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REGENERATIVE CAPACITY OF SPEARGRASS (*Imperata cylindrica* (L.) P.Beauv.

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ABSTRACT

Imperata cylindrica (L.) P.Beauv. is a noxious perennial grass that has invaded many countries in Africa. In Tunisia I. cylindrica is an invasive perennial species that has spread widely in oasis and riparian areas where it has altered wildlife habitats, compromised water conservation efforts and affected flood control. I. cylindrica is a dominant, competitive and difficult weed to control, particularly in date palm plantations. Its management has been a significant challenge because of large rhizome and buds reserves in the soil. In Tunisia, no information is available on the biology and behaviour of I. cylindrica particularly its regenerative capacity and growth patterns. Laboratory trials under controlled conditions were conducted in the Institute of Agronomical Science at Chott-Mariem, Tunisia, about regenerative capacity of I. cylindrica from 2003 to 2007. I. cylindrica has an extensive rhizome network and it is able to regenerate from these rhizomes. The bud viability decreased by burying. The fragmentation of rhizomes increased the regenerative potential of I. cylindrica and decreased the apical bud dominance effect. The age and the length of the rhizome had an effect on the regenerative capacity.

Keywords: Biology, correlative inhibition, Imperata cylindrica (L.) P. Beauv., regenerative capacity, rhizomes.

INTRODUCTION

Imperata cylindrica (L.) P.Beauv. (speargrass) is a C_4 perennial grass with persistent aggressive rhizomes that are reported to be the main mechanism for survival and local spread. Speargrass rhizomes are resistant to high temperatures and have characteristics that enable them to conserve water and resist breakage.

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I. cylindrica is considered to be one of the most troublesome and problematic weedy species in the world (Holm *et al.,* 1977). This aggressive rhizomatous perennial grass is generally considered a pernicious pest due to its ability to successfully disperse, colonize, spread and subsequently compete with and displace desirable vegetation and disrupt ecosystems over a wide range of environmental conditions (Holm *et al.,* 1977; Brook, 1989; Bryson and Carter, 1993; Dozier *et al.,* 1998). The explanation of this vegetation displacement may be caused by the production of phenolic compounds that together with competition may inhibit growth and survival of other plants (Akobundo and Ekecleme, 2000). The species is found throughout tropical and subtropical regions, generally in areas disturbed by human activities. Vegetative reproduction from rhizomes is a significant factor in human spread of a species because these are often found in dirt moved as fill. This pernicious species, considered one of the top ten worst weeds in the world, has been reported by 73 countries and on all six continents as a pest in a total of 35 crops (Holm *et al*., 1977). *I. cylindrica* has been found in a broad range of crops and soils under different management practices. Over 100 common names have been associated with this species that is named Diss in Tunisian dialect. In Tunisia, *I. cylindrica* occurs in riparian habitats, sub-humid and humid grasslands and open woodlands where it forms mono-specific swards (Omezine, 1998). It thrives in areas of minimum tillage, such as orchards, lawns and roadsides. *I. cylindrica* is a major impediment to date palm plantation efforts in the South West of Tunisia. *I. cylindrica* causes loss of native habitat in Tunisia and infested areas are increasing (Omezine, 1998). Management efforts are restricted to several mechanical strategies.

I. cylindrica possesses several features that foster its rapid spread and persistence. It produces new rhizomes with total length ranging from 1.5 to 3 m per year, facilitating the plant's spread at newly colonized sites. However, rhizomes fragments do not survive well under regular deep tillage. *I. cylindrica* is a prolific producer of wind-blown seeds, most of which are viable and highly germinable with almost no dormancy. Seed longevity is very short; less than 3 months Seed number is as high as 3000 per seed head and disperse over long distances into a variety of habitats.

In the world, several biological studies have been carried out on this species, but in Tunisia, no studies have been conducted on either its biology or control strategies. Date palm farmers consider *I. cylindrica* as one of the most serious weed. The farmers indicated that they lack resources to effectively manage it, and urged development of improved technology which does not demand monetary investment should be a priority. Since there is not sufficient data on *I. cylindrical*, in Tunisia, the instant work on *I. cylindrica* constitutes the first one that will be conducted in Tunisia to understand biological behaviour and elucidate management strategies. The objective of this study was to improve the understanding of the biology of *I. cylindrica* in relation to weed management strategies. The basic biology of *I. cylindrica* particularly with respect to growth and propagation will be studied. This work will improve integrated mechanical and chemical management for smallholder farmers.

