considers this to be similar to the sylleptic growth of many tropical and temperate fruit trees. Stage (II) may be described as partial, e.g. bean and wild-type petunia (Cline, 1997), where some branching is normal even without decapitation. In the most extreme cases, apical dominance is complete as in *Helianthus*, *Tradescantia* and *Ipomea* and no bud outgrowth occurs without decapitation (Sachs, 1991).

Stage (III), the release of apical dominance, may be promoted by direct application of cytokinin, e.g. BAP (benzylaminopurine) to the bud (Pillay et al., 1983) or suppressed by application of auxin to the cut stump after decapitation of the shoot apex (Thimann et al., 1934). In contrast to this, soon after apical dominance has been released and lateral bud elongation is underway (stage IV), the developing lateral shoot will begin to produce its own auxin, which may enhance elongation further (Thimann et al., 1934). Gibberellic acid may also stimulate bud outgrowth once apical dominance is released (Prochazka et al., 1984), although tiller growth in sorghum was inhibited by gibberellic acid (Isbell et al., 1982).

It can be seen from the previous paragraph that timing of treatments relative to the physiological state of the axillary buds is critical. Thus, a treatment applied immediately after removal of apical dominance (stage III), will have a very different effect if it is applied 24hrs later when bud outgrowth has begun stage (IV). For instance, Wickson et al., (1958) found only a small suppression of bud outgrowth of isolated pea buds if auxin was applied to the cut stump 24hrs after decapitation. Several workers (Shein et al., 1971; Stimart, 1983; Cline, 1997) have raised concerns that sufficient distinction is not made between the initiation of axillary bud outgrowth and the subsequent shoot elongation in the apical dominance literature. Sachs et al. (1967) demonstrated that these processes are almost certainly mediated by different plant hormones. According to Cline (1997), lateral bud formation is promoted by cytokinin (stage I), the outgrowth of lateral buds is prevented by auxin (stage II), release of apical dominance is mediated by loss of auxin and promoted by cytokinin (stage III) and both auxin and gibberellin promote shoot development (stage IV).

Also, Cline (1997) considers that a mistake commonly made by workers investigating the mechanism of release of apical dominance is that data obtained days or weeks after decapitation, by which time branch development is well underway, is interpreted on the basis of physiological processes occurring within a few hours of release from dominance. It is important to understand that branch development is much more than just release of apical dominance. As branch development is affected by different hormones to those that affect dominance release and bud outgrowth.

Dormancy

Dormancy is an important factor in bud outgrowth, and the intensity of inhibition between terminal and axillary buds can differ. In apple and related *Malus* species, axillary buds are apparently less endodormant (winter dormant) than are terminal buds (Hauagge et al., 1991). Cook et al., (2001), demonstrated that the rate of bud outgrowth was greater from lateral buds that were released from apical dominance by decapitation prior to chilling than in lateral buds that were released from apical dominance after chilling. It was concluded that in intact shoots, distal tissues appeared to inhibit the chilling response (dormancy-breaking) of lateral buds. Usually, branching in apple is predominantly acrotonic, i.e. branches form from distal buds. Basitonic branching, (branches from proximal buds) is only expressed under specific conditions e.g. gravimorphisms (Cook et al., 1998). Also, arching apple shoots during the autumn, followed by re-orientation to the original position before bud burst in the spring, caused proximal buds that had been uppermost, to break in spring, thus changing the normal acrotonic branching pattern of apple (Crabbe, 1987).

Under normal conditions proximal bud break is inhibited by effects of the distal tissues, i.e. paradormancy (Zieslin et al., 1976; Champagnat, 1983; Suzuki et al., 1989; Cook, 1998). However, in his classic work, Champagnat (1955) pointed out that it was commonly known that pruning (decapitation) of flushing shoots did not always release lateral buds and that other influences originating from outside the terminal bud must be responsible. Similarly, Cline et al. (1999) suggest that apical dominance does not play a primary role in lateral bud outgrowth in some species. Champagnat (1986) described winter dormancy as the “last cascade of correlative inhibitions” and Cline et al. (1999) commented that it is mandatory that the paradormic processes be carefully studied for the species of concern, if there is to be a beginning of understanding of the endodormic (winter dormancy) mechanisms, i.e. the factors which often override apical dominance in some species must be identified.

Accumulation of abscisic acid (ABA) in *Malus* buds of increasing age has been identified as a potential overriding factor in bud dormancy (Theron et al., 1987). However, Cline et al. (1999) suggests that lack of sufficient twig vigour (or growth rate) is perhaps the most common attribute associated with lack of lateral bud outgrowth. However, the causes of this deficiency, though obviously dependent on light, water and nutrition, are difficult to quantify.

Clearly, dormancy is a major influence in determining when and how bud-break and outgrowth occur and consequently in determining plant morphology. It is of interest that the orientation of axillary buds affects dormacy release, (this is clearly visible in partially fallen trees, in which shoots invariably arise from all nodes on the uppermost surfaces of the branches and trunk). These observations raise questions about the timing and duration of treatments required to release buds from dormancy and whether orientation effects could be utilised as a tool in HNS production.

