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BOTANY

INFLUENCE OF α-NAPHTHYL ACETIC ACID, SUCROSE AND BORIC ACID ON THE FLOWER DROP OF *LUPINUS POLYPHYLLUS LDL.*

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1. INTRODUCTION

Because of its attractive shape and colour *Lupinus polyphyllus* Ldl. is a popular border plant. As a cut flower however, it is almost of no importance. Undoubtedly the main cause for this is the rapid drop of flower buds and the unfertilized flowers. In his efforts to remedy this WARNE (24) showed that flower drop could be retarded by a 0.04–0.08 % spray of indol acetic acid (IAA) or α-naphthyl acetic acid (NAA). This effect of growth substances on the drop of turgid flower parts is rather exceptional (1, 2). When the method was applied in the course of the present work, its results proved to be uncertain and insufficient. It has been shown (1, 2) that the drop of turgid petals (e.g. with *Antirrhinum majus*, *Lathyrus odoratus*, *Rosa* and *Tulipa*) and of turgid florets (e.g. *Laburnum anagyroides* and *Ribes sanguineum*) could be retarded or prevented by the addition of sugar.

This led us to test the effect of sugar on the fall of florets of *Lupinus*. The effect of boric acid was also studied, as according to TORSSELL (23) 'the complexes between boric acid and carbohydrates control the deposition of oriented cellulose micells and the accompanying stiffening of the cell wall'.

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2. MATERIALS AND METHODS

All experiments were conducted with 3 inflorescences of a blue and 3 of a white variety of *Lupinus polyphyllus*. As the differences between the two varieties were not larger than those between the different plants of one variety, the averaged data of the 6 inflorescences are given here. The inflorescences were cut when the first flowers had just opened. Immediately after cutting they were completely defoliated.

NAA, sucrose and boric acid were supplied to the water in the vase. NAA was also given by a dip shortly after cutting. As a basal solution was used: 0.003 % $AgNO_3$ + 0.1 % $Ca(NO_3)_2.4H_2O$ + 0.06 % citric acid

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Summary: see p. 331-332.

+ 0.025 % cladox (with 2:4-dinitrorhodane benzene) + 0.001 % AAradon (organic mercurial) (2). The flowers were placed in a rather dark laboratory room at a temperature of 15–23° C.

The length of the naked part of the inflorescence was expressed in % of the total length of the flower stalk that was originally covered with flowers and flower buds. Thus a comparable and easily determinable measure for the flower drop was obtained.

3. Results

As shown in fig. 1 flower drop could be retarded considerably by sucrose in high concentrations (6–8 %) as well by a dip into the solution of a growth substance (NAA). The greatest effect of NAA was obtained when

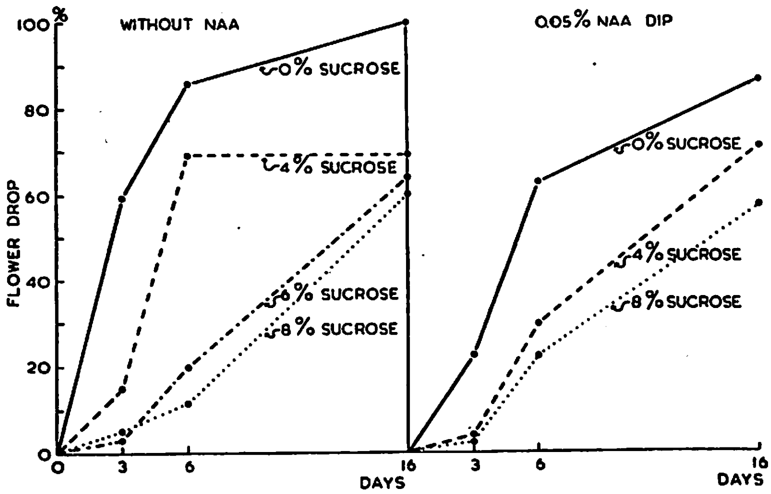

Fig. 1. Influence of sucrose concentration on flower drop of *Lupinus polyphyllus*. Left without, right in combination with a 0.05 % NAA dip.

sucrose had been applied simultaneously. Without sucrose flower drop could be retarded by NAA no longer than 3 days. In combination with 4 % sucrose its effect was considerably more pronounced, but with 8 % sucrose no influence of NAA could be established (see also fig. 2).