MATERIALS AND METHODS

Experimental materials and sites

Rhizomes were collected from a pure stand of *I. cylindrica* located in Tunisia at the Institute of Agronomical Sciences, Chott-Mariem. Healthy rhizomes with different colours (white, creamy, brown, black) were stored in plastic bags in a refrigerator for not more than 4 days prior to being used in the assigned experimental treatments. Each experiment was conducted in a completely randomized design with five replicates and in each replicate five rhizome fragments were used. Four experiments were conducted in the present study.

All propagules were planted in pots filled with standard potting soil mix (sand, peat moss, vermiculate, V/V) in greenhouse equipped with ventilation system. The pots were watered every two days to avoid water stress.

Experiment 1: Spatial distribution of I. cylindrica rhizomes into the soil horizons and viability test.

The spatial distribution of *I. cylindrica* rhizomes into the soil was studied at the Institute Superior of Agronomical Sciences, Chott-Mariem (Tunisia). To obtain quantitative information about rhizome distribution in soil horizons, prism monoliths about 20 x 20 x 10 cm were taken with a spade and transported to the laboratory for rhizome separation from soil by washing (Wolfgang, 1979). Then, the rhizomes of each horizon were weighed, counted and immediately planted in containers filled with potting soil media to determine their viability. The containers were put in greenhouse at 25 ± 2°C. Before excavation of the root system from the soil, the above ground parts of the plants were weighed.

Experiment 2: Correlative inhibition and fragmentation of rhizomes.

To determine the effect of the growth of one bud on another, called correlative inhibition, rhizomes one year old (white rhizomes with pointed apex) were collected from solitary stands of *I. cylindrica.* These rhizomes were planted in a growth chamber filled with sterilized sandy soil. After emergence, the number of buds sprouted and emerged in shoots or not sprouted were counted. The ammonium nitrate was added to the first half of the pots @ 2 g kg^{-1} of standard horticultural soil mix and the second half of the pots was without ammonium nitrate as a control.

The effect of fragmentation of rhizomes was studied beside the first experiment. Rhizomes were cut into three pieces: apical zone, middle zone and basal zone, and buried at 2 cm in containers. Each container contained 5 pieces. The containers were inspected weekly to recorded emergence time of each plant. After the growth period, all plants were harvested simultaneously. The buds in each piece that sprouted were counted.

In another experiment, rhizomes of the same length and same number of buds were planted in containers in order to study shoot dominance effect. These rhizomes fragments were placed in a greenhouse under a ventilation system but without a mist system. Watering was done by hand every two days or where the containers needed water to avoid water stress. The length of growth from each bud was taken at the end of the experiment after three months from experiment establishment. Each rhizome fragment has nine buds.

Experiment 3: Regenerative capacity.

To determine the regenerative capacity of *I. cylindrica* rhizomes, two separate experiments were conducted in the greenhouse. Rhizomes were collected from solitary stands of *I. cylindrica* at the Institute of Agronomical Sciences and stored in a refrigerator for 1 to 4 days in a plastic bag until assigned to the experimental treatments.

In the first experiment, to determine the smallest viable rhizome length, rhizomes were cut into fragments of different lengths that are 1(one bud), 3 (2 buds), 6(4 buds), 9(8 buds), 12 cm (12 buds).

In the second experiment, rhizomes were cut into fragments of the same length but of different ages based on the colour: white fragments that have an age less than one year old, creamy fragments that have an age between one and two years or creamy to black fragments have an age more than three years.

Experiment 4: regenerative growth pattern.

Seeds were collected from a pure stand of *I. cylindrica* in June and immediately planted in 8 cm diameter pots to determine the regenerative growth pattern. The pots were placed in greenhouse under a ventilation system and watered by hand when needed.

Statistical analysis

These experiments were conducted in greenhouse at a temperature as indicated above. They were assigned in completely randomized design with ten replicates. The analysis of variance and least significant difference were used.