Leaf Inhibition

Other factors that may suppress lateral bud outgrowth have been identified, for example, Cozens et al. (1966), and Tinklin et al. (1970) clearly distinguish between the inhibitory effects of apical dominance and those of leaf inhibition of lateral bud outgrowth in blackcurrant. Defoliation experiments with blackcurrants indicated that leaves, both young and mature, inhibit bud outgrowth and consequently must be considered as a possible source of bud-growth inhibitors and/or competitors for water and nutrients (Borcher, 1991; Crabbe, 1970; Crabbe et al., 1996).

Recently, McIntyre (2001) proposed that the main factor limiting bud outgrowth was the water potential gradient between the stem and lateral bud, as this limited the availability of nutrient (both carbohydrate and nitrogen). Removing the leaf adjacent to a bud may affect the water potential gradient that may, in part, explain the leaf inhibition of bud outgrowth.

Juvenility and maturity

Branching habit is affected by the physiological age of woody plants, typically, juvenile plants (seedlings) exhibit a more apically dominant, less branched phenotype, than mature (flowering) plants (Doorenbos, 1965; Hackett, 1985). At first sight this appears to be in conflict with the overall aim of the nurseryman in his attempts to produce high quality plants of the desired form. While other juvenile-like characteristics such as high vigour and rooting potential are desirable, reduced branching is not. Fortunately, it appears that the more highly branched growth habit of mature plants is not always affected during rejuvenation procedures. For example, Cameron et al (1994) compared the branching habit of rooted cuttings prepared from seedlings and epicormic shoots of 5-, 10- and 30-year old birch trees. Rooted cuttings derived from epicormic shoots produced nearly twice as many lateral branches as cuttings raised from seedlings. However, the authors considered that this was not solely an effect of maturation. However, Fennessy et al. (2000) demonstrated that Sitka spruce cuttings produced fewer branches, had a poorer root:shoot ratio and were less cold tolerant than seedling transplants. This is in contrast with results obtained by Decourtyre et al. (1988) who compared grafts of neoformed buds from the roots of rooted apple cuttings, (i.e. by the accepted definitions the buds were juvenile), with the mother trees (mature) and found significantly increased branching as well as other differences in growth habit.

There is clear evidence that the physiological age of the plant can affect its branching habit and the balance of evidence seems to suggest that cuttings derived from a mature, but rejuvenated source are most likely to produce well-branched plants. The effects of applying gibberellins to stock plants, that has been shown to induce juvenile-like growth on mature plants (Ford et al., 2002), or other rejuvenating treatments may offer an opportunity to increase the branching ability of cuttings.

Syllepsis

Sylleptic shoots are short lateral shoots that arise from lateral meristems of strongly growing terminal shoots without an intervening rest period. They occur in many tropical woody species and a few temperate trees (Halle et al., 1978; Wheat, 1980) and in some young fruit trees (Barlow, 1970; Tromp, 1996). Halle et al. (1978) suggested that syllepsis would occur when certain threshold levels of parent shoot growth rate are exceeded. However, as Champagnat (1961) and Genard et al. (1994) have pointed out, such rapid growth of the main stem would be expected to be accompanied by high auxin production and transport levels. According to the traditional ‘auxin inhibition’ view of apical dominance, such conditions should inhibit shoot formation rather than promoting it. Sachs et al. (1967) and Genard et al. (1994) suggest that the sensitivity to auxin may decrease as the shoot growth rate increases, but this decrease in sensitivity has never been demonstrated. Tromp (1996) observes that the phenomenon of sylleptic growth is difficult to reconcile with the hormonal version of the apical dominance concept and he is doubtful if the phenomenon of apical dominance is an important factor in sylleptic shoot formation.

While sylleptic shoots are of considerable importance in fruit trees, they are unlikely to be of importance in HNS production, since they result from strongly growing terminal shoots, which are not desirable features of HNS.

Light

Light is one of the fundamental requirements for plants to grow and develop fully. In general, with increased shading, plants are taller and less branched, although many plants are adapted to life in partial shade e.g. *Rhododendron*, *Camellia*, etc. Plants can sense the quality, quantity and direction of light and use it as a signal to optimise their growth and development in a given environment. In addition to its role in photosynthesis, light is involved in the natural regulation of how and where the photosynthetic products are used within the developing plant; i.e. light is a key component of photomorphogenic, photoperiodic and phototropic responses. Light-dependent development of plants is a complex process and beyond the scope of this review, but can be considered in three parts and all aspects can be of practical use to the nurseryman. The first effects to be considered are those resulting from changes of the intensity of the incident light. In addition, we must also consider the effects of photoperiod and of the spectral quality of light.

