CHAPTER 6

GENERAL DISCUSSION AND CONCLUSION

6.1 Discussion and Generalizations

A true indigene of South-east Asia, *Scirpus grossus* in a scourge and weed of economic importance in rice fields, abandoned and derelict wet-marshy areas, farmlands, river banks, drainage and irrigation canals, and other water bodies in Malaysia and elsewhere. The sedge is a principal weed species in rice fields and poses a major threat to rice fields in Malaysia. The present sets of studies were undertaken with the principal objective to fill up the limited or paucity of information on this rhizomatous clonal plant with the focus on general growth patterns, demography and modelling of structural modules of the weed based on synthetic populations established in the fields as influenced by selected agro-environmental factors, mediated through time and space. Further, assessment on spatio-temporal dynamics of aerial ramets and subterranean rhizomes, and phenology of the sedge mediated through soil type, fertilizer application, water depth and their interactions were also made.

Rhizomatous plants like *S. grossus* grows and reproduces clonally by rhizomes, from which active nodal buds sequentially grow to form aerial ramets. Clonal branches are formed from the reiteration of the basic units, while flowers and inflorescences come from the reiteration of units bearing modified leaves (Harper 1977; Horn 1978). The population dynamics of many rhizomatous plants is dominated more by the flux of clonal modules. The ability of a single genotype to form fragmented phenotypes is just one of the variants in the life patterns of a modular organism (Harper and Bell 1979; Alderman 2011). The process of new growth is often subjected to different pressures, including the change in soil nutrients, and resource capture ability among individual plants and their modules. Remobilization of internal nutrient helps to support new growth and is a key mechanism to explain the improved performance of nutrient-loaded plants (Salifu *et al.* 2008). It is through this rhizomatous growth at the nodes that aerial ramets proliferate above ground displaying phalanx (*sensu stricto* Baki 1986) growth strategy in concordat with lateral proliferation of rhizomes through soil layers or lattices in search of space for further exploration and intake of nutrients in nutrient pools. These latter display of growth strategy mimicking the guerilla (*sensu stricto* Baki 1986) tactics of the clandestine communist guerilla army in search of the enemy during the war of attritions comparable to the conventional warfare among phalanx of armies of tactical divide. In actual field situations, phalanxes of aerial ramets of *S. grossus* when growing sympatrically with crops or other weed species are actually competing for space, while the subterranean rhizomes are competing for space in the soils in search for nutrients. The highest clonal growth rate in peat soil, in general, was between 10-18 weeks. An outcome similar to the results reported previously by Baki (1988) for time-mediated weekly increase in emerged ramets. At the end of the 24 weeks of study period, when the plots are completely filled with *S. grossus* plants, the total average gross number of emerged ramets in fertilized soils were 126.75 ramets m^{-2} and 117.83 ramets m^{-2} in unfertilized soils, respectively, although these readings were not significantly different at $p < 0.05$. (HSD tests). The parallel figures for the sedge growing in paddy soils were 97.08 ramets m^{-2} in fertilized and 83.67 ramets m^{-2} in unfertilized soils, and these readings were not significantly different at $p < 0.05\%$ (HSD tests).

Under Malaysian environment, *S. grossus* grows in moist soils or under inundated or water-logged conditions. It is these conditions that may impact on the growth performance of this sedge, particularly when subjected to wet and dry soil fluxes or when subjected to different depths of inundation under the natural environment in drainage and irrigation canals, abandoned rice fields, or even as a weed in rice crops. Application of fertilizer had a significant impact on the overall growth performance of generally with regard to population fluxes of the sedge, especially on ramets mortality number, but not on the overall gross populations and net populations as well. The addition of NPK fertilizer at a concentration of (100:30:30) had a significant effect on clonal growth with dramatically increase in the population fluxes of the weed. Likewise, the NPK fertilizer reduced mortality of ramets, and this was similar to the findings of Baki (1988 under paddy soils of the Bungor series.