Each experiment was set up as a completely randomised design. The original intent was to analyze growth of sprouts using analysis of variance appropriate to this experiment. However, because of the frequency of failure to sprout, it was decided to analyze the proportion sprouted. Because each experimental unit was a five rhizome fragments, it was either sprouted or not sprouted. To calculate proportion sprouted it was necessary to combine replicates and calculate the % of the five replicates that sprouted. The data were subjected to Analysis of Variance Test and subsequently means were separated (Little and Hills, 1978).

RESULTS AND DISCUSSION

Experiment 1 : *Spatial distribution of I. cylindrica rhizomes in the soil horizons and viability test.*

This work indicates that rhizomes of *I. cylindrica* penetrates into the soil (Table-1) up to 50 cm deep, although the majority of rhizomes remain in the top 20 cm, and more than 80% of shoots originate from the rhizomes less than 15 cm below the soil surface. Wilcut *et al.* (1988) reported that *I. cylindrica* is unlikely to send up shoots from deeper than 8 cm. However, in other studies rhizomes may penetrate soil up to 1.2 m deep, although the sheer rhizome mass generally occurs in the top 20 cm in heavy clay soils, and 40 cm in sandy soils (Holm *et al.*, 1977; Bryson and Carter, 1993). The present studies showed that rhizome biomass had reached 6 tons of fresh weight ha^{-1}, whereas, other studies indicate that rhizome biomass can reach 7 to 40 tons of fresh weight ha^{-1} (Soerjani,1970; Terry *et al.*, 1997). Moreover, 30 tons were found as above ground fresh weight produced by *I. cylindrica*. The viability of *I. cylindrica* rhizomes increased with depth (Table-1**)**. Consequently, tillage and cultivation destroy the rhizome system and bring up the deeper rhizomes at the superior horizons where they are able to re-grow and bring down the superficial rhizomes to deeper horizons where they will not be able to sprout.

Table-1. Spatial distribution of rhizomes into the soil horizons and sprouting.

Depth (cm)	No. of rhizomes (%)	Sprouting(%)
0-5	22.5 ± 1.2	16.5 ± 1.6
5-10	15.2 ± 1.5	15.5 ± 1.2
10-20	24.4 ± 2.3	06.8 ± 07
20-30	22.9 ± 1.4	02.3 ± 0.5
30-40	10.5 ± 1.9	02.5 ± 0.9
40-50	6.2±	00.0

± * Standard deviation

Experiment 1: Correlative inhibition and fragmentation of rhizomes

The inhibiting effect of one bud on another, termed correlative inhibition, is widespread among vegetative regenerating parts of weeds. In this experiment with *I. cylindrica*, the apical meristem inhibited the growth of the axillary buds at the nodes along the rhizome. This inhibiting effect of the apical meristem, although not usually that of complete inhibition of other buds, is nevertheless very pronounced. The presence of the apical meristem allowed only 9.2% germination of the axillary buds. Removing the apical meristem allowed more than a two fold increase in germination of the axillary buds (Table-2).

Also the results show a correlative inhibition effect among shoots. This effect is for one or a few shoots to inhibit or completely prevent the growth of other buds on the same rhizome fragment. In Figure 1 the shoot originating from the bud number 6 has restricted the growth of the other buds and almost completely prevented growth of the buds at 2 and 5 nodes. The addition of ammonium nitrate did not eliminate the apical and the shoot dominance effects but the growth was improved.

Table-2. Influence of the apical meristem on the sequence bud sprouted of three- *I. cylindrica* rhizome pieces (results in percentage).

	Rhizomes non fragmented		Rhizomes fragmented
Bud position	Rhizomes without apex	Rhizomes with apices	
Apical	42.0 ± 1.2	75.2 ± 2.3	22.1 ± 3.5
Middle	36.2 ± 2.3	15.6 ± 1.5	23.5 ± 1.8
Basal	21.8 ± 1.6	9.2 ± 0.9	26.2 ± 3.5