Changes in the intensity of light can affect branching and, with few exceptions, apical dominance is greater at lower light intensities than at higher intensities (Rubinstein et al., 1976). For example, *Dracaena marginata* plants grown in full sun produced an average of 4.3 basal branches per plant, while those grown under 50% shade produced no branches (Donselman et al., 1982). Also, an average of 3.9 branches per plant were induced on Canary Island ivy by increased light intensity, while the plant rarely branches under normal conditions (Al-Juboory et al., 1998). In chrysanthemum, increases in the number of lateral shoots of 'pinched' plants were attributed to an increase in photosynthetic photon flux and air temperature (Schoellhorn et al., 1996) and in *Ficus elastica* the number of branches decreased as shading increased (Conover et al., 1978). Effects of low light intensity have been ascribed tentatively to lack of carbohydrate for bud growth based on work with garden pea (Wickson et al, 1958), *Agropyron* (McIntyre, 1977) and *Verbascum* (Lortie et al., 1997).

The duration of the photoperiod can also affect branching patterns; generally apical dominance is favoured under long day lengths, whereas short day lengths tend to promote lateral branching (Phillips, 1969). Support for this statement comes from work by Holcomb et al. (1987) who reported that roses grown under short days had more branches than those grown under long days, while Moe (1988) reported that day extension inhibited lateral bud growth of roses. Additional support was gained from work with Canary Island ivy which does not branch under normal conditions, but produced an average of 3.9 branches per plant under a short-day, high-intensity light regime (Al-Juboory et al., 1998). However, there are exceptions, in carnations short day treatments could inhibit lateral branching if applied too early (Healy et al., 1983) and saplings of *Plumeria rubra* broke dormancy under 13 hour photoperiods, while those under11.7 hour photoperiods remained dormant.

The effects of spectral quality of light on plant growth and development is well established and has been reviewed many times (for examples, see Smith, 1990; Aphalo et al., 1999; Ballare et al., 2000; Tong et al., 2000; Christie et al., 2001). Also, modifications to the spectral quality of incident light have been used under glasshouse conditions to modify plant growth, for instance, reductions in the height of Easter lillies (Kambalapally et al., 1998), chrysanthemum (Rajapakse et al., 1993) and bell peppers (Li et al., 2000). Modifying spectral quality was also reported to reduce transpiration and alter the growing season in chrysanthemum (Li et al., 2000). Growing potted miniature roses under light modified by passage through a copper sulphate solution to reduce the red:far red wavelengths and increase the red:far red, blue: far red and blue:red ratios, resulted in plants of reduced height with increased lateral branching (Rajapakse et al., 1994). Furthermore, rose plants growing with supplementary lighting from high pressure sodium or metal halide lamps increased the numbers of flowering stems by 64% compared with plants growing under filtered high pressure sodium lamps which increased the red:far red ratio (Roberts et al., 1993). However, daylength extension with incandescent lamps, which provided a low red:far red ratio inhibited lateral bud growth and induced blind shoot formation in glasshouse cut-rose production, while lighting with fluorescent lamps (high red:far red ratio) had the opposite effect (Moe, 1988).

The growth effects observed when plants are subjected to illumination with light of altered spectral quality depends very much on the species, and the magnitude of effects can depend on the cultivar under test. However, generally comparisons of the responses of different species to spectral quality and irradiance have not been undertaken, but work has concentrated on optimising conditions for single plant species. A few comparative trials have been reported, for example, Marks et al. (1999) performed a series of experiments *in vitro* and demonstrated significant differences between the responses of *Crataegus oxyacantha*, three *Rhododendron* cultivars and *Disanthus cercidifolius*, to different levels of illumination and spectral quality. Red light promoted shoot extension and axillary branching, while blue light inhibited stem growth and branching in the sensitive cultivar *Rhododendron* cv. Dopey. Differences in responses were explained by reference to the normal habitats of the species tested, i.e. *Crataegus* is a plant that is naturally adapted to growing in an open environment, while *Rhododendron* and *Disanthus* plants are shade tolerant. Also, Healy et al (1980) investigated the influence of photoperiod and light quality on lateral branching of eight different vegetatively propagated plants and reported that short days promoted branching and cutting production in *Pilea* cvs Moon Valley and Panamegia. Long days and night lighting treatments promoted lateral branching and cutting production in *Alternanthera amoena*, *Coleus*, *Hedera helix*, *Pelargonium* and *Peperomia.*