Mortality of emerged ramets set in 8 weeks after planting of the mother plant with eventual plunging of net populations in the ensuing weeks up to the 24th week, especially in the unfertilized plots. Mortality of aerial ramets also set in the fertilized plots, albeit at a slower rates and lower in numbers (Fig. 2.10a and 2.10b). The numbers of dead ramets recorded were 30.33 ramets in unfertilized peat soils and 8.67 ramets in fertilized soils after 24 weeks (Table 2.1), while the net population of ramets were 87.5 ramets m^{-2} in unfertilized soils and 116.08 ramets m^{-2} in fertilized soils, and these differences were significant at $p<0.05$ (HSD tests) (Fig. 2.10a and 2.10b). These differences in ramet mortality in fertilized *vis-a-vis* unfertilized soils perhaps explain the relative fitness of those cohorts, indicating higher turn-over of aerial ramets in the unfertilized peat soils compared with those in the fertilized plots. It must be recorded here that at the end of experimentation, scores of aerial ramets still emerged outside the 2 m x 2 m plots, but these were not taken into account in the analysis. At this juncture to speculate whether there is some forms of trade-offs between the production of aerial ramets (as a means of resource capture of light and above- ground space) and the subterranean growth of rhizomes and roots through soil lattices (as a means of lateral exploitation and exploration of space, water and nutrients) is superfluous. From previous studies by Harper J. L. and his school (Sagar 1974; Harper 1977; Franco and Silvertown 1996; Baki 1986, 1988; Faravani and Bakar 2007), *inter-alia*, indicated a mechanism generally known as the "integration of modules" prevailed in modular plants, where trade-offs occurs among modules in the partitioning of resources, made more readily available to young growing points (leaves, roots, etc.) compared with older modules, to enable the former to grow in anticipation of resource capture for ensuing growth. In the case of *Oxalis corniculata* (Baki 1986) or *S. grossus*, the active nodal growing points, as represented by the stolons and rhizomes, respectively are located in the peripheries

It was very apparent that the sub-sequent recruitments of aerial ramets appeared convergent (Table 2.3 and Fig. 2.11), where the highest average plant (ramet) height in unfertilized peat soils was 161.67 cm while in fertilized peat soils it was 160.67 cm, after 24 weeks of growth, but these differences were not significantly different at $p < 0.05$ (HSD tests). The parallel figures recorded for paddy soils were shown in Table 2.3 and Fig. 2.11 where the highest mean plant height in unfertilized soils was 172.67 cm, while in fertilized counterparts it was 175.33 cm, again not significantly different at $p < 0.05$ (HSD tests).

Aerial ramets growing in unfertilized soils started to flower 16 weeks after transplanting, while in fertilized peat soils, *S. grossus* started to flower at week 13. At the end of the 24 weeks study period, the average number of flowering ramets in unfertilized peat soils stood at 38.75 ramets m^{-2} *vis-a-vis* 51.58 ramets m^{-2} for those with fertilizer application (Table 2.4 and Fig. 2.12). However, time-mediated measurable differences were observed in the number of flowering ramets between those receiving fertilizers compared with those non-augmented with fertilizer application. The sedge in the unfertilized paddy soils started to flower 16 weeks after transplanting, while in fertilized paddy soils, *S. grossus* started to flower at week 13. At the end of the

24 weeks study period, the average number of flowering ramets in unfertilized paddy soils stood at 16.42 ramets m^{-2} and this was not significantly ($p<0.05$, HSD tests) lower *vis-a-vis* 23.67 ramets m^{-2} for those fertilizer application (Table 2.4 and Fig. 2.12). It appears that the NPK fertilizer, which contained 30% of phosphate, is known to boost flowering in plants, increased the flowering number of the weed. A similar observation was reported by Baki (1988).

Baki (1988) experimented with NPK fertilizer application to assess its possible effect on the phenology of *S. grossus* and reported enhanced flowering among the sedge populations. In the present experiments, time-mediated measurable differences were observed in the number of flowering ramets between those receiving fertilizers compared with those devoid of fertilizer application. At the end of the 24 weeks study period, the average number of flowering ramets in unfertilized peat soils stood at 38.75 ramets m^{-2} *vis-a-vis* 51.58 ramets m^{-2} for those with fertilizer. The parallel figures for the sedge in the paddy soils 16.42 ramets m^{-2} in non-augmented with fertilizer *vis-a-vis* 23.67 ramets m^{-2} for those fertilizer application. There is plethora of data in the literature that the addition of N and P to the soil can play an important and significant role in increasing plant growth and development (Miller *et al.* 2006; Gundale *et al.* 2008; Levi *et al.* 2011). Kolb *et al.* (2002) reported that the exotic annual weed *Lolium multiflorum* grew at a faster rate and increased its competitive effectiveness more than the perennial native weed *Hordeum brachyantherum* in the presence of nitrogen.