± * Standard deviation

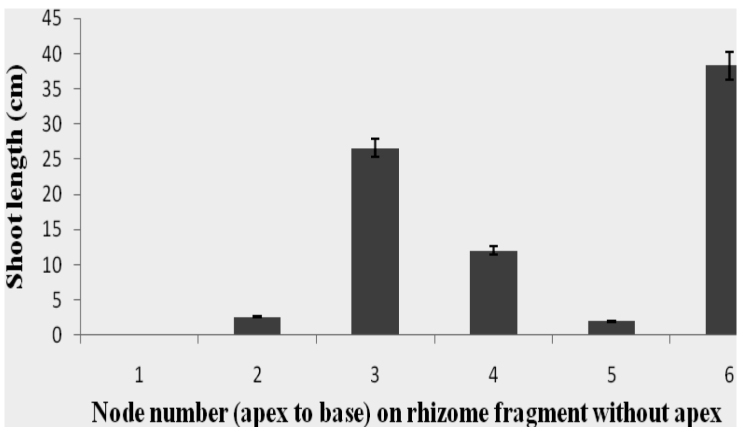

Fig.1. Shoot dominance effect of *I. cylindrica* among shoots on a rhizome fragment (Vertical bars are standard errors).

Experiment 2: Effect of rhizome length and of physiological rhizome age on regenerative capacity.

The growth potential of rhizomes is a critical issue in development of control strategies. Regeneration from rhizomes segments has been observed. White rhizome fragments without the apex did not sprout at all, therefore the white rhizomes fragments with apex did grow but they had the least regenerative capacity. The creamy and the creamy to black ones were grown in different proportions. The best growth was observed for creamy rhizome fragments (Table-3). White rhizome fragments did not have visible buds and roots. Creamy and creamy to black did have visible buds and same roots for nutrient uptake, moreover, certain buds which are present on creamy to black rhizome fragments were not only non-survived but also depleted from food reserves by repeated previously sprouting and growth of rhizome mother. Success of rhizome fragment regeneration is determined by its age such as the original location of the segment on the rhizome, including proximity to/inclusion of, axillary and apical buds.

Table-3. Effect of physiological rhizome age on regenerative capacity.

Physiological age based on colour	Regenerative capacity (%)*
White without apex	00.0
White with apex	12.3 ± 1.6 a
Creamy without apex	59.2 ± 3.1 b
Creamy to black without apex	14.3 ± 1.3 a

± * Standard deviation

Moreover, the germination of buds was correlated directly with the vegetative reproductive rhizome fragments. The percentage of buds that sprouted decreased as the length of rhizome fragments increased. However, the number of buds that sprouted increased. A significant positive relationship existed between rhizome fragment length and bud germination. These relationships are shown in Figures 2 and 3**.** The best sprouting of regenerative reproductive part was with rhizome fragments which had only one bud. The percentage dropped from 80 % to 40 % for 12 cm rhizome fragments but the number of buds increased from 28 to 96. The explanation for this observed effect is likely to lie in the fact that as the length of rhizome fragments is reduced, the dominance relationship is reduced.

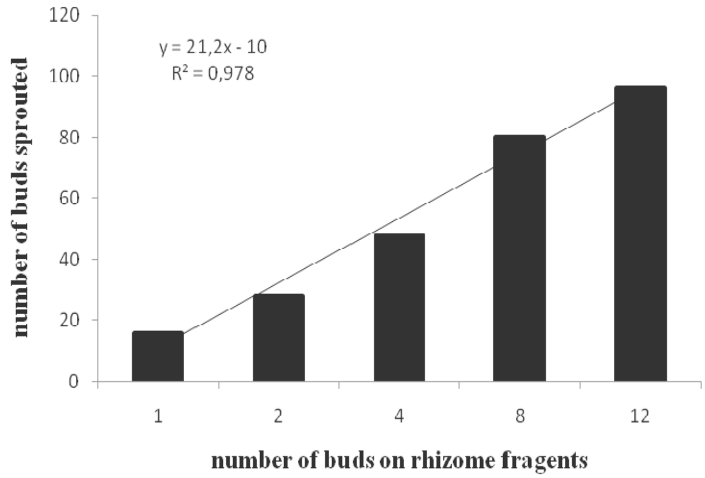

Fig.2. Positive relationship of buds sprouted to the number of buds on the rhizome.