Fig. 2 shows at the same time that introduction of NAA into the transpiration stream in concentrations too low to be toxic has no effect on the flower drop, not even in combination with sugar.

In these experiments it was observed that flowers on the verge of opening were the first to fall off. This fact in combination with the beneficial effect of sugar suggested that competition for food within the spike could play a role, young growing buds competing with older ones and affecting the fall of the latter. Indeed the removal of the uppermost 3–4 cm of the spike (in fig. 3 -top) retarded the fall of the rest of the florets. If sucrose was added, this effect was masked. After 9 days almost all florets had fallen, also when the top had been removed, unless sugar had been applied.

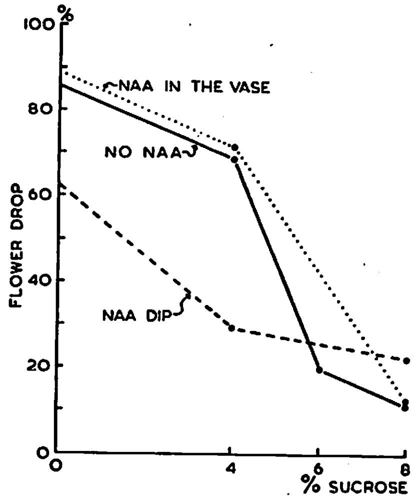

Fig. 2

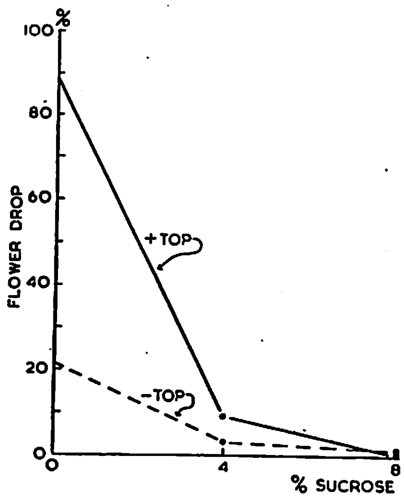

Fig. 3

Fig. 2. Flower drop of *Lupinus* as influenced by sucrose concentration and growth substance, applicated by dip and with the transpiration stream. Condition after 6 days. ——— without NAA; ----- 0.05 % NAA dip; ...... continuously in 0.01 % NAA.

Fig. 3. Influence of the removal of the upper 3 cm (top) of Lupinus spikes on flower drop in combination with different sucrose concentrations. Condition after 5 days.

Boric acid induces a regular and lasting retardation of the flower drop. Maximal inhibition could be obtained with ± 0.1 % of boric acid (fig. 4). Other data, not given here, show that 0.2 % or more boric acid was harmful to the flowers and the flower stalk.

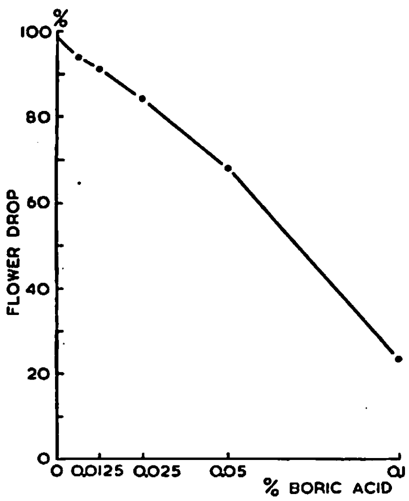

Fig. 4. Influence of boric acid (0–0.1 %) on flower drop of *Lupinus polyphyllus*. Condition after 13 days.

