The Effect of Irradiance, Defoliation, and Bulb Size on Flowering of *Nerine bowdenii* W. Watson (Amaryllidaceae)

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Abstract. Large *Nerine bowdenii* bulbs (>14 cm in circumference) were exposed to low light intensities for different periods during two successive growing seasons. The flowering percentage and number of florets in the current season's inflorescence were recorded at anthesis. Small and large bulbs were subjected to continual defoliation starting at different times during the growing season. Bulbs were dissected at planting (26 Sept. 1992) and on 12 Jan. 1993 (nondefoliated control bulbs) to determine growth and developmental stage. At anthesis, inflorescences were harvested and the florets per inflorescence were counted. After anthesis in the fall, all bulbs were dissected and the following variables recorded: 1) percentage flowering, quiescence, or abortion of the current season's inflorescence; 2) developmental stage of quiescent inflorescences; 3) number of florets in the outermost inflorescence; 4) developmental stage of the innermost inflorescence; 5) number of leaves or leaf bases in each growth unit; 6) number of daughter bulbs; and 7) dry weight of new leaf bases. There were three reasons for nonflowering of the bulbs, viz., failure to initiate an inflorescence, inflorescences remaining quiescent, and inflorescence abortion. Individual florets that had not reached stage "Late G" (gynoecium elongated, carpels fused) at the start of rapid inflorescence elongation aborted. The more florets that aborted, the greater the probability that the entire inflorescence aborted. The inflorescence was more vulnerable to stress during the first half of the growing season due to its relatively weak position in the hierarchy of sinks within the bulb.

Nerine bowdenii (Amaryllidaceae) is a fall flowering, synanthous, perennial bulbous plant indigenous to southern Africa (Du Plessis and Duncan, 1989). It is an excellent cut flower, but low flowering percentages severely limit its share in the market place (Berghoef and Van Brenk, 1983). According to Rees (1985), inflorescence initiation occurs regularly in bulbs 12 to 14 cm in circumference, and the low flowering percentages are due to the failure of inflorescences to elongate. A number of factors are responsible for nonflowering: storage above 2C (Sytsma, 1971), long storage at 2C, and storage at relative humidity below 80% (Van Leeuwen, 1988). Berghoef (1983), Rees (1985) and Van Brenk (1988) reported that the developmental stage of inflorescences was critical to achieve successful flowering. Large bulbs (>14 cm in circumference) have a higher flowering percentage than small bulbs (12 to 14 cm in circumference) (Best, 1985; Rees, 1985; Theron and Jacobs, 1992). Water stress or high soil temperatures before inflorescence elongation also reduced flowering (Best, 1985). Berghoef (1983) planted bulbs in the fall and found a decrease in flowering, which he attributed to low light intensities in winter.

Constant temperatures above and below 17C during the growing season reduced the percentage of plants that flowered (Berghoef and Van Brenk, 1983). At a constant temperature of 25C, the flowering percentage of the current season was not affected, but inflorescences contained fewer florets. Replanting these bulbs resulted in a greatly reduced flowering percentage in the next season.

In this paper we report on the effects of low light intensity stress and defoliation at different times during the growing season on the development and flowering of large and small bulbs of *N. bowdenii*.

Materials and Methods

Plant material. Bulbs from a commercial planting of *N. bowdenii* were used. They were grown in a shadehouse in the Elgin region in the western Cape (latitude 33°54'S). The Elgin climate is Mediterranean with cool, wet winters, and dry, hot summers. The average annual rainfall is about 1000 mm (Dept. of Agriculture and Water Supplies, 1989). Bulbs were stored at 2C for 3 months before planting in the fall. They were irrigated, fertilized, and treated for pests according to standard commercial practices.

Terminology. *Nerine* bulbs are composed of a series of growth units (Van Brenk and Benschop, 1993). A growth unit has a vegetative phase during which leaves are formed and a reproductive phase during which the apex is transformed into an inflorescence. At anthesis in the fall, there are more than three growth units per bulb. The oldest growth unit consists of the current season's inflorescence (N), which is subtended by leaf bases. The second growth unit is composed of a developing inflorescence (N+1). The N+1 inflorescence reaches anthesis the next fall, and is subtended by fully expanded leaves that senesce during winter. Developing inflorescence (N+2), subtended by young, unexpanded leaves, constitute the third growth unit. The leaves of growth unit N+2 expand after winter; whereas, the inflorescence N+2 reaches anthesis in the second fall. Two to three leaf primordia develop in the fourth growth unit (N+3) and the apex is vegetative (Theron and Jacobs, 1994a).

