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5. IMPERATA CYLINDRICA (L.) BEAUV

5.i. Introduction

I. cylindrica variously known as lalang, cogon grass or spear grass is a widespread perennial particularly serious as a weed of rubber in Malaysia. There have, however, been few studies of its growth or of the rhizome system. The underground rhizomes branch freely and terminate in a very sharp structure of scale leaves which enclose the apex. Nodes occur at varying intervals along the rhizome, being two or three cm apart on mature sections. In pots, branching is observed to occur most frequently in the region of an apex which has begun to ascend vertically to form an aerial shoot.

Work on the regeneration of rhizome fragments has been recently conducted by Soerjani and Soemarwoto (1969). Rhizome which was collected in Indonesia was found to possess buds at every node in the region of the apex. Rhizome diameter and the position of the bud on the prepared fragment were factors found to have little or no influence on regeneration. Bud colour, considered an indication of age, was associated with the capacity of fragments to regenerate. Fragments with white buds germinated much better than those with dark brown buds, the latter presumed to be the older. Size also had an effect. While fragments 1 cm long regenerated well, fragments only 0.5 cm gave much poorer results. The resulting shoot length was found to be linearly related to the length of fragment; the longer the fragment, the longer the shoot.

These workers found light to stimulate bud germination but the increase over dark controls was only statistically significant ($P=0.05$) when fragments were placed with the bud facing the light. When the buds were placed facing downwards buried in the supporting agar media, a reduced regeneration resulted.

I. cylindrica may spread by seed. Santiago (1965) reports that 95% germination is possible for seed within a week of harvest. However, viability is retained for less than a year.

Work at WRO has been concerned with rhizome regeneration. Various factors thought likely to influence regeneration were studied. Preliminary studies concerned effects of substrate, fragment type, fragment size, season and the temperature at which stock plants were grown. The effects of season and plant age were assessed in an experiment of comparable design to that used for the other species.

5.ii. Preliminary studies on regeneration

Methods

A clone was established from rhizome material originally obtained from Malaysia. Stock plants for the experiments were produced by dividing existing plants using large portions of the rhizome system with attached aerial shoots. These portions were potted into John Innes potting (J.I.P.) compost No. 2 using 15 and 25 cm diameter pots for young and old plants respectively. The stock plants were grown at 21°C for a preliminary period to encourage rhizome production after which some were transferred to a lower temperature of 10°C. The dates of potting and the duration of the temperature periods are shown in Table IX. Where experiments did not involve comparisons of stock plant treatments the material was obtained from mature plants grown at 21°C.

Except for an initial experiment comparing fragment sizes, all fragments were 9 cm long and consisted either of a 9 cm length with an apex

Table IX

Treatment of I. cylindrica stock plants

Time of potting	Months of growth at 21^{o}C min	Months of growth at 10^{o}C min	Description of material	Date of experiment
Oct. 1965	8	0	Old - warm	June 1966
	4	4	Old - cool	
Oct. 1965	12	0	Old - warm	Nov. 1966
June 1966	5	0	Young - warm	
Oct. 1965	16	0	Old - warm	Feb. 1967
Oct. 1965	4	12	Old - cool	
Nov. 1966	4	0	Young - warm	
Oct. 1965	21	0	Old - warm	July 1967
Oct. 1965	4	17	Old - cool	
Feb. 1967	5	0	Young - warm	

(apical fragments) or a 9 cm length taken 9 cm back from the apex (sub-apical fragments).

The fragments were planted 1.25 cm deep in 9.0 cm pots and placed in a glasshouse at 21^{o}C minimum temperature. There were 10-15 fragments per treatment.

Results

In an initial experiment comparing one and two-node fragments (3 and 5 cm long) planted in October 1965 using JIP compost, all fragments failed to regenerate and succumbed to rotting. Larger fragments up to 15 cm taken in January 1966 grew and produced a variable number of shoots: of these fragment sizes, a length of about 9 cm was the smallest to regenerate well and provided the best opportunities for utilising the limited amount of material then available.

Substrate, fragment type, and the condition of the stock plant were investigated initially in a 2 x 2 x 2 factorial experiment in June 1966. The substrate type was the principal factor of interest at this stage. The results are shown in Table X.

The substrate type did not affect the number of pots in which plants were established.

Sand was included with the object of reducing the possibility of rotting but this did not appear an important factor. The greatest shoot number after 30 days occurred with JIP compost and the difference between sand and JIP had increased at 60 days when JIP had almost twice as many shoots as sand.

Apical fragments established much better than sub-apical fragments and produced approximately three times as many shoots.

There were only small differences due to stock plant temperature conditions, with the "warm" plants giving rise to approximately one third more shoots than "cool" plants. These differences were not significant.

Table X

Effects of substrate, fragment type and stock plant condition on the regeneration of <u>I. cylindrica</u>

(three fragments per pot, five replicate pots per treatment)

		Sand				J.I.P.			
		Number of pots with plants established		Total shoot numbers per treatment		Number of pots with plants established		Total shoot number per treatment	
Number of days from planting		30	60	30*	60⁄	30	60	30*	60⁄
Stock plants cool	Apical fragments	5	5	13	19	4	4	16	26
	Sub-apical fragments	1	3	2	5	2	3	4	9
Stock plants warm	Apical fragments	5	5	10	16	5	5	15	40
	Sub-apical fragments	3	3	5	7	4	4	6	16

* L.S.D. = 8.0 (P = 0.05)
⁄ L.S.D. = 9.0 (P = 0.05)

Apical and sub-apical fragments taken from stock plants of two ages, twelve and five months' old established in 25 cm and 15 cm diameter pots respectively were planted in November 1966 in J.I.P. compost. The results are shown in Table XI. Establishment was generally poor. Shoot numbers were low and showed a decrease from thirty to sixty days after planting. Many fragments rotted and root production on those fragments which survived was poor. The use of apical fragments again led to increased survival.

With old rhizome, apical fragments proved best, while all sub-apical fragments rotted. With young rhizome material apical fragments were poorer than sub-apical fragments.

The effects of stock plant age were not significant.

A factorial experiment involving apical and sub-apical fragments and three stock plant treatments was conducted in both the winter and in the summer to measure the effect of season on establishment, and on any interaction with the other factors. The results of the experiment which was non-orthogonal with respect to stock plant age and temperature treatments are shown in Table XII.

Of the main effects, fragment type proved the most important with apical fragments giving both increased regeneration and shoot production. The overall percentage of fragments regenerating was 78% and 23% for apical and sub-apical fragments respectively.

