

Impact of Crude Oil Pollution on Population Dynamics of *Limoniastrum monopetalum* (L.) Boiss

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Abstract: Population demography and dynamics analysis of *Limoniastrum monopetalum* were carried out in crude oil polluted and unpolluted sites located in the western Mediterranean desert of Egypt (Al-Hamra Petroleum Station, the main crude oil pipeline terminal in Al-Alamein). The aim was to investigate the impact of crude oil pollution on the population dynamics of *Limoniastrum monopetalum* in order to assess its role in the phytoremediation and rehabilitation of petroleum-contaminated sites. The contribution of old individuals in the polluted site to the population was greater than the contribution of similar age classes in the normal unpolluted site, while young individuals contribution in the unpolluted site outweighed the contribution of similar individuals in the polluted site. Seedlings and youngest adult age class are not represented in the polluted site population indicating lack of regeneration due to oil pollution. The adult individuals are least affected by crude oil pollution than seedlings and juveniles. The survivorship curves exhibited a Deevey type-III, where reproductive survivorship stages from flower bud to germinable seed stages in population of the unpolluted site occurred over a shorter time period than in the oil polluted site. The reproductive dynamics occurred over shorter time period in the polluted site than in the unpolluted site. The highest expectations of future life were reached by adult individuals of age 12 years old in the unpolluted site population, while reached 10.50 in adults of age 8 years old in the polluted site population. The net reproductive rate is 0.457 and 0.246 for populations in unpolluted and polluted sites, respectively. The intrinsic rate of increase per capita per year is negative and calculated as -0.019 and -0.025 in unpolluted and polluted sites populations, while the generation time estimated as 40.67 and 55.27 years for unpolluted and polluted sites populations, respectively. Population established on the polluted site is characterized by vigorous vegetative growth of adult plants, absence of seedlings and juveniles, expanded reproductive cycle and better flowering, fruiting and seed output. The population dynamics, survivorship, reproductive value and expectation of future life as well as resistance to crude oil pollution are dependent on the plant's age and stage of growth. This does not compellingly diminish the potential of this species for its use in phytoremediation and rehabilitation programs of oil polluted soils. A point of interest obtained from the present investigation is the increase of flower number per spikelet to reach up to 4 in the polluted site. The recorded number of flowers in *L. monopetalum* normally ranges from 1 to 2 per spikelet. Further investigations, genecological in particular are required to determine whether the new form of *L. monopetalum* with more than 2 flowers per spikelet is a habitat form or an ecotype.

Key words: Demography • Life table • Fecundity schedule • Phenology • Mediterranean • Egypt

INTRODUCTION

Contamination of soils by crude oil causes drastic changes in its physical and chemical properties. Development of vegetation and growth of plant populations on contaminated areas may be prevented, retarded, or accelerated depending on changes taking

place in soil properties [1,2]. When oil pollution is present at a concentration that affects the physiological processes or biotic interactions among plants, the negative outcome of competition increases [1,3]. In a widely scattered literature on the effects of crude oil contamination on plants, little attention has been drawn to the effects on population dynamics [4,5] with almost

none have been published on effects on plant populations in saline or salt affected habitat types in arid regions [1,6-8]. On the other hand, most of previous studies covered mainly the general phytotoxic effect which results in a decreased plant biomass production [9,10].

Prior to contamination, the present study natural population of *L. monopetalum* was associated with *Arthrocnemum macrostachyum*, *Zygophyllum album* and *Suaeda pruinosa* [11-13]. Crude oil pollution resulted in the elimination of most species in the natural vegetation, except *L. monopetalum*. This may explain the oil-adaptation characteristics and the competitive balance of *L. monopetalum* as a medium-sized shrubby species, commonly living in coastal salt marshes or salt affected dry habitats with circummediterranean distribution [8, 14].

Crude oil residues from maintenance drainage of floating storage tanks and from ballast waters of tankers operating between Al-Alamein and Alexandria Harbor were dumped during the period from 1985 to 1995 into 20 acres of land at Al-Hamra Petroleum Station. Crude oil is a complex mixture of many compounds. When it is released to the environment, various physical, chemical and biological alterations occur, which collectively called weathering. The geochemical study, carried out in the same study site [2], revealed that more than 99.6% of the total polycyclic aromatic hydrocarbons (PAHs) were lost in the weathered oil residue. Degradation processes have changed the physical appearance of the residual spilled oil as they varied in appearance, depending on the degree of weathering, from yellowish/gray fine sediment, through sticky dark brown/black viscous oil and tar, to black charred residue.

