J. AMER. SOC. HORT. SCI. 116(3):574-579. 1991.

Dwarf Flower Stalk in Onion: Characterization, Genetic Control, and Physiological Response to Ethephon and Gibberellic Acid

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Additional index words. scape, seed production, *Allium cepa*

Abstract. **Recently, a dwarf scape mutant was found in 'Autumn Beit-Alpha' onion *(Allium cepa* L.). The development of dwarf scape in onion, the genetic control of this attribute, and its response to external application of ethephon and GA_3 were studied. Data from segregating populations conclusively showed that a single recessive gene, designated *dw*, controls scape dwarfness in onions. Its expression is slightly modified by minor genes. Relatively slow growth and early cessation of cell elongation are the characteristics associated with scape dwarfness. A similar developmental pattern characterized emerging normal flower stalks treated with ethephon. GA_3 application at 50 ppm had no effect on scape elongation of dwarf plants. In each of 3 years, dwarf genotypes always produced scapes about half the length of normal ones. The marked expression stability of the *dw* gene will facilitate its introduction into onion cultivars. Providing there is no negative pleiotropic effect, the dwarfness gene is expected to reduce lodging and, thus, improve mechanical harvest of onion seed. Chemical names used: 2-chloroethyl phosphoric acid (ethephon), gibberellic acid (GA_3).**

Seed stalks of most onion cultivars reach a length of 1 to 2 m (Currah, 1981) and are prone to lodging. When this occurs, mechanical seed harvesting is obstructed, and yield losses are common. The introduction of genes restricting excessive scape elongation successfully controlled lodging in many crops (Hendrich et al., 1985; Hiroshi, 1972; Phinney, 1985; Pinthus and Levy, 1983). When a source for dwarf scape in onion was identified by H. Feldner in 'Autumn Beit Alpha' onion (Rabinowitch et al., 1984), a similar solution to scape lodging was considered. Our preliminary studies indicated that this type of dwarf scape is controlled by a single recessive gene, which we named *dw*. We also concluded that the expression of *dw* is modified by minor genes (Rabinowitch et al., 1984). In a complimentary work, Horobin (1986) crossed the same mutant with long-day 'Rijnsburger' onions and demonstrated a similar expression of the *dw* gene in a different genetic background.

Dwarfism in some barley mutants was attributed to low endogenous levels of gibberellins (Hiroshi, 1972; Reid and Potts, 1986), and in wheat genotypes, to a lack of sensitivity to gibberellins (Stoddart, 1984). Chemical treatments have been used to control .scape height and lodging in many crops. External application of gibberellic acid (GA_3) promoted stem elongation of many barley dwarf mutants (Phinney, 1985). In onions, GA_3 at 50 to 1000 ppm enhanced flowering of normal genotypes and improved seed yields, but had little effect on final length of seed stalks (Corgan and Montano, 1975; Loper and Wailer, 1982; Naamni et al., 1980; van Kampen and Wiebosch, 1970). Ethephon at 500 to 5000 ppm has been used to suppress scape elongation in onions and to reduce lodging (Corgan, 1975; Corgan and Izquiedro, 1979; Corgan and Montano, 1975; Levy et al., 1972). However, this treatment has never been adopted by seed producers as a standard procedure, possibly due to the potential of plant tissue damage by ethylene (Levy et al., 1972).

The present report provides detailed information on the development of dwarf scape in short-day onions, the genetic control of this characteristic, and the physiological response to external application of ethephon and of GA_3.

Materials and Methods

The spontaneous dwarf-scape mutant 'Autumn Beit-Alpha 52/1' is maintained by Hazera Seed Co., Haifa, Israel. The mutant was crossed with short-day 'Barletta' and ' Grano' onions and with 'Dehydrator #86'. The 'Grano' and 'Barletta' crosses were made using GA_3 as a gametocide (van der Meer and Van Bennekom, 1973). Pollination took place in small cages using flies as pollinators. The dwarf plant was the male parent in both cases. The third combination was produced using a male sterile line of 'Dehydrator #86'. No reciprocal crosses were made. Later, individual F_1 plants were selfed in small cages using flies as pollinators. The tested populations were grown either from seed or from bulbs, as detailed in the results, in an experimental plot at Beit Yitzhak (the Sharon Valley) that had been fumigated with 500 kg methyl bromide/ha. Standard agricultural practices for onion seed production were used throughout.