Irradiance studies 1991–92. A preliminary trial was conducted to establish the effect of reduced irradiance at different periods during the growing season on inflorescence abortion. Bulbs (> 14 cm in circumference), were planted on 26 Sept. 1991 at a density of 160 bulbs/m² in a 64% shadehouse. The irradiance inside the

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house was $440 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 1100 HR on a sunny day in late summer (20 Feb. 1992). A steel-framed cage (580 mm high $\times$ 620 mm wide $\times$ 1430 mm long), covered with dense shade cloth yielding $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at midday, was placed over the plants to induce a severe low-irradiance stress. The cage was left for a three-week period and then moved to another location. This was carried out nine times from 15 Oct. 1991 to 22 Apr. 1992. About 96 bulbs were covered each time. The cage was placed within the bed at random. The percentage of bulbs reaching anthesis was recorded during the normal flowering time.

Irradiance studies 1992–93. Bulbs (12 to 14 cm in circumference) were planted on 26 Sept. 1992 at a density of 120 bulbs/m² in a 30% shadehouse. The irradiance in the shadehouse was $1055 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 1100 HR on a sunny day in late summer (1 Feb. 1993). Steel-framed cages (580 mm high $\times$ 620 mm wide $\times$ 1430 mm long), covered with 70% shade cloth, were used to induce a low-irradiance stress. The light intensity inside a cage was $284 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant level. The treatments were as follows: 1) control, 2) shading from 6 Oct. 1992 (just before leaf emergence) until anthesis, 3) shading from 6 Oct. 1992 until 12 Jan. 1993, and 4) shading from 12 Jan. 1993 until anthesis. The four treatments were replicated four times in a randomized complete-block design. At anthesis, the percentage bulbs flowering and the number of florets per inflorescence were recorded.

Defoliation. Large (> 14 cm in circumference) and small (10 to 12 cm in circumference) bulbs were planted in a 30% shadehouse on 26 Sept. 1992 at a density of 160 bulbs/m². Plants were defoliated every 2 weeks starting 20 Oct. 1992, 1 Dec. 1992, 12 Jan. 1993, 23 Feb. 1993, and 6 Apr. 1993. Defoliation was done by cutting all leaves a few millimeters above the neck of the bulb with secateurs. Nondefoliated bulbs served as a control. The six treatments were replicated five times in a randomized complete-block design with 16 bulbs per treatment per block. Nondefoliated control bulbs of both size groups were sampled randomly at planting (35 bulbs) and on 12 Jan. 1993 (25 bulbs) for further

analysis. At planting, bulbs were sampled at random from the sorting table, and on 12 Jan. 1993 bulbs were removed (five per block) from buffer rows between the treatment rows. The following variables were recorded: 1) bulb circumference, 2) number and dry weight of leaf bases N, and 3) the outside dimensions and developmental stage of inflorescences N and N+1, according to the terminology proposed by Beyer (1942). At anthesis, the number of florets per inflorescence was counted. After anthesis, when leaf senescence started, all bulbs were lifted, and the following variables were recorded: 1) bulb circumference, 2) number of leaf bases N and N+1, 3) number of leaves N+2, 4) dry weight of leaf bases N and N+1, 5) outside dimensions and developmental stage of inflorescences N+1 and N+2, 6) number of daughter bulbs (without expanded leaves and roots), and 7) whether inflorescence N had reached anthesis, remained quiescent or aborted.

Data analysis. All data were analyzed using SAS's (SAS Institute, Cary, N.C.) General Linear Models procedure.

Results

Irradiance studies 1991–92. Bulbs were more sensitive to low-light-intensity stress during the first half of the new growing season than the second half (Fig. 1). Fewer bulbs flowered when plants were subjected to low-light-intensity stress for 3 weeks from 5 Nov. 1991 until 7 Jan. 1993. Shade applied during the first 3 weeks after the emergence of the leaves or after the end of January 1992, did not decrease the flowering percentage (Fig. 1).

Irradiance studies 1992–93. Shading during any period of growth reduced flowering percentage compared to the control (Table 1). Shading during the first half of the growing season produced only 33% of flowering bulbs compared to the 58% that flowered when shaded during the second half of the season. These results were comparable to those of the initial experiment (Fig. 1). The inflorescences contained about one floret less when shading was applied either continuously or during the second part of the

Fig. 1. Effect of reduced irradiance ($20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for 3-week periods during the growing season on flowering percentage of *Nerine bowdenii* (96 bulbs per treatment). Observations for periods 26 Nov.–17 Dec. and 28 Jan.–18 Feb. were lost due to bulb decay.