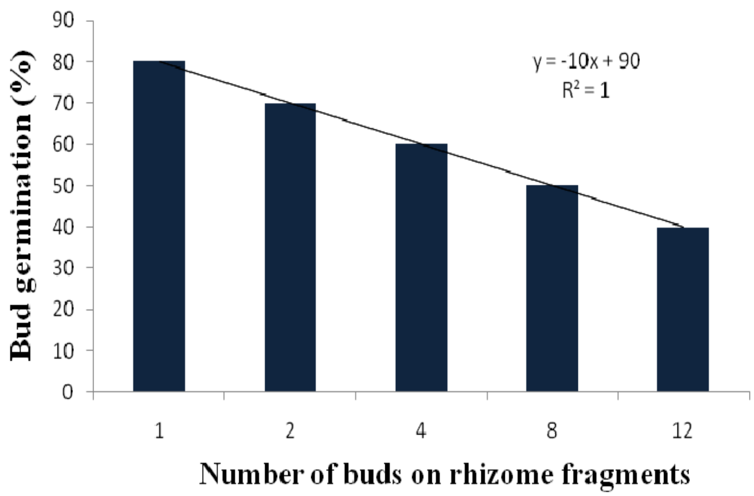

Fig.3. Inverse relationship of bud germination to the number of buds on the rhizome to the number of buds on the rhizome.

Experiment 3: Vegetative growth pattern and life cycle.

The vegetative growth pattern of *I. cylindrica* (Figure 4) was studied in greenhouse. Careful observation of plants grown from mature rhizome fragments indicated that a young plant initiates new rhizomes between the third and the fourth leaf stage. Rhizome growth is determinate (the rhizome tip turns up to form a shoot), with the apical bud forming a shoot and sub-apical buds forming rhizomes branches. Under favourable conditions apical and sub-apical buds develop simultaneously, but under stress the growth of the apical bud is favoured. Root and bud development occurs on the distal nodes of the young rhizomes long after the rhizome has been formed.

Rhizome development generally starts between the third and the fourth leaf stage. Early rhizome growth is plagiotropic, or vertical, with growth by the fifth leaf stage becoming horizontal when rhizomes develop scale leaves (cataphylls). The tips of the rhizomes grow upward (negatively orthogeotropic) between the fifth and the sixth leaf stage. A second generation shoot arises from the apical bud, and rhizomes form from sub-apical buds. Most buds are located at the distal end of the rhizomes, in nodes in the apical region. No buds are formed until the diageotripic rhizome growth stage. Root development also begins at this stage with a fibrous system forming at the rhizome nodes. Second generation shoots and rhizomes form simultaneously on strong plants. In weaker plants, the shoots forms first, whereas buds on the convex side form shoots much later or remain suppressed.

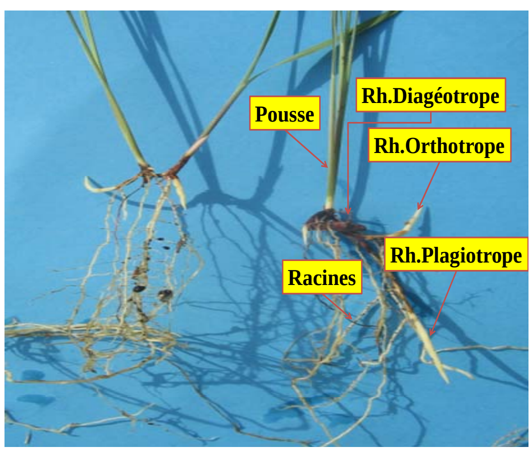

Fig.4: **Growth patterns of *Imperata cylindrica* (L.) Beauv.**

The life cycle of *I. cylindrica* is very complex (Figure 5). The growth pattern comports 6 cycles of growth (a,b,c,). Three of them are sexual cycles and three are vegetative cycles (d,e,f).
cycle a: 1,2,3,4,5,6.
cycle b: 1,2,7,8,9,3,4,5,6.
cycle c: 1,2,10,11,12,8,9,3,4,5,6.
cycle d: 7,8,9
cycle e: 14,11,12.
cycle f :11,13

In Tunisia, *I. cylindrica* is a pernicious costing hundreds of millions of Tunisian Dinars to control; with its only documented beneficial use is a thatch for building huts and roofs. This species has been considered as among the first 18 world's worst invaders (Holm *et al.,* 1977) and the first of 10 Tunisian's worst weeds (Omezine, 1990). Earlier, *I. cylindrica* was used for covering the top of plates containing food or for erosion control in date palm plantations thus spread in large areas.

