

proximal older leaves.

Our evidence for phloem transport of Ca in young apple seedlings or rooted layers should be verified for older trees. Even though Ca is considered to be immobile in the mature bean plant, it has been shown that there is redistribution of Ca from the cotyledons during germination and early seedling growth (2). The age at which the nutrient distribution pattern is established for apple plants is not known.

Literature Cited

1. Bell, G. W., and O. Biddulph. 1963. Translocation of calcium. Exchange versus mass flow. *Plant Physiol.* 38:610-614.
2. Bukovac, M. J., and A. J. Riga. 1962. Redistribution of cotyledonary phosphorus, calcium and zinc during germination and early seedling

development of *Phaseolus vulgaris* L. *Proc. XVIth International Hort. Congress* 2:280-285.

3. Koontz, H. V., and Foote, R. E. 1966. Transpiration and calcium deposition by unifoliate leaves of *Phaseolus vulgaris* differing in maturity. *Physiol. Plantarum* 19:313-321.
4. Mason, T. G., and Maskell, E. J. 1931. Further studies on transport in the cotton plant. I. Preliminary observations on the transport of phosphorus, potassium, and calcium. *Ann. Bot.* 45:125-173.
5. _____, _____, and E. Phillis. 1936. Further studies on transport in the cotton plant. III. Concerning the independence of solute movement in the phloem. *Ann. Bot.* 50:23-58.
6. Perring, M. A. 1968. Mineral composition of apples. VII. The relationship between fruit composition and some storage disorders. *J. Sci. Fd. Agr.* 19:186-192.
7. Shear, C. B., and M. Faust. 1970. Calcium transport in apple trees. *Plant Physiol.* 45:670-674.

Snapdragon Stem Tip Breakage as Related to Stem Lignification and Flower Color¹

David G. Adams and Wesley A. Urdahl²
South Dakota State University, Brookings

Abstract. Breakage in the floret area of the stem which occurs during harvesting or post-harvest handling in commercially mature snapdragons was investigated. The point of breakage was not influenced by the number of open florets on the stem, provided many unopened buds remain at the apex. Breaking occurred lower on the stem in crops harvested during fall as opposed to summer months. The break point appears to be related to the end of the concentric column of safranin stainable, lignified xylem. Although not without exception, breakage also appears related to flower pigmentation in that anthocyanin (red) containing cultivars tend to break high whereas aurone (yellow) containing cultivars break low in the floret area. These factors suggest a competition for phenyl propanoid precursors which are consumed in both lignification and pigmentation.

Production of weak, succulent-stemmed ornamentals in the greenhouse has been a perpetual problem and most often noticed during months of low light intensity. Breakage of stems in the floret area during harvesting or post-harvest handling in the snapdragon, *Antirrhinum majus* L., is usually clean, without much tearing of tissues. This suggests that lignification has not taken place. Most problems concerning snapdragon quality have been approached from the standpoint of environmental or cultural manipulation.³ Such factors as nutrition, withholding water (7, 8), temp and photoperiod manipulation (15, 20, 23), spacing or increasing illumination per plant (2), and cultivar selection have been common areas of investigation.

We studied stem breakage within the area of the florets as it relates to xylem lignification in the stem and to flower color. Lignification and flower pigmentation were investigated because of their mutual dependence on phenyl propanoid precursors. Research and review articles on the biosynthesis of lignin (1, 4, 16, 21, 22, 25) and plant pigments (5, 9, 10, 11, 18) clearly show that precursors such as p-coumaric, ferulic, and caffeic acids, and other phenyl propanoid compounds derived from the shikimic acid pathway are principal components of both processes.

Materials and Methods

Snapdragons were greenhouse-grown in raised beds and were flowered during spring, summer, fall, and winter. Normal spacing and feeding, and temp of 50-55°F, when possible, were maintained for each crop. Within each cropping period, several

cultivars were grown. Cultivars were planted in single rows across the bench and were randomly mixed. Guard rows were used only on bench ends. Samples of 10 stems each were pulled from the bed when individual stems had 6 or more, (often 15-20) fully open florets. Stems were taken randomly from all positions within the row and bench as flowering commenced.

In order to determine if stem breakage was correlated with stem lignification, individual stems were physically broken by hand, often in several places. The recorded point of breakage (hereafter referred to as "break-point") was determined as that point on the stem furthest from the apex which broke cleanly and without visible tearing of the xylem tissues.