In the case of increased water depths, the population increase of ramets of *S. grossus* were severely curtailed with parallel increase in mortality. Employment of an effective flooding survival strategy, either quiescence or escape, is thus crucial for plant competitive vigour and survival. Physiological studies have revealed that the gaseous plant hormone ethylene, which rapidly accumulates within flooded organs attributable to the reduced gas exchange underwater, is one of the main drivers regulating both strategies. Indeed, ethylene is considered to be the most reliable and earliest indicator of the flooded status of a plant (Voesenek and Sasidharan 2013). On the contrary, there is no concrete evidence from the experimental data that *S. grossus* instituted such escape or quiescence strategy to increase population number of ramets, enhanced biomass production or increased plant height with increased water depth. In fact, with increased depths of inundation, population number of ramets decreased, irrespective of fertilizer regimes. However, there are evidences from the experiments conducted that plants of *S. grossus* have a remarkable ability to alter their development in response water depth regimes. This phenotypic plasticity allows them to continually adapt to their local environment, a necessity for plants as sessile organisms. Further, deep or transient flood conditions favour species with growth-suppressing behaviour upon submergence by limiting carbohydrate consumption and elongation growth, the so-called quiescent strategy (Fukao *et al.* 2006; Akman *et al.* 2012). This situation seems prevalent among *S. grossus* populations subjected to increased depth of flooding or inundation, where mortality rates were increased accordingly.

The results of experiments in Chapter 3 on chlorophyll content in *S. grossus* leaves in fertilized and unfertilized peat and paddy soil have shown that, although the chlorophyll content was slightly higher in the fertilized soil, the differences were not significant. (Fig. 3.4. and 3.7.) Similarly experiments investigating the biomass of *S. grossus* leaves, stem and flowers grown in fertilized and unfertilized peat and paddy soils also showed no significant differences when *S. grossus* was grown on the same soil. However when grown on paddy soil *S. grossus* developed larger leaves stem and flowers (Fig. 3.5. and 3.8.) With regard to chlorophyll fluorescence, which reflects the photosynthetic capacity of the plant, no significant difference was recorded between *S. grossus* grown in fertilized and unfertilized soils, although it was noticeably slightly higher in plants grown in paddy soil (Fig. 3.6. and 3.9.) The latter experiments showed that photosynthesis was not significantly influenced by the addition of fertilizers, nor by the different soil types used in this study.

These observations may be due to the elemental resources present in the soil, necessary for plant growth, being enough and thus the addition of fertilizers did not bring about any significant differences, in chlorophyll content of the leaves and the photosynthetic ability of the plants. In addition, the use of the NPK fertilizer did not result in the development or growth of larger leaves, stem and flowers when grown on the same soil, although these plant parts were significantly larger when *S. grossus* was grown on paddy soil. This indicated that the paddy soil was more suitable for the growth of *S. grossus*, because it is also naturally found growing in rice fields. The observations recorded in this study is different from what has been reported in many previous studies which have shown that the application NPK fertilizer can effect clonal growth of crop plants, such as in wheat (Ognjanovic *et al.* 1994; Biberdzic *et al.* 2011). This probably indicates that *S. grossus* grows optimally only in a soil in soil inundated with water, such as the paddy soil. Baki (1988) had earlier reported that the growth of *S. grossus* was affected by the depth of inundation with water.

Both leaf chlorophyll content and chlorophyll fluorescence parameters. (Fv/Fm) can be considered to be “stress indicators” (Maxwell and Johnson, 2000), and any significant changes can be taken to indicate a negative/positive impact on the plant of the different fertilizer treatments in this study. According to the literature typical Fv/Fm parameter values for dark-adapted non-stressed healthy leaves in C3 plants are in the region of 0,80 to 0,83 (Bown *et al.* 2009; Murchie *et al.* 2009). The Fm/Fv values observed in this study were slightly lower than these values ranging between 0.71-0.79. As pointed out above this probably indicates that the soil on which the *S. grossus* plants were grown had sufficient macro and micro nutrients to support healthy growth during the period of exprimentation. In a study on the effects of fertilizer on the leaf chlorophyll fluorescence parameters, chlorophyll content in *Carya cathayensis,* Song *et al.* (2011) reported a slight increase in both parameters during the early growth period (30-60 days), but a remarkable decrease in mid and later growth periods (75 - 120 days).