With 0.1 % boric acid the flowers remained at the stalk, but turned brown after about 5 days. This is in contrast to the experiments with sugar, where the flowers did not drop and also remained completely fresh for a much longer time. If however, 0.1 % boric acid was combined with 2 % sucrose, which by itself is too low a concentration, the flowers did not fall and remained fresh during 10–14 days (see fresh weight in table 1). Table 1 shows that with addition of sugar also a normal elongation of the stem could be obtained and that also in this respect 0.1 % boric acid had almost no harmful effect.

TABLE 1

Influence of 0.1 % of boric acid with (+) and without (—) 2 % sucrose on flower drop, keepability (fresh weight) and flower spike elongation. Condition after 10 days

	Flower drop %		Fresh weight in % of original weight		Growth in length of the inflorescence %	
0.1 % boric acid / 2 % sucrose	—	+	—	+	—	+
—	97.4	0	74.4	85.9	41.6	36.5
+	54.0	0	104.4	124.6	76.0	71.4

It is highly probable that the optimal sugar concentration to prevent flower drop is higher than the optimal concentration to prolong flower life. Boric acid, however, affects only the flower drop and almost not the keepability. By the combination of both sugar and boric acid good results are obtained, while only a small amount of sugar is required. With boric acid concentrations below the optimum (e.g. 0.05 %) the effect of sugar and boric acid on flower drop is cumulative (fig. 5). At higher concentrations both of boric acid and sugar this cumulative effect cannot appear.

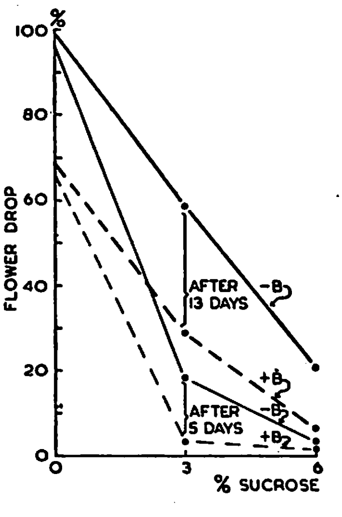

Fig. 5. Influence of sucrose with (+ B) and without (— B) 0.05 % boric acid on the flower drop of *Lupinus polyphyllus*. Condition after 5 and 13 days.

4. Discussion

It has been shown several times that growth substances cannot exhibit their influence when the carbohydrate level in the plant is too low. This can be illustrated here by one of my own observations: Cut flower spikes of *Muscari armeniacum* react strongly to a dip in a solution of 0.1–0.01 % NAA. The flower stalk shows hypertrophic swelling and at higher concentrations curvatures occur; the perianth becomes fleshy and deformed, while its life is considerably prolonged. All these growth substance effects occurred only when the flowers were placed in a solution containing 2 % or more sucrose.

As has been shown by Heinicke (13) and Brown and Addicot (6), the abscission of debladed petioles could be retarded by putting a droplet sugar solution at the stump. Went and Carter (25) found that the flower drop occurring in tomato at high night temperatures, could be prevented by a sugar spray, not by growth substances. Heinicke (13) thought that sugar by its osmotical force would restore the disturbed transpiration stream. Brown and Addicot (6) showed however, that the sugar was mostly accumulated at the proximal side of the abscission layer. In the present experiments sugar did not disturb the transpiration stream in the neighbourhood of the flower at all.

The experiments with *Lupinus polyphyllus* clearly show that the level of carbohydrates in the plant is of practical importance in the control of flower, leaf or fruit drop with growth substances. At extremely low carbohydrate levels growth substances cannot exert their influence. At extremely high levels abscission does not occur, so that in this case growth substances have no visible effect. Perhaps this can explain the irregularity of the effect of growth substances on flower and fruit drop under different weather conditions [Blair and Nelson (5), Whiteman (27)]. Whiteman (27) for instance could retard the petal drop of cut *Paeonia* flowers with growth substances in a normal year, but not in a very rainy or very sunny one.