Table XI

Effects of stock plant age and fragment type on the regeneration of I. cylindrica

(two fragments per pot, 10 replicate pots per treatment)

	Old plants				Young plants			
	Number of pots with plants established		Total shoot numbers per treatment		Number of pots with plants established		Total shoot numbers per treatment	
Number of days from planting	30	60	30*	60⁄	30	60	30*	60⁄
Apical fragments	8	7	10	7	3	2	3	3
Sub-apical fragments	0	0	0	0	5	5	7	8

* L.S.D. = 5.6 (P = 0.05)

⁄ L.S.D. = 6.2 (P = 0.05)

Season had a significant effect on aerial shoot numbers only, with summer production being more than double that of the winter.

Differences due to stock plant condition were not significant, although there were interactions with the other factors. During the summer sub-apical fragments gave a much reduced percentage regeneration and a low shoot number compared with apical fragments. Differences in the winter were small.

Table XII

Effects of season, fragment type and stock plant condition on the regeneration of I. cylindrica

(one fragment per pot, 10 replicate pots per treatment)

Stock plant condition	Winter (Feb. 1967)				Summer (July 1967)			
	Apical fragments		Sub-apical fragments		Apical fragments		Sub-apical fragments	
	*i	*ii	i	ii	i	ii	i	ii
Old - cool	100	10	0	0	90	19	10	1
Old - warm	40	4	0	0	90	23	40	7
Young - warm	60	6	70	7	90	15	20	3

* i % of fragments regeneration. L.S.D. = 32% (P = 0.05)

* ii total shoot number per treatment. L.S.D. = 7.5 (P = 0.05)

Season had a significant effect on aerial shoot numbers only, with summer production being more than double that of the winter.

Differences due to stock plant condition were not significant, although there were interactions with the other factors. During the summer sub-apical fragments gave a much reduced percentage regeneration and a low shoot number compared with apical fragments. Differences in the winter were small.

There were only small differences resulting from the temperature treatment of old stock material with fragments planted in the summer, when the "warm" material did best. In the winter differences were greater and the "cool" material was the most satisfactory. Again all sub-apical fragments taken from both the old stock treatments completely failed to grow in the winter.

A small experiment in June 1966 compared establishment of rhizome fragments possessing an aerial shoot with that of apical and sub-apical fragments without such shoots. Eighteen days after planting, the original shoot, which had begun in most cases to die, was cut off leaving new shoots to develop. Establishment of such material was good, (Table XIII).

Table XIII

Effects of shoot retention on establishment of <u>I. cylindrica</u> rhizome fragments

(15 fragments per treatment)

Fragment type	Percentage of fragments regenerating	Mean shoot number per fragment planted
Apical fragments plus aerial shoot	100	3.5
Apical fragment minus aerial shoot	60	0.7
Sub-apical fragment minus aerial shoot	30	0.3

5.iii. <u>Effects of season and plant age on rhizome production and reproductive potential</u>

<u>Methods</u>

The methods of culture and design of the experiment were identical to those used for the other species apart from some differences in the method of fragment preparation and the assessment of rhizome growth and regeneration. Apical fragments 9.0 cm in length were used exclusively in testing regeneration and for the establishment of the stock plants. As the number of nodes on the rhizome was unrelated to the number of fragments obtainable from the plant this measure was not obtained when the rhizome was being assessed.

Results

The production of rhizome by I. cylindrica appears to be largely influenced by season. Data presented in Table XIV shows that there were fluctuations in the amount of rhizome, in both length and weight, which can be related to seasonal conditions. Except in the case of the June planting rhizome length reached a peak in September. There then followed a decline from September to December after which the amount of rhizome increased.

The most favourable three-month period for rhizome growth depended somewhat on the time of planting (Table XV). Overall, June to September was most favourable while conditions between September and December were associated with a decline in the amount of rhizome.

The amount of aerial growth increased steadily with the age of the plant. The rhizome/aerial shoot weight ratio was seasonally dependant, being highest for June assessments and falling to a low level in December. The percentage of rhizome by weight was high compared to other species, the mean value for all treatments being 28.6%.

Regrowth of rhizome fragments was not found to occur readily on fibre-glass in the dark and so comparable tests were conducted also:

a) on fibre-glass in the light;

b) in pots in the light;

c) in pots in the dark.

Fragments in pots (9.0 cm diameter) were inserted vertically, with the apex exposed in J.I. compost and were sub-irrigated by standing on fibre-glass. Due to slowness of growth a 40-days assessment period was used. Fragments tested were from plants of three ages. In all cases, fragment placed in the light in the glasshouse showed improved regeneration over those placed in the dark (Table XVI). In the glasshouse the fibre-glass technique gave better regeneration than pots. (The mean percentage regeneration improved also with plant age, from 32% for three months, to 39% for six, and 66% for nine month old plants). Any further tests were therefore conducted in the light on fibre-glass.

Results of the three-monthly assessments of regeneration are shown in Fig. 4. Regeneration showed a tendency to improve during the summer months and to decline in mid-winter. June-planted material however, did not follow this pattern. The number of apical fragments available was variable and not consistently related either to age or season. Regeneration was not related to rhizome weight per unit length.

5.iv. Conclusions

Preliminary experiments have established that fragment type is one of the most important factors influencing regeneration. Apical fragments regenerate better than sub-apical fragments of comparable length from mature plants (8 - 12 months old). For younger plants (4 months old) apical fragments are best in the summer whilst sub-apical fragments give the best results in the winter.

Regeneration is benefited in the winter if stock plants are grown at a 10°C minimum temperature instead of 21°C. This may be a result of reducing the depletion of carbohydrate reserves. There is no advantage accruing from such treatment in the summer.