The objective of this study is to investigate the impact of crude oil pollution on the population dynamics of *Limoniastrum monopetalum* at different life stages and phenological phases. Results are expected to assist in the evaluation of *L. monopetalum* role in the phytoremediation and rehabilitation of petroleum-contaminated sites.

MATERIALS AND METHODS

Study area: The study area is located in the saline depression of Al-Hamra Petroleum Station, which is the main crude oil pipeline terminal in Al-Alamein at 120 km west of Alexandria. The two study sites (polluted and normal unpolluted) are adjacent and occur under the same environmental conditions. Before dumping the crude oil, the two sites constituted one plant community

(Plate. 1a&b). The climate is Mediterranean, with mean annual rainfall around 100mm; mostly occurs from December to March. The mean annual temperature and relative humidity are 22.5°C and 65%, respectively [15].

Soil: Physical and chemical properties of the soil, in both sites, at depth of 20-30 cm were analyzed following [16,17]. Soil texture analysis was estimated using Boyquous hydrometer method. Soil water extracts of 1:5 were prepared for the determination of electrical conductivity (EC) and soil reaction (pH) using a direct indicating salinometer (Simpson Scientific Co., YSI-33) and pH meter (Crison pH meter, PH 25). Total organic matter was determined by loss-on-ignition at 450°C, calcium carbonates by Bernard's calcimeter. Soil extracts of 5 gm air-dried soil samples were prepared using 2.5% v/v glacial acid for estimating P, K, Ca, Na and Mg. Flame photometer was used to determine K, Ca and Na concentrations. Molybdenum blue and Indo- phenol blue methods were applied for the determination of phosphorous concentration using spectrophotometer (340-UMEDIC). Mg concentration was determined using atomic absorption (Varian, spectra AA220).

Plant population: Demographic analysis of *Limoniastrum monopetalum* populations was carried out in ten randomly chosen quadrats per site, each of 10 x 10 m. The growth stages from seedlings, juveniles and adult plants of different size classes were categorized according to crown volume into size classes. Plant crown volume was measured by the crown diameter method [18,19]. Demographic observations covered the number of individual plants per size class, number of inflorescences per individual, number of flower buds, flowers, fruits and seeds per inflorescence. The number of each item per individual was multiplied by the total number of individuals to give the total number per size class. Then summation of numbers for each size class gave the total per population. Age of the plants was estimated by observing the stem xylem vessel groups in hand cross-sections [20]. Eight size classes were categorized for the adult individuals; < 0.5, 0.5-1.0, 1-2, 2-3, 3-4, 4-5, 5-10 and > 10 m³.

Life table and fecundity schedule: Data of the life table and fecundity schedule were calculated [21,22]. The first column of the life table (Appendix 1 & 2) sets out the various stages including flower buds, flowers, fruits, seeds, germinable seeds, seedlings and juveniles, and adults of different ages. The second and third columns



(a)



(b)

Plate 1: a) The normal unpolluted site; b) Crude oil polluted site



(a)



(b)

Plate 2: a) Plant inflorescence from the polluted site (left)- note the dense flowers, and from the normal unpolluted site (right)- note the fewer number of flowers per inflorescence; and b) An inflorescence and spikelet with four flowers from the polluted site (Herbarium sheet).

list the estimated age in years (x) and the corresponding number per stage (N_x). The data is standardized in the fourth column starting with value of 1.0, where the proportion of the original age class surviving to the start of each stage (l_x) obtained. The proportion of the original age class dying during each stage (d_x), stage specific mortality rate (q_x) and expectation of future life (e_x) were calculated. The fecundity schedule was estimated from the seed output. The reproductive value (V_x), the net reproductive rate (R_0), the generation time (T), and the intrinsic rate of increase per capita (r) were calculated.

