Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

THE PHYSIOLOGY OF SPROUTING AND FLOWERING IN ONION BULBS: PHOTOPERIOD AND TEMPERATURE EFFECTS

D. S. Bertaud

Thesis submitted in partial fulfilment of the requirements for Master of Science in Plant Science, Massey University

February, 1988

Abstract

Onion bulb growth and development are affected by photoperiod, light quality and light interception. In short-days no bulbs are formed; in long-days large bulbs are formed, but take some time to mature; in very long-days small bulbs are formed and mature quickly. The effect of photoperiod depends on light quality; bulb growth is stimulated by far-red light. In conditions favourable to bulbing, sucrose and oligosaccharides accumulate in the bulb. Bulb growth and carbohydrate accumulation depend on current environmental conditions and cease if conditions are no longer favourable. High light intensity and leaf area enhance bulb growth.

Photoperiod and temperature effects on sprouting and floral development, and the effect of duration of chilling at 8°C on inflorescence development, were investigated in three cultivars of onion. The cultivars used were early maturing ('Sakigake Yellow'), midseason ('Gladalan Brown') and late maturing ('Early Long Keeper'). These cultivars were subjected to treatments comprising all combinations of two photoperiods (8 h and 14 h) and two constant temperatures (15°C and 20°C), except that 'Sakigake Yellow' was subjected to constant 8°C in 8 h days instead of 15°C and 14 h days. 'Sakigake Yellow' sprouted readily under all conditions except 8°C; 'Gladalan Brown' sprouted much faster in short-days than in long-days; and 'Early Long Keeper' sprouted poorly in all conditions. In long-days, some 'Gladalan Brown' plants showed evidence of remobilisation of assimilates, leading to growth of new bulbs within the original one, without growth of leaf blades.

'Early Long Keeper' plants were slow to develop roots as well as to sprout. Leaf appearance rates after sprouting were affected by photoperiod in 'Sakigake Yellow', and in 'Gladalan Brown' they were affected by both photoperiod and temperature. Rates were lower in long-days, and photoperiod had more effect at 15°C than at 20°C. It appears that bulbs of 'Sakigake Yellow' and 'Gladalan Brown' were ecodormant when planted, requiring only sufficient water to begin growth; however, leaf appearance in 'Sakigake Yellow', and both sprouting and leaf appearance in 'Gladalan Brown', showed a photomorphogenetic response to photoperiod. 'Early Long Keeper' bulbs were very slow to root and to sprout, indicating that they required more than the availability of water to begin growth, and were therefore not simply ecodormant when planted. The effects of duration of chilling at 8°C and subsequent photoperiod and temperature on floral initiation and development in three onion cultivars were investigated. Four weeks of chilling at 8°C followed by four weeks of growth at 15°C was sufficient for floral initiation in 'Gladalan Brown' and 'Early Long Keeper', but the bolting-resistant cultivar 'Sakigake Yellow' required eight weeks of chilling at 8°C followed by four weeks of growth at 15°C. With all cultivars, subsequent emergence of inflorescences was more rapid in 14 h days than in 8 h days, but at 20°C there was abortion of some inflorescences in 14 h days. Development of the emerged inflorescence to anthesis was also rapid in 14 h days, and faster at 20°C than at 15°C. There was apparent competition between leaf growth and inflorescence development in 8 h days, with resultant abortion of some inflorescences. At 15°C in 8 h days many of the inflorescences had bulbils or malformed florets in the inflorescence. Mature onion bulbs may be brought into flower in 35 weeks by sprouting them for 8 weeks in 15°C and 8 h days, followed sequentially by 8 weeks chilling at 8°C, 10 weeks at 15°C and 8 h days (until most plants have emerged inflorescences), and 8-10 weeks at 20°C in 14 h days. Knowledge of the responses of specific cultivars would allow the time to flowering from planting to be reduced further. Malformations occurring during floral development in unfavourable conditions are described; these are compared with floral development in *Allium cepa* var. *proliferum*. A conceptual model for dry weight partitioning in onion bulbs is described.

Keywords: photomorphogenesis, *Allium cepa* L., dormancy, bulb sprouting, inflorescence initiation, floral initiation, inflorescence development, floral development, light interception, phytochrome, red/far-red ratio, plant growth models.