According to the gradient theory of Addicot and Lynch (3) abscission occurs, when the growth substance concentration at the proximal side of the abscission zone is higher than at the distal side. In the case of fig. 6 for instance the petiole would drop. The observation that applications of growth substances with the transpiration stream had no influence on *Lupinus* flower drop, is in accordance with this theory. With *Alnus*, however, catkin drop could be prevented by this method (1) and Steyer (22) could retard petal drop of *Coleus* by growth substance application at the style, that is to say proximal. Laibach (18) on the other hand, working with *Papaver rhoeas*, found an acceleration of petal drop, when auxin was applied to the style.

Gaur and Leopold (9) showed that growth substances applicated proximally as well as distally retarded abscission in high concentrations but accelerated it in low concentrations. According to Haccius and Nies

(11) growth inhibitors retard abscission in low concentrations and accelerate it in higher ones. If it is also taken into consideration that auxins are transported faster basipetally than acropetally, this hypothesis can completely explain the experiments of ADDICOT and LYNCH (3).

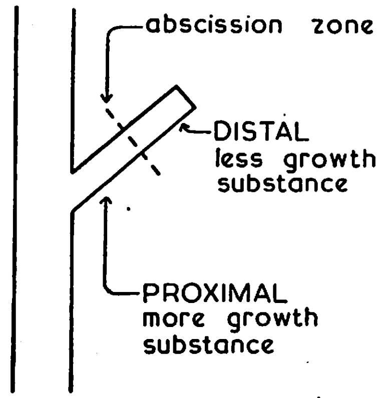

Fig. 6. Scheme of growth substance distribution leading to abscission. According to ADDICOT and LYNCH (3).

JACOBS (14) found with *Phaseolus* that the abscission of debladed petioles was accelerated by the presence of leaves, especially the young growing leaves of the terminal shoot. Out of these leaves growth substances would be transported, thus raising the concentration at the proximal end of the debladed petiole and accelerating abscission. However, the results of JACOBS as well as the present ones with *Lupinus* may also be explained by assuming competition for food among the growing parts of the plant, or in other words, an insufficient amount of sugar to be the cause of abscission.

According to the auxin-ethylene balance theory of GAWADI and AVERY (10), byproducts of the aging process (e.g. ethylene) combined with a relative shortness of growth substances would induce abscission. Ethylene induced abscission has been frequently reported (10), but for instance with tomato abscission of leaves could not be induced by ethylene (7). Detached (12) or damaged (28) leaves can give off rather considerable amounts of ethylene; however, as in *Lupinus* (and also in *Antirrhinum*) the abscission occurs very rapidly, when the flowers are still completely turgid, it does not appear very likely that ethylene is the cause of the abscission. As BIALE a.o. (4) have pointed out for ripening fruits, the formation of ethylene seems rather more a consequence, than the primary cause of the aging process. In fruits there is no connection between sugar content (17) and ethylene production. It may be possible, however, that such a relationship exists in leaves or flowers. Therefore, it would be of some importance to investigate whether addition of sugar or boric acid to cut flowers would retard or decrease the production of ethylene. However, the fact that with boric acid the flowers wilt, but do not abscise, renders also ethylene production improbable as a cause of abscission. Also the fact that in many species growth substance applications have no effect whatsoever on flower shed makes the general acceptance of the auxin-ethylene balance theory impossible.

Considering the likelyhood of the theories of ADDICOT and LYNCH (3) and GAWADI and AVERY (10), one must conclude that they give only an explanation of the conditions leading to abscission, but not of the mode of action by which growth substances and ethylene cause the middle lamells to weaken. A noteworthy attempt to do so has been made by SACHER (20). He reports that in debladed *Coleus* petioles the air was driven out of the intercellular spaces by water before the stumps would abscise. Both water leaching and abscission were prevented by application of IAA. From this he concludes that the growth substances act by maintaining the membrane integrity.