Free hand cross sections of the same turgid stems were immediately cut and stained with a dilute safranin solution. Sections were made from internodal tissue approx half way between individual florets. Usually, 5-8 sections were made from each stem. The point on the stem where a continuous ring of stainable xylem ceased and individually stainable bundles continued was designated as the "stain-point." Above this point stainable xylem was found only in isolated bundles and below, it was a continuous ring. Records based on hand breakage and stain acceptability were taken on each of the 10 stems in a sample. Samples were replicated 2-4 times depending on quantity of material.

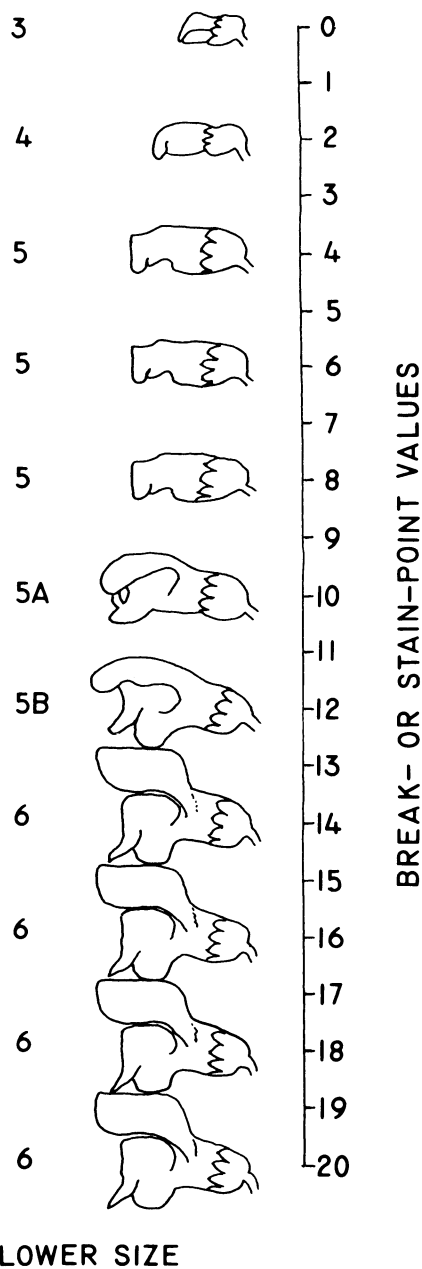
Locations of break- and stain-points were also recorded in relation to floret size and openness to establish an external index for xylem lignification and point of breakage. The system used for characterizing size and degree of floret openness was modified from Schmidt (21); fully open floret "6," floret more than half open "5B," floret beginning to open "5A," floret full size but prior to opening "5," sizes "4, 3, 2, 1" as per Schmidt (Fig. 1).

Floret development was compared with break- and stain-points on an arbitrary scale (Fig. 1). A numerical value of 13 was assigned to those samples which broke or stained at the internode between the last fully open floret (size 6) and the first

¹Received for publication December 27, 1971. Approved for publication by the Director, Agr. Expt. Sta., S. Dak. State Univ., Brookings, as Journal Series No. 1050.

²Associate Professor of Horticulture and Assistant-in-Horticulture, respectively.

³Grower Circle News. April, 1967 and Jan., 1968. Yoder Brother Inc., Barberton, Ohio.



FLOWER SIZE

Fig. 1. Schema of snapdragon flower spike indicating floret size and stain- or break-point values used to identify location of xylem lignification and points of stem breakage, respectively. Even numbers associated with floret positions, odd numbers with internodes. Floret size "6" fully open, "5B" more than half open, "5A" beginning to open, etc. Adapted from Schmidt (21).

partially open floret (size 5B). Smaller values were used acropetally and larger values basipetally from this central position. For example, a cultivar with a stain- or break-point value of 9 would exhibit a continuous ring of lignified xylem or would break cleanly between a floret which was beginning to open and one not yet starting to open (5A/5) (Fig. 1). Three size 5's were used on the scale (Fig. 1) because snapdragons normally have several florets in this stage of development at any given time.

Results and Discussion

The number of open florets on a stem at sampling had little effect on break- and stain-point locations. Samples with as many as 20 open florets were found to break and stain similar to those with only 5-6 open florets provided many unopened buds

remained at their apices, Table 1. Cultivars sampled during periods of high light intensities, consistently showed smaller break- and stain-point values than those sampled during periods of low light (Table 2, 6/68 vs. 11/68). These data indicate that xylem lignification occurred closer to the apex in June samplings than in plants sampled in November. Salim (19) and Torrey (26) have shown that when linear growth of root tips is inhibited by either physical or chemical means, xylem lignification occurs very near to the root apex. Different rates of linear stem growth during summer and winter would be expected because of a lack of photoinhibition during periods of low light intensity, short photoperiods, and low growing temp in winter (20).