Table XIV

Rhizome and aerial shoot productivity of <u>I. cylindrica</u>

(data are means of three plants)

Month of planting	Plant age in months	Month of assess-ment	Rhizome length (cm/plt)	Rhizome fresh weight (g/plt)	Aerial shoot fresh weight (g/plt)	Rhizome fresh weight per cm length (mg)	Rhizome/shoot fresh weight ratio	Rhizome as a % by weight of rhizome plus aerial shoot
Sept. 1967	3	Dec.	46	3	7	61	0.39	30.0
	6	March	559	35	45	63	0.79	39.9
	9	June	2060	182	285	88	0.64	39.0
	12	Sept.	2463	160	349	65	0.46	31.4
Dec. 1967	3	March	54	1	3	26	0.47	25.0
	6	June	981	92	135	94	0.68	40.5
	9	Sept.	1896	133	376	70	0.35	26.1
	12	Dec.	1585	109	544	68	0.20	16.7
March 1968	3	June	574	50	61	87	0.81	45.1
	6	Sept.	2302	140	287	61	0.49	32.8
	9	Dec.	1368	104	441	76	0.24	24.0
	12	March	1445	84	391	58	0.22	17.7
June 1968	3	Sept.	678	36	97	53	0.37	27.1
	6	Dec.	625	24	199	38	0.12	10.8
	9	March	1445	67	252	46	0.26	21.0
	12	June	1734	157	361	90	0.43	30.3

Table XV

Increments in rhizome length of I. cylindrica during three-monthly periods of growth

(data are means of three plants)

Period of growth	Month of planting				Total
	September	December	March	June	
	Length in cm/plant				
September - December	46	-311	-934	-53	-1252
December - March	513	54	77	820	1464
March - June	1501	927	574	289	3291
June - September	403	915	1728	678	3724

Table XVI

The influence of incubation environment on the regeneration of 9.0 cm apical rhizome fragments of I. cylindrica

(means of three plants)

Age of parent plant in months	Environment	Mean fragment number tested	Number of fragments regenerating roots and shoots		% of fragments regenerating roots and shoots	
			20 days	40 days	20 days	40 days
3	Pots:					
	GH	5.7	1.7	2.0	30	35
	C.E.R.	5.7	0.7	0.7	12	12
	Fibre-glass:					
	GH	5.3	2.7	4.3	51	81
	C.E.R.	6.0	0	0	0	0
6	Pots:					
	GH	8.0	3.3	4.0	41	50
	C.E.R.	8.0	1.3	1.3	16	16
	Fibre-glass:					
	GH	7.7	4.0	4.3	52	56
	C.E.R.	8.0	1.7	2.7	21	34
9	Pots:					
	GH	19.3	12.7	14.7	66	76
	C.E.R.	19.3	4.0	4.7	21	24
	Fibre-glass:					
	GH	19.7	17.3	18.7	88	95
	C.E.R.	19.7	10.0	13.0	51	66

GH = glasshouse (20 - 27°C)

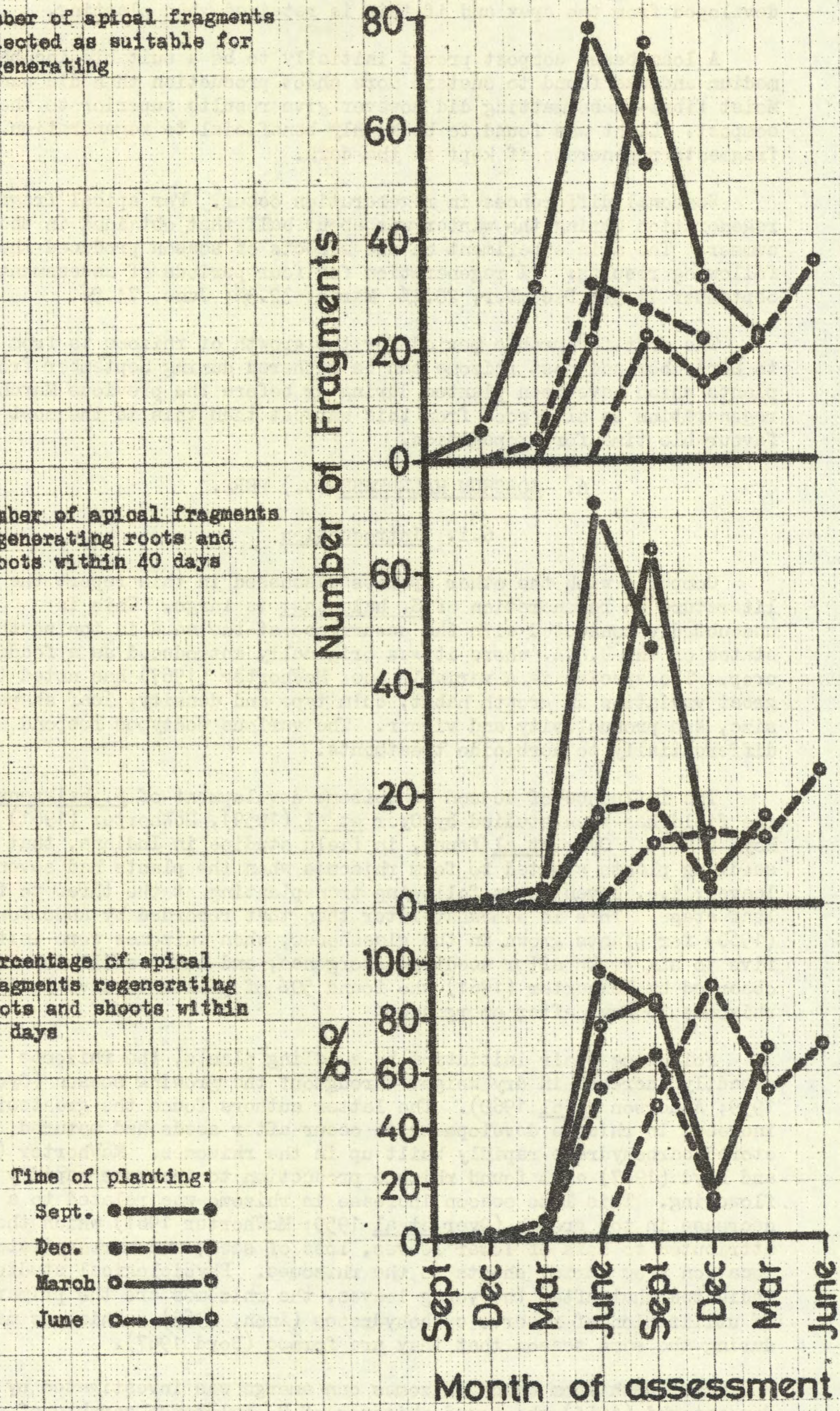
C.E.R. = dark constant environment room (23°C)

Fig. 4. Reproductive potential of rhizome of Imperata cylindrica

a. Number of apical fragments selected as suitable for regenerating

b. Number of apical fragments regenerating roots and shoots within 40 days

c. Percentage of apical fragments regenerating roots and shoots within 40 days



Division remains an alternative technique to the use of fragments. Establishment of apical fragments is aided if the shoot has already developed from the apex and if this is retained when planting.