Table 1. Effect of reduced irradiance (284 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) on percentage of bulbs flowering and number of florets per inflorescence N of *Nerine bowdenii*.

Treatment	Percentage ^a bulbs flowering	No. of florets per inflorescence
Control	71 a ^a	8.3 a
Shade (6 Oct.–12 Jan)	33 c	8.6 a
Shade (6 Oct.–anthesis)	36 C	7.5 b
Shade (12 Jan.–anthesis)	58 b	7.8 b

^aLogit transformation performed.

^bMean separation by LSD ($P=0.05$).

growing season compared to shading during the first half of the growing season and the control (Table 1).

Morphology of large and small bulbs. The composition of large and small bulbs was determined on the date of planting (26 Sept. 1992) and 15 weeks after planting on 12 Jan. 1993 (Table 2). Dissection of the small bulbs revealed that about 42% did not contain the following year's inflorescence (N+1). Also the inflorescences N in small bulbs that did not contain inflorescence N+1 were less 'advanced'. Inflorescence N of large bulbs was more advanced in floret number than small bulbs. Differences in number of florets in inflorescence N were also reflected in the length of the inflorescence and the number of florets that had advanced to the stage "Mid G" (carpels elongated) and stage "Late G" (gynoecium elongated, carpels fused). At planting, 44% of the small bulbs without inflorescence N+1 had less than six florets in inflorescence N, 68% of the small bulbs containing inflorescence N+1 had eight or more florets in inflorescence N, and 17% of the large bulbs had less than nine florets in inflorescence N (data not presented).

At planting, the length of inflorescence N+1 in small bulbs was slightly shorter than in large bulbs (Table 2). By 12 Jan. 1993, this difference was pronounced. This difference was also reflected in the number of florets in inflorescence N+1.

In small bulbs without inflorescence N+1 it was impossible to distinguish clearly between growth units N+1 and N+2. Therefore, leafbases were considered to belong to unit N+1 and the unexpanded leaves to unit N+2. At planting, the number of leaves in growth unit N+1 was 5.1, 8.8, and 9.6 in small bulbs without inflorescence N+1, small bulbs with inflorescence N+1, and large bulbs respectively (Table 2). The leaf numbers in growth unit N+1 did not change during the season.

Effect of defoliation on the current season's inflorescence (N). Only 44% of the small, nondefoliated bulbs without inflorescence N+1 flowered. In bulbs that did not flower, inflorescence N remained quiescent and did not abort (Table 3). Quiescent inflorescences N in nondefoliated bulbs were comparable in appearance and developmental stage to inflorescence N+1 in small nondefoliated bulbs. Aborted inflorescences N appeared translucent and shrivelled. In contrast, small bulbs containing inflorescence N+1 had a flowering percentage of 65%. However, lack of flowering was mainly due to flower abortion (29%) and not to quiescent inflorescences. Most of the large, nondefoliated bulbs flowered (84%). Lack of flowering in large bulbs was due to flower abortion since no quiescence occurred in inflorescence N in large bulbs (Table 3). The developmental stage of quiescent inflorescences N depended on the date that the defoliation was initiated. Quiescent inflorescences in control bulbs were 1.6 mm long, contained 7.7 florets, and the oldest floret was at stage "Mid G". The earlier bulbs were defoliated, the smaller and less developed was the quiescent inflorescence N (Table 3).

Continual defoliation of small bulbs from 20 Oct. 1992 or 1 Dec. 1992 resulted in nonflowering small bulbs. All inflorescences aborted in bulbs containing inflorescence N+1. Whereas, in bulbs without inflorescence N+1, most inflorescences N aborted, with 7% and 29% remaining quiescent for the two dates respectively. In large bulbs, most of the inflorescences aborted, with only 8% and 18% reaching anthesis (for the two defoliation dates respectively). When the defoliation was delayed until 12 Jan., 23 Feb., and 6 Apr. 1993, flower abortion decreased with a concurrent

Table 2. Composition of small (10 to 12 cm in circumference) and large (>14 cm in circumference) bulbs of *Nerine bowdenii* sampled at planting (26 Sept. 1992) and on 12 Jan. 1993.