While the use of copper sulphate solutions has clearly demonstrated the potential for the modification of normal daylight to manipulate plant morphology, the technology needed for such systems is prohibitively expensive and the solutions are phytotoxic (Rajapakse et al., 1999). However, the use of coloured plastic films and shade nets offers an alternative approach to spectral modification that has shown considerable promise. For example, Rajapakse et al. (1999) report excellent control of plant height by filtering light with films of different spectral quality in a study using chrysanthemum, bell pepper and watermelon, but unfortunately no data on branching habit was presented. However, Oren-Shamir et al. (2001) investigated the effects of spectral modification by coloured and neutral density shade nets on shoot production of *Pittosporum variegatum*. These authors reported that red nets promoted branch elongation, blue nets dwarfed plants and grey neutral-density nets promoted branching. Also, Patil et al (2001) demonstrated that plant morphology was effected by the interaction of selective plastic films and alternating day and night temperatures. The effects of light quality and quantity and the effects of shading on quality of chrysanthemum has been reviewed recently (Carvalho et al., 2001), and these authors suggest that increased assimilate levels as a result of increased irradiance promoted lateral branching most effectively. However, Oyaert et al. (1999) reports that blue filters resulted in the smallest numbers of axillary shoots in chrysanthemum and Song et al. (1997) report that all coloured filters used (red, blue, green and semi-transparent) reduced the number of lateral branches compared with natural light or transparent films in *Hibiscus syriacus.* Preliminary results from the HDC-funded project HNS 108: Spectral Filters for Hardy Nursery Stock, suggest that bud-break may be improved by selection of the correct plastic film for the crop being raised. In this project alpines performed best under the film with the highest level of light transmission, while conifers and *Philadelphus*, *Lithospermum* and *Saxifraga* produced most breaks under an infra red filter. While blue film reduced internode length and promoted bushiness, but it is not clear whether this is just a visual improvement as a result of branches being less separated by the shorter internodes.

Control of plant growth habit by manipulation of the spectral quantity and quality of light appears to offer considerable scope for exploitation after some additional work. It is effective on a wide range of species, environmentally acceptable and applicable to organic growing systems. The ability to manipulate desirable characteristics by manipulation of the environment also provides a 'way in' for the scientist to understand the genetic control of these characters.

Temperature

Temperature can influence bud-break in two main ways. First, there are the direct effects of temperature on rate of growth of the parent shoot and development of the newly produced axillary buds. Secondly, dormant buds of perennial plants often require a cold period to allow them to break dormancy and grow away in the spring.

Went (1953), suggested that in some species there was a mechanism of thermoperiodic control of branching, but Hillman (1984) argued that "without critical research it is not possible to state whether true thermoperiodic control of branching exists". Since then there has been considerable interest in the control of plant growth, including branching, by manipulation of day and night temperatures (Cockshull et al 1995; Myster et al., 1995; Langton et al., 1997; Langton, 1998). For instance, there were greater numbers of lateral branches produced when petunias were grown under red-rich light and a higher day temperature than night temperature, than when plants were grown under a higher night temperature than day temperature regime (Kubota et al., 2000). The difference between day and night temperature is known as DIF, positive DIF is when day temperature is greater than the night temperature and negative DIF, when day temperature is lower than night temperature. Also, chrysanthemum plants produced greater number of side-shoots under positive DIF than under negative DIF (Patil et al., 2001), although earlier work had reported that air temperature had no effect on branching in chrysanthemum (Schoellhorn et al., 1996). However, axillary bud development in poinsettia was inhibited by high air temperature (Faust et al., 1996). Although axillary shoot growth was promoted by high temperature, when the axillary shoots were used as cuttings, the percentage of nodes developing lateral shoots was 21% compared with 74% from cuttings of plants raised at lower temperatures. Earlier, Heide (1974) demonstrated that the temperature at which buds of Norway Spruce developed was crucial to the performance of the plant in subsequent years, and the effects were detectable for up to three years after treatments were applied.

Dormancy in container-grown kiwifruit vines was broken most efficiently by storing plants for two months at low temperature, under these conditions both the numbers of flower buds and the number of vegetative buds breaking dormancy were maximised (McPherson et al., 1995). These authors noted that chilling in excess of the requirement resulted in a decline in bud-break and shoot development. Also, Mahmood et al. (2000) noted that excess chilling resulted in reduced bud-break in sweet cherry, and also demonstrated that chilling requirements were cultivar dependent. Bud dormancy may also be broken by short-duration high temperature treatments. For instance, when dormant Japanese pear cuttings were allowed to acquire different numbers of chill units and were then subjected to a temperature of 45°C for 4 hours, dormancy was broken in both vegetative and floral buds (Tamura et al., 1993). Similarly, near lethal heat stress (47°C for 1 hour) overcame dormancy in intact *Cornus sericea* shoots when applied either early or late in the dormancy cycle, while treatments during deep dormancy were less effective (Shirazi et al., 1995).

In addition it has been reported that root temperature can alter root morphology as well as influencing axillary bud break and shoot formation. For example, when *Rosa hybrida* were grown in three divergent root temperature regimes, higher root temperatures favoured axillary bud break and basal shoots were produced earlier (Dieleman et al., 1998). However, their hypothesis that high root zone temperatures increased bud break and shoot growth through enhanced cytokinin production in the roots was not supported.

Anecdotal evidence suggests that frost damage to newly emerging shoots of woody species including *Camellia* and rose can promote branching to a greater degree than pinching at a similar growth stage. We were unable to locate reports of any controlled experiments investigating this phenomenon, but Cline et al., (1999) state in their report that “a late frost promoted vigorous outgrowth of lateral buds of white and green ash," while decapitation did not promote lateral bud outgrowth, however, the effect was not quantified.