A loam-based compost proved initially to be a suitable incubation medium and was found to sustain more shoot production than did sand. Moist fibre-glass matting did however give results superior to the compost. Light was found to be highly beneficial to regeneration. Few fragments regenerate if kept in the dark.

Seasonal differences in regeneration occur. For apical fragments regeneration during the winter was about half that obtained in the summer. The main experiment on the effects of season produced the following results: (% regeneration for four periods of assessment) September 71.3%; December, 28.4%; March, 32.3%; June, 74.5%.

The most favourable period for the growth of rhizome is from June to September and most rhizome can be gathered during September from plants which have been planted during or before the previous March. As regeneration is also good from this harvest then this is the most favourable time for propagation.

6. SORGHUM HALEPENSE (L.) PERS.

6.i. Introduction

Compared with the other species discussed in this report the literature on regeneration of S. halepense is large. This is undoubtedly connected with the occurrence of the weed in the southern states of the U.S.A. where it was originally introduced as a fodder crop. The species is a variable one; McWhorter (1967) has noted the great variation in growth habit, culm type and density, leaf shape and size, see productivity and vigour. The various ecotypes respond differentially to herbicide treatments.

The influence of season on rhizome development of S. halepense in the field has been studied by Oyer et al (1959), McWhorter (1961) and by Boyd (1967). Oyer et al found, in field studies in Indiana, that seedling plants started to form rhizomes when the plants had seven leaves; i.e. seven weeks following transplanting at the three to four leaf stage. This is somewhat later than that recorded by Anderson et al (1960) for plants grown in the glasshouse, when rhizomes were initiated five to six weeks after seedling emergence, and later still than that observed by McWhorter (1961) who found 50% of plants to have initiated rhizomes 18 days after emergence.

Following their initiation by seedling plants, the rhizomes steadily increase in dry weight throughout the growing season (Oyer et al 1959; Anderson et al 1960). The latter authors found the greatest increase in rhizome development to occur after seeds had matured, and stored carbohydrate rapidly built up in the rhizomes. McWhorter (1961) and Boyd (1967) also found rhizome production to increase rapidly after flowering. This late season increase in rhizome was related to a decrease in top growth (Oyer et al 1959; McWhorter 1961) which the former attributed to loss of lower leaves, loss of seed, and carbohydrate translocation from aerial shoots to the rhizomes. Physiological studies have indicated that after the young leaves, the rhizomes are the primary sites of utilization of reserve carbohydrates (Anon, 1965). Rhizomes may decay during the same season that they are formed (Boyd 1967).

The depth from which rhizomes can emerge was investigated by Pop-antoski (1954) who found rhizomes of S. halepense capable of emerging from a depth of 60 cm.

Both Oyer et al (1959) and McWhorter (1961) found plant development from single-node rhizomes to be similar to that of seedlings although plants from rhizomes were generally slower growing than from seed (McWhorter 1961).

The quantity of rhizome produced was found by Anderson et al (1960) to be exemplified by an internode number exceeding 5,200 for a 4.5 month old plant. McWhorter (1961) reports that after approximately five months growth a mean of 8070 g and 212 linear feet of rhizome was produced per plant. Stamper (1957) estimated, on the basis that ten miles of rhizome weighs one ton, that 15 tons or 150 miles of rhizome could be produced per acre. Individual rhizome could be up to 7 - 9 ft long. This indicates the tremendous development the rhizome system can undergo.

Regeneration of one-node rhizome fragments was found, by Ingle and Rogers (1957), to be favoured by darkness and high temperatures. At a given temperature the percentage of fragments sprouting decreased as the photoperiod increased. At 16°C less than 25% of fragments sprouted while at 32°C over 80% sprouted. Hull (1966) also found 15°C to be too low to induce bud germination. The response to temperature, which had a greater effect than light, was later found to differ according to the source of the material (Ingle and Rogers 1961); rhizomes from Michigan showed a greater response at low temperatures than rhizomes from Indiana.

It was noted (Ingle and Rogers 1961) that rhizome buds always gave rise to aerial shoots and never to rhizomes. Adventitious roots appeared at the base of these shoots but their appearance was not general within the 14 days duration of the experiments.

Boyd (1967) found there to be no differences between herbaceous and woody rhizomes in either their ability to regenerate roots and shoots or in their carbodyrate content. Carbohydrate content did however vary seasonally; soluble sugars were found to increase during the winter. A seasonal variation in the regeneration of fragments also occurred. Rhizomes when tested early in the year gave 100% regrowth decreasing to 70% in late summer and rising to 100% again in the autumn and winter. This is coincident with the "late-summer dormancy", a normal phenomenon in the field. This dormancy has been considered by Hull (1966) to be controlled by apical dominance (bud activity declines once shoots have emerged); also being influenced by the supra-optimal temperatures which prevail. Hull found that rhizome pieces with apical meristems produced aerial shoots by development of the meristem in 100% of cases while only 67% of basal buds developed and such development was normally delayed. The number of buds developing decreased along the rhizome in the direction of the apex.

Competition between nodes of multi-node fragments without apices does not appear to occur according to results of Anderson et al (1960). The total number of shoots produced was found to be much the same whether the rhizome were cut into 8-internode pieces or further fragmented into one-node pieces; indeed slightly more shoots were produced when the rhizome pieces were left intact.

In a study of the effect of desiccation on rhizome regrowth it has been found that drying to 40% of the original weight represented the critical limit below which few shoots developed (Anderson et al 1960).

Inhibitors have recently been found in rhizome extracts as well as in those of the leaf (Abdul-Wahab 1967). This is possibly an additional factor favouring establishment at the expense of other species.

Thus, much is known of the growth and regenerative behaviour of this species in the field. Investigations described below were restricted to studying the effects of age and season on the growth and regeneration of pot-grown material.

6.ii. Effects of season and plant age on rhizome production and reproductive potential

Methods

Stock plants of S. halepense were established from material imported from Israel. The experiment was conducted in a manner identical to that for C. dactylon and D. scalarum. Rhizome fragments were, however, given 40 days in which to regenerate as their progress was slow compared to the other two species under the same conditions.

Results

Rhizome and aerial shoot growth records are shown in Table XVII. Rhizome growth increased steadily with age; planting in December giving the greatest quantity. The most productive period for rhizome growth proved to be from March to June while a reduction in amount of rhizome occurred during September - December (Table XVIII).

Aerial shoot weights continued to increase during the life of the plants. The rhizome/shoot weight ratio showed a dependence on season, being greatest for June and September and low for December and March.

