The population biology of wrinklegrass (*Ischaemum rugosum* Salisb.) - Seed and seedling dynamics

[Biologi populasi rumput colok cina (*Ischaemum rugosum* Salisb.) – Dinamik biji benih dan anak benih]

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Abstrak

Penyelarasan populasi, satu proses yang menetapkan ketentuan individu, wujud di dalam sesuatu persekitaran. Kerap kali tapisan persekitaran yang menyelaras silih ganti populasi individu di dalam sesuatu populasi sama ada bergantung pada kepadatan atau masa melalui fasa-fasa pengeluaran biji benih, serta kemunculan dan pertapakan anak benih. Kajian telah dijalankan untuk menilai dinamik populasi biji benih dan anak benih rumput colok cina (*Ischaemum rugosum* Salisb.) dari segi kepadatan dan masa.

Daya pengeluaran biji benih generasi pertama dan kedua bagi populasi sintetik rumput colok cina tidak ketara berbeza berbanding dengan populasi asal induk, meskipun hubungan purata hujan biji benih sepokok adalah berlawanan dengan peningkatan selari kepadatan taburan atau hujan biji benih. Satu genet rumput colok cina yang tumbuh sendirian tanpa jiran mengeluarkan sehingga 6 000 biji benih bagi satu kitaran hidup selama 4 bulan atau 18 000 biji benih setahun. Nilai selari bagi kadar tabur pada kepadatan 1 000–6 000 biji benih/m di dalam generasi pertama populasi sintetik adalah di dalam lingkungan 48–62 biji benih sepokok. Daya pengeluaran biji benih rumput colok cina berkurangan sebanyak 50% bagi dua kali peningkatan selari kepadatan hujan biji benih. Kejayaan penjelmaan anak benih daripada hujan biji benih adalah masing-masing pada kadar 85% dan 90% bagi generasi pertama dan kedua.

Penyelarasan populasi melalui mortaliti anak benih yang bergantung pada kepadatan atau pengurangan sendirian populasi, dan pengurangan populasi dari segi masa wujud di kalangan generasi pertama dan kedua populasi sintetik anak benih. Kadar kejayaan bagi anak-anak benih yang muncul bertapak menjadi dewasa ialah 80.8% dan 22.8% masing-masing bagi populasi generasi pertama dan kedua. Purata jumlah berat biji benih bagi dua generasi berturut-turut rumput colok cina adalah seiringan dengan Hukum Hasil Akhir Konstan Kira.

Abstract

Population regulation, an important process determining the fate of individuals, prevails in an environment. Quite often the environmental sieves regulating the population fluxes of individuals in a population are either density- or time-mediated through the phases of seed production, seedling emergence and

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establishment. Studies were conducted to assess the density- and time-mediated dynamics of synthetic seed and seedling populations of wrinklegrass (*Ischaemum rugosum* Salisb.).

Seed production capacity of the first, and second generation synthetic populations of wrinklegrass did not vary significantly with the initial parental population, although the mean seed rain per plant was inversely related to the corresponding increase in sowing or seed rain density. A single genet of wrinklegrass grown devoid of neighbours, produced up to 6 000 seeds within a growth cycle of 4 months or 18 000 seeds per year. The parallel figures for the respective sowing densities of 1 000–6 000 seeds/m^2 in the first generation synthetic population ranged from 48–62 seeds/plant. Invariably, the seed production capacity of wrinklegrass was reduced by 50% with twice the corresponding increase in seed rain density. The respective success rate of seeds from the seed rain emerging as seedlings were 85% and 90% in the first and second generation populations.

Population regulation via density-dependent mortality or self-thinning, and time-mediated decrease prevailed among emerged seedlings in the first and second generation synthetic populations. The success rates of emerged seedlings becoming established plants in the first and second generation populations were 80.8% and 22.8%. The mean total seed weights of two successive generations of wrinklegrass were in line with the Kira's Law of Constant Final Yields.

Introduction

Seeds are the fundamental unit for propagation and continued survivorship in most annuals (Mortimer et al. 1989) and the seed phase represents the longest stage in their life cycles (Chauvel and Darmency 1989). For annuals and perennials alike, the most common demographic phases and parameters include seed bank, emerged seedlings, mature plants, seed rain, and seed dispersion (Sagar and Mortimer 1976; Mortimer 1983; Baki 1986, 2001; Fernandez-Quintanilla 1988; Grannados and Garcia 1993; Nabi 1999). The seed bank is considered the most critical phase among the demographic phase of annual weeds (Baskin and Baskin 1983; Yuguang et al. 1994; Nabi 1999).