Although, *I. cylindrica* is sufficiently deep rooted to have considerable drought resistance, most of its rhizomes are found relatively close to the surface. The mean of several excavations reported by Ivens (1976) showed that the total proportions of the rhizome dry weight were 24, 70, 99, and 100 % of rhizome dry weight down to depths of 7.5, 15, 22.5, 30 cm, respectively. Comparable figures for the total proportions of shoots originating down to the same levels 7.5, 15, 22.5, 30 cm were 49, 91, 100 percent, and 100 % of rhizome dry weight, respectively. No shoots were found to reach the surface from below 22.5 cm and evidence was obtained that the older, deeper rhizomes were of low viability. With *I. cylindrica*, Soerjani (1970) and Eussen and Wirjahardja (1973) reported that the great majority of the rhizomes were situated in the topmost 20 cm of soil and that fewer of the older rhizome buds sprouted.

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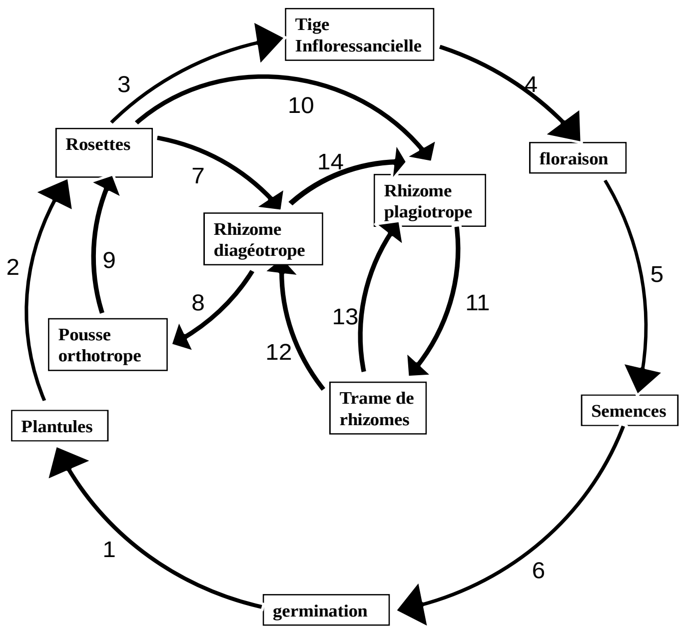

Fig.5. Life cycle of *Imperata cylindrica* (L) Beauv

Both Soerjani (1970) and Ivens (1976) reported loss of viability after exposure for two or three days at relative humidity between 50 and 78 %. Because most of the rhizomes are produced only a short distance below ground and dry up rapidly when disturbed, cultivation can be an effective treatment as long as it is carried out deeply enough. Aboaba (1967) reported a high degree of long-term control from three rotary cultivations at one-month intervals, the final cultivation reaching a depth of 20 cm. Likewise, Adegbola *et al.* (1970) achieved 95 % control by ploughing to a depth of 15 cm early in the dry season.

The effectiveness of cultivation is also related to the degree of fragmentation of the rhizomes. The proportion of rhizomes sections producing shoots was generally low, but increased with the number of buds in the sections, from 4 % with sections of 2-nodes to 27 % with sections with 8 nodes. For a given length of rhizomes the number of separate plants growing after cutting into lengths of 4 nodes or more was about 50 % greater than that developing from the larger number of 2- and 3-nodes sections. There is a greater difference in plant vigor, however, and whereas 80 % of the 2- and 3 –node sections planted at 7.5 cm had died without sprouting after two months, only 30 % of the 5-node and none of the 9-node sections had died.

The percentage of sections sprouting in this work is very much lower than in that reported by Soerjani and Soemorwoto (1969). In the work of Aboaba (1967), however, rhizome sections were taken at random whereas Soerjani and Soemorwoto (1969) selected apical sections with large, healthy buds. The later studies also reported that the longer sections produced the more vigorous shoots. Thus, with this species there is evidence that the more thoroughly the rhizome system can be broken up by cultivation, the better the degree of control is likely to be achieved.

The rhizomes are responsible for the survival and short-distance spread of *I. cylindrica*. Rhizomes are very resistant to mechanical tillage and breaking. Repeated tillage operations which disconnected rhizomes with or without apex from mother plants in new date plantations and the lack of safe use and selective herbicides had increased the extension and the position of underground system of this pernicious weed. This disconnection has also an important effect on regenerative capacity. A major obstacle to *I. cylindrica* control is this regeneration from buds on rhizomes that have been disconnected from mother plants. The disconnection of rhizomes from mother plants released buds from correlative inhibition. *I. cylindrica* rhizome fragments which had at least one visible bud sprouted, but the growth of buds differed according to the number of buds on the rhizome fragments and the presence or absence of apex.