Upon emergence of the scape, plants were individually sprayed until runoff with either GA_3 (Berlex; Machteshim, Beer Sheva, Israel) at 50 ppm (Naamni et al., 1980) or ethephon (Agan, Ashdod, Israel; 48% active material) at 2500 ppm (Corgan and Montano, 1975; Levy et al., 1972), with addition of 0.1% surfactant. Ten plants were treated from each of the four cultivars and from each of the two F_1 populations.

The dates of scape emergence and flowering were recorded, and the length of scapes was measured two or three times a week, according to the rate of stalk elongation. Scape length was measured from the top of the bulbs (lst year) or from the

Received for publication 2 Feb. 1990. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked ***advertisement solely*** to indicate this fact.

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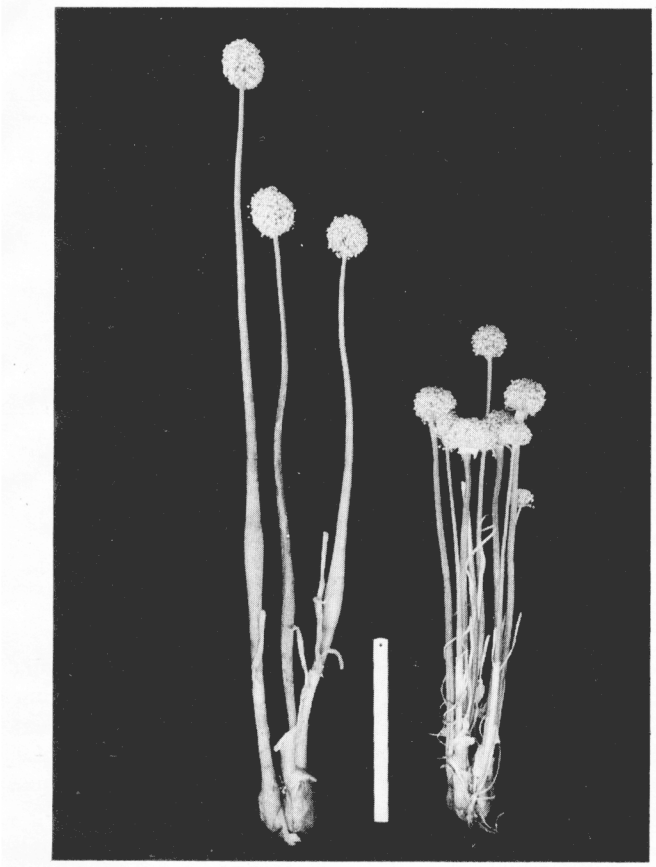


Fig. 1. Normal ('Dehydrator 86') and dwarf ('Autumn Beit Alpha 52/1') plants flowering from bulbs in the 2nd year of their development. The picture was taken July 1990. In the center there is a standard 30-cm ruler.

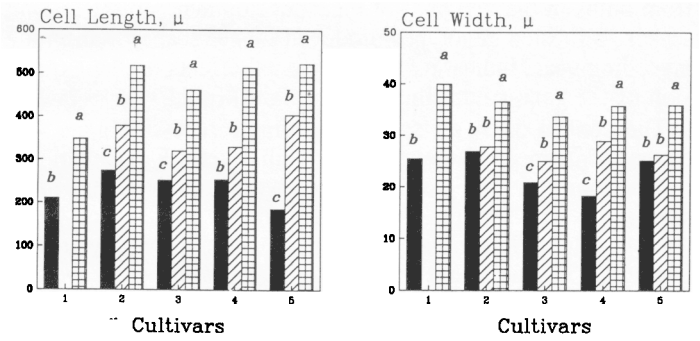


Fig. 2. Length **(left)** and width **(right)** of epidermal cells of normal and dwarf onion scapes at three stages of development. Observations were made on samples from both the top of the scape (just below the inflorescence) and the midheight region. Three scapes of each genotype were sampled at three stages of development: a) at the emergence of the stalk (■), b) stalks reached half of their estimated final length (❑) the end of the elongation phase (ES). Cultivars: 1 = 'Autumn Beit Alpha 52/1'; 2 = 'Dehydrator #86'; 3 = 'Barletta'; 4 = 'Grano'; 5 = F_1('Grano' × 'Autumn Beit Alpha 52/1').