In arable fields, the seed bank of annual weeds is in the state of continuous dynamic state. This state is reflected in fluxes of seeds from seed rain of the vegetation *in situ*, or/from adjacent fields, and from external sources such as farm equipment, contaminated crop seeds, animals, wind or manure (Fenner 1995;

Buhler et al. 1997), and seed population depletion and lost through natural seed decay, predation, ageing, and germination (Kremer 1993; Fenner 1995; Buhler et al. 1997; Nabi 1999). The longevity of weed seeds, the size of soil seed bank, and species composition are governed by the totality of the prevailing environmental factors, seed dormancy characteristics, and prevailing management practices, mediating through their influence on seed dormancy and seed germination.

Seed population depletion through germination in undisturbed soils is mainly attributed to seed germination (Fenner 1992) - an important element in bio-economic weed management models (King et al. 1986). This loss has been estimated to be 22% per year in undisturbed soils compared to 30–36% per year in disturbed soils (Roberts 1962; Roberts and Dawkins 1967; Shaffer and Chilcote 1970). Others maintained that seed loss through germination following soil disturbance ranges from 1% to 50% for a given year (Roberts and Ricketts 1979; Roberts and

Potter 1980; Forcella et al. 1992; 1997; Cousens and Mortimer 1995). Reliance on seedling emergence for depleting the soil seed bank is based on the fact that the seedling phase in the life of a plant is usually considered the most hazardous (Harper and White 1974).

Modern weed control techniques require a thorough understanding of the population dynamics of dormant viable weeds in the soil seed bank (Roberts 1963). Seed bank population dynamic models are important elements in the weed management variable inputs. Such models are of paramount importance in predicting potential seedling densities and weed competition, crop losses, necessary inputs and financial returns (Forcella et al. 1992). Seedling emergence models could be used to predict weed infestation patterns in future crops and aid in decision-making on the use of preventive measures when losses are expected to exceed an economic threshold (Roberts and Ricketts 1979; Ball and Miller 1989; Chauvel and Darmency 1989; Forcella et al. 1992; Prostko et al. 1997; Buhler et al. 1997). Population regulation is an important process in determining the fate of individual seed, seedlings, and established plants in an environment. Quite often the environmental sieves regulating the population fluxes of individuals in a population are either density- or time-mediated through the phases of seed production, seedling emergence and establishment.

This paper reports on a series of study to investigate the seed and seedling dynamics of wrinklegrass based on synthetic populations grown in an insect-proof house.

Materials and methods
Experiment 1. The establishment of first generation synthetic population
This study was conducted in an insect-proof house in the Institute of Biological Sciences, University of Malaya, Kuala Lumpur, Malaysia in April 1997 to June 1998 with mean daily temperature of 27 °C, RH of 85%, and the mean daily sunshine of 11.30 h.

A total of 12 wooden boxes measuring 1 m x 1 m x 40 cm previously lined with polythene sheets were filled with moist silt loam paddy soils of the Java series to a depth of 35 cm. These boxes were arranged in three rows of four boxes. The physico-chemical characteristics of the soil have been described elsewhere (Nabi 1999). A 1 m x 1 m quadrat previously lined with wire strings at 10 cm x 10 cm spacings was placed on top of each box, thereby dividing it into 100 equal size sub-compartments.

Fresh matured seeds of wrinklegrass (*Ischaemum rugosum* Salisb.) previously collected from rice fields in Pulau Pinang, Malaysia were heat treated for 1 week at 30 ºC in an oven in the laboratories of the Institute of Biological Sciences, University of Malaya, Kuala Lumpur. The first generation synthetic population of wrinklegrass was established by sowing the oven-dried pre-soaked seeds at random into the soils in each box on 15 April 1997. These boxes were sorted out into four sets of three replicates, and each set was randomly assigned to one of the four density regimes sown with 1 000, 2 000, 4 000 or 6 000 seeds/m^2. The seeds were then covered with a thin layer of soils. The boxes were watered twice daily from above using a fine spray. Monthly supplements of urea (N), muriate of potash (K_2O) and triphosphates (P_2O_5) at the respective rates of 100, 30, and 20 kg/ha were appllied to the soils in the boxes.

The number of emerged seedlings in each box was recorded every 3 days for 2 weeks using randomly chosen 10 sub-compartments/quadrats or seedlings until the cessation of emergence. Data pertaining to wrinklegrass seedling establishment (survivorship) and mortality were recorded every 2 weeks until no mortality cases were recorded among the established plants. Prior to seed set, 1.8 m high polythene sheet barriers were erected around each box. Sixteen weeks after sowing, watering was ceased to allow the plants to desiccate. Two weeks after cessation of watering, the aerial

plant parts were clipped and removed from the boxes. The polythene sheet barriers were then removed. A second set of similar experiment was conducted in April 1999–June 2000.