In experiments 3.4.7 and 3.4.8 chlorophyll content in the leaves of *S. grossus* was subjected to different water depth levels for 16 weeks. As reported above, it was observed that increasing the level of water depth had significant effect on the content of chlorophyll in the leaves of *S. grossus*. However, Osborne *et al.*, (2002) reported that in *Zea mays* L., there was an inverse relationship between water depth and chlorophyll content, with chlorophyll content decreasing with increasing water depth. The negative effects of water on photosynthesis has been reported previously by Tripathy *et al.* (1981) and Pandey and Sharma, (2002).

Wersal and Madsen, (2011) reported significant decline in biomass and plant length as water levels increased, suggesting that submersed leaves alone cannot sustain *M. aquaticum* growth for long periods of time. Earlier, Salvucci and Bowes, (1982) reported optimal photosynthetic rates of *M. aquaticum* was observed in the emergent form and *M. aquaticum* can not remain as a submersed plant for long periods of time as the photosynthetic rate of submersed leaves may not be sufficient to support plant growth.

Previous studies have reported that leaf photosynthetic rates are reduced in plants grown under water probably providing some evidence for an energetic cost involved in heterophyllous plants (Cook and Johnson 1968), However, in this study it was observed that there was a decrease in chlorophyll content in the leaves of *S. grossus* when increasing fertilizer concentrations were added to plants grown under 20 cm water depth. This could be due to several reasons, as has been reported in many studies previously, such as the low rates of photosynthesis observed in *M. aquaticum* as the leaves are flooded for extended periods (Salvucci and Bowes 1982). They suggested that the rate of photosynthesis of the immersed leaves was probably not sufficient to support plant growth. It was also suggested that the growth of the submersed leaves was transient and only utilised for short overwintering periods and times of reduced light and temperature (Sytsma and Anderson 1993a). Another study reported that the presence of algae can lead to reduced hydrocarbon content, and works as a contraceptive light and thus inhibiting the growth of *Botryococcus braunii* (Deng *et al.* 2012).

As mentioned earlier, in this study it was observed that water depth did not affect the chlorophyll content. However when NPK fertilizer was added to plants grown under a depth of 20 cm, a decrease in chlorophyll content was observed, with a greater decrease in increasing fertilizer concentrations and subsequently to the death of the plant. The latter observation could be due to several reasons such as the plant is unable to grow normally under a depth of 20 cm when the fertilizer added becomes poisonous for some reason.