ACKNOWLEDGEMENTS

My thanks to D. J. Woolley and I. J. Warrington, for supervision and many useful discussions; also to D. Grant, who supplied the onion bulbs; to G. Arnold, for help with the experimental design; to G. S. Wewala, for assistance with the statistical analysis; to M. Christensen, who identified the fungi growing on unhealthy plants; to K. G. McNaughton, D. Halford and B. Hayman, for help with the mathematical discussion; to C. J. Stanley, H. J. L. Coenders and J. P. de Boer, for help in keeping the plants alive; and to the Climate Laboratory Technical Services Group, who kept the equipment running.

Contents

		Abstra	ac	t.,	• •	• •		•	•		•	• •	•	·	•	• •	•	•	•	•	•	•	•		•	÷	•	•	•		ii
		Ackno	ow	ledg	eme	ents		•	•						•								•						•	•	v
2	Intr	oducti	io	n																											1
	1.1	REFE	ER	ENG	CE			•	•		•		•	•	•	• •	•		•	•	·	·		÷			÷	•	•	•	2
2	Oni	on phy	ys	iolo	gy																										3
	2.1	THE S	SI	RU	CTI	URE	0	F.	AN	1 (ON	IO	N	P	L.A	AN	T														3
	2.2	THE 1	Eł	FFE	CTS	S OI	r Li	IG	H7	r (ON	В	UJ	LB	I	10	ι.		•			•			•		•		•		6
		2.2.1	I	Phot	ope	riod	eff	ect	S		•		•	٠	•		•	•	•	•		•			•	•			•		6
		2.2.2	I	ligh	t qu	ality	r ef	fec	ts		•		•	•	•	• •					•	•			•	•	•	•			13
		2.2.3	I	ligh	t int	erce	pti	on	ef	fec	cts		•	•	•				•		•	•			•	•	•	•	•	·	15
		2.2.4	I	mpl	icati	ions	for	bı	u]}	o s	pro	out	in	g	•			•		•	•		•	٠	•	•	•	•	•		16
	2.3	FLOW	WE	CRIM	٢G			•	•				•		٠		•			•	٠						•	•			17
		2.3.1	I	nitia	atio	n an	d e	me	erg	en	ce																				17

		2.3.2 Development after emergence	18
	2.4	REFERENCES	19
3	Effe	ect of light quality and daylength	24
	3.1	INTRODUCTION	24
	3.2	MATERIALS AND METHODS	25
	3.3	RESULTS	27
	3.4	DISCUSSION	29
	3.5	REFERENCES	30
4	Spr	outing	32
	4.1	INTRODUCTION	32
	4.2	MATERIALS AND METHODS	33
	4.3	RESULTS	35
		4.3.1 Sprouting	35
		4.3.2 Leaf appearance	39
	4.4	DISCUSSION	42
		4.4.1 Sprouting	42
		4.4.2 Leaf appearance	46
	4.5	CONCLUSIONS	46
	4.6	REFERENCES	47

vii

5	Flov	vering		49
	5.1	INTRO	DDUCTION	49
	5.2	MATE	CRIALS AND METHODS	51
	5.3	RESU	LTS	54
		5.3.1	Floral initiation	54
		5.3.2	Inflorescence emergence	57
		5.3.3	Flowering	59
		5.3.4	Rate to emergence and from emergence to flowering \ldots .	60
		5.3.5	Seed production	64
	5.4	DISCU	JSSION	66
		5.4.1	Stage of floral development	67
		5.4.2	Rate to emergence and from emergence to flowering \ldots .	68
		5.4.3	Development of protocols for use in breeding programmes	69
6	Org	an dev	relopment	72
	6.1	INTRO	DDUCTION	72
	6.2	LEAF	DEVELOPMENT	73
	6.3	DEVE	LOPMENT OF THE INFLORESCENCE	74
		6.3.1	Long-days and warm temperatures	74
		6.3.2	Short-days and cool temperatures	78

viii

		6.3.3	Long-days and cool temperatures	79
		6.3.4	'Tree onions'	79
	6.4	DISCU	USSION	36
		6.4.1	Leaf development	36
		6.4.2	Floral development	86
	6.5	REFE	RENCES	87
7	Moo	delling	onion growth 8	9
	7.1	INTRO	ODUCTION 8	39
	7.2	ONIO	NS: THE PHYSIOLOGICAL PROBLEM	0
	7.3	RELA	TIONSHIPS BETWEEN MATHEMATICAL MODELS 9	92
		7.3.1	Stochastic models	92
		7.3.2	Size density distributions	93
		7.3.3	Deterministic models	94
		7.3.4	Compartment models	94
		7.3.5	Models involving environmental forcing functions 9	95
	7.4	A DES	SCRIPTIVE DRY WEIGHT MODEL	99
		7.4.1	Growth of individual bulbs 10)0
		7.4.2	Discussion)1
		7.4.3	Leaf initiation - a term for the apex)2