Experiment 2. The demography of seeds and seedlings over 3 generation populations

Ten cylindrical soil-core samples (2.5 cm diameter and 10 cm deep) were taken at random from each box. These samples were placed in polythene bags and taken to the laboratory for wrinklegrass seed bank analysis using the methods of Baki (1986). Each sample was crumbled with fingers into small fractions and placed in a beaker standing on a fine sieve. High-pressure tap water was applied to the soil in the beaker and the overflowing water containing soil and plant materials and seeds were filtered by the sieve. Plant and soil debris other than the wrinklegrass seeds were removed.

Total seed counts from each soil sample were made, separating viable seeds from dead or empty ones. Those seeds believed to be healthy were placed in petri-dishes lined with moistened filter paper. These petri-dishes were placed in a growth chamber, maintained at a constant temperature regime of 30 °C and light intensity of 630 Em^2s. Germinated seedlings were counted and removed daily for a period of 10 days. Seeds failing to germinate were re-examined individually. The remaining non-germinated seeds were subjected to viability tests using 2,3,5-triphenyl tetrazolium chloride.

Following the removal of the aerial plant parts and recommencing of watering of the soils in the boxes, census on seedling emergence, survivorship, and/or mortality of the second generation population from the seed rain provided for by the first generation population commenced using the same method described earlier. Prior to the seed set, a 1.8 m high polythene sheet barrier was erected around each box. Watering ceased 16 weeks after seedling emergence of the

second generation population, followed by removal of the aerial plant parts 2 weeks later. Census of soil seed bank derived from the second generation population was undertaken using the same procedures outlined earlier for the first generation soil seed bank. The procedures were repeated or the census of the seed, seedling, and established plant of the third generation population.

Similar procedures in the demographic studies of seeds and seedlings from the second set of experiment of the first and subsequent generation populations of wrinklegrass were repeated.

Collated data pertaining to seedling emergence, seedling mortality, and survivorship of the first, second, and third generation populations from the two sets of experiments were subjected to multifactorial ANOVA while the seed rain and seed bank data were analysed using one-way ANOVA. Where appropriate, data transformation was undertaken to homogenise the variance prior to ANOVA. Tukey's tests were used to compare the means of seedling emergence, mortality and survivorship, and seed populations as influenced by density regimes.

Results and discussion
Seedling emergence, mortality and survivorship of wrinklegrass

In the first generation population, seedling emergence of wrinklegrass in all density regimes ceased 6 days after sowing, and was density independent $(p < 0.05)$. The mean percentages of emerged seedlings were 79–88%, and these were insignificantly different from each other, irrespective of the density regimes of 1 000–6 000 seeds/m^2. The failure of 12–21% seeds to germinate could be attributed to their inability to secure safe sites (*sensu* Harper 1977) for successful germination, or those seeds could have germinated but failed to emerge, or had emerged but failed to establish as seedlings (Baki 1986). Further, these fractions of viable but non-germinating seeds could have

acquired induced dormancy due perhaps to inappropriateness of the optimum temperature and moisture range for germination at that particular time and space. Seed viability tests with 2,3,5-triphenyltetrazolium chloride indicated that these retrieved non-germinating seed fractions were indeed viable.

The multifactorial ANOVA indicated that the number of wrinklegrass survivors in the first generation population decreased significantly *(p <0.05)* with time after sowing, and increased in sowing density *(Figure 1)*. Mortality set in 6–10 weeks after seedling emergence. The number of survivors among emerged seedlings 14 weeks after sowing registering only 66, 29, and 19% for the respective sowing densities of 2 000, 4 000 and 6 000 seeds/m^2 among first generation seedling population.

However, no time-mediated decrease or density-dependent mortality occurred among emerged seedling populations with the sowing density of 1 000 seeds/m^2. Significant *(p <0.05)* time-mediated density-dependent mortality of self-thinning also prevailed among emerged seedlings in the second and third generation populations after seedling emergence *(Figure 2)*. Mortality set in 8–12 weeks after seedling emergence, inflicting losses ranging from 34% to 81% to the second generation population, with the equivalents of 76–84% in the third generation population occurring between 6–12 weeks following seedling emergence. Such mortality incidences reflect the truism of Harper's contention that the seedling phase is the most hazardous and vulnerable period in a given plant's life cycle (Harper 1977). Others maintained that seedling mortality may be attributed to direct consequence of the prevailing physical characteristics of the substratum (Baki 1986); lack of safe sites for establishment of newly-emerged seedlings (Sagar and Mortimer 1976), attacks by biotic agents (Miles 1972) or interference from neighbouring plants (Putwain and Harper 1970; Baki 1986; 1995).