The percentage of prepared fragments which regenerated generally increased steadily with age although there was some decline for older plants. Regeneration was not dependent on the time of harvest (Fig. 5b). Also, regeneration was not related to variations in the fresh weight of rhizome per node. September planting gave the highest percentages of regeneration. Planting in December, however, gave the greatest number of regenerating fragments as more fragments were available for testing from these plants (Fig. 5a); a mean of 81.8 compared to 44.9, 35.1 and 45.7 for March, June and September respectively was obtained.

6.iii. Conclusions

Work in the USA has shown that S. halepense produces much rhizome in the field and has a relatively rapid rate of spread. The rhizome is active in regenerating new shoots but may enter a period of dormancy in the late summer. Laboratory studies indicate that regeneration of rhizome fragments is both a light and a temperature sensitive process. Regeneration is favoured by darkness and by high temperatures.

In pots under glass in UK rhizome growth is greatest if planting is done in December. Also, December planted material yields the greatest number of regenerating fragments even though the percentage of regenerating fragments is greater with September plantings.

Regeneration appears to be related to age with the more mature rhizome having the better chance of regrowth than rhizome from very young plants.

Table XVII

Rhizome and aerial shoot productivity of S. halepense

(data are means of three plants)

Month of planting	Plant age in months	Month of assess-ment	Rhizome length (cm/plt)	Rhizome fresh weight (g/plt)	Aerial shoot fresh weight (g/plt)	Number of distinct nodes on rhizome (per plant)	Rhizome fresh weight per cm length (mg)	Mean length of rhizome per node (cm)	Rhizome/shoot fresh weight ratio	Rhizome as a % by weight of rhizome plus aerial shoot
Sept. 1967	3	Dec.	10	3	163	7	262	1.5	0.02	1.8
	6	March	155	52	259	93	330	1.7	0.20	16.7
	9	June	484	145	357	332	300	1.5	0.41	28.9
	12	Sept.	708	179	467	661	253	1.1	0.38	27.7
Dec. 1967	3	March	2	1	123	2	200	1.2	0.01	0.8
	6	June	576	137	354	253	238	2.3	0.39	27.9
	9	Sept.	1029	239	541	536	232	1.9	0.44	30.6
	12	Dec.	923	177	492	452	192	2.0	0.36	26.5
March 1968	3	June	94	32	326	52	341	1.8	0.10	8.9
	6	Sept.	398	117	352	220	295	1.8	0.33	25.0
	9	Dec.	369	84	423	253	227	1.5	0.20	16.6
	12	March	411	96	490	205	233	2.0	0.20	16.4
June 1968	3	Sept.	166	32	264	90	194	1.8	0.12	10.8
	6	Dec.	112	32	339	90	287	1.2	0.10	8.6
	9	March	331	76	372	200	228	1.7	0.20	17.0
	12	June	877	261	472	586	298	1.5	0.55	35.6

Fig. 5. Reproductive potential of *Sorghum halepense*

a. Number of fragments selected as suitable for regenerating.

b. Number of fragments regenerating roots and shoots within forty days.

c. Percentage of fragments regenerating roots and shoots within forty days.

Time of planting:

Sept. ●———●

Dec. ●– – –●

March ○———●

June ○– – –●

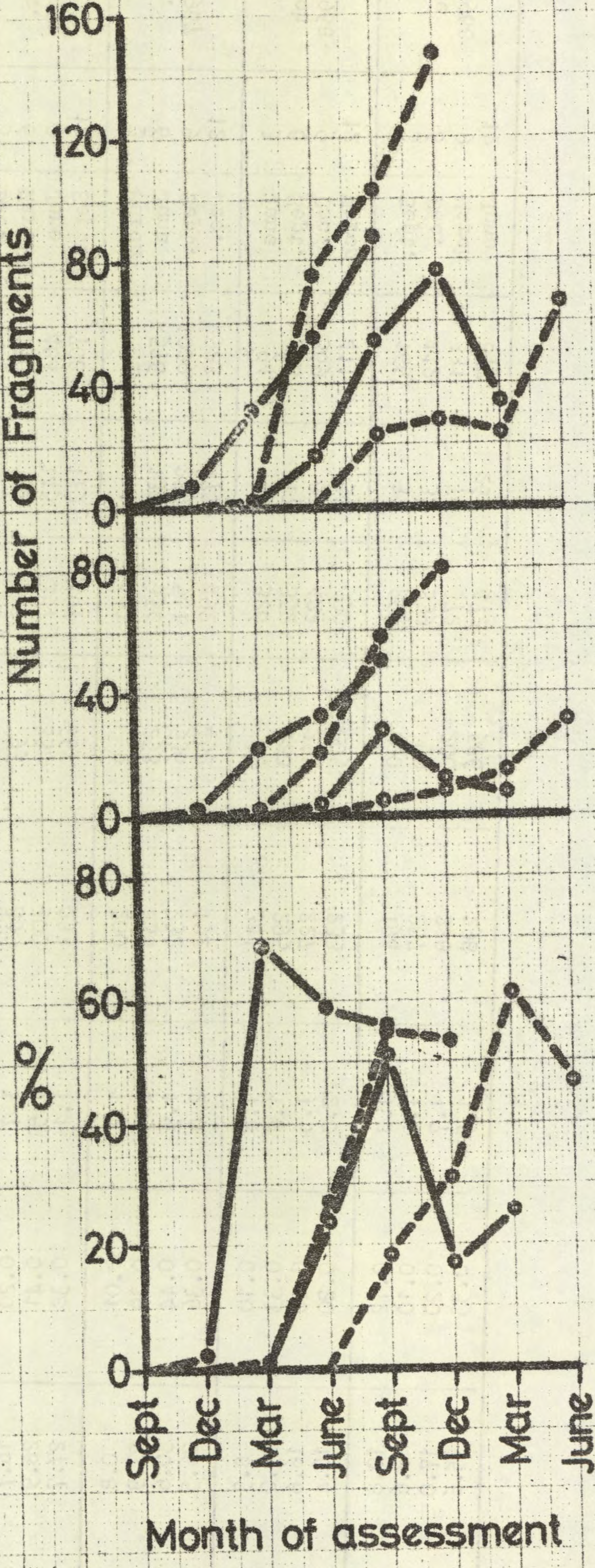


Table XVIII

Increments in rhizome length of S. halepense during three-monthly periods of growth

(data are means of three plants)

Period of growth	Month of planting				Total
	September	December	March	June	
	Length in cm/plant				
September - December	10	-106	-29	-54	-179
December - March	145	2	42	219	408
March - June	329	574	92	546	1543
June - September	224	453	304	166	1147

7. GENERAL DISCUSSION

Rhizomes are very efficient as perennating and reproductive organs. Their subterranean origin places them in a physically protective environment while their diageotropic growth habit maintains this and serves to extend laterally the plant's domain. Their regenerative ability is displayed both in the intact plant by the emergence of new shoots, often some distance away from the original stock, and more dramatically in the fragmented plant by the stimulation of sprouting of buds on detached fragments. Regeneration of detached fragments is dependent on physiological factors, largely unknown but which presumably include the status of bulk food reserves in the rhizome. The aerial assimilatory parts of the plant determine rhizome growth, condition, and hence ability to regenerate both when intact and fragmented. Rhizome growth and regeneration may thus be related to the general metabolic processes, in particular the photosynthetic efficiency and growth-substance status of the aerial shoots.