Phenology: Observations on phenology were carried out on 10 randomly labeled individuals per population. The selected individual plants covered the different size classes. Five phenophases were followed up: vegetative, flower bud, flowering, fruiting and seed dispersal. Data were collected at monthly intervals (biweekly during flower bud to fruiting phases) over one year from January to December 2006.

RESULTS

Soil: The physical and chemical characteristics of the soil in the two study sites are shown in Table 1. The soil texture in both polluted and unpolluted sites are loamy sand. Silt and clay fractions were significantly higher in polluted than in unpolluted site. Generally, soils are alkaline (pH: 7.70-8.17) and calcareous (CaCO_3 : 50.13-56.20%) with higher values in the unpolluted site. Similarly, phosphorous concentration was significantly higher in the unpolluted site. The electrical conductivity was comparable in both sites, while the total organic matter, potassium ion concentrations and water content were higher in the polluted site than in the unpolluted one. As for magnesium and sodium ions, the values were insignificantly different.

Population demography: The total population in polluted site is greatly reduced compared to that in the unpolluted site. Total number of individuals recorded was 72 per 500 m^2 in the unpolluted site, with age range from 4-68 years old, while 42 individuals recorded in the same area in the polluted site with age range from 8-72 years old (Fig. 1a). In the unpolluted site, adults of up to 4 years old contributed 36% of the total population, while have no contribution in the polluted site. In contrast, the oldest size classes in the polluted site

Table 1: Mean \pm standard error of physical and chemical properties of the soil supporting *Limoniastrum monopetalum* populations in the polluted and normal unpolluted sites. *= $p < 0.05$

Soil character	Polluted site	Unpolluted site	r-value
Physical properties:			
Gravel (%)	09.15 \pm 2.05	10.36 \pm 2.41	0.3518
Coarse sand (%)	46.79 \pm 3.19	50.82 \pm 3.64	0.5602
Fine sand (%)	28.50 \pm 3.15	27.60 \pm 2.73	0.3723
Silt (%)	09.31 \pm 0.85	07.40 \pm 0.65	0.8699*
Clay (%)	06.25 \pm 0.26	03.82 \pm 0.18	0.9258*
Chemical properties:			
pH	7.70 \pm 0.20	8.17 \pm 0.40	0.9897*
EC (mS/cm)	14.37 \pm 6.27	13.20 \pm 0.44	0.2598
Organic matter (%)	9.10 \pm 4.29	0.50 \pm 0.17	0.9492*
CaCO_3 (%)	50.13 \pm 6.17	56.20 \pm 5.87	0.9596*
Ca^{+2} (mg/100 g)	40.40 \pm 7.90	38.00 \pm 1.11	0.8196
Mg^{+2} (mg/100 g)	40.00 \pm 15.90	42.17 \pm 0.81	0.0413
Na^{+2} (mg/100 g)	42.62 \pm 5.93	46.97 \pm 6.35	0.4643
K^{+} (mg/100 g)	39.70 \pm 2.57	13.13 \pm 4.35	0.9995*
P (mg/100 g)	0.49 \pm 0.14	9.90 \pm 2.12	0.9992*
Water content			
(% oven dry weight)	19.56 \pm 2.91	10.46 \pm 1.35	0.8146*

contributed 29% of total individuals in the population, while individuals of similar age in the unpolluted site were not represented in the population. Generally, the contribution of old individuals in the polluted site to the population was greater than the contribution of similar age classes in the normal unpolluted site, while young individuals contribution in the unpolluted site outweighed the contribution of similar individuals in the polluted site.

The vigorous growth of adult individuals as reflected by the increased crown size was accompanied by better flowering and fruiting success. The number of flowers per spikelets reached up to 4 in polluted site and ranged from 1 to 2 in the unpolluted site (Plate 2a&b). The number of flowers and fruits per population in the polluted site reached 3425514 and 2404772, while values in the unpolluted site population estimated as 146250 and 125788, respectively (Appendix 1&2). Estimates of the percentage seed contribution of different adult age classes in the normal unpolluted site increased with age and reached maximum values at age range of 42-56 years old individuals (Fig. 1b). The same trend was found in the population of the polluted site with maximum seed contribution attained by individuals at age 62 years old.