In most cases the point of record followed a color pattern. It was nearest the stem apex in red, rose, and white cultivars and furthest from the apex in bronze and yellow. Pink and ivory

Table 1. Representative samples of commercially mature snapdragon stems depicting influence of number of open florets on break-point (BP) and stain-point (SP) values.

Open florets Size "6"	Cultivars, break- and stain-point values					
	Montezuma		Snowman		Treasure Chest	
	BP	SP	BP	SP	BP	SP
6					13	12
7						
8	7	10				
9	9	9			7,10	7,10
10	10	9				
11	9	13	15	13	13	13
12	11	10				
13	12	12	13, 13	9, 13	7	10
14	9	9			11	8
15	15	15			7	7
16	9	13	13, 15	13, 10	11	11
17	10	10				
18			10, 10	10, 15	12	9
19			13, 17	13, 15		
20			13	13		
21						
22						
23					12	12
Average	10.1	10.1	13.2	12.4	10.3	9.9

were intermediate (Table 2). It is of interest to note that the genetics of flower pigmentation in snapdragon follows a very similar pattern (5, 6, 13). The dominant or homozygous colors are red (anthocyanin), yellow (aurone), and white (albino-no pigment, complete recessive); rose, pink, and bronze are mixtures of anthocyanins and aurones. Flower pigmentation may be an important factor in regard to stem breakage because of its relationship to lignin production. Esters of p-coumaric and ferulic acids and several similar substances with phenyl propane structures are precursors of both lignin and flower pigments of snapdragon (1, 4, 5, 9, 21). Moreover production of both of these materials requires light (10, 12, 16, 17, 21).

Lawrence and Scott-Moncrieff (14) in a study of the genetics and chemistry of flower color in dahlia, summarized with the following statement: "Balanced pigment production points to a limited common source for both anthocyanins and flavones, while interaction and suppression indicate that this source is limited in such a way that it is competed for by all the factors present, the actual proportions of pigments produced depending upon the specific claims of the various factors." Although the above work was not quantitative, Jorgensen and Geissman (13) did measure the relative quantities of anthocyanin and aurone pigment in 25 of 27 possible color genotypes of snapdragon. They found that anthocyanin concn was inversely related to aurone concn. Competition for biochemical substances is well

known in all fields of plant growth and development (10).

Red cultivars which exhibit anthocyanin pigmentation throughout the entire plant, (stem, leaves, and flowers) exhibited small break- and stain-point values. These plants are therefore capable of producing large amounts of pigment and lignin at the same time throughout the entire plant. Yellow cultivars, and the genetically related orange, bronze, and ivory, produce aureusidin, the primary yellow pigment, only in floral tissue (6). These cultivars exhibit poor lignification in the floral area of the stem (large break-point values), at a time when the florets are also requiring large quantities of precursor common to pigmentation and lignification. Since pigment synthesis is

carried out only in flowers and not in stems and leaves as in the red forms, the total precursor synthesizing system may likewise be greatly restricted in quantity and distribution.

Although the aurone, aureusidin, is generally believed to be the principle yellow pigment in snapdragons, several other yellow pigments are known (3, 6, 9, 13, 24). All are thought to be formed from the same precursors; however, the synthesis pathway of aureusidin is believed to differ significantly from other yellow pigments (13). This may account for the wide variations in break- and stain-point values found between yellow cultivars such as 'Golden Spike' and 'Montezuma' (Table 2). The genetic backgrounds of these 2 cultivars may also differ

Table 2. Flowering dates and average stain-^Z and break-point^Y values of snapdragon cultivars grown during various periods of the year.