Of the four species studied here three have shown a similarity in pattern of rhizome growth and reproduction, whilst that of the fourth, I. cylindrica, differs somewhat from the others. While two and even one-node fragments of D. scalarum and S. halepense readily regrow, multi-node fragments containing an apex are required to achieve comparable success in the case of I. cylindrica. It is the apex which continues the growth of fragments of this species. Sub-apical buds are seldom encouraged to sprout in the absence of the continued growth of the apex. This contrasts directly to the behaviour of the other species.

Photosynthetic tissue is quickly produced when apical fragments of I. cylindrica are incubated in the light, and light appears to be necessary if roots are to be initiated and the fragment is to survive. Also if a fragment already has an established green shoot then chances of survival are increased further (Table XIII). In the dark the leaf tissue underlying the other scale leaves of the apex may not expand or only slightly expand and of course will remain without chlorophyll.

Once the apex of I. cylindrica rhizome has resumed growth some of the sub-apical buds may begin to grow so that the fragment establishes several shoots. This is similar to the behaviour of the intact plant where branching occurs just behind an upturned apex of the rhizome with the buds at the position of a "bend" producing new shoots. Buds lower down the rhizome do, however, remain dormant. This is a dominance system in reverse to the usual pattern such as is found with e.g. D. scalarum fragments. Here the common pattern of apical dominance occurs with the most distal bud of a fragment inhibiting the growth of the proximal bud(s). This is consistent with the concept of polar flow and is displayed both in the initial sprouting and the subsequent growth of the buds. It has been found with D. scalarum that the environment in which fragments are placed for regeneration influences this dominance pattern. Although there are several differences in the environment between planting in soil and laying on moist fibre-glass (e.g. temperature, aeration) it is probable that light is the major one. In the light both proximal and distal buds sprout equally and the shoots they produce appear equal on casual observation. This tendency for both buds to sprout in light has also been observed with stolon fragments of Agrostis stolonifera L. (Henson, 1969). However, further measurement of D. scalarum has shown that in terms of shoot fresh weight the distal node is still dominant. These modifications by light and possibly other factors of the growth and expression of dominance in fragments of I. cylindrica and D. scalarum are of obvious significance in the physiology of regeneration of these species and warrant further study.

The position from which fragments are taken did not, in the case of D. scalarum, effect greatly their capacity to regenerate. Only the apical fragments too immature and too small to possess adequate reserves, failed to grow. Apart from this instance variation in the bulk of rhizome, as measured by its fresh weight, did not influence the regenerative capacity of the bud, for buds with the greatest bulk of rhizome associated with them did not necessarily give the best regeneration. The physiological state of the tissue was therefore of more importance.

The rate at which fragments regenerated differed, being rapid for C. dactylon and D. scalarum and slow for I. cylindrica and S. halepense (Fig. 6). It is probable, from the work of Ingle and Rogers (1957), that for S. halepense temperatures used were sub-optimal for most rapid regeneration.

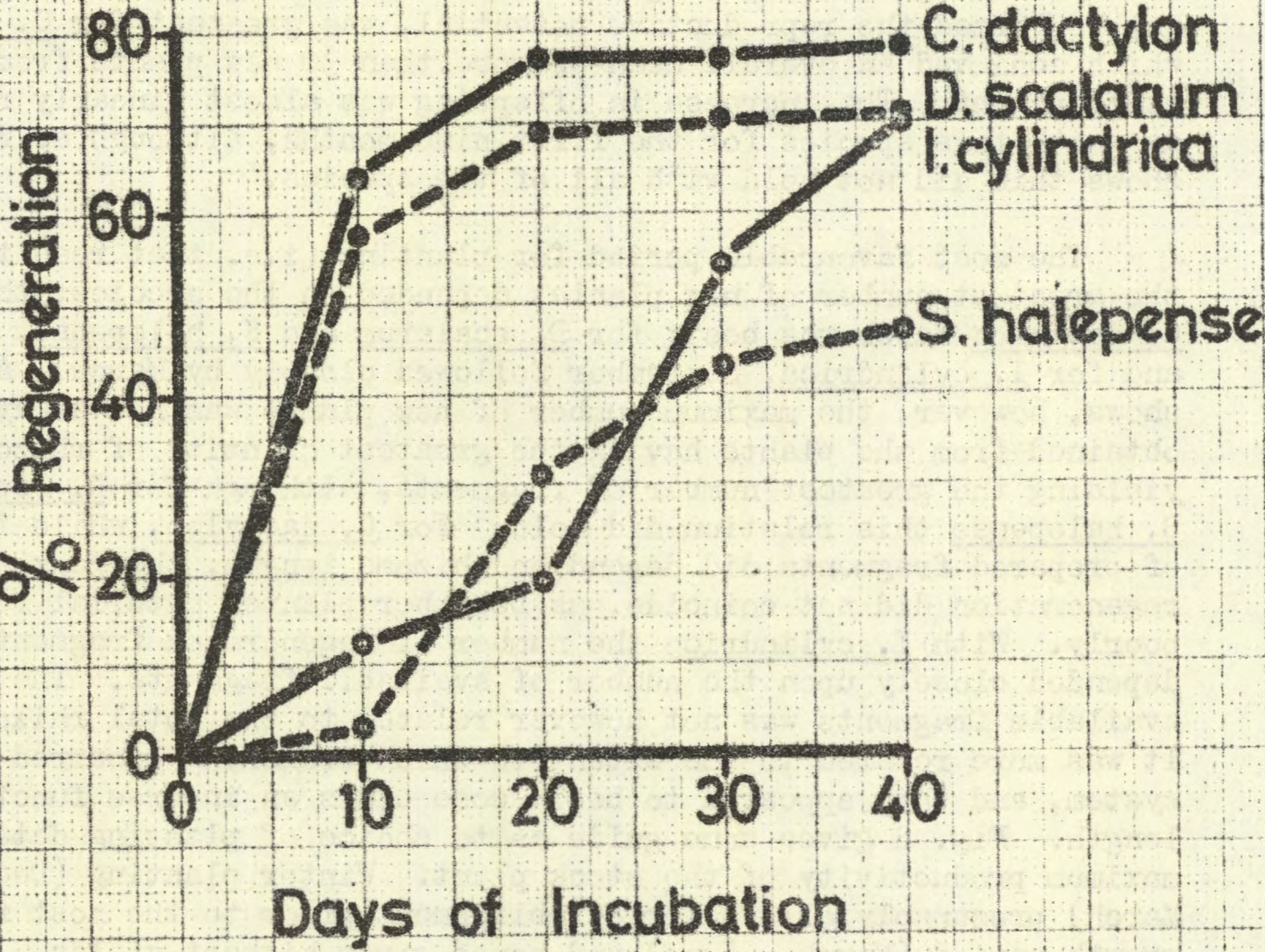
The state of the rhizome and its suitability for propagation may be influenced by age and/or season. The experiments designed to determine the importance of these factors high-lighted interesting differences between the species. The regeneration of D. scalarum fragments was governed largely by seasonal influences and regeneration was poor in mid-winter. This was generally the case also with C. dactylon and I. cylindrica. S. halepense was less influenced by the time of year and age appeared a more important factor. Fragments from young plants often gave poor results.