The comparative meta-analyses in the spatial spread and proliferation of aerial ramets and sub-terranean modules of *S. grossus* were attempted through fractal dimensions, plant topography, response surface, dispersion and directionalilty analyses in plots of peat and paddy soils form the body of experimental results and discussions in Chapters 4 and 5. As displayed in Figs. 4.3 – 4.26 the time-mediated emergence and ensuing growth of aerial modules (ramets) of *S. grossus* with or without fertilizer applications on peat and paddy soils of Jawa series, with sub-terranean rhizomes radiated from the points of origin, the respective mother plants, originally into two quadrants bifurcating away from each other as early as in the first two months after transplanting of the mother plants (Figs. 4.5 – 4.26) . It was from these nodal points that aerial ramets emerged, again initially in the two quadrants, only to form very apparent four quadrants of growth points (Figs. 5.4-5. 26). These aerial ramets registered and displayed growth patterns essentially the reverse of Kurosaki's "*rich periphery, poor center"* (*sensu* Kurosaki *et al.* 2003) phenomenon with time- and space-mediated ensuing growth heavy loads of population pressure in the centre of the 2 m x 2 m plots among cohorts of S. *grossus.,* while in the periphery the opportunistic strategy of continuing exploitation space, and "edge effect" (*sensu* s*tricto* Baki 1986) prevails unabated. Interestingly when the growth patterns of subterranean rhizomes were examined, it was very apparent that the ensuing growths of rhizomes, radiated into "two quadrants" then into "four quadrants" from the centre, i.e. mother plant, by placing themselves "away" from their respective cohorts so as to avoid intra-modular competition between them, while searching for peripheral spaces and exploitation of resources. This growth strategy in the exploitation of space and resources by the subterranean rhizomes with or without fertilizer application, irrespective of soil types is indeed akin to "*poor in the centre, rich in the periphery*" (*sensu* Kurosaki *et al.* 2003), phenomenon, expounded by Kurosaki *et al.* (2003). Further, this phenomenon is exactly the opposite by those phalanxes of aerial ramets, as illustrated in Chapter 4 (pp. 199-225). These cohorts were not detached from the mother plant in the centre, and linkages between young and old cohorts still prevailed. The basic question arising from this juxtaposition of aerial and sub-terranean modules, is how are nutrients being strategized to achieve optimal growth, or is there any optimal growth at all at a particular point of time and space? The fact that these cohorts are not detached but interconnected from each other, points to the arguments proposed by Baki, (1986, 1988) that some kind of integration modules occurs so as to allow, more active growth not in the centre of the 2 m x 2m plots but in the peripheral growing points for more emergence of new modules. In similar veins, it would serve another research frontier to have radio-tracer technique studies under controlled environment perhaps with C^{14} to autoradiograph the nutrients pathway fed from the centre and follow through their movements in both aerial and subterranean modules. Equally enchanting will be further research pursuits to understand the compensation points and possible trade-offs between the aerial exploration of space together with the ability of produce photosyntates not only to serve the aerial ramets but also the subterranean rhizomes of the sedge within the framework of "source" and "sink" mechanics. This would be an interesting exercise to test the hypothesis that there is a possibility of "integration of modules'' (*sensu* Baki 1986) taking place in *S. grossus* as a "safety mechanism" to ensure that young-growing subterranean modules (in this case represented by rhizomes) in the peripheries do get better access to nutrients *vis-à-vis* the older ones in the centre. These theoretical considerations and their possible experimental proofs will help understand better the growth and survival strategy of this weed as influenced by agro-environmental variables namely, water depths, soil traits, fertilizer application, and management practices, particular among rice farmers to manage this weed. Equally interestingly, this divisive, time-mediated mutual avoidance growth strategy displayed by the rhizomes of *S. grossus* is also akin to the "guerrilla" (*sensu* Baki 1986) growth strategy by other rhizomatous plants like *Cyperus malaccensis* Lamk. (Baki, *unpublished* data) or stoloniferous plants like *Oxalis corniculata* L. (Baki 1986) or "a-mile-a-minute" *(Mikania micrantha* HBK) or *Mimosa longihirsuta* Baki, Mohamed & Noormawati (Baki, *unpublished data*).

In the plant topography-fractal dimensions analysis, fractal dimensions of the time-mediated emerged aerial ramets are analysed to generate three-dimensional (3D) shape and other information (Sarkar and Chaudhuri 1992). Using Excess Green minus Excess Red (ExG − ExR), coloured vegetation (in this case the emerged ramets of the sedge) can be separated from the various field backgrounds, and the corresponding gray-level images with a uniform background are acquired (Wu *et al.* 2009). It was obvious that there was an inverse relationships between gray-level and fractal dimensions (Figs. 4.28, 4.29). This indicates that more spaces are occupied by the ramets in the centre of the plots compared with the peripheries, some akin to the reverse of Kurosaki's "*rich in the periphery, poor in the centre*" (*sensu* Kurosaki *et al.* 2003) phenomenon with time- and space-mediated ensuing growth heavy loads of population pressure in the centre of the 2 m x 2 m plots among cohorts of S. *grossus.* Interestingly, more dispersed distribution of these ramets prevailed in the non-fertilized plots of the peat soils, compared with the fertilized counterparts. In paddy soils, heavier phalanxes of ramets were observed in the centre compared to the peripheries in fertilized plots than the non-fertilized plots, and the latter case signified the attempts by subterranean rhizomes in search of nutrients away from the centre, through which emergence of aerial ramets from the rhizome nodes occurred.