Cultivar and color		Stain-point ^{ZX}	Break-point ^{YX}	Stain-point ^Z	Break-point ^Y
Flowering dates		(6/68)	(6/68)	(11/68)	(11/68)
A. ^w	Virginia white	5.0 a	6.5 a	B. 7.2 a	11.1 a
	Panama white	10.5 bc	10.3 b	12.6 b	13.7 ab
	Tucson lavender	11.8 bcd	13.1 bc	---	---
	Tennessee red	13.3 cd	12.3 b	15.0 bc	13.9 ab
	Potomac Yellow yellow	13.7 cd	13.1 bc	20.3 d	20.1 c
	Hawaii ivory	14.0 d	13.2 bc	19.1 d	17.3 bc
	Pan. Am. Sum. Pink pink	15.1 de	13.7 bc	17.8 cd	17.4 bc
	Kansas bronze	17.5 e	16.6 c	18.3 cd	19.2 c
Average		12.6	12.4	15.8	16.1
Flowering dates		(4/69)	(4/69)	(5/69)	(5/69)
C.	Montezuma yellow	8.7 a	10.1 a	D. 9.1a	11.1 a
	Apache red	9.9 ab	13.3 b	11.1ab	11.0 a
	Treasure Chest rose	10.9 abc	10.7 a	12.5 b	11.5 a
	Native Dancer pink	11.2 abc	12.6 b	11.2 ab	10.9 a
	Snowman white	11.7 bc	12.5 b	11.3 ab	11.9 a
	Galant Fox bronze	13.2 c	13.6 b	12.8 b	11.8 a
	Golden Spike yellow	16.4 d	13.5 b	16.0 c	13.4 b
Average		11.7	12.3	12.0	13.4
Flowering dates		(9/68)	(9/68)		
E.	Potomac Red red	10.7 a	12.1 abc		
	Pan. Am. Sum. Pink pink	10.8 a	11.3 ab		
	Panama white	14.1 b	15.2 cdef		
	Potomac Rose rose	14.6 b	14.4 bcde		
	Potomac Yellow yellow	14.7 b	16.4 def		
	Monterey white	15.1 b	18.4 f		
	Veracruz yellow	15.4 b	16.9 ef		
Average		13.6	14.9		
Flowering dates		(4/69)	(4/69)		
F.	Rosita rose	9.3 a	11.4 a		
	Sierra white	9.9 a	12.8 a		
	Buccaneer red	10.0 a	11.9 a		
	Doubloon yellow	11.2 a	12.1 a		
Average		10.1	12.1		

^ZValues indicate most acropetal point of concentric ring of stainable, lignified xylem in the floret area of commercially mature stems.

^YValues indicate most basipetal point of clean breakage (without tearing of xylem tissues) in floret area of commercially mature stems.

^XNumbers not associated with the same letter within a column are significantly different at the 5% level as determined by method of least squares and multiple range test.

^wDesignations "A" through "F" indicate individual cropping periods. Group "C" differs from "F" in that because of poor growth, the former was pinched and later trimmed to one stem for flowering.

Table 3. Mean squares and F values developed during analysis² of stain- and break-point values for cultivars flowered at designated periods.

Value	Flowering groups periods		MS	F	Significance level
Stain-point	6/68	A	43.85	13.51	**
Stain-point	11/68	B	46.49	14.32	**
Error	A & B		3.2		
Break-point	6/68	A	27.38	6.39	**
Break-point	11/68	B	25.44	5.93	**
Error	A & B		4.29		
Stain-point	4/69	C	13.46	6.41	**
Stain-point	5/69	D	18.03	8.59	**
Error	C & D		2.10		
Break-point	4/69	C	4.79	4.71	**
Break-point	5/69	D	3.06	3.01	*
Error	C&D		1.01		

²Least squares analysis of variance; * and ** indicate 5% and 1% significance levels, respectively.

greatly.

Paper white snapdragons are genetically and biochemically different from other forms in that their florets are truly albino and possess no recognizable pigments. They do, however, contain esters of p-coumaric and ferulic acid and other phenyl propanoid compounds (5, 11, 21). These precursors have been found in relatively high concn in albino florets when compared to colored controls. Some competition between developing flowers and stem lignification would therefore be expected but would probably be less than that experienced by ivory, bronze, and yellow cultivars since the precursors in the albino forms would not be depleted by pigment synthesis.

In an effort to determine if the stain- and break-point methods were similar for determining the exact point of stem breakage, both statistical and practical aspects were considered. Statistically, the stain- and break-point values were not well correlated (0.45). On the other hand, 82% of the average break-point values (Table 2) were within 1 floret distance of their corresponding stain-point value, the rest were within 2 florets distance (Fig. 1 and Table 3). Half of these break-point values were larger and half were smaller than their corresponding stain-point values. Table 3 shows the mean square values and error terms for groups A, B, C, and D. The larger F values shown for the staining method indicate a higher degree of precision for this method as opposed to hand breakage. Sampling precision is also shown in Table 2 in that stain-point values (group A) are statistically divided into 5 categories (a-e) while only 3 exist (a-c) in the corresponding break-point group. Groups B, C, and D show a similar response. This would be expected since factors such as differences in stem diam, turgidity and closeness of florets make hand breaking a rough estimate at best of the exact break-point. Since the stain-point corresponds with the end of the continuous column of lignified xylem, and for all practical purposes is closely related to the break-point, it is felt that the stain-point method is a more precise estimate of the actual point of breakage than is hand breaking. It seems probable therefore that stem breakage in the floral area is a function of xylem lignification and flower pigmentation.