I. cylindrica rhizomes exhibited apical and shoot dominance. *I cylindrica* bud meristems are regulated by apical dominance. The earliest work (Hubbard *et al*., 1944), however, had indicated that shoots grow from even small rhizome segments. Subsequent work (Peng, 1984) reported little to no sprouting from short speargrass rhizome fragments. Four years later, Wilcut *et al.*, (1988) determined that *I. cylindrica*, unlike other weedy grasses, lacks axillary bud formation along the length of the rhizome, suggesting that *I. cylindrica* rhizomes are unable to send up new shoots following apex damage. More recently Gaffney (1996) has revealed that rhizomes with intact apices produce a small number of new shoots only in the area nearest the undamaged apex, whereas rhizomes that have had the apices removed produce, over several weeks more shoots that have located along the entire length of the rhizome. This result from *I. cylindrica* is in concordance with those found with quackgrass (Leakey *et al.*, 1978), however, it contradicts the result from Chancellor (1974). It appears that the nutrient content of rhizome has a greater influence than the nitrogen added to the soil mix.

Rhizome length and number of buds on that rhizome did not contribute significantly toward subsequent bud growth as shown in many other studies. Vegetative reproduction is believed to be responsible for localized spread of *I. cylindrica* populations as well as establishment of new populations when rhizome pieces are dispersed. The stage of *I. cylindrica* rhizome growth was one amongst main features determining the regenerative capacity of the propagule. Regenerative capacity of rhizomes has been shown to be positively correlated with increased in age, weight, length and thickness of the rhizomes as well as the number of visible buds thereon. Regrowth capacity increased with rhizome maturity, weight. On the basis of regenerative capacity, *I. cylindrica* rhizomes were classified into young, mature and old rhizomes. Success of segment regeneration is determined by the original location of the segment on the rhizome, including proximity to, inclusion of, axillary and apical buds. The young rhizome which had white colour did not sprout since no visible buds existed on it and without roots for up-taking necessary nutrients. However the creamy rhizome which had visible buds and certain roots has a regenerative capacity very high. The probable explanation of decreased sprouting of creamy to black rhizomes is in the repeated growth of buds and the depletion of food reserves from these rhizomes (Vengris, 1962; McWhorter, 1972). The effect of rhizome fragment length on germination of buds is significant for management and control strategies since it is something that can obviously be affected by the type and the amount of tillage, and it may offer an opportunity for preventive approaches through tillage and other production practices. Earlier, work on quackgrass and Johnsongrass showed that the size of the rhizome influenced the germination and the emergence of buds. The buds on short rhizome fragments sprouted the best (Vengris, 1962; McWhorter, 1972).

Regrowth potential of rhizomes is a critical issue in development of control strategies. To eliminate *I. cylindrica*, the rhizomes must be destroyed to avoid regrowth and to deep plough or disc several times during the dry season to desiccate the rhizomes and exhaust the food reserves. It is essential to cut to a depth of at least 15 cm to ensure that most, if not all the rhizomes have been cut, and bring up the cut rhizomes to the soil surface to be exposed to sun light (Terry *et al.,* 1997).

In conclusion, the information obtained from this study of the rhizome system suggests that successful control of *I. cylindrica* by cultivation depends on disturbing the soil to a depth of at least 15 cm under conditions favorable for rhizome desiccation and on breaking the rhizomes into the smallest possible pieces. In the absence of sophisticated machinery, such as rotary cultivation, the former requirement is probably more important but it may possible to improve the degree of rhizome fragmentation by several cultivations with simpler implements. Smaller rhizome fragments are not only less likely to survive at the surface of the soil, but are also less likely to re-establish successfully when buried. The results of this work have greatly expanded our understanding of the environmental effect leading to these conclusions: separating rhizomes from plant mother increases the apical dominance effect, dividing the rhizomes into pieces reduces, but does not completely eliminate bud dominance; the apex dominance effect is reduced by nitrogen fertilization added to culture medium.

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