The manner in which season affects the ability of the rhizome to regenerate is not known but presumably the conditions governing photosynthesis play a large part. Light and temperature are the major varying factors and an effect of temperature on the capacity for regeneration by I. cylindrica stock material has been mentioned. If plants are grown cool (at 10°C) during the winter, regeneration of the fragments prepared subsequently is improved. This may be the result of ensuring a more favourable balance between photosynthesis and respiration under the low light intensity of the English winter; this increases the quantity of assimalates available for fragment regrowth. There is no advantage of such a treatment with plants during the summer when light intensity is increased.

Growth of rhizome is also under the dual influence of plant age and seasonal environmental variations. The quantity of rhizome continued to

Fig. 6. The rate of regeneration of rhizome fragments

(Fragments taken from 12-month old plants established June 1968)



increase as the plants matured despite the somewhat restrictive influences of the pot. Rhizome grew most rapidly during March to June for C. dactylon and S. halepense and from June to September for D. scalarum and I. cylindrica. There were cases when the amount of rhizome diminished. These losses occurred in the winter months; all species showed decrements in length of rhizome between September and December, while rhizome in one planting of D. scalarum decreased also between December and March. These losses in total length must be due to decomposition, but there were also losses in fresh weight unaccompanied by a decline in length, notably by I. cylindrica, which may have been due to depletion or redistribution of reserves.

Partition of growth between aerial shoots and rhizome varied and was found to be most efficient in I. cylindrica. The mean % of rhizome by weight was lowest with D. scalarum. The figures were: D. scalarum, 6.7%; C. dactylon, 15.6%; S. halepense, 18.7% and I. cylindrica, 28.6%. However, the productivity as measured by the numbers of regenerating fragments (and hence new plants) obtained, which may be termed the reproductive potential, was greatest for C. dactylon which achieved an overall mean of more than 30 new plants from each stock parent. The increase in offspring was almost linearly related to age with this species for the first nine months, although as Fig. 7 shows this did not hold with all of the species.

The most favourable period for planting (i.e. that resulting in the greatest number of new plants) depended on the species; thus for C. dactylon March was best; for D. scalarum and S. halepense, December and for I. cylindrica, September followed closely by March. As Fig. 8 shows, however, the maximum number of new plants was not always obtained from the plants having the greatest quantity of rhizome or yielding the greatest number of fragments, although for D. scalarum and S. halepense this relation did hold. For C. dactylon, while the number of prepared fragments did depend on rhizome length, the peak for regeneration did not coincide, as December planted material regrew but poorly. With I. cylindrica the number of regenerated fragments depended closely upon the number of available fragments. The number of available fragments was not however related to the total rhizome length. It was more related to the extent to which branching occurred in the system, and this appeared to be in some cases an inverse function of length. Fig. 8 gives some guide as to choice of planting date for maximum productivity of the stock plant. Winter planting (December or March) presumably allows for establishment prior to the most favourable growth period (March - June) and hence gives highest yields.

As mentioned previously there is a general lack of information on the growth and regeneration of the rhizome system of these species, except for S. halepense. There is thus much need for such studies on this aspect of the biology of these weeds. Pot experiments of the kind reported here can never be a substitute for field studies but they can serve as an indication of trends to be expected in the field, and are useful in the comparisons of species and clones, and can be used to investigate critical effects of environmental factors. Field studies on C. dactylon, Cyperus rotundus L. and S. halepense are indeed at present in progress in Israel at the moment (Horowitz, unpublished communication 1968) but similar work needs to be done in other areas of the tropics and sub-tropics if the results are to be widely applicable.