Sampling date	Inflorescence IV				Inflorescence N+1			
	Length (mm)	No. of			Length (mm)	No. of		
		Florets	Florets	Florets		Florets	Leaves	Bases
			at	at			N + 2	N + 1
			Mid G	Late G				
Small bulbs without inflorescence N + 1								
26 Sept. 1992	6.5	5.6	0.4	0	---		2.6	5.1
SE	0.56	0.28	0.16	0	---		0.45	---
12 Jan. 1993	10.0	7.1	1.3	2.1	---	---	6.1	5.1
SE	1.27	0.39	0.34	0.81	---		0.59	---
Small bulbs with inflorescence N + 1								
26 Sept. 1992	10.3	7.9	3.1	0	2.0	1.4	2.5	8.8
SE	0.37	0.17	0.20	0	0.23	0.33	0.26	0.26
12 Jan. 1993	15.5	8.8	2.0	5.3	3.6	4.1	5.1	8.8
SE	0.85	0.22	0.18	0.22	0.26	0.34	0.32	0.25
Large bulbs								
26 Sept. 1992	13.4	9.3	4.5	0	2.2	2.4	3.2	9.6
SE	0.24	0.13	0.13	0	0.08	0.12	0.13	0.18
12 Jan. 1993	19.6	10.2	2.8	6.4	5.2	5.1	6.7	9.6
SE	0.42	0.20	0.14	0.11	0.31	0.20	0.28	0.15

^aCurrent season's inflorescence (N), developing next season's inflorescence (N+1); carpels elongated (Mid G), gynoecium elongated, carpels fused (Late G).

increase of the inflorescences remaining quiescent in small bulbs without inflorescence N+ 1. The flowering percentage of these bulbs ranged from 11% to 16%. In small bulbs with inflorescence N+1 and in large bulbs, the flowering percentage increased and inflorescence abortion decreased with a delay in defoliation (Table 3).

Individual florets aborted when bulbs were defoliated. There was a linear increase in the number of aborted flowers in large bulbs with earlier initiation of defoliation (Table 4). At the time of planting, there were on average 9.3 florets in inflorescence N in large bulbs (Table 2). Small, nondefoliated bulbs had at anthesis 7.6 florets per inflorescence N, while those defoliated from 12 Jan. had 5.8 and those defoliated from 23 Feb. and 6 Apr. 1993 had 7.2 and 7.5, respectively (Table 4). At planting, the number of florets in small bulbs with and without inflorescence N+1 was 7.9 and 5.6, respectively (Table 2).

Effect of defoliation on the following year's inflorescence (N+1). Inflorescence N+1 did not abort following defoliation. Continual defoliation from 20 Oct. 1992, 1 Dec. 1992, and 12 Jan. 1993 delayed the initiation of florets. The number of florets in nondefoliated large and small bulbs was similar, at 8.9 and 8.8 florets, respectively. The number of florets was comparable to the floret number found in inflorescence N+ 1 when defoliation was delayed until 23 Feb. or 6 Apr. 1993 (Table 4). This implies that all the florets in inflorescence N+ 1 of nondefoliated bulbs had been formed by 23 Feb. 1993.

Effect of defoliation on growth cycle N+2. When the bulbs were dissected after anthesis, inflorescence N+2 in all nondefoliated

bulbs had advanced to stage Pr (first phase of floret initiation) (Table 5). There were 2.0 leaf primordia in unit N+3 in large and small bulbs with inflorescence N+ 1, and 2.3 primordia in small bulbs without inflorescence N+1 (data not presented). In large bulbs, 11.3 leaf primordia preceded inflorescence N+2, while in small bulbs containing inflorescence N+1 this was 10.8 (Table 6). At planting, growth unit N+2 of small bulbs without and in small bulbs with inflorescence N+1 and in large bulbs contained 2.6, 2.5, and 3.2 leaves, respectively. By 12 Jan. 1993, the number of leaves in growth unit N+2 had increased to 6.1, 5.1, and 6.7, respectively (Table 2). In small, nondefoliated bulbs without inflorescence N+1, there were 10.6 leaves in unit N+2 (Table 6). All bulbs defoliated late (23 Feb. or 6 Apr.) completed the vegetative unit N+2 with a full complement of leaves (about 10 to 11), and reproductive development had advanced to the Sp (spathe valve initiating) or Pr stage (Table 5). In bulbs defoliated from 6 Apr. 1993, growth unit N+3 in large and small bulbs (with and without inflorescence N+1) contained 0.5, 1.4, and 1.1 leaf primordia, respectively (data not presented). When bulbs had been defoliated earlier during the growing season, growth unit N+2 only had 5.4 to 8.6 leaves in small bulbs with inflorescence N+1, 8.8 to 10 in large bulbs, and 6 to 9.5 in small bulbs without inflorescence N+1 (Table 6) and they were still vegetative (Table 5). Only some of the bulbs defoliated from 12 Jan. had a reproductive apex at stage II. All the other bulbs were still vegetative (stage I) (Table 5).