There is considerable scope for further research into the effects of temperature on branching in HNS. Work on herbaceous species has demonstrated considerable potential for manipulating both branching habit and plant stature. Although consideration must also be given to the effects of the temperature at which stock plants are grown on the subsequent performance of cuttings. The anecdotal evidence available suggesting that branching may be enhanced by frosting should also be considered further.

Water

Water plays a key role in the growth and development of most terrestrial plants, in their natural environments plants are normally expected to tolerate varying degerees of water-stress. As part of a stress-tolerance mechanism, active meristems have the competitive ability to obtain water at the expense of the mature parts of the plant (Hillman, 1984). McIntyre (1977) indicated that competition for water might play a critical role in apical dominance, since water availability and high humidity promote axillary bud growth in *Agropyron*, *Helianthus*, *Phaseolus* and *Pisum*, and recent work suggests that water and nutrients are the key factors in release of apical dominance (McIntyre, 2001).

Branching of *Quercus petraea*, *Fraxinus excelsior* and *Pinus sylvestris* was increased, when seedlings were grown under two irrigation regimes over a three-year-period (Broadmeadow et al., 2000). However, water deprivation in *Linum* cultivars, reduced branching and ultimately crop yield (Foster et al., 1998), but the degree of reduction was species dependent. Hipps et al. (1995) demonstrated that maintenance of soil moisture content at of 50% field capacity promoted shoot growth and increased sylleptic branching in 1-year-old peach trees. Steinberg et al. (1990) reported a reduction or a termination of lateral shoot and new leaf production when young peach trees were subject to significant water stress. Also, excess water, i.e. prolonged flooding, was shown to inhibit branching in *Platanus occidentalis* seedlings, in spite of the fact that the plants exhibited some adaptations to flooding (Tang et al., 1982). However, Cameron et al. (1999) demonstrated that manipulation of stock-plants could be used to create pre-branched cuttings as ‘designer liners’. This concept, of taking a holistic view of plant production is being advanced by using controlled water stress. Water stress is applied as partial root drying (PRD) or regulated deficit irrigation (RDI) to increase plant quality, including branching, and efficiency of production and to reduce water consumption (Dr Ross Cameron, HRI- East Malling, personal communication).

Quite clearly water availability can strongly affect the branching habit of plants and minimising water stress appears to promote branching, while controlled water stress appears to be a useful tool in the production of HNS. These apparently contrasting results suggest that great care must be taken in the application of water stress treatments that minimise shoot elongation to ensure that branching potential is not compromised.

Nutrients

Nutrients, including carbon dioxide, have been shown to promote bud-break and branching. Most work pertaining to elevated carbon dioxide does not specifically detail branching habit, but describes increased biomass production in terms of numbers of leaves etc. produced (for reviews, see Taylor et al., 1994; Morrison et al., 1999). However, elevated levels of carbon dioxide have been reported to diminish apical dominace and consequently, to promote lateral branching in some species; *Pisum* (Andersen, 1976), *Quercus petraea*, *Fraxinus excelsior* and *Pinus sylvestris* (Broadmeadow et al., 2000), *Lonicera japonica* and *Lonicera sempervirens* (Sasek et al., 1991) and red mangrove (Farnsworth et al., 1996). In contrast, Hattenschwiler et al. (1997) noted that mature *Quercus ilex* growing in a carbon dioxide-enriched atmosphere around natural CO_2 vents since the seedling stage showed a moderate, age-dependent increase in stem biomass production, but had significantly lower biomass of 6-year-old branches and decreased branching compared with control trees at a nearby unenriched site.

The availability of nitrogen has been recognised as an important factor affecting lateral bud growth and effects of increasing the nitrogen status of low nitrogen growing media can often be observed within 48 hours of treatment (Phillips, 1975; Rubinstein et al., 1976). The cytological changes observed in buds of *Tradescantia,* released either by decapitation or increased nitrogen availability were closely similar (Yun et al., 1973) and McIntyre (1977) postulated that nitrogen was a limiting factor in bud growth, as increases in bud total-nitrogen accompany increases in bud-elongation and bud dry weight. However, Hillman (1984) suggests that the increased nitrogen content of a bud could result from, rather than cause, bud growth. Other nutrients that may play an important role in bud growth after release from apical dominance and Kramer et al. (1980) was able to demonstrate that one of the earliest changes to occur around axillary nodes after decapitation was the accumulation of potassium ions.

Nutrient status of growing media have been reported to influence branching and in a six nursery-site trial of various fertilizers and watering regimes on three plant species (Fashion azalea, Japanese holly and Pacific Juniper) 'Osmocote' 18-6-13 produced plants that were most visually acceptable, with the most branches (Whitcomb, 1991). In *Verbascum thapsus*, branching was increased by shoot apex removal and the degree of branching was increased by the addition of nutrients, but only in detipped plants (Lortie et al., 1997).