Despite the larger number of seed output (921891) and potentially germinable seeds (28857) in the

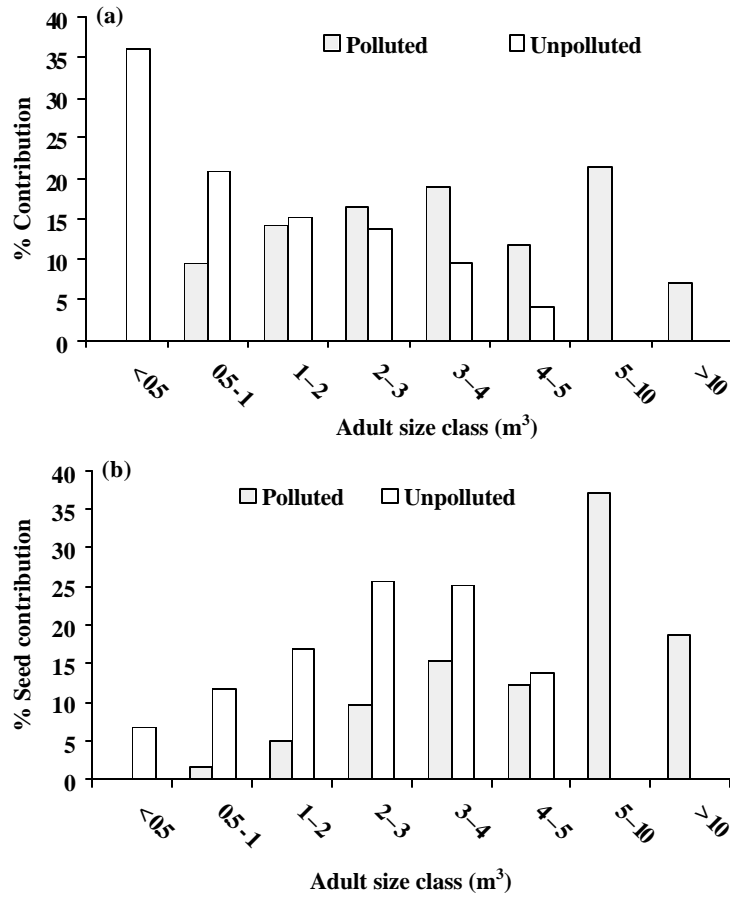


Fig. 1: (a) Size class distribution of *Limoniastrum monopetalum* population and percentage contribution of different classes to the total population in the polluted and normal unpolluted sites. (b) Percentage seed contribution of different size classes to the total population in the polluted and normal unpolluted sites.

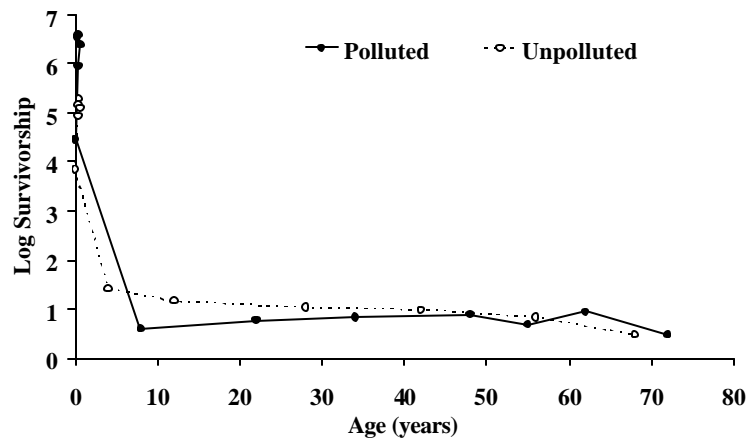


Fig. 2: Survivorship curve (log scale) for the different individuals of the two study populations in polluted and normal unpolluted sites.