The *Fractal Dimension Analysis* of subterranean rhizomes through *Fractal Dimensions Software's Box-Counting Method* by ImageJ program on *S. grossus* in peat and paddy soils showed no significant differences in peat soils (fractal dimension between 1.52 ± 0.53 and 1.50 ± 0.59) in unfertilized and fertilized plots. (Table 5.5 and Fig. 5.29). However, it was observed that there were significant differences in the direction of growth in peat until 12 weeks in fertilized plots, where we can see two different directions of growth (Table 5.5 and Fig. 5.29). Also, it was found that in peat soils there was more space between emerged ramets (Fig. 5.30), indicating the extra ability of rhizomes to penetrate further the peat soils lattices *vis-à-vis* the paddy soils. Ultimately, monthly-fractal analyses of rhizomes indicated the fractal dimensions of rhizomes in fertilized peat soil plots were measurably shorter than those rhizomes in the non-fertilized plots. The reverse cases were registered for fractal dimensions in paddy soils.

Further attempts to assess the modular growth of the sedge in time and space were made based also on aerial ramets populations and sub-terranean rhizome lengths as parameters, and time- and replicate-mediated observations as the functions of fertilizer applications, and soil types using *Response Surface Analysis* (RSA). The response surface is embedded in the time- and replicate-dimensional data space, which is the set of all promising response vectors that could be generated independently of any model. The response surface is a hyper plane for a linear model but may be curved when the model is nonlinear (Myung 2000). In this study, the density functions for both peat and paddy soils, with fertilizer applications of otherwise were obtained with corresponding R^2 values.

The RSA density function stationary points for best location and time obtained for the unfertilized plots of peat soils was at x-distance = 0.03 m, y-distance = - 0.06 m and time = 9.8 months, and this function predicted a maximum density of 178 plants m^{-2} to occur at the location and time. For the fertilized plot, the stationary point was at x-distance = 0.20 m, y-distance = - 0.82 m and time = 11.31months. The predicted density obtained was 291.02 plants m^{-2}. The disparities in maximum densities and extent of spread of the sedge are indicative of the higher potentials of the sedge to spread and proliferate in fertilized plots *vis-a-vis* those devoid of fertilizer applications.

In paddy soils, the parallel figures for fertilized plots were the stationary point obtained for the fitted surface was at x-distance = -0.13 m, y-distance = 0.20 m and time = 8.48 months. However, results of ridge analysis indicated that maximum density increased with time and location (x-distance and y-distance). The models point out to direction of density changes in ramet populations which followed southwest from the mother plant during 3.5 to 6 months period. The data for non-fertilized paddy soils registered lack of fit at $p < 0.09\%$ (Chi-Square tests). The stationary point obtained for the fitted surface was at x-distance = 0 m, y-distance = -0.14 m and time = 8.16 months. This function predicted a density of 28 plants per m^2 to occur at the stationary point. The results of canonical analysis, indicated that the predicted response surface was shaped like a saddle. Because the canonical analysis resulted in a saddle point, the estimated surface does not have a unique optimum. Further, the results of ridge analysis, indicated that maximum density increased with time and location (x-distance and y-distance). The models point out to direction of density changes in ramet populations which followed northeast from the mother plant during the 3.5 to 6 months period.

The dispersion and directionality analyses of aerial ramet populations of *S. grossus* in peat and paddy soils, fertilized or otherwise with NPK generated no special preferences in the direction of modules or emerged ramets as explained based on circular statistics attributes of Rayleigh’s *r,* Rayleigh’s *z,* and mean angle of dispersion (Tables 5.3, 5.4), although there were heavier concentrations of ramets in the eastern sector of the plot, presumably due to phototropic effect of sunlight (Figs. 5.28, 5.29).

The present set of studies on rhizomatous clonal plant species like *S. grossus* opens up new frontiers for further research on population biology of plants, especially on modular dynamics as the functions of agro-environmental and edaphic factors. The sedge responds displayed positively to increased fertilizer application with enhanced growth. The response was somewhat reduced with increasing water depths, despite augmentation with fertilizer. The question arises as to the possibility of reduced uptake of the nutrients with water depths with parallel reduction in bud breaks or these buds remain dormant *in S. grossus*. In other words, the plants are in “quiescence mode”, or activate “escape strategy” mechanism with reduced growth to escape increased mortality or even eventual depth under those growth conditions. These intrigues remain a new frontier for research.