Population regulation among wrinklegrass seedlings through density-dependent mortality mechanism is a negative feedback acting to limit population size within narrow limits than the range of starting densities. This mechanism acts as a buffer to maintain wrinklegrass population more constant than would be produced by
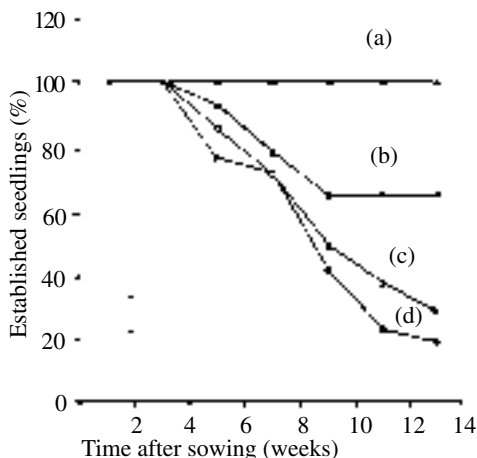

Figure 1. Mean percentages of established seedlings of the first generation population of wrinklegrass sown at (a) 1 000, (b) 2 000 (c) 4 000, and (d) 6 000 seeds/m^2 as a function of time after sowing. Bar represents HSD value at p <0.05
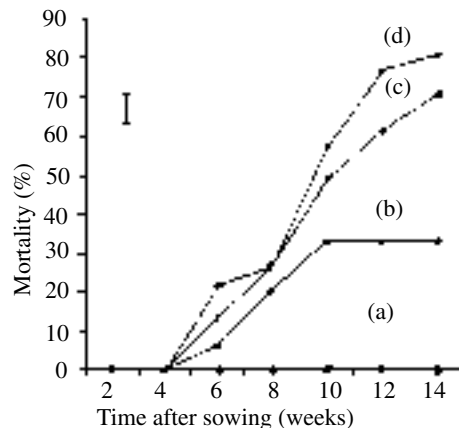

Figure 2. Mean percentages of seedling mortality of the first generation population of wrinklegrass sown at (a) 1 000, (b) 2 000 (c) 4 000, and (d) 6 000 seeds/m^2 as a function of time after sowing. Bar represents HSD value at p <0.05

natural variations in seed production and dispersal. The number of established plants/m^2 of wrinklegrass in the first, second, and third generations conformed remarkably well to Deevey's type III survivorship curve (Deevey 1947), denoting high mortality among young individuals in a population *(Figure 3)*. These curves are common among species growing in habitats that are subjected to frequent disturbance (Silvertown 1982). There were evidences of a slight build up of population size, albeit inconsistencies, in the second population. For example, 14 weeks after sowing there were 880 established plants from the first generation population from plots sown with 1 000 seeds/m^2 compared to 1 333
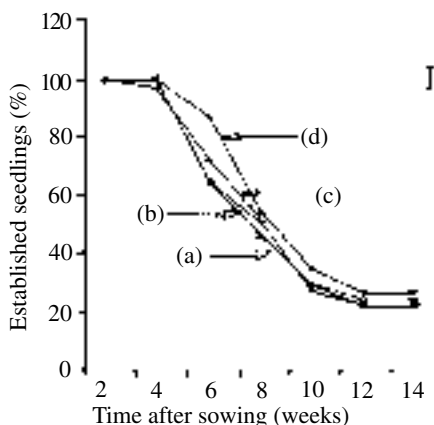

Figure 3. Mean percentages of seedlings of the second generation population of wrinklegrass established from first generation population sown at (a) 1 000, (b) 2 000, (c) 4 000, and (d) 6 000 seeds/m^2 as a function of time after sowing. Bar represents HSD value at p <0.05

established plants/m^2 in the second population. The parallel figures for plots sown with 6 000 seeds/m^2 were 1 467 and 1 488 plants/m^2 *(Table 1)*. Evidently, despite the discrepancies in the initial population of wrinklegrass in the sowing densities of the first generation population, density-dependent regulation of population size prevailed across densities in the second population, approaching similar values in the final established plant population number. The dry weights of established plants irrespective of the starting densities were fairly constant *(Table 2)*, in conformity with Kira's Law of Constant Final Yields (Kira et al. 1953). This implies that the variations in wrinklegrass sowing densities are largely compensated for by variations in the amount of growth accomplished by individual plants.

Seed rain and seed bank of wrinklegrass
Seed production capacity of the first, and second generation synthetic populations of wrinklegrass did not vary significantly *(p <0.05)* with the initial parental population, although the mean seed rain/plant was inversely related to the corresponding increase in sowing or seed rain density. A single genet of wrinklegrass grown devoid of neighbours, produced up to 6 000 seeds within a growth cycle of 4 months or 18 000/year (Nabi 1999). The parallel figures for the respective sowing densities of 1 000 – 6 000 seeds/m^2 in the first generation synthetic population ranged

Table 1. Mean number of established seedlings in the first generation synthetic population of wrinklegrass emerging from different initial densities