In an 'opinion' paper, McIntyre (2001) argues that apical dominance is partially controlled by limiting nutritional factors, including water and nitrogen, but that the water potential gradients between the main stem, leaf and lateral buds are the prime determinants of bud outgrowth. It is, however, acknowledged that further research on a wide range of species is necessary to examine the general validity of this hypothesis.

Beneficial microbes and pathogens

Microbes that enhance branching in plants may be divided into two classes, those that are symbiotic, i.e. both plant host and microbe gain benefit from the association and those that cause damage to the plant host (i.e. pathogens). Arbuscular and ectomycorrhizas are the main representatives of the first class and their beneficial effects on plant growth are well documented, although it is their effects on root growth and nutrition that have received most attention (for reviews, see Harley et al., 1983;Taylor et al., 2002). However, in tomato, transplants inoculated with *Glomus mosseae* had greater dry weight and almost double the number of nodes, lateral branches and leaves as non-mycorrhizal transplants (Khaliel et al., 1987). A comparison of the effects of nine species of arbuscular mycorrhizal fungi on growth and nutrition of red raspberry demonstrated that in some instances branching was significantly increased (Taylor et al., 2000). In addition, bacteria associated with mycorrhizas, known as mycorrhiza helper bacteria have been reported to increase the colonisation of roots by the fungus (Garbaye et al., 1989; Garbaye, 1994). Poole et al. (2001) noted that the species of bacteria could modify the host plant morphology, including promotion of leaf initiation, and consequently the number of axillary buds and potential branches available for outgrowth.

Other biological agents have been reported to promote branching, including the root-knot nematode in *Arabidopsis* (von Mende, 2000), weevils in Verbascum (Lortie et al., 2000) and phytoplasmas, the causal agent of witches broom disease and, most importantly, highly branched cultivars of poinsettia (Bradel et al., 2000; Lee et al., 1997; Lee et al., 1996). Lee et al. (1997) described the branching induced in poinsettia, as the first example of a pathogenic phytoplasma as a causal agent of a desirable and economically important trait.

Many plants form symbiotic relationships with mycorrhizal-forming fungi. Although *Glomus* species are the predominant fungal partner there are many other fungi that form mycorrhizae. Most research has investigated the role of mycorrhizae in root branching, plant nutrition and the ability of plants to establish in contaminated land. The observation that mycorrhizal infection can promote branching in raspberry suggests that further research would be profitable, especially as infection with specific arbuscular mycorrhizal fungi can promote rooting to a significantly greater degree than synthetic auxins in some species (Thanuja et al., 2002). It is also possible that infection of stock plants with specific mycorrhizal fungi may increase the rooting ability of cuttings.

Chemical treatments

The use of plant growth regulators is more prevalent in ornamental crops than in edible crops and they are used to promote a number of beneficial processes including the modification of branching habit (Halevy et al., 1995). Chemical treatments to modify branching have been in commercial use for several years, (for example see, Kozel, 1968) and they can be divided into groups according to their mode of action (Wade, 1976). While there are many classes of chemicals that are used as plant growth regulators, only a limited number of them promote branching. Therefore, in this review we will concentrate on chemicals that have been shown to exhibit beneficial effects on branching in several plant species.

Chemicals with cytokinin-like activity may be used to promote the release of lateral buds from apical dominance in the presence of the intact tip. Chemical pruning and pinching agents exert their effects either by selectively killing shoot apices or by strongly inhibiting shoot elongation, thus allowing lateral buds to break dormancy and begin outgrowth. Also, there are other growth regulating chemicals including several 'one-off' chemicals that have been shown to affect branching, although their modes of action are not always clear.

There are many reports of bud-break and branching being induced by use of synthetic cytokinin sprays either alone or in admixture. For example, benzyladenine (BA, also known as benzylaminopurine, BAP) was used to promote branching in geranium (Carpenter et al., 1972), non-branching poinsettia (Semeniuk et al., 1985), *Ilex crenata, I. Vomitoria*, *Photinia* and *Nandina domestica* (Keever et al., 1990), florist azaleas (Bell et al., 1997) and apple (Ono et al., 2001). Combinations of benzyl adenine with gibberellin $A_{(4+7)}$, as Promalin for example, can increase lateral branching in woody species (Keever et al., 1990) and in ivy (Al-Juboory et al., 1990) and may be used to manipulate acrotony in deciduous fruit trees (Cook et al., 2000). Benzyladenine has also been shown to promote basal breaks in roses (Parups, 1971; Faber et al., 1977; Jayroe-Cournoyer et al., 1995) and to promote shoot initiation in empty leaf axils of *Stellaria media* (Tepper, 1992). In contrast, benzyladenine failed to promote branching in *Camellia* and *Rhododendron* (Richards et al., 1984) or *Columnea microphyla* (Lyons et al., 1987). Other synthetic cytokinins, such as thiadiazuron, CPPU (2-chloro-4-pyridyl-3-phenylurea) and PBA (6-benzylamino-9-tetrahydropyran-2-yl-9H-purine) are available, and they have been shown to promote lateral branch formation *in vivo* (for eaxample see, Ryan, 1974) and adventitious shoot formation *in vitro* (for example see, Kapchina-Toteva et al., 2000).