Effect of defoliation on daughter bulbs. Defoliation reduced the number of daughter bulbs formed. The only exception was large

Table 3. Effect of defoliation on behavior of the current season's inflorescence N in small (10/12 cm, in circumference) and large bulbs (> 14cm, in circumference) of *Nerine bowdenii*.

Treatment ^y				Quiescent inflorescence N		Developmental ^z stage of oldest florets
	Percentage			Length (mm)	No. of florets	
	Flowering	Aborted	Quiescent			
<i>Small bulbs without inflorescence N + I</i>						
Control	44	0	56	1.6 ± 0.05 ^x	7.7 ± 0.14	Mid G
20 Oct.	0	93	7	0.6 ± 0	5.0 ± 0	P ₂
1 Dec.	0	71	29	0.8 ± 0.04	5.7 ± 0.40	A ₂
12 Jan.	14	72	14	0.9 ± 0	7.0 ± 0.99	A ₂ /Mid G
23 Feb.	16	34	50	1.0 ± 0.06	7.3 ± 0.41	Early G
6 Apr.	11	22	67	1.4 ± 0.11	8.4 ± 0.21	Mid G
<i>Small bulbs with inflorescence N + I</i>						
Control	65	29	6			
20 Oct.	0	100	0			
1 Dec.	0	100	0			
12 Jan.	7	93	0			
23 Feb.	59	41	0			
6 Apr.	73	27	0			
<i>Large bulbs</i>						
Control	84	16	0			
20 Oct.	8	92	0			
1 Dec.	18	82	0			
12 Jan.	48	52	0			
23 Feb.	88	12	0			
6 Apr.	83	17	0			

^xMid G= carpels elongated; Early G = gynoecium initiating, three carpel initials visible; A₂= second whorl of androecium initiating; P₂= second whorl of perianth initiating.

^yDate on which defoliation treatment was started.

^zSE

Table 4. Effect of defoliation on floret number in inflorescences N and N + 1 at anthesis in large (> 14 cm in circumference) and small bulbs (10 to 12 cm in circumference) of *Nerine bowdenii*.

Treatment	No. of florets per inflorescence			
	N		N + 1	
	L ^z	S ^y	L	S
Control ^x	8.9	7.6	8.9	8.8
20 Oct.	5.4	---	5.4	4.0
1 Dec.	6.6	---	6.1	4.4
12 Jan.	7.4	5.8	6.8	6.1
23 Feb.	8.4	7.2	8.0	7.6
6 Apr.	8.3	7.5	8.9	8.5
Contrasts ^w				
Control vs. rest	0.0020	---	0.0001	0.0001
Defoliate linear	0.0001	---	0.0001	0.0001
Defoliate quadratic	0.1849	---	0.1092	0.5627

^zBulbs (> 14 cm in circumference).

^yBulbs (10 to 12 cm in circumference).

^xDate on which defoliation was started.

^wSignificance level.

Table 5. Effect of defoliation on stage of development of inflorescence N + 2 in large (> 14 cm in circumference) and small (10 to 12 cm in circumference) bulbs of *Nerine bowdenii*.

Treatment ^y	Developmental stage of inflorescence N + 2 ^z		
	Large bulbs	Small bulbs	
		With inflorescence N + 1	Without inflorescence N + 1
Control	Pr	Pr	Pr
20 Oct.	I	I	I
1 Dec.	I	I	I
12 Jan.	I/II	I/II	II
23 Feb.	Sp	Sp	Sp
6 Apr.	Pr	Pr	Pr

Pr = florets initiating; Sp = spathe valves initiating; II= apex enlarging; I = apex vegetative.

^yDate on which defoliation treatment was started.

bulbs, with delayed defoliation until 6 Apr. 1993. No daughter bulbs formed when bulbs were defoliated on 20 Oct. or 1 Dec. 1992. When defoliation started on 12 Jan. 1993, only 0.3 and 0.4 daughter bulbs formed within small and large bulbs, respectively (Table 7).

Effect of defoliation on storage tissue. More leaf bases of growth unit N were present in defoliated bulbs (data not presented), but they weighed less than in control bulbs (Table 7). Leaf bases of growth unit N+1 failed to accumulate reserves in appreciable amounts. The dry weight of the leaf bases (N+ 1) in bulbs defoliated on 20 Oct. 1992 was 8% and 23% of the dry weight in nondefoliated control bulbs in small and large bulbs, respectively. When defoliation was delayed to 6 Apr. 1993, dry weights were only 54% and 66% of that of control bulbs in small and large bulbs, respectively. Smaller bulb diameter in defoliated bulbs also reflected the failure of the N+ 1 leaf bases to accumulate dry weight (Table 7).