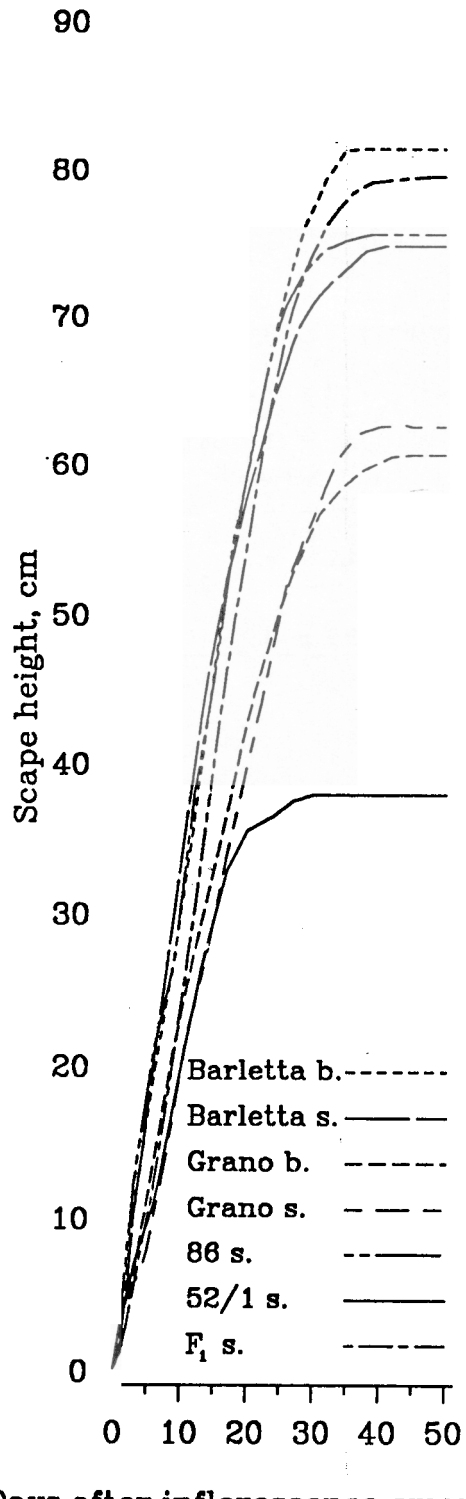


Fig. 3. Elongation rates of normal and dwarf onion flower scapes, 1982-83 season. The length of scapes was measured twice or three times a week, in accordance with the rate of stalk elongation. Measurements were taken from the top of the bulbs. For each plant, the tallest flower stalk was used throughout; b = plants grown from bulbs, s = plants grown from seeds.

soil surface (2nd and 3rd years) to the base of the umbel. Scape diameter was measured with a Vernier (PAV, Prazisions-Apparatebau-Aktiengesellschaft, Furstentum Liechtenstein) caliper at the widest zone of the stalk at the same frequency. After seed set was complete and no further increase in scape length could be noticed, the tallest flower stalk of each plant was selected for measurement.

Anatomical observations were made on tubular sections, 1.5 cm long, sampled from both the top of the scape just below the

Table 1. Final scape height of parental lines and of the F_1 and F_2 progenies for normal and dwarf onion plants.

Plant material	Scape length (cm; mean ± SE) Normal	Dwarf	No. plants Normal	Dwarf
	1st year			
Barletta[z]	81.3 ± 1.3	---	14	0
Barletta[y]	74.6 ± 4.4	---	14	0
Dehydrator #86[z]	75.4 ± 3.1	---	10	0
Beit Alpha 52/1[y]	---	35.8 ± 1.4	0	10
F_1 (Dehydrator #86 x Beit Alpha 52/1)[y]	79.4 ± 3.4	0	10	0
F_2 (Dehydrator #86 x Beit Alpha 52/1)[y]	73.0 ± 11.2	38.8 ± 7.2	54	19
F_2 (Barletta x Beit Alpha 52/1)[y]	72.1 ± 11.7	38.6 ± 7.0	47	19
	2nd year[z]			
Barletta	101.1 ± 2.6	---	10	0
Dehydrator #86	87.9 ± 3.9	---	10	0
Grano	84.1 ± 4.2	---	10	0
Beit Alpha 52/1	---	52.9 ± 2.8	0	10
F_1 (Grano x Beit Alpha 52/1)	95.9 ± 3.9	---	10	0

[z]From bulbs.
[y]From seeds.