Sowing density (no. seeds/m^2)	Weeks after sowing						
	2	4	6	8	10	12	14
1 000	880a	880a	880a	880a	880a	880a	880a
2 000	1 680a	1 547b	1 480b	1 253c	1 053d	1 053d	1 053d
4 000	3 587a	3 587a	3 193b	2 640c	1 786d	1 053e	1 053e
6 000	4 903a	4 903a	4 220b	3 560c	2 046d	927e	925e

Values sharing a common letter in a row are not significantly different from each other at *p <0.05* (HSD tests)

Table 2. Mean weight of 1 000 seeds, and mean dry weight of established plants of wrinklegrass in the first and second generation populations as the function initial sowing density

	Generation	Sowing density (no. seeds/m^2)			
		1 000	2 000	4 000	6 000
Mean weight of	1st	211.4a	216.7a	225.3b	228.4b
1 000 seeds (g)	2nd	236.3a	266.7b	273.6bc	288.2c
Mean dry weight*	1st	2.395a	2.415a	2.456b	2.467b
(kg/m^2)	2nd	2.393a	2.867b	2.886b	2.932b

Values sharing a common letter in a row are not significantly different from each other at
p <0.05 (HSD tests)
*Aerial dry weight

Table 3. Effects of different sowing densities on the number of seeds produced per plant (in brackets), and rates of fecundity (number of seeds/m^2) by the first and second generation populations of wrinklegrass

Generation	Sowing density (no. seeds/m^2)			
	1 000	2 000	4 000	6 000
	Seed rain (x10^4)/m^2			
First	5.27aA	5.36aA	5.70cA	5.54bA
	(53)a	(27)b	(14)c	(9)d
Second	6.40bB	6.30bB	7.20cB	5.90aB
	(59)a	(30)b	(15)c	(10)d

Values sharing a common lower case letter in a row, and a common upper case letter in a column, are not significantly different from each other at
p <0.05 (HSD tests)

from 9–53 seeds/plant, depending on density. Invariably, the seed production capacity of wrinklegrass was reduced by 50% with twice the corresponding increase in seed rain density. The respective number of seeds produced for each seed sown in the first generation synthetic population were 53, 27, 14, and 9 for the initial sowing density of 1 000, 2 000, 4 000, and 6 000 seeds/m^2 *(Table 3)*. The parallel figures for the second generation population were 59, 30, 15, and 10 seeds, indicating a slight build-up of seeds in the seed bank.

The build-up of seed bank population was also exemplified by the marginal increase in the mean seed weight/m^2 in the second generation population ranging from 236 to 288 g/m^2, respectively, compared to 211–228 g/m^2 registered in the first generation population *(Table 2)*. Irrespective of the initial sowing densities, and the

resultant established populations therein, the mean seed weight/m^2 produced was fairly constant in each of the three generations of wrinklegrass. Kira's Law of Constant Final Yields (Kira et al. 1953) also prevailed based on the fairly constant values mean seed weight/m^2 across density regimes in the first, second and third generation populations of wrinklegrass. Again, this implies that the variations in wrinklegrass sowing densities are largely compensated for by variations in the amount of growth accomplished by individual plants manifested here in the seed production capacity.

The authors believed that the number of viable seeds recovered from the seed bank for each generation was an underestimate of the real seed population generated by the established plants of wrinklegrass. The underestimation could
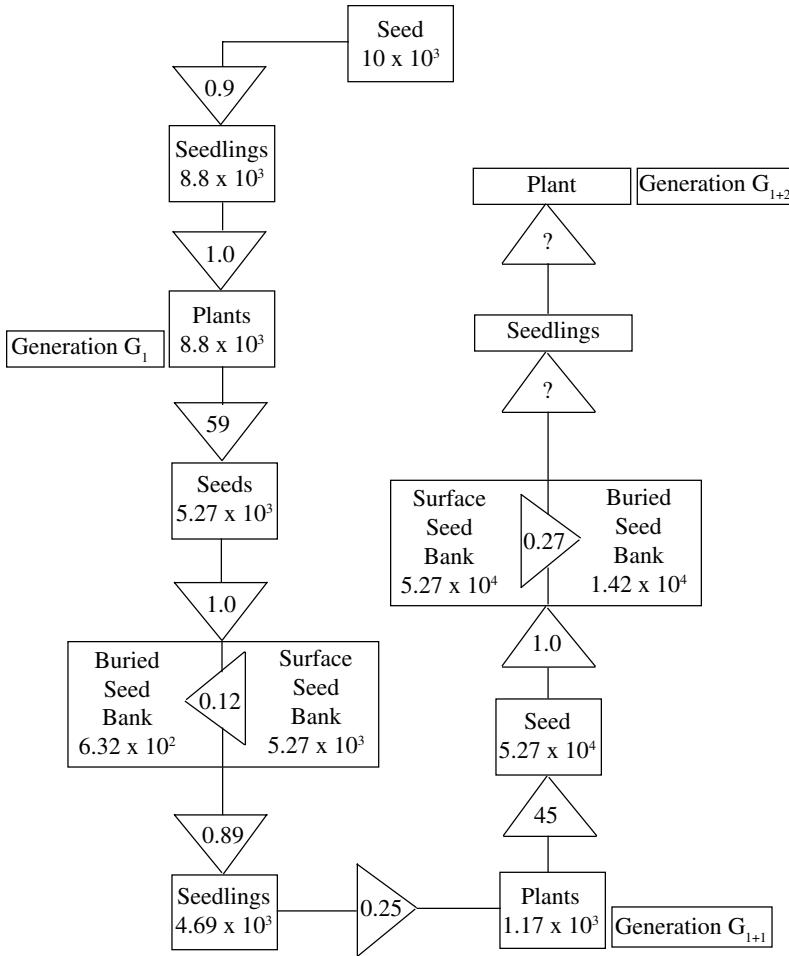
Figure 4. A schematic diagram of the dynamics of synthetic populations of wrinklegrass in the first (G_1), and second (G_{1+1}) populations 32 weeks after sowing at the initial density of 1 000 seeds/m^2 (numbers/m^2)