Discussion

Failure to initiate an inflorescence. Small and large bulbs contained inflorescences N at the time of planting (Table 2). However, 42% of the small bulbs did not contain the following

year's inflorescence N+ 1. Therefore, nonflowering could be due to a bulb's failure to initiate an inflorescence. In bulbs dissected during this and previous studies, (Theron and Jacobs, 1994a, 1994b) six or more leaves were present before an inflorescence initiated. This result agrees with earlier reports (Rees, 1985). Therefore, a minimum of six leaves has to form before inflorescence initiation can take place. Small bulbs without inflorescence N+1 contained only 5.1 leaf bases in growth unit N+1. Thus, they failed to initiate inflorescence N+1 (Table 2). The factors for producing the small number of leaves in growth unit N+1 is unknown. Perhaps the plastochron was longer than the 1 month reported by Theron and Jacobs (1994a) and Van Brenk (1988). Therefore, fewer plastochrons occurred than required for inflorescence initiation during the previous growing season. A longer plastochron could be due to suboptimum environmental conditions and/or endogenous factors. Plants with an internal induction (self-induction) system often depend on the completion of a minimum number of plastochrons before inflorescence or flower initiation occurs, e.g., *Haemanthus katherinae* (now *Scadoxus multiflorus* subspecies *katherinae*) (Rees and Rünger, 1985) and tulip (De Hertogh et al., 1983).

At planting, growth unit N+2 had on average 2.5 and 3.2 leaf primordia in small and large bulbs, respectively, and an additional

Table 6. The effect of defoliation on the number of leaves in vegetative phase of growth unit N + 2 in large (> 14 cm in circumference) and small (10 to 12 cm in circumference) bulbs of *Nerine bowdenii*.

Treatment ^x	No. of leaves in growth unit N + 2		
	Large bulbs	Small bulbs	
		With inflorescence N + 1	Without inflorescence N + 1
Control	11.3	10.8	10.6
20 Oct.	8.8	5.4	6.0
1 Dec.	8.9	5.7	6.4
12 Jan.	10.0	8.6	9.5
23 Feb.	11.1	10.2	10.3
6 Apr.	11.3	10.3	10.5
Contrasts ^y			
Control vs. rest	0.0071	0.0001	0.0001
Defoliate linear	0.0001	0.0001	0.0001
Defoliate quadratic	0.8972	0.2207	0.0063

^xDate on which defoliation treatment was started.

Significance level.

eight leaves formed before an inflorescence was initiated (Tables 2 and 6). However, when bulbs were defoliated on 20 Oct. or 1 Dec. 1992, only three to five additional leaf primordia formed in small and large bulbs, respectively, and inflorescences were not initiated (Tables 2 and 6). When defoliation was delayed until 12 Jan. 1993, an additional six to seven leaf primordia formed after planting (Tables 2 and 6), and when the bulbs were harvested, half were reproductive (Table 5). It appears that, after planting, at least six new leaf primordia must form before inflorescences can be initiated. Van Brenk (1988) found that bulbs containing one leaf primordium at planting, and grown at 17C during the season formed an additional 6.5 primordia before the inflorescence was initiated. About eight additional leaf primordia initiated after planting when defoliation was delayed until 23 Feb. or 6 Apr. 1993 (Tables 2 and 6), and inflorescence differentiation had advanced to stages Sp and Pr for the 23 Feb. and 6 Apr. 1993 defoliation, respectively (Table 5). This was comparable to the development in nondefoliated control bulbs (Table 5 and 6). It is not clear why more than six additional leaves initiated before the apex became reproductive. Van Brenk (1988) found that when bulbs were exposed to 25C constantly during the growing season an additional 9.9 leaves formed before inflorescence initiation occurred. This was an additional three leaves compared to bulbs kept at a constant 17C. In *Scadoxus multiflorus* subspecies *katherinae*, an increase in the number of leaf initials was observed when bulbs were exposed to 25C after leaf senescence and inflorescence initiation did not occur (Peters, 1971). Easter lilies produce more leaves before flower initiation when grown at warmer temperatures (Lin and Wilkins, 1975). In carnation, flower initiation was delayed and more leaves were formed under low light intensities (Bunt and Cockshull, 1985). The planting in this study was grown under 30% shade, whereas, *N. bowdenii* usually grows in full sun (Du Plessis and Duncan, 1989). These data imply that two conditions must be met before inflorescence initiation commences. First, at least six additional leaves must initiate in the growing season and, second, the environmental conditions must be optimal, i.e., high light and favorable temperatures.