Since wide variations in breaking susceptibility exist between commercial cultivars of similar color, it is suggested that this staining procedure might be used as a means of evaluating new cultivars for commercial use.

Literature Cited

- Brauns, F. E., and D. A. Brauns. 1960. The chemistry of lignin, Supp. Vol. Academic Press, New York, 804 p.
- Carpenter, W. J. 1964. Response of snapdragons and chrysanthemums to supplemental reflective light. *Proc. Amer. Soc. Hort. Sci.* 84:624-629.
- Dayton, T. O. 1956. The inheritance of flower colour pigments. I. The genus *Antirrhinum*. *J. Genet.* 54:249-260.
- Freudenberg, K., and A. C. Neish. 1968. Constitution and biosynthesis of lignin. Springer-Verlag, New York, 129 p.
- Geissman, T. A., and J. B. Harborne. 1955. The chemistry of flower pigmentation in *Antirrhinum majus*. IV. The albino (-mm-*nn*) form. *Arch. Biochem. Biophys.* 55:447-454.
- _____, E. C. Jorgensen, and B. L. Johnson. 1954. The chemistry of flower pigmentation in *Antirrhinum majus*. Color genotypes. I. The Flavonoid components of the homozygous P,M,Y color types. *Arch. Biochem. Biophys.* 49:368-388.
- Hanan, J. J. 1965. Efficiency and effect of irrigation regimes on growth and flowering of snapdragons. *Proc. Amer. Soc. Hort. Sci.* 84:681-692.
- _____, and R. W. Langhans. 1964. Soil water content and the growth and flowering of snapdragons. *Proc. Amer. Soc. Hort. Sci.* 84:613-623.
- Harborne, J. B. 1963. Plant polyphenols. X. Flavone and aurone glycosides of antirrhinum. *Phytochemistry* 2:327-334.
- _____. 1967. Comparative biochemistry of the flavonoid. Academic Press, London, 383 p.
- _____, and J. J. Corner. 1961. The cinnamic esters of *Antirrhinum majus* flowers. *Arch. Biochem. Biophys.* 92:192-193.
- Hillis, W. E., and T. Swain. 1957. Influence of illumination on the synthesis of leuco-anthocyanins in leaves. *Nature* 179:586-587.
- Jorgensen, E. C., and T. A. Geissman. 1955. The chemistry of flower pigmentation in *Antirrhinum majus* color genotypes. III. Relative anthocyanin and aurone concentrations. *Arch. Biochem. Biophys.* 55:389-402.
- Lawrence, W. J. C., and Rose Scott-Moncrieff. 1935. The genetics and chemistry of flower colour in dahlia: a new theory of specific pigmentation. *J. Genet.* 30:155-226.
- Miller, R. O. 1962. Variations in optimum temperatures of snapdragons depending on plant size. *Proc. Amer. Soc. Hort. Sci.* 81:535-543.
- Pearl, I. A. 1967. The chemistry of lignin. Marcel Dekker, New York, 339 p.
- Phillips, E. W. J. 1954. Influence of leaf activity on the composition of wood cell wall. *Nature* 174:85-86.
- Robinson, T. 1964. The organic constituents of higher plants. Burgess Publishing Co. Minneapolis, 306 p.
- Salim, K. M. 1966. Relationship between linear growth and the distance of initiation of lignification behind the root-tip in *Lepidium sativum* L. *J. Exp. Bot.* 17:185-194.
- Sanderson, K. C., and C. B. Link. 1967. The influence of temperature and photoperiod on the growth and quality of a winter and summer cultivar of snapdragon, *Antirrhinum majus* L. *Proc. Amer. Soc. Hort. Sci.* 91:598-611.
- Schmidt, H. 1962. Chemische Untersuchungen uber den Biosyntheseweg der Blütenfarbstoffe in Mutanten von *Antirrhinum majus*. *Biol. Zentralblatt* 81:213-226.
- Shubert, W. J. 1965. Lignin biochemistry. Academic Press, New York, 131 p.
- Seeley, J. G. 1965. Soil temperature and the growth of greenhouse snapdragons. *Proc. Amer. Soc. Hort. Sci.* 86:693-694.
- Seikel, M. K., and T. A. Geissman. 1950. Anthochlor pigments. VII. The pigments of yellow *Antirrhinum majus*. *J. Amer. Chem. Soc.* 72:5725-5730.
- Siegel, S. M. 1953. On the biosynthesis of lignins. *Physiol. Plant* 6:134-139.
- Torrey, J. G. 1953. The effect of certain metabolic inhibitors on vascular tissue differentiation in isolated pea roots. *Amer. J. Bot.* 40:525-534.