10.

ix

		7.4.4	Leaf appearance and death	104
		7.4.5	Flowering	106
	7.5	A MO	DEL USING FORCING FUNCTIONS	108
		7.5.1	Introduction	108
		7.5.2	A compartment model for an onion plant	108
		7.5.3	Bulbing	109
		7.5.4	Sprouting and floral initiation	113
		7.5.5	Discussion	114
		7.5.6	References	117
8	Con	clusio	ns	120
	8.1	Onion	physiology	120
	8.2	Develo	opment of protocols for use in breeding programmes	121
	App	oendix	: Statistical methods used in data analysis	123
	A.1	ANAI	YSIS OF UNBALANCED DATA	123
		A.1.1	Generalised linear models	123
	A.2	ANAI	YSIS OF CATEGORISED DATA	124
		A.2.1	χ^2 tests for homogeneity	124
		A.2.2	Generalised linear models	124

х

List of Figures

2.1	Schematic drawing of an onion plant, showing growth habit \ldots .	5
2.2	Schematic drawing of the inflorescence on an onion plant	7
2.3	Effect of photoperiod on onion bulbs	8
2.4	Leaves from an onion transferred from long to short-days \ldots .	11
2.5	Leaf from an onion transferred from short to long-days	12
2.6	Effect of light quality on sugars	14
4.1	Cumulative relative frequency of times to sprouting for 'Sakigake Yellow'	36
4.2	Cumulative relative frequency of times to sprouting for 'Gladalan Brown'	37
4.3	'Gladalan Brown' bulbs in 20°C and 14 h days. Note swelling and splitting of unsprouted bulbs	38
4.4	Mean leaf number per shoot with time for 'Sakigake Yellow'	40
4.5	Mean leaf number per shoot with time for 'Gladalan Brown'	41
5.1	Flow chart of protocol for flowering experiment	52

5.2	Effect of duration of chilling on (a) rate to inflorescence emergence and (b) rate to flowering for cultivar 'Early Long Keeper'	61
5.3	Effect of duration of chilling on (a) rate to inflorescence emergence and (b) rate to flowering for cultivar 'Gladalan Brown'	62
5.4	Effect of duration of chilling on (a) rate to inflorescence emergence and (b) rate to flowering for cultivar 'Sakigake Yellow'	63
5.5	Cage for pollinating onion flowers with blowflies	65
6.1	Leaf of plant transferred from short-days to long-days	75
6.2	Leaves from a plant transferred from long-days to short-days \ldots .	75
6.3	Abortion of inflorescences in long-days	76
6.4	Bulbil produced in inflorescence in long-days	76
6.5	Spathe of plant transferred to long-days	77
6.6	Spathe of plant developing in short-days	80
6.7	Deformed pedicels produced in cool short-days	80
6.8	Bulbils formed in cool short-days	81
6.9	Abnormal florets produced in cool short-days	81
6.10	Three inflorescences on one shoot in cool short-days	82
6.11	Leaf with multiple blades produced in cool short-days	83
6.12	Fasciated inflorescence produced in cool short-days	84
6.13	Bulb-inflorescence formed in cool long-days	84

xii

6.14	Inflorescence of Allium cepa var. proliferum	85
7.1	Compartment model for onion leaf	96
7.2	Section through apex of onion	103
7.3	Leaves appear through a hole at the top of the sheath of the previous leaf	105
7.4	The reproductive apex	107
7.5	Compartment model for onion plant	110
7.6	Compartment model for onion plant undergoing reproductive development	115
A.1	Contingency table for sprouting data in Chapter 3	125

xiii

List of Tables

3.1	Numbers of bulbs of each cultivar per treatment	26
3.2	Effect of light quality and photoperiod on sprouting of four onion cultivars	28
3.3	Effect of light quality and photoperiod on time to emergence of inflo- rescences, measured from the end of chilling at 8°C	29
4.1	Development details for onion bulbs used in this study \ldots .	34
5.1	Effect of chilling on stage of floral development	56
5.2	Effect of subsequent temperature on manifestation of effect of chilling duration	57
5.3	Effect of photoperiod on stage of floral development at 15°C	58
5.4	Effect of temperature on stage of floral development in 14 h days	59