Atrinal (dikegulac) and Off-Shoot-O are examples of chemical pinching agents that have found use in the promotion of lateral branching. Atrinal was demonstrated to promote branching in several woody species including azaleas and *Rhododendrons* (Miller, 1975; Orson et al., 1978; Ticknor et al., 1991; Bell et al., 1997), *Camellia* (Scott, 1981; Song et al., 1995) and rose (Jayroe-Cournoyer et al., 1995). Greater numbers of cuttings were obtained from azaleas treated with dikegulac and the cuttings produced greater numbers of new shoots than cuttings taken from untreated mother plants (Schnall, 1980). However, dikegulac treatments did not improve basal shoot production in rose (Jayroe-Cournoyer et al., 1995). Off-Shoot-O (methyl esters of fatty acids) was one of the first chemical pinching agents to be used, initially in tobacco culture. However, it has also been used to promote lateral branching in woody plants, including fruit trees (Quinlan, 1978; Quinlan et al., 1978), *Camellia* (Kagira, 1975), *Rhododendrons* and azaleas (Ryan, 1974; Cohen, 1978). Other chemicals that have been used to promote lateral branching include paclobutrazol and uniconazole, although these compounds tend to inhibit both terminal and lateral shoot growth strongly and their effects may persist for several seasons (Keever, 1994).

Ethylene generating chemicals, such as ethephon, have also shown beneficial effects on promotion of lateral branching (Carpenter et al., 1971; Ryan, 1974; Ellabban et al., 1977) and, in particular, on the formation of basal-breaks in rose (Deen, 1972; Deen,1973; Zeislin et al., 1972; Hassan et al., 1976; Marczynski et al., 1979; Burgess, 2001). Also, ethephon induced the formation of axillary shoots in branchless chrysanthemum, *Dendranthema grandiflorum* cv Kitamura, but was inactive in branchless stock (*Matthiola incana* cv Akinobeni (Shin et al., 1996).

However, concerns about the use of chemical plant growth regulators have been raised (Keever, 1994). These relate mainly to inconsistent results that have been reported in the literature, particularly differences in dose-response curves for different cultivars of the same species, (for instance see, Grzesik et al., 1985a; Grzesik et al., 1985b;Ticknor et al., 1991; Andrews, 1996). However, there are also reports of phytoxicity (Sachs et at., 1975; Jacyna, 1996; Bell et al., 1997) and some cultivars displayed severe symptoms while other cultivars were unaffected (Jacyna, 1996; Bell et al., 1997). McAvoy (1989) attempted to rationalise the variation in response that had been observed by considering three groups of factors. Group 1: plant factors, includes the cultivar, the physiological stage of development, the physical condition of the plant. Group 2: environmental factors, including light and temperature, growing medium, water quality and nutrition. Group 3: physical and chemical factors, that must be considered, including residual effects, spray droplet size and crop coverage.

Chemical treatments to increase branching are an attractive option for the nurseryman, but there are risks involved and many of the chemicals are relatively expensive. While chemical sprays have mostly been applied directly to the plants to increase branching, there are indications that pretreatment of stock plants with cytokinins and/or gibberellins may be of benefit. For instance, axillary shoots were stimulated in cotyledonary nodes of mung beans following preconditioning with benzylaminopurine (Avenido et al., 2001). While, Ford et al. (2002) demonstrated that pretreating growing shoots on *Prunus avium* stock plants with GA increased the number of cuttings that rooted and the number of roots per rooted cutting compared to untreated control plants.

Summary and Conclusions

During the course of this review, we have considered the progress being made towards understanding and controlling branching at the basic, strategic and applied levels of science and technology. There is quite clearly a demand from the horticultural industry for 'tools' and techniques that will enable the manipulation of branching. The research effort on bud-break and branching has been somewhat patchy. Our literature search revealed a total of some 2000 references to work on pruning, growth regulating chemicals, apical dominance and branching in scientific journals. In comparison, basic research associated with vegetative bud initiation, and outgrowth is relatively unexplored. We found only ca. 30 references to initiation of buds and the genetic control of branching; in comparison to basic research on flowering this is but a drop in the ocean.

However, the work of Christine Beveridge and co-workers will eventually lead to the cloning of genes that control lateral bud outgrowth and consequently branching. Also, work is in progress to isolate and clone genes from mutants of antirhinum that demonstrate either acrotonic, mesotonic or basitonic branching patterns (Dr CGN

Turnbull, Imperial College at Wye, personal communication). These cloned genes may then be inserted to create new genotypes with the desired branching characteristics. New genotypes may be used directly or, where appropriate, they may be used as branch-inducing rootstocks. For example, in rose bush production, a clonal rootstock that promoted basal break formation would be of great value in increasing the efficiency of production of desirable older cultivars that currently yield low numbers of basal-breaks when grafted to traditional *Rosa laxa* rootstocks.