Simple canonical and ridge analyses on the spatio-temporal spread of the sedge, indicated that the predicted response surface indicated that maximum densities, in peat and paddy soils, either augmented with fertilizer or otherwise increased with time and location (x-distance and y-distance). These optimum values in time and space, generated by these analyses did not actually help to explain the actual roles of fertilizer or soil types (actual key constituents and attributes) in population spread of aerial and subterranean modules. Further field experimentations on the growth, spread and ramification of these modules as influenced by key soil attributes and agronomic factors and practices, followed by the more robust Canonical Correspondence Analysis (CCA), or Canonical Discriminant Analysis (CDA), or Principal Component Analysis (PCA) will show which of the key soil attributes and agronomic factors and practices influence the time- and space-mediated growth patterns of the sedge.

Plant architectures are affected by endogenous factors such as hormone signals and trophic competition between organs, but exogenous factors such as light distribution, temperature, soil water and nutrient regimes also influence the time-mediated resultant architecture produced. Plant morphology can as well be artificially modified. Many efforts have been made in the last decade to model the structural development of plants taking into account their plasticity, that is, their ability to adapt their shape and to regulate their functions in a changing environment (Baki 1986, 1988; Cieslak *et al.* 2011; Pallas *et al.* 2011; Yan *et al.* 2011). In this study on the architectural models of *S. grossus,* it is unknown whether there is such thing as compensation points in the vertical growth of aerial ramets with the parallel growth of lateral subterranean rhizomatous counterparts. If there is, when will the plant switch on their hormonal signals favouring either one of the growth mechanics, and continue the exploitation of space and nutrients to sustain growth. Perhaps in their exploration and exploitation of space and nutrients in different soil types, the sedge manifest itself in growth trade-offs favouring either the phalanxes of aerial ramets for maximization of photosynthates production, or producing more rhizomes to strategize "guerrilla" type in maximization nutrients and space exploitation underground. The existence of these two strategies in the sedge may serve another frontier of research, popularly known as "integration of modules" (*sensu* Baki 1986) in many clonal plants. As deliberated in the preceding Chapters 2 and 4, it would be an interesting exercise to assess the nutrient pathways by employing C^{14} radio-tracer techniques from the mother plant to the peripheries of the rhizomes under controlled environment to test the hypothesis that there is a possibility of "integration of modules' (*sensu* Baki 1986) taking place in *S. grossus* as an "safety mechanism" to ensure that young-growing subterranean modules (in this case represented by rhizomes) in the peripheries do get better access to nutrients *vis-à-vis* the older ones in the centre.

The above studies may also help to explain the growth strategies of *S. grossus* in the exploitation of space and resources by the subterranean rhizomes with or without fertilizer application, irrespective of soil types the theoretical considerations of "*poor in the centre, rich in the periphery*" (*sensu* Kurosaki *et al.* 2005) phenomenon, expounded by Kurosaki *et al.* 2005). In addition, the preliminary topography-fractal analyses carried out in this study pointed out to the fact that irregularity of spacing and empty spaces prevail among emerged ramets of the sedge under different fertilizer and soil regimes. It would serve another research pursuit as to the differential degrees of penetration, hence their respective hardiness, by the growing points of rhizomes in the sub-terannean lattices of peat and paddy soils. Intriguingly the differences in the fractal dimensions of *S. grossus* plants growing under different soil and fertilizer regimes warrants further research and explanation.

6.2 General Conclusions

Under the prevailing experimental conditions in the studies, the following conclusions can be drawn, *viz:*

(i) The optimal period of clonal growth for *Scirpus grossus*, in general was between 10-18 weeks after planting;

(ii) Augmentation with different NPK fertilizer concentrations and at different water depths had the following effects on *S. grossus* growth in both fertilized and unfertilized peat and paddy soils, (a) Increased rate of natality and the population number of ramets, fortified by enhanced proliferation of subterranean rhizomes; (b) Decreased rates of ramets mortality; (c) Increased rate and production of inflorescence of the weed; and (d) Enhanced production of biomass *vis-a-vis* the control of various plant components. However, the NPK fertilizer treatment did not have a significant impact on the plant height; chlorophyll content; and chlorophyll fluorescence, registering non-significant difference in both fertilizer and control plants.