have been attributed to (i) errors in seed bank sampling techniques in which uniform spatial seed distribution was assumed and the soil cores were taken accordingly; (ii) the two weeks of fallow dry period might have led to seed population decay through natural seed death, predation by seed predators or infection by fungi and other microorganisms; and (iii) lack of soil distribution agents (and seeds) analogous to those occurring in the agro-ecosystems as a result of management practices, although natural macro-pores or soil cracks occurred following the dry fallow period, resulting in

some seeds being buried in deeper soil profiles.

Seed, seedling, and established plant dynamic models of the synthetic population of wrinklegrass

The diagrammatic scheme which best describes the behaviour of the three generation synthetic populations of wrinklegrass in a closed ecosystem where no migration prevails, is the modified scheme for perennials proposed by Sagar and Mortimer (1976), and Lindquist and Kropff (1995). A population of wrinklegrass may be
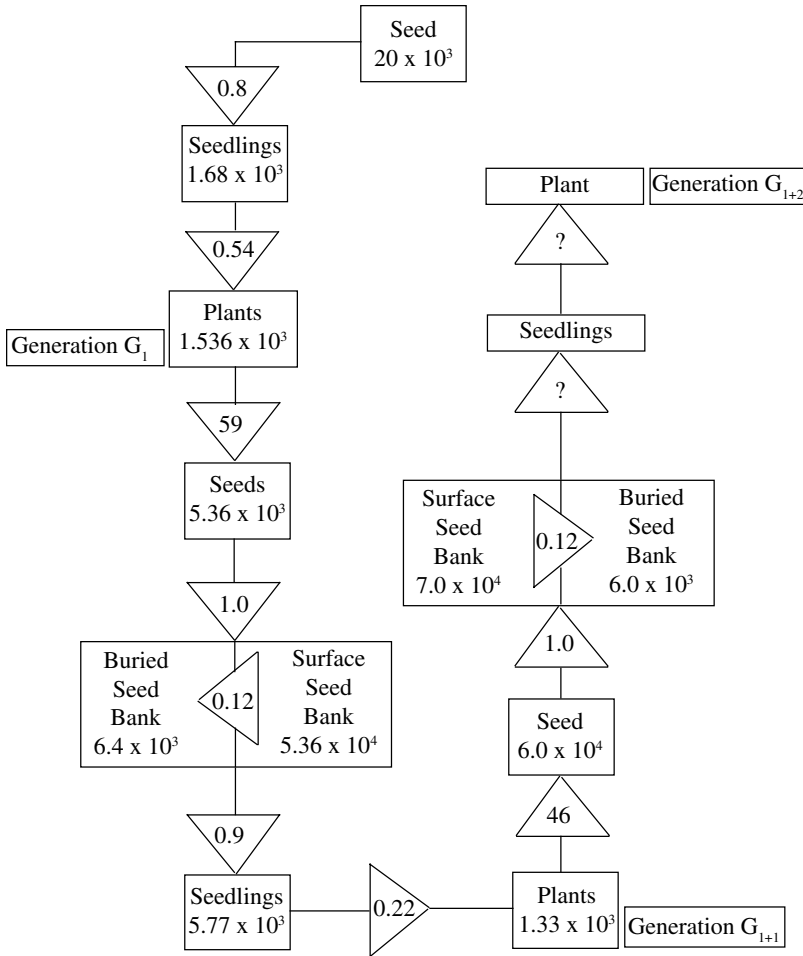
Figure 5. A schematic diagram of the dynamics of synthetic populations of wrinklegrass in the first- (G_1), and second- (G_{1+1}) populations 32 weeks after sowing at the initial density of 2 000 seeds/m^2 (numbers/m^2)

envisaged as a series of cohorts *(Figures 4–7)* in which the fates of individual plants are measured by their probability of survivorship to maturity and their fecundity expressed as an average number of seeds produced in a given growing season.