Quiescence of inflorescence N. No reports on the quiescence of inflorescence N exist (Van Brenk and Benschop, 1993). It was not observed either in large or in small bulbs containing inflorescence N+1, with the exception of one small bulb in the 22 bulbs dissected.

At planting, inflorescence N was less advanced in small bulbs without inflorescence N+1 than in either small bulbs containing inflorescence N+1 or in large bulbs. It was observed that inflorescence N had not yet completed the floret initiation phase and floret initiation continued after planting. There was an increase in the number of florets in inflorescence N when bulbs were dissected on 12 Jan. 1993 (Table 2). Theron and Jacobs (1994a) showed that the oldest floret in an inflorescence reached stage "Mid G" when about 7 to 8 florets had formed. At planting, large bulbs contained eight or more florets and no quiescence was observed. Small bulbs containing inflorescence N had six or more florets at planting and by 12 Jan. 1993 all bulbs contained eight or more florets. Only 6% of these bulbs contained a quiescent inflorescence. In contrast, at planting, 44% of small bulbs without inflorescence N+1 had less than six florets per inflorescence N, and on 12 Jan. 1993, and 5670 contained only six florets per inflorescence N (data not presented). These values correspond to the percentages of bulbs with quiescent inflorescences, i.e., 56% of nondefoliated control bulbs, 50% with defoliation on 23 Feb. 1993, and 67% with defoliation on 6 Apr. 1993 (Tables 2 and 3). The size, number, and developmental stage of florets in quiescent inflorescences N in small, nondefoliated bulbs were similar to that in inflorescence N+1 in bulbs containing this inflorescence (Tables 3 and 4). Therefore, when inflorescence N contains six or less florets at planting, the probability is high that it will remain quiescent and not develop to anthesis. This lack of development is probably due to the same conditions or factors that led to a slow development of growth cycle N+ 1, and this resulted in an insufficient number of leaves for reproductive development. Berghoef and Van Brenk (1983), reported high temperature stress during the growing season reduced flowering in the following season. The reduction was ascribed to in florescence abortion. However, bulbs were not dissected and quiescence of the in florescence may have occurred. After high temperature stress in the previous growing season, it is possible the inflorescences were underdeveloped at planting containing only five to six florets. The oldest floret was at stage A when the bulbs were replanted (Berghoef and Van Brenk, 1983).

Floret and inflorescence abortion. At anthesis, inflorescences from large bulbs contained fewer florets than at the time of planting or at 12 Jan. 1993. Individual florets in inflorescence N had aborted after planting and, more specifically, after 12 Jan. 1993 (Tables 2

and 4). Hartsema and Leupen (1942) found that up to 16 florets are initiated in *Amaryllis belladonna* L., but only 9 to 12 florets developed fully per inflorescence. Theron and Jacobs (1994a) found that advanced florets were arrested at stage "Mid G", while younger florets continue to develop to the same stage after planting. This synchronized the developmental stages of the individual florets in an inflorescence. The number of florets at either stage "Mid G" or "Late G" on 12 Jan. 1993 corresponded to the floret number in inflorescence N at anthesis (Tables 2 and 4). This suggests that under developed florets aborted. The probability of inflorescence abortion decreased with an increase in the number of florets per inflorescence at stage "Late G". Three factors support this conclusion. First, the large difference between the number of florets per inflorescence at planting and the number at anthesis decreased when defoliation was delayed. This indicates that progressively more florets had reached stage "Mid G" and "Late G", and in florescence abortion decreased. Second, the flowering percentage of nondefoliated bulbs (44%, 65%, and 84% in small bulbs without inflorescence N+1, with inflorescence N+1, and large bulbs, respectively) followed the trend of floret numbers at stage "Mid G" at planting (0.4, 3.1, and 4.5, respectively) and to the number of florets at stage "Late G" on 12 Jan. 1993 (2.1, 5.3, and 6.4, respectively) (Tables 2 and 3). Third, low light intensities during the early part of the growing season (until 12 Jan. 1993) resulted in many nonflowering bulbs (Table 1). Inflorescences with few florets at stage "Mid G" aborted. When low light intensities were applied during the later half of the growing season, the flowering was 57%, which indicates that more florets had reached stage "Late G". These in florescences contained fewer florets at anthesis indicating that florets were further advanced in their development when low light intensity stress was applied later in the season. This enhanced the sink strength, accounting for in florescences with fewer florets reaching anthesis. Since five florets was the minimum found in an inflorescence at anthesis (data not presented), this suggests that it is the minimum number required at stage "Late G" to support the growth of inflorescence N to anthesis.