(iii) Fertilizer concentration with water depth did have a significant impact on the following parameters; namely (a) plant height; and (b) inflorescence number.

(iv) Aerial modular growth, dispersion, response surface, plant topography-fractal analyses on emerged ramets, and fractal dimension boxing analyses of subterranean rhizome modules confirmed that the fertilizer treatment (at NPK 100:30:30) did not have a significant impact on the growth patterns of *S. grossus.*

6.3 Future Studies

The present studies open new venues for further research on rhizomatous plants like *S. grossus.* With the display of dualism in growth strategy several intriguing questions could serve as potential areas in future research. Interestingly, how and when does this weed optimise resource capture via its subterranean rhizomes vertically and horizontally? Theoretically the plant's rhizomes could dig deep in the soils in search of more nutrients, but perhaps at the expense of lesser chances of bud breaks, emerging as aerial ramets through time and space. In similar veins, when will it be the optimum time to emerge as aerial ramets for above-ground resource capture? A relevant issue would be the compensation point in resource capture with possible trade-offs if any between aerial phalanx phalanx and guerrilla growth pattern and strategies *vis-a-vis* the subterranean guerrilla growth pattern and strategies of the rhizomes. This is quite pertinent to the related issue on the optimization of population concentration in a unit area be ascertained without compromising for any trade-offs on clonal growth *vis-à-vis* reproductive growth? Further, how could horizontal clonal growth (as manifested by time- and space-mediated ramification of rhizomes) and vertical growth (as displayed by emergence of ramets population) be in synchrony with each other (with or without any trade-off between them) for regulated optimization of resource capture? Another issue in hand would be the possible role of phenological patterns and reproductive growth in their affects on rhizomatous clonal growth of the weed, or *vice-versa*.

We have seen the impact of NPK fertilizer application, soil types and water depths on the population dynamics and sequential growth of the weed. Interestingly these effects were demonstrated by a series of population models of aerial ramets and architectural models of subterranean rhizomes of *S. grossus*. The factorial analyses of growth and population data complement such models in the attempt to understand the growth strategies of the weed. Such analyses and models do not actually explain the cohort dynamics within the realm of spatio-temporal cohort fitness. Cohort fitness helps to explain the age-mediated survivorship pattern as influenced by agronomic factors like fertilizer regimes, water depths, and soil types. The actual positioning of all emerged cohorts and their sequential monitoring within the duration of the experiments would generate pertinent information on the actual dynamics and phenological patterns through time and space as the functions of agro-environmental variables.

Our study generate valuable information on the population patterns and dynamics of *S. grossus* devoid of other weed species or crops that may grow in sympatric with each other under field situations. Future studies should explore growth and survivorship for *S. grossus* plants under limited resources in the presence of intra- and inter-specific competition from neighbours in the continuing effort to understand optimization of resource capture. No information was made available on the biomass allocation and resource partitioning of different plant components of *S. grossus* as influenced by agro-environmental variables through time and space from the present study. Monitoring the biomass allocation and resource partitioning of these plant components would help to explain the possible change in growth strategy and capture of the weed to ensure continuous survival into new generations. Further, monitoring of resource capture through C^{14} and other elemental radiographs would help to trace the concentration of carbon and other elements in the different plant components of the weed, given the growth conditions that they are subjected to. These studies serve another venues for further research.

In effect these future studies entail in the generation of life-tables of *S. grossus* as influenced by agro-environmental variables tracing cohort fitness and survivorship patterns mediated through time and space. These life-tables serve the understanding of spatio-temporal population dynamics of rhizomatous plants like *S. grossus*, better.

PUBLICATIONS

Journal Articles

Majrashi, A. A., Nasrulhaq, A., Jaafar, A. M., Khandaker, M. M. and Bakar, B. B. 2013. Structural demography, modular dynamics and growth patterns of above-ground populations of *Scirpus grossus* L. on paddy field. *Bulgarian Journal of Agricultural Science* **19**:03-24.

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Conferences

Majrashi, A.A., Nasrulhaq, A., Jaafar, A.M. And Bakar, B.B. 2011. Allometry and growth patterns of *Scirpus grossus* L. on peat. *Proc 23rd Asian-Pacific Weed Science Conference, 25-30 September 2011, Cairns, Australia*, pp. 340-349.

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