Table 2. Segregation of F_2 populations extracted from individual self-pollinated F_1 populations between genotypes with normal and dwarf scapes. Plants were considered dwarf if the height of their scape was equal to or less than the mean value ± LSD unit of the 'Autumn Beit Alpha 52/1' plants grown concomitantly in the same experimental plot.

F_2 population	Progeny distribution Normal	Dwarf	χ^{2z}	Probability
	1st year[y]			
F_2 (Barletta x Dwarf)[x]	31	10	0.0008	$0.95 > P > 0.90$
F_2 (Barletta x Dwarf)[x]	33	11	0.0000	$P = 1.0$
F_2 (Grano x Dwarf)[x]	32	14	0.7200	$0.50 > P > 0.30$
F_2 (Grano x Dwarf)[x]	33	10	0.0690	$0.80 > P > 0.70$
F_2 (Grano x Dwarf)[w]	18	10	1.7080	$0.20 > P > 0.10$
	2nd year[v]			
F_2 (Grano x Dwarf)[x]	52	17	0.0048	$0.95 > P > 0.90$
F_2 (Grano x Dwarf)[x]	43	15	0.0229	$0.90 > P > 0.80$

[z]χ^2 distribution assuming a single gene for dwarfness.
[y]Mean height of 'Autumn Beit Alpha 52/1' plants was 35.2 cm, LSD = 11.9.
[x]From bulbs.
[w]From seeds.
[v]Mean height of 'Autumn Beit Alpha 52/1' plants was 52.9 cm, LSD = 8.4.

inflorescence and from the mid-height region. In the spring, individual scapes of each genotype were sampled at one of three development stages: a) at the emergence of the stalk, b) when stalks reached half of their estimated final length, and c) at the end of the elongation phase (see Fig. 3 for time reference). Similarly, samples were taken from plants treated with growth regulators. These tissues were preserved in lactic acid until they were needed for microscopic measurements. Then, the epidermal layer was stripped, and cell dimensions were measured without any staining.

Table 3. Length and width (microns) of epidermal cells sampled from midheight and top of normal and dwarf scapes.[z,y]

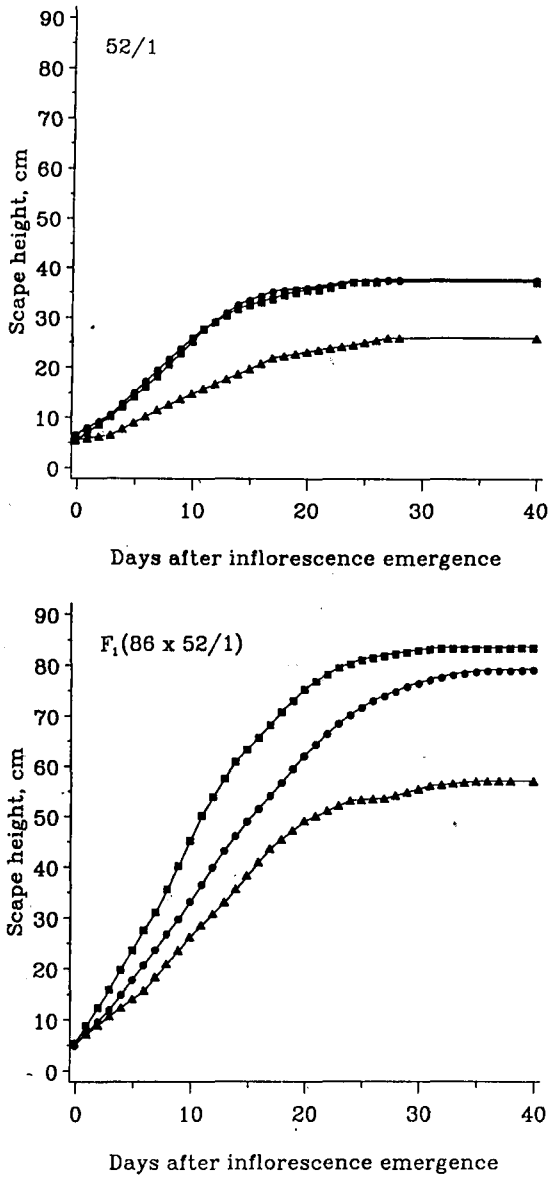
Genotype	Cell length Midheight	Top	Cell width Midheight	Top
Beit Alpha 52/1	329.9 at	366.0 av	39.1 as	40.8 ar
Barletta	446.7 ars	475.2 atu	37.2 as	30.2 bt
Dehydrator #86	508.7 ars	524.7 ast	41.8 as	31.2 bst
Grano	497.1 brs	574.2 arst	36.2 as	31.2 ast
F_1 (Grano x Beit Alpha)	437.5 bs	606.8 ar	39.4 as	32.2 bst
F_2 (Grano x Beit Alpha)[x]	331.7 bt	454.5 au	41.5 as	39.2 ar
F_2 (Grano x Beit Alpha)[w]	497.1 ar	540.9 astu	45.8 ar	37.0 brs