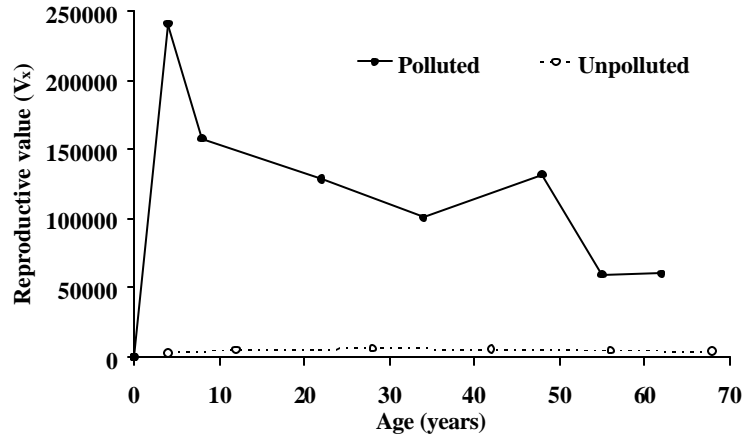


Fig. 3: Age dependent expectation of future life for the different individuals of the two study populations in polluted and normal unpolluted sites.

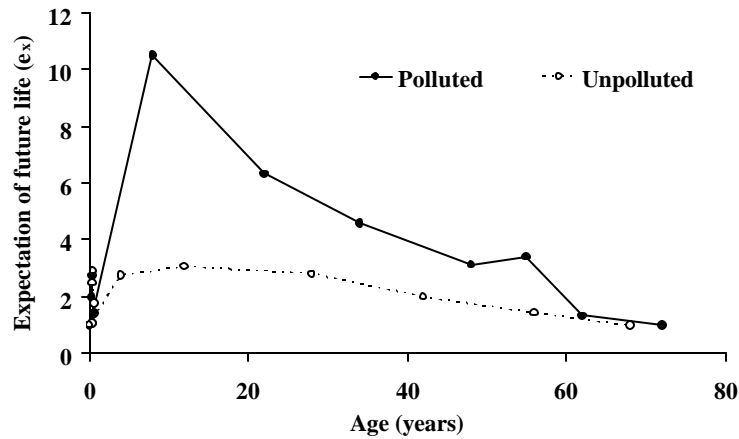


Fig. 4: Age dependent reproductive value for the different individuals of the two study populations in polluted and normal unpolluted sites.

Phenophase	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Vegetative	Shaded			Horizontal lines								
Flower buds	Horizontal lines			Shaded						Horizontal lines		
Flowering	Horizontal lines			Shaded						Horizontal lines		
Fruiting	Horizontal lines			Shaded			Horizontal lines					
Seed dispersal	Horizontal lines			Shaded			Horizontal lines					

Fig. 5: Phenological spectrum of *Limoniastrum monopetalum* populations in the polluted (shaded bars) and normal unpolluted (horizontal lines bar) sites.

polluted site population compared to the unpolluted site population where values of 88052 and 7044 obtained respectively, seedlings and youngest adult age class were not represented in the polluted population (Appendix 1&2), indicating lack of regeneration.

Population dynamics: The overall survivorship (l_x) curves were similar in the two populations of polluted and unpolluted sites, where the two curves exhibit a Deevey type-III curve, that shows sharp decline during the early stages of growth and reproduction (Fig. 2). In the unpolluted site, the population survivorship decreased from value 192555 in flower bud stage to 7044 in germinable seeds, while for the polluted site population values decreased from 3917210 to 28857 in flower bud and germinable seeds, respectively. This sharp decline was followed by a plateau of low mortality in adult stages. The major differences between the two populations is that the reproductive survivorship stages from flower bud to germinable seed stages in population of the unpolluted site occurred over a shorter time period than in the polluted site population.

The stage specific mortality rate (q_x) experienced by the two populations varied among the different reproductive stages and adult cohorts (Appendix 1&2). For the unpolluted site population, the q_x values showed irregular pattern of variation among all stages, while the polluted site population demonstrated a pattern of increase from flower bud towards germinable seed stage, followed by decreased values in the adult stages. The highest q_x values were obtained in the germinable seeds stage for the two populations in unpolluted and polluted sites.

The expectation of future life (e_x) for different growth stages surviving to successive ages are shown in Fig. 3. In the reproductive stages (flower bud to seed) the e_x values decreased from 2.91 and 2.73 in flower bud stage of unpolluted and polluted site populations, respectively to value of about 1.0 in the germinable seeds stage of the two populations. The highest e_x values were reached by adult individuals of age 12 years old in the unpolluted site population, while reached 10.50 in adults of age 8 years old in the polluted site population. The e_x values decreased over the remaining adult stages and attained the minimum value of 1.0 in the oldest age class in the two populations.