It was suggested before (2), in connexion with the action of sugar and boric acid in preventing wilting of cut flowers, that these compounds would be helpful in maintaining protoplasmatic structure. If this is true, they would have the same influence as growth substances.

JERMYN and ISHERWOOD (15) showed that in the cell walls of fruits during ripening not only decompositions occur but also synthesis. The cell wall would be in dynamic equilibrium with the cytoplasm. According to this idea sugar could directly influence the changes of the cell wall that lead to abscission.

TORSSELL (23) stated that boric acid too prevents changes in the cell wall. Indeed SPURR (21) reported that boron deficiency is accompanied by abnormal structure of the cell wall.

Apart from the different ways that have been mentioned, boric acid could act by facilitating sugar (8) or auxin (19) transport. The central question is: Do growth substances, sugar and boric acid interact, or can they prevent abscission independent of each other? Perhaps this can be discovered by simultaneous application of NAA and boric acid at different places. Apart from this it would be interesting to know whether boric acid affects flower drop in species that react to growth substances but not to sugar, e.g. *Alnus glutinosa*, or that behave in the opposite manner, like e.g. *Ribes sanguineum*.

Nothing is known about the possibilities of boric acid applications, alone or with other substances, to control flower or fruit drop in other species. It has been stated however, that boron deficiency sometimes causes flower drop in pear (16).

SUMMARY

The flower drop from cut branches of *Lupinus polyphyllus* can be prevented by sucrose in high concentrations (6–8 %). Dipping the branches into a NAA solution (0.05 %) retards the drop. This effect of the growth substance is enhanced when the flowers are placed in 3–4 % sucrose

solution. At lower sugar concentrations influence of the growth substance is slight, at high concentrations it is undetectable. Introduction of NAA into the transpiration stream has no effect.

Removal of the top of the flower spike retards the drop of the remaining florets.

Flower drop can be prevented almost completely by 0.1 % boric acid. However, sugar must be supplied at the same time, otherwise the flowers placed in a boric acid solution, although they do not fall off, remain fresh for a very short period only. A combination of 0.1 % boric acid and 2 % sucrose gives good results with regard to flower drop and keepability. The addition of boric acid therefore saves a considerable amount of sugar.

Neither the auxin gradient theory of ADDICOT and LYNCH (3), nor the auxin-ethylene balance theory of GAWADI and AVERY (10) gives a completely satisfactory explanation of these findings. Growth substance, boric acid and sugar may each affect cell wall structure, but they can also accelerate the transport or mobilisation of each other. Therefore the question rises whether these three compounds act independently or not.

Perhaps the use of boric acid shows new perspectives in the control of premature leaf, flower or fruit drop. For practical applications to *Lupinus polyphyllus* a basal solution (p. 10) + 2 % sucrose + 0.075–0.1 % boric acid is recommended.

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LITERATURE

1. AARTS, J. F. TH.: De ontwikkeling en houdbaarheid van afgesneden bloemen. Meded. Dir. Tuinb. 20, 1957: 690–701.
2. AARTS, J. F. TH.: Over de houdbaarheid van snijbloemen. Meded. Landbouwhogeschool, Wageningen 57 (9), 1957: 1–62.
3. ADDICOT, F. T. and LYNCH, R. S.: Physiology of abscission. Ann. Review Plant Physiol. 6, 1955: 211–238.
4. BIALE, J. B., YOUNG, R. E. and OLMSTEAD, A. J.: Fruit respiration and ethylene production. Plant Physiol. 29, 1954: 168–174.
5. BLAIR, D. S. and NELSON, S. H.: Use of chemicals in apple production. Reduction of preharvest and harvest drop in apples by spraying with growth regulating substances. Hortic. Div. Centr. Exp. Farm, Ottawa. Progress Report 1949–1953: 44–49.
6. BROWN, H. S. and ADDICOT, F. T.: The anatomy of experimental leaflet abscission in Phaseolus vulgaris. Am. Journ. Bot. 37, 1950: 650–656.
7. DIMOND, A. E. and WAGGONER, P. E.: The cause of epinastic symptoms in Fusarium wilt of tomatoes. Phytopathology 43, 1953: 663–669.
8. GAUCH, H. G. and DUGGER Jr., W. H.: The role of boron in the translocation of sucrose. Plant Physiol. 28, 1953: 457–466.
9. GAUR, H. and LEOPOLD, A. C.: The promotion of abscission by auxin. Plant Physiol. 30, 1955: 487.
10. GAWADI, A. G. and AVERY Jr., G. S.: Leaf abscission and the so-called "Abscission layer". Am. Journ. Bot. 37, 1950: 172–180.