Berghoef and Van Brenk (1983) exposed plants to a constant 25C during the entire growing season. They found a reduced floret number in inflorescence N, without increased inflorescence abor-

tion. This suggests that high temperature stress during the early part of the growing season was not as harmful as a low light intensity stress. At the time bulbs were replanted in spring, inflorescence N+1 contained fewer and less-developed florets compared to plants kept at a constant temperature of 17C. Most of the inflorescences at 25C did not reach anthesis. This also indicates that floret number and developmental stage determine the probability of anthesis (Berghoef and Van Brenk, 1983).

Hierarchy of plant sinks. During the growing season more than one sink is active in a *N. bowdenii* bulb at any one time. Since inflorescence N+1 does not abort, it is concluded that this inflorescence is a stronger sink than inflorescence N. Defoliation reduced the rate of floret initiation in inflorescence N+1 more than it reduced the rate of leaf primordia initiation in growth unit N+2 (Tables 2, 4, and 6). This implies that the formation of leaf primordia in growth unit N+2 is a stronger sink than floret initiation in inflorescence N+1. Defoliation reduced the number of daughter bulbs (Table 7). The number of daughter bulbs formed was comparable to daughter bulb number in nondefoliated bulbs only when defoliation was delayed until 6 Apr. 1993. Flower abortion was similar to that in control bulbs when defoliation was delayed until 23 Feb. 1993. Therefore, inflorescence N is a stronger sink than daughter bulbs (Tables 3 and 7). Dry weight (reserves) in leaf bases N+ 1 never reached the levels found in control bulbs, even when defoliation was delayed until 6 Apr. 1993. Thus, it appears that daughter bulbs are stronger sinks than mother bulb storage tissue (Table 7).

This study excluded roots. However, in apple trees, roots are just above storage tissue in the hierarchy of sinks (Wright, 1989). It is known that leaf development in growth unit N+ 1 is a sink, for a short period, thereafter, it becomes an exporter and source of carbohydrates (Theron and Jacobs, 1994b, 1995). If roots in *N. bowdenii* are comparable to the apple, the hierarchy of sinks is as follows: formation of leaf primordia N+2 > formation of floret primordia N+1 > inflorescence N > daughter bulbs > roots > storage tissue.

Berghoef and Van Brenk (1983) could not deduce from their study whether high temperatures during the growing season produced a reduced inflorescence development due to more leaf initiation, or if the reduced inflorescence development resulted in increased leaf initiation. In their study, the plastochron for leaf

Table 7. Effect of defoliation on number of daughter bulbs, bulb diameter, and dry weight of leaf bases N and N + 1 in *Nerine bowdenii*.

Treatment ^z	No. of daughter bulbs		Bulb diam (mm)		Dry wt of leaf bases			
					N		N + 1	
	L ^y	S ^x	L	S	L	S	L	S
Control	1.63	2.34	48.9	45.3	3.31	2.83	7.70	4.62
20 Oct.	0.02	0.00	41.3	33.4	2.27	1.12	1.79	0.37
1 Dec.	0.03	0.03	39.7	32.9	2.24	1.07	1.76	0.41
12 Jan.	0.38	0.30	41.2	36.0	2.30	1.68	2.27	1.07
23 Feb.	1.08	1.31	44.5	41.9	2.46	1.95	3.41	1.85
6 Apr.	1.80	1.67	47.0	42.7	2.86	2.18	5.09	2.48
Contrasts ^w								
Control vs. rest	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Defoliate linear	0.0001	0.0001	0.0001	0.0001	0.0003	0.0001	0.0001	0.0001
Defoliate quadratic	0.0128	0.5627	0.0001	0.0095	0.0200	0.6596	0.0082	0.0003

^zDate on which defoliation was started.

^yBulbs (>14 cm in circumference).

^xBulbs (10 to 12 cm in circumference).

^wSignificance level.

initiation in growth unit N+2 was not affected by high temperature, but the growth rate of inflorescence N+1 was severely reduced from planting until 120 days after planting. Afterwards it again increased. Therefore, inflorescence N+1 was affected negatively by 25°C, whereas, leaf initiation in growth unit N+2 was not (Van Brenk, 1988). This confirms the position of inflorescence N+1 relative to the formation of leaf primordia in the sink hierarchy of the *N. bowdenii* bulb.

In conclusion, the relatively low position of inflorescence N in the sink hierarchy of the bulb makes it vulnerable to stress conditions. Defoliation stress, low light intensities, water stress, and high soil temperature (Best, 1985), especially during the early part of the growing season, could produce high percentages of nonflowering bulbs.

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