Fecundity schedule: Fecundity was estimated based on seed production. The schedule demonstrate the contribution made by the fraction of adult individuals in

the two populations to a relative measure of reproductive value (V_x) based on sexual reproduction (Appendix 1&2). The net reproductive rate (R_0) was 0.457 and 0.246 for populations in unpolluted and polluted sites, respectively. The intrinsic rate of increase per capita per year was negative and calculated as -0.019 and -0.025 in unpolluted and polluted sites populations, respectively indicating that the two populations are declining. The population of the polluted site is declining in a faster rate than the normal population. The generation time (T) estimated as 40.67 and 55.27 years for unpolluted and polluted sites populations, respectively.

The reproductive value (V_x) of the polluted site population gradually decreased from 240477 in eight years old individuals to 59858 in 62 years old individuals showing that seed production was not evenly distributed over the different adult stages (Fig. 4). The population in the unpolluted site showed remarkable low seed output and more evenly distributed over the different adult stages with values ranged from 3386 in four years old individuals to 6526 in 28 years old individuals.

Population phenology: Five phenophases were recognized in the two study populations; vegetative, flower bud, flowering, fruiting and seed dispersal stages (Fig. 5). Vegetative growth of the study populations occurred from mid November to mid March in the polluted site and to mid April in the unpolluted site. The three stages: flower buds, flowering and fruiting started consequently during April and lasted in August / September with about two weeks lag between every two consecutive phases. The three phases started at least two weeks earlier in the polluted site than in the unpolluted site population. The seed dispersal phase lasted from mid June to mid November in the polluted site, while continued from early July to mid October in the unpolluted site population.

DISCUSSION

Population established on the polluted site is characterized by vigorous vegetative growth of adult plants, absence of seedlings and juveniles, i.e., lack of regeneration and expanded reproductive cycle and better flowering, fruiting and seed output. The adult individuals are least affected by crude oil pollution than seedlings and juveniles. The stage-specific survivorship of the unpolluted site population occurred over shorter time period than in the polluted site. The established adult plants in the polluted site revealed deep root systems below the soil surface, this is together with the

increased soil water content compared to the normal unpolluted site, where most plants appear stunted with small root systems confined to the upper soil surface.

Besides the toxic effect of petroleum hydrocarbons there are several related factors that influence root morphology [23]. In case of petroleum-contaminated soil, the phytoremediation effect is assumed to be based on stimulation of degrading microorganisms in the rhizosphere, called phytostimulation or rhizo-degradation [24]. Consequently, changes in root morphology can influence the stimulation and thus the oil degradation by microorganisms in the rhizosphere. As such, the observed increase in root length of *L. monopetalum* in the polluted site increases its potentialities as a phytoremediator species. Moreover, adult individuals survived crude oil pollution showed lower mortality, and higher reproductive value and expectation of future life than the individuals of similar age in the unpolluted site.

In the present investigation, it worth noting that the number of flowers recorded for *L. monopetalum* (up to 4 flowers per spikelet) in the polluted site is a new record for this species. The number of flowers in *L. monopetalum* normally ranges from 1 to 2 [14,25,26]. This reflects a defense mechanism developed by the study species against crude oil ecotoxicity. The allocation of resources towards sexual reproduction at the expense of vegetative reproduction was also recorded in salt affected land in the Nile Delta [27]. Further investigations, genecological in particular are required to determine whether the new form of *L. monopetalum* with more than 2 flowers/spikelets is a habitat form or an ecotype.

Soils contaminated with the crude oil develop striking physical and chemical characteristics. In severe cases, soil aggregates are broken down, i.e., the crumb structure of the normal soil is lost and dispersion results as soil becomes puddled. The soil has a hard, waxy appearance when dry and resists wetting from the surface unless cracked. However, once these soils are wetted, they tend to remain wet for long time [1]. The higher moisture content in polluted soil than in the unpolluted soil could be attributed to the increase water retention.