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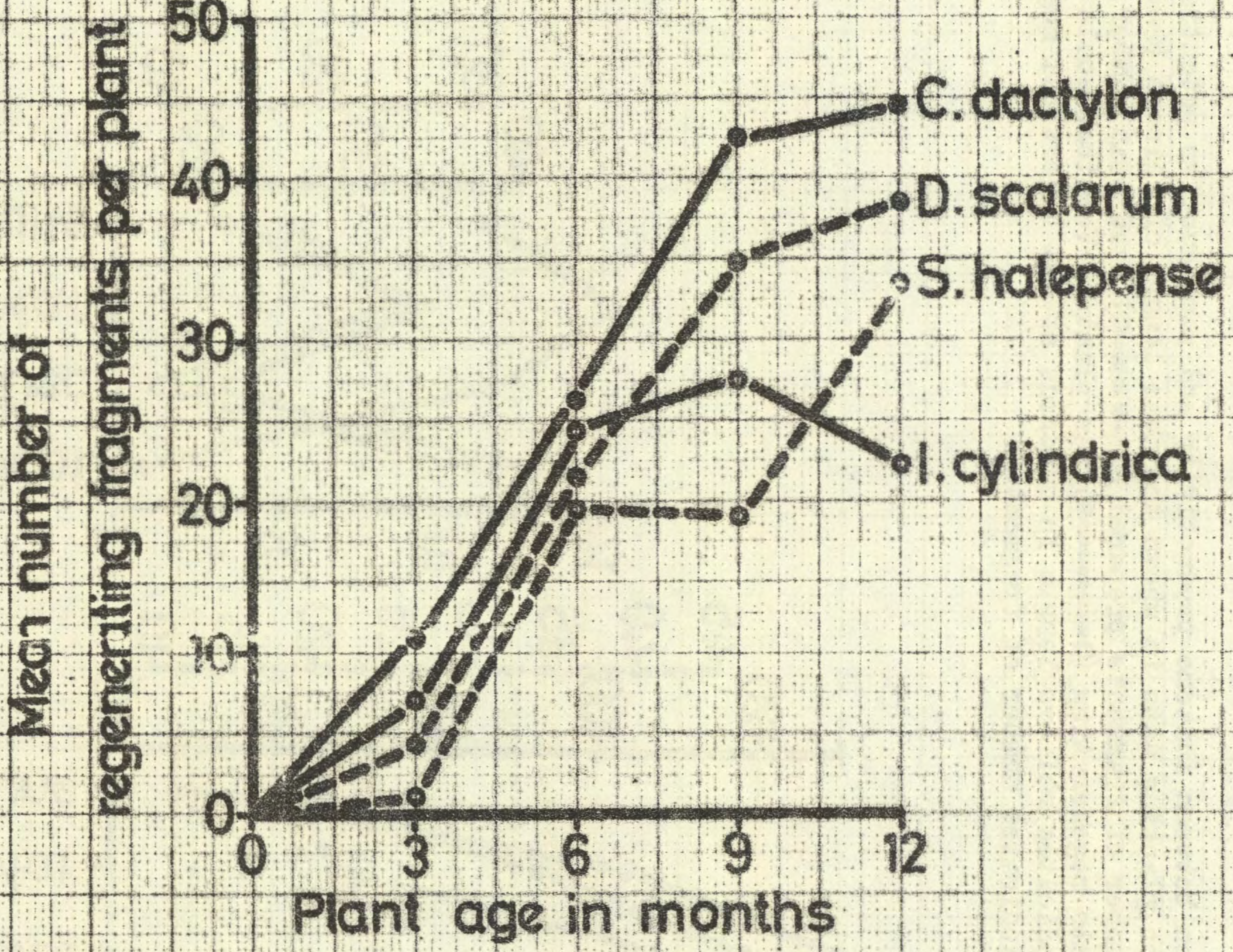
Fig. 7. The increase with plant age in the number of regenerating fragments obtained.
(means of four planting dates)



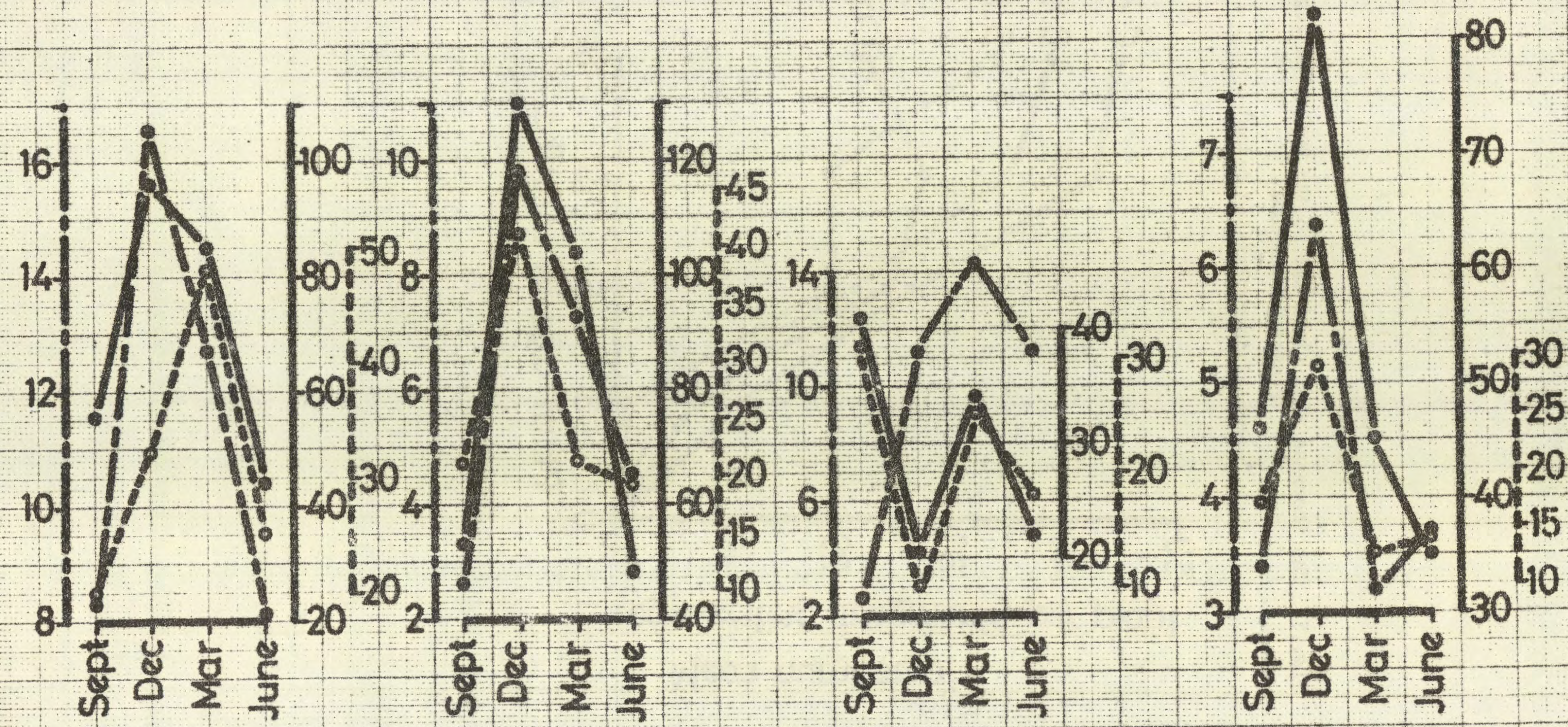


Fig. 8. Relation between rhizome productivity and reproductive potential. For each planting date is shown the mean length of rhizome (●— — —●), mean number of fragments prepared (○- - - - -○), and mean number of fragments regenerating (○———○) per plant. Vertical scale on left indicates rhizome length in hundreds of cm. Vertical scales on right indicates number of fragments.

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