[z]a, b = For each dimension, within each row, mean separation at $P = 0.05$.
[y]r, s, t, u = Within each column, mean separation $P = 0.05$.
[x]Dwarf scape.
[w]Normal scape.

Results

The final height of the onion scapes of dwarf and normal plants could easily be distinguished in both years (Table 1, Fig. 1). Similar data were collected in a third season (data not shown). Whether grown from seeds or from bulbs, dwarf scapes of 'Autumn Beit Alpha 52/1' reached about half the length of those of normal genotypes. F_1 plants between 'Autumn Beit Alpha 52/1' and normal cultivars developed long scapes similar to those of the normal parent. The segregating F_2 populations could also be divided into two distinct groups in a 3 normal :1 dwarf scape ratio. Hence, it was concluded that dwarf onion scape is an inherited recessive trait, relatively stable under a variety of weather conditions (three seasons), and expressed in both bolting onions (flowering directly from seeds) and onions flowering from bulbs in the 2nd year of their development. In the second season, all tested genotypes produced longer scapes than in the preceding year, indicating environmental effects on the expression of the gene controlling scape height (Table 1).

The control of dwarf scape by a single recessive gene was further confirmed in an experiment with several F_2 populations. Seeds from various F_1 combinations were harvested and sown separately. The resulting bulbs were transplanted to the field. To guarantee 100% bolting, one F_2 population was seeded in September. Scape height was measured, as described above, for each F_2 plant within a cross. Each season, the mean value for 'Autumn Beit-Alpha 52/1' + LSD was used to define dwarfness (Table 2). Chi-square analyses of individual families supported the expected 3 normal: 1 dwarf ratio, indicating single recessive gene control of dwarfness. However, because of the relatively small size of each family, we further tested the validity of the null hypothesis, using three additional χ^2 tests: a) χ^2 test measuring the inconsistency of the deviations of the sample ratios from the hypothetical, i.e., the heterogeneity test, $\chi^2(n = 6) = 2.167$, $0.90 < P < 0.95$; b) the pooled value of χ^2 of the seven families was $\chi^2(n = 7) = 2.533$, $0.90 < P < 0.95$; and c) χ^2 calculated from the pooled data of the seven tested families was $\chi^2(n = 1) = 0.366$, $0.50 < P < 0.75$. These results emphasized the conformity of the progenies to the 3:1 ratio, confirming the earlier tentative conclusion that a single recessive gene, named *d w*$_l$ (Rabinowitch et al., 1984), controls dwarfness. The data also showed some variation in scape height within and between genotypes, thus suggesting a modifying effect of the general



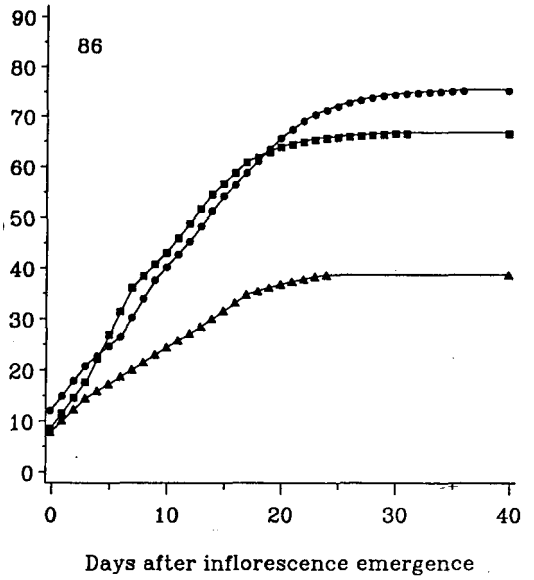


Fig. 4. Effect of GA_3 and ethephon on the development of 'Autumn Beit Alpha 52/1', 'Dehydrator #86', and F_1 hybrid onions between them, 1983–84 season. (●—●) Control, (■—■) GA_3, (▲—▲) ethephon. Each point is the mean of 10 readings. Experimental details as in Fig. 2.

genetic background on the expression of this attribute (Horobin, 1986; Rabinowitch et al., 1984).