11. HACCIUS, B. and NIES, H.: Über die Wirkung von 2,3,5-Trijodbenzoesäure und von 2,4,6-Trichlorphenoxyessigsäure auf die Abgliederung entspreiteter Blattstiele. Planta 47, 1956: 613–624.

12. HALL, W. C.: Studies on the origin of ethylene from plant tissues. Bot. Gazette 113, 1951: 55–65.

13. HEINICKE, A. J.: Concerning the shedding of flowers and fruits and other abscission phenomena in apples and pears. Proc. Am. Soc. Hort. Sci. 16, 1919: 76–83.

14. JACOBS, W. P.: Studies on abscission: The physiological basis of the abscission-speeding effect of intact leaves. Am. Journ. Bot. 42, 1955: 594–604.

15. JERMYN, M. A. and ISHERWOOD, F. A.: Changes in the cell wall of the pear during ripening. Biochem. Journ. 64, 1950: 123–132.

16. JOHNSON, F., ALLMENDINGER, D. F., MILLER, V. L. and POLLEY, D.: Fall application of boron sprays as a control for blossom blast and twig dieback of pears. Phytopathology 45, 1955: 110–114.

17. KIDD, F. and WEST, C.: Physiology of fruit. I. Changes in the respiratory activity of apples during their senescence at different temperatures. Proc. Royal Soc., London, Series B, 106, 1930: 93–109.

18. LAIBACH, F.: Über das Verblühen der Mohnblüte und seine Beeinflussbarkeit. Ztschr. f. Bot. 45, 1957: 123–144.

19. MITCHELL, J. W., DUGGER Jr., W. M. and GAUCH, H. G.: Increased translocation of plant-growth-modifying substances due to application of boron. Science 118, 1953: 354–355.

20. SACHER, J. A.: Relationship between auxin and membrane-integrity in tissue senescence and abscission. Science 125, 1957: 1199–1200.

21. SPURR, A. R.: Boron in morphogenesis of plant cell walls. Science 126, 1957: 78–80.

22. STEYER, G.: Über die Ursachen des vorzeitigen Abwurfes von Blütenteilen bei Coleus. Beiträge Biologie Pflanzen 31, 1957: 15–26.

23. TORSSELL, K.: Chemistry of arylboric acid VI. Effects of arylboric acids on wheat roots and the role of boron in plants. Physiol. Plantarum 9, 1956: 652–664.

24. WARNE, L. G. G.: Bud and flower dropping in Lupine. Journ. Royal Hort. Soc. 72, 1947: 193–195.

25. WENT, F. W. and CARTER, M.: Growth response of tomato plants to applied sucrose. Am. Journ. Bot. 35, 1948: 95–106.

26. WHITE-STEVENS, R. H.: Carbohydrate metabolism in relation to boron nutrition. Proc. Am. Soc. Hort. Sci. 36, 1938: 537–543.

27. WHITEMAN, T. M.: Sodium alpha-naphthyl acetate tests on life of cut flowers. Flor. Exchange 112, 1949: 16.

28. WILLIAMSON, C. E.: Ethylene, a metabolic product of diseased or injured plants. Phytopathology 40, 1950: 205–208.