Bud-dormancy can be manipulated by many environmental effects, including temperature, nutrition and orientation. Under protected conditions, temperature, nutrition and light are routinely controlled, but re-orientation of plants to induce bud-break seems to have been largely unexplored. Also, we noted that in abstracts of reports detailing nutrition studies, particularly those reporting the effects of elevated carbon dioxide concentrations, the results often detailed increases in biomass or numbers of leaves, yet in the body of the text reference was made to alterations to branching habit. Further research in this area would undoubtedly yield useful information. In other areas, branching and bud-break have been considered and useful results obtained, for instance both spectral quality and quantity of light, as well as photoperiod, affect branching habit and offer a method for manipulation. Similarly nitrogen nutrition and carbon dioxide supply affects branching and may be used as a management tool in susceptible species.

The use of mycorrhizae as tools to manipulate plant growth is an area that offers considerable promise as a non-GM approach to manipulating plant growth habit. Benefits, such as improved branching, reduced fertilizer requirements and increased disease resistance may result from infection of cuttings with specific fungi at an early stage during rooting. Also, stock plants grown in association with specific fungi may produce greater numbers of cuttings that may root more readily and require less fertilizer or pest and disease control.

Chemical treatments, in common with pruning and pinching techniques, appear to be very variable in their effects, even between different cultivars. This makes generic approaches difficult to formulate, as even small changes in any of the parameters that govern bud-outgrowth will effect the result of chemical, pinching or pruning treatments. However, the use of growth regulators as ‘pretreatments’ prior to cutting collection or budding has not been fully explored.

Practical Recommendations

- At the genetic level the nurseryman is limited by the species and cultivars he wishes to grow, but clonal variation may allow the selection of individuals that exhibit higher degrees of branching, for use as stock plants. Also, in species where grafting or budding is the preferred method of propagation, selection of rootstocks that promote a high degree of branching in the scion is clearly a desirable objective. In future, genetic manipulation of branching habit will be plausible and it will be possible to develop new scions or rootstocks with the desired characteristics.
- In protected crops, manipulation of the quantity and quality of light may prove a useful manipulative tool. For instance, high ratios of red/far red to blue wavelengths of light have been shown to enhance shoot growth and prevent bud outgrowth. Screening plants from late evening light in the summer, would reduce the red light perceived by the plant and shorten the daylength, both of which are reported to promote branching. In the field it is desirable to ensure that the maximum light possible is intercepted by lateral buds to promote bud break, for

instance by minimising shading. Also, the orientation at which plants are grown or over-wintered may provide opportunities to manipulate bud-break.

- Nutrition and water requirements should be carefully controlled, and foliar feeding at the appropriate time may promote bud-break. Clearly water plays a critical role in the development of the plant, but too much water can result in leggy unsaleable plants, while too little may result in decreased bud-break and little branching.
- Synthetic cytokinins, dikegulac and ethephon have most consistently promoted branching and may provide beneficial effects in combination with other treatments, including pinching and pruning.

For consideration by HDC

It is apparent that when considering projects relating to production of HNS, it is important to consider a 'holistic' view of the process. For example, projects that address only 'stock plant' issues, should grow cuttings on to ensure that there are no detrimental effects (i.e. poor branching habit) on development of the new plant. Similarly, treatments that affect cutting development may lead to undesirable 'carry-over' effects if the cuttings are destined for use as new stock-plants. That which is gained on the swings, must not be lost on the roundabouts!

Clearly there are 'gaps' in the strategic work being undertaken currently and to fully understand the process of apical dominance it is important that the unknown root to shoot and the shoot to root signals are identified. Chemicals that mimic or block the transport of these signals may be expected to affect the branching habit of plants. Opportunities to identify these signals are offered by various plant systems, for instance the *rms* pea mutants and other plants in which branching can be manipulated by spectral quality or perhaps mycorrhizal infection.

Mycorrhizae will, perhaps not only affect branching, but also provide other beneficial effects on propagation, such as increased rooting of cuttings. Also, it is possible to raise stock-plants that are infected with arbuscular mycorrhiza-forming fungi that will, for example, promote rooting ability in cuttings collected from the stock plants as well as reducing the need for additional fertilizers. Modification of the spectral quality and quantity of light offer a method for manipulation of branching, but it is unclear as to the duration of treatment needed. Also, manipulation of spectral quality may promote the success of other branch inducing treatments such as chemical pinching and controlled nutrient and water supply or possibly a temporary increase in carbon dioxide levels.

While many processes of plant growth, for example, flowering, rooting and pollination, have been featured as themes for international conferences of the ISHS, shoot branching has not been addressed as a ‘main stream’ issue. This must be amended if substantial progress is to be made and the profile of control of branching as an area of scientific research must be enhanced. A conference or workshop dedicated to branching would best achieve this goal. Such an event should feature presentations from grower representatives to define the problems that need to be addressed as well as from scientists with international reputations to attract wide scientific participation. This would achieve the dual objectives of raising the awareness of the need to understand the process of branching and bringing together scientists, growers and, hopefully, funding agencies with a common goal.

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