In the first generation synthetic populations (G_1) *(Figures 4–7)* wrinklegrass sown at densities of 1 000, 2 000, 4 000 and 6 000 seeds/m^2 generated 8.8 x 10^3, 1.68 x 10^3, 3.59 x 10^3 and 4.9 x 10^3/m^2 seedlings, respectively, of which only 8.8 x 10^3, 1.54 x 10^3, 1.17 x 10^3 and 1.7 x 10^3/m^2 of the seedlings established and reached maturity, and the rest failed to establish as a result of

density-dependent mortality. These plants had produced a soil surface bank amounted to 5.27 x 10^4, 5.36 x 10^4, 5.69 x 10^4 and 5.64 x 10^4 seeds/m^2, respectively, as seed rain onto the soil surface to form the constituents of the soil surface seed bank. About 12, 13, 10 and 10% of the surface seed bank of the density regimes of 1 000, 2 000, 4 000 and 6 000 seeds/m^2, respectively, were incorporated in soil to form the constituents of the soil seed bank (Nabi 1999). The detailed seed bank dynamics have been presented elsewhere (Nabi 1999; Baki and Lajili 2003). The probabilities of successful transition from
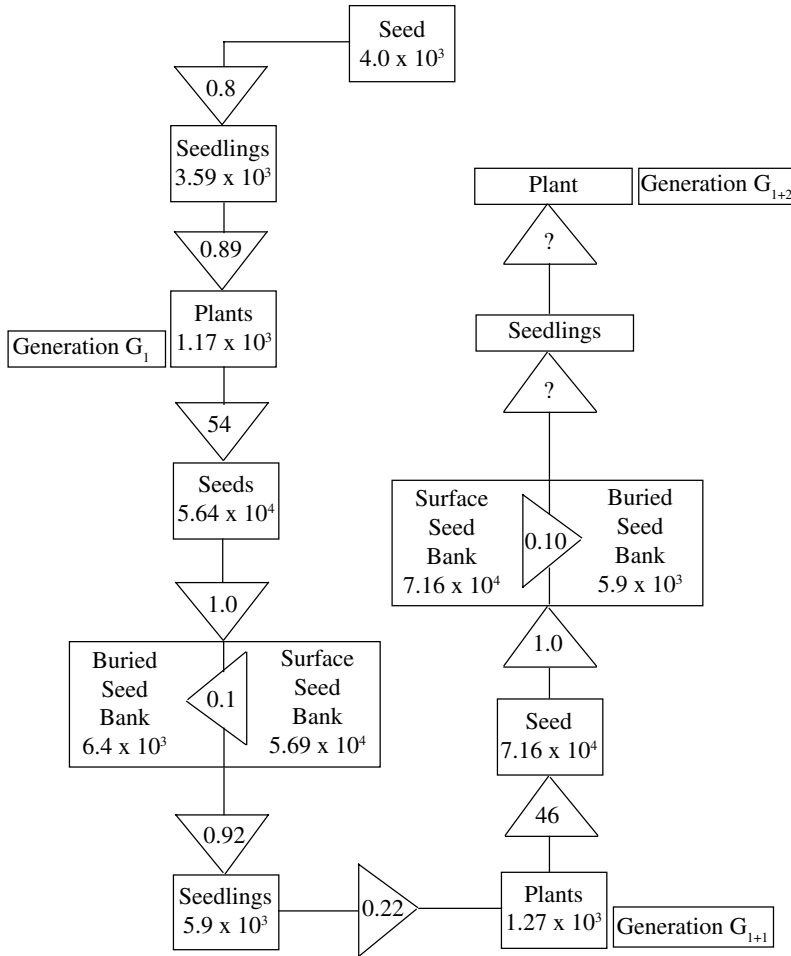
Figure 6. A schematic diagram of the dynamics of synthetic populations of wrinklegrass in the first- (G_1), and second- (G_{1+1}) populations 32 weeks after sowing at the initial density of 4 000 seeds/m² (numbers/m²)

total seedbank to seedling emergence were 89, 90, 92, and 89% respectively for density regimes of 1 000, 2 000, 4 000 and 6 000 seeds/m². Of the emerged seedlings, 25, 22, 22 and 22% for the same density regimes respectively established and completed their life cycles. These figures were of higher magnitude than those recorded for other plant species such as *Echinochloa crus-galli* (Baki 1988; Baki and Suhaimi 1995; Baki et al. 1995a, b) or *Oxalis corniculata* (Baki 1986), *Mimosa quadrivalvis* var. *leptocarpa* Barneby (Baki 2001) or *Ranunculus* spp. (Sarukhan 1974).