There was a marked variation in scape diameter within each population (data not shown). No relationship between scape diameter and height and between time of emergence and height was apparent when plants with dwarf scapes were compared to plants with normal scapes in the two F_2 populations between 'Autumn Beit Alpha 52/1' and 'Barletta' and 'Grano', respectively (data not shown). We conclude, therefore, that the factor(s) controlling scape height have no effect on scape width or date of their emergence.

The size of the epidermal cells increased with scape growth, reaching a maximum when scapes reached their final size (Fig. 2). Cells were longer at the top and wider at the midheight section of the scape than the reverse (Table 3). GA_3 had no effect on the dimensions of the epidermal cells (data not shown). Cells of ethephon-treated normal plants and of the dw_1/dw_1 from F_2 populations segregating for dwarfness were significantly shorter than normal genotypes (78% and 84% of control scapes, respectively).

The fast linear phase of scape development continued for more than 30 days in the normal plants. In the dwarf type, it lasted only 20 days (Fig. 3). A single application of GA_3 at 50 ppm had little, if any, effect on rate of linear elongation or on final height. Two exceptions were noted, however. GA_3-treated F_1 hybrid plants between 'Dehydrator #86' and 'Autumn Beit-Alpha 52/1' grew significantly faster and were ≈10% taller than the nontreated controls (Fig. 4). Similar, but not significant, results were also obtained with bolting plants of 'Grano', but not with those that developed from bulbs (data not shown). These results indicate a possible interaction between gibberellin, genotype, and plant physiological age. These results require more investigation.

Ethephon treatment of normal genotypes caused both slower growth and early cessation of scape elongation, much like the pattern observed with the untreated dwarf genotype. Plants of 'Autumn Beit-Alpha 52/1' responded in a similar way, resulting in even shorter scapes (Figs. 4 and 5).

Discussion

Data from segregating populations, both in Israel and in England, conclusively show that a single recessive gene controls scape dwarfness in onions. We named this gene dw_1 (Rabinowitch et al., 1984). The main expression of this trait is slightly modified by the genetic background and is also affected