In the second (G_{1+1}) generation synthetic populations, the emerged seedlings were subjected to density-dependent mortality. The number established plant for density regimes of 1 000, 2 000, 4 000 and 6 000 seeds/m² were 1.17 x 10³, 1.3 x 10³, 1.27 x 10³, and 1.47 x 10³/m², respectively, and these in turn produced 5.89 x 10⁴, 6.0 x 10⁴, 5.9 x 10⁴ and 6.0 x 10⁴ seeds/m², respectively. Of the seeds which were assumed to form the soil surface seed bank 27, 12, 10 and 10% of these seeds were buried to form the constituents of buried soil seed bank which upon emergence form part
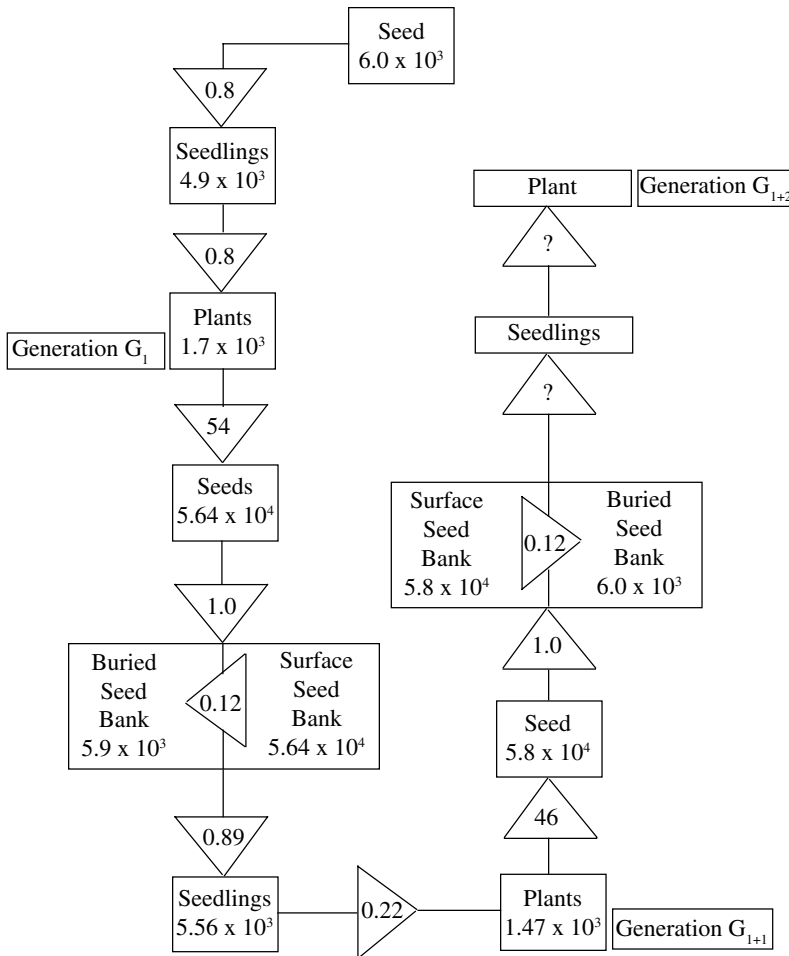
Figure 7. A schematic diagram of the dynamics of synthetic populations of wrinklegrass in the first- (G₁), and second- (G₁₊₁) populations 32 weeks after sowing at the initial density of 6 000 seeds/m² (numbers/m²)

of the third (G_{1+2}) generation life cycle. The parallel figures of wrinklegrass establishing to maturity among the third generation population were 1.38×10^3, 1.41×10^3, 1.47×10^3, and 1.56×10^3/m², and these represented only a marginal portion of seeds produced by the plants across density regimes. This indicates the importance of environmental sieves in regulating the population numbers of wrinklegrass, and in so doing ensuring only the fittest among them to survive establishment to maturity. It is important to notice that only the seeds which incorporated in the soil seed bank

were protected by the soil and most of these seeds emerged as seedlings, given the right environmental conditions. The emerged seedlings are subjected to juvenile mortality, leaving only a small fraction to establish and produce seeds (Baki 1986). There were evidences of a slight build up of population size, albeit inconsistencies, in the second, and third generation populations based on the number of established plants in each generation as displayed in *Figures 4–7* across the initial sowing densities in the first generation population. The lower number of the established wrinklegrass plants coupled

with vigorous vegetative growth, high seed production per plant arguably enabled this weed to survive and spread in the rice granaries of Malaysia.

Acknowledgement

The authors thank the two anonymous referees for their invaluable suggestions on the manuscripts, and Mr Zainal Mustapha for the technical help.

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