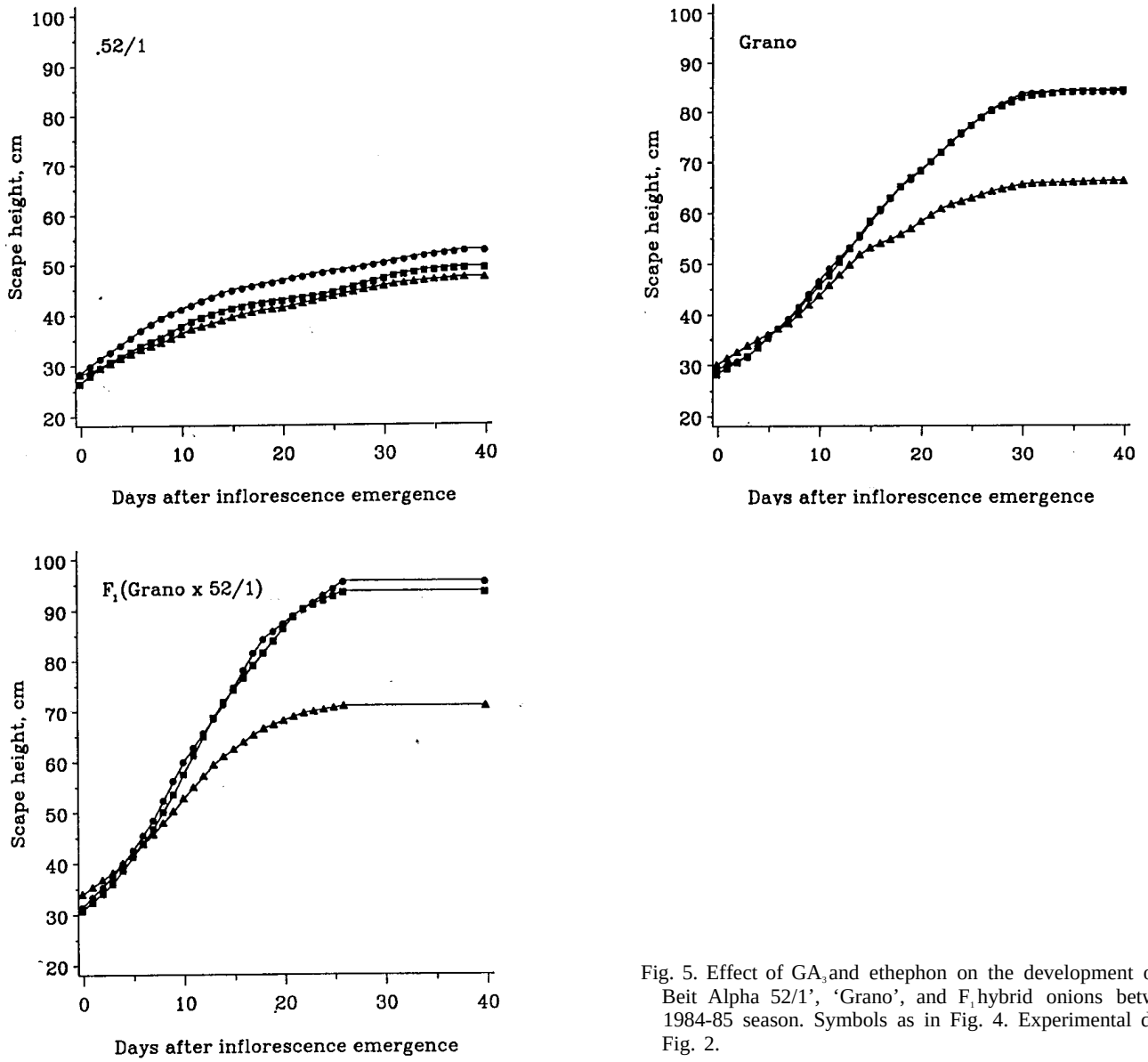


Fig. 5. Effect of GA_3 and ethephon on the development of 'Autumn Beit Alpha 52/1', 'Grano', and F_1 hybrid onions between them, 1984-85 season. Symbols as in Fig. 4. Experimental details as in Fig. 2.

by year-to-year variation. However, regardless of environment, dwarf genotypes always produce scapes about half the length of normal ones (Table 1, Figs. 3–5). Hence, this gene can be easily identified in segregating populations. Wherever lodging of seed stalks occurs, dw_1/dw_1 cultivars would allow more efficient mechanical harvesting and would reduce seed losses, providing there are no negative pleiotropic effects. Ethephon treatment did not cause a reduction in onion seed yield (Levy et al., 1972). Others showed negative effects of ethephon on seed yields, particularly for rates that produce very short scapes (Corgan, 1981).

Relatively slow growth (Fig. 2) and early cessation of cell elongation (Table 3) are the characteristics that can be directly linked. to scape dwarfness. Similar results were obtained when emerging normal flower stalks were treated with ethephon. These effects of ethylene on the rate of scape elongation and on final height, caused by early cessation of cell elongation, imply that this plant hormone may be involved in the regulation of scape height in dw_1/dw_1 plants. Ethylene has been shown to affect other growth processes in onion, such as bulbing (Levy et al., 1973), bolting (Izquierdo and Corgan, 1980), and senescence (Levy et al., 1972). No information is available on the endogenous changes in the concentration of this plant hormone during scape elongation and inflorescence development. To determine whether endogenous ethylene is involved in the expression of the dw_1 gene, the following need to be investigated: the exact timing of ethylene activity, as well as the possible direct or indirect interaction with other hormones, especially gibberellins, which are known to be antagonistic to a number of ethylene-regulated processes, such as sex expression in cucumbers (Rudich, 1985) and lycopenogenesis in tomatoes (Dostal and Leopold, 1967).

Gibberellin application had no significant effect on scape elongation of 'Autumn Beit-Alpha 52/1' dwarf plants, but partially affected those of some other genotypes, e.g., 'Grano' and F_1 ('Dehydrator #86' × 'Beit-Alpha 52/1'). This result may imply that dw_1/dw_1 plants lack sensitivity to gibberellin. However, since we tested only a single concentration of only one kind of gibberellic acid (GA_3), this conclusion may be premature. Further experiments on endogenous hormone levels and varietal differences are needed to better understand the physiology of scape elongation and its control.

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