The feasible explanation for the increased adult plant growth and the more efficient and expanded reproductive cycle of the population in the polluted site seems to result from the increased microbial activity due to crude oil contamination and the accompanying increase in organic matter and soil water holding capacity, and increased supply of nitrogen [28,29]. The pronounced damage to seedlings and juveniles seems to result from the increase in exchangeable ions to toxic levels in the

root zone area. Also, the relatively lush and vigorous growth of adult individuals in polluted site, apparently because of the warm microclimate that is associated with the dark soil surface [5,30]. The susceptibility of *L. monopetalum* seedlings and juveniles to crude oil pollution could be attributed to its shallow rooting with undeveloped underground organs. The resistance of adults seems to be a competitive advantage in recovering from oil pollution as a result of their fast growth and cushion forming habit with robust and deep underground organs [30]. The vigorous growth, increased crown size and flowering / fruiting success of adult plants in the polluted site compared to the normal unpolluted site is in agreement with the findings of other studies [31-33] on saline environment plants.

When the time factor is considered, the consequence of stages in survivorship (l_x) and reproductive dynamics from flower bud to seed dispersal phenophases occurred over shorter time period in the unpolluted site, while the reproductive value (V_x) and expectation of future life (e_x) occurred over faster rate in the polluted site. This behaviour indicates that evolutionary significance of population dynamics in response to crude oil pollution depends on the distribution of age classes within the population. The seedlings, juveniles and young adult age classes are the most affected by crude oil pollution. Ironically, old individuals flourish and gain better growth in response to oil pollution [1,6,27]. On bringing together the survivorship and reproductive cycle, *L. monopetalum* is characterized by Deevey's type-III curve, with extremely heavy mortality in the early reproductive stages in the study two populations. But the fewer adult individuals survived the crude oil pollution have lower mortality, and higher reproductive value and expectation of future life than the individuals of similar age in the unpolluted site.

The delayed survivorship and reproductive cycle of the population inhabiting the polluted site, presents an advantage for *L. monopetalum*. From the ecological perspective, this delay allows plants to produce seeds under variable environmental requirements that favour the species persistence. This was proved true in other studies [27,34-37].

Despite the better reproductive value (V_x) and expectation of future life (e_x) in polluted site population, the negative intrinsic rate of increase (r) and net reproductive rate (R_0) of the whole population describe its potential for persistence. An (r) value of -0.025 and (R_0) value of 0.246 indicate a potential decreased chance in seed production and population persistence. An

important aspect of the reproductive value (V_x) data interpretation is that, although the polluted site population maintained higher values than the unpolluted site population, it exhibited a negative intrinsic rate of increase. This indicates that high fecundity of adult individuals in the polluted site does not ensure persistence of the population. This behaviour was previously proved for another species in the same family, *limonium delicatulum* [20].

Considering the population phenology, the vegetative period in the unpolluted site exceeded the polluted site by at least six weeks. In contrast, the remaining phenological phases in the unpolluted site population were shorter than that in the polluted site by about 4-6 weeks. In general, the reproductive dynamics occurred over shorter time period in the polluted site than in the unpolluted site. The population dynamics and survivorship of *L. monopetalum*, the reproductive value and expectation of future life as well as its resistance to crude oil pollution are dependent on the plant's age and stage of growth. However, this does not compellingly diminish the potential of this species for its use in phytoremediation and rehabilitation programs of oil polluted soils.

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Appendix 1: Life table and fecundity schedule calculated for *Limoniastrum monopetalum* from data on naturally growing population in normal unpolluted site at Al-Hamra, Al-Alamein, Egypt. x = estimated age in years, N_x = number per stage (age class), l_x = proportion of original cohort surviving to the start of each stage, d_x = proportion of original cohort dying during each stage, q_x = stage-specific mortality rate, e_x = expectation of future life, b_x = average number of seeds per individual, v_x = reproductive value, R_0 = net reproductive rate, T = generation time, and r = intrinsic rate of increase

Stage	x (years)	N_x	l_x	d_x	q_x	e_x	b_x	$l_x b_x$	$x l_x b_x$	V_x
Flower buds	0.48	192555	1.00000000	0.24047675	0.24	2.91				
Flowers	0.35	146250	0.75952325	0.10626574	0.14	2.51				
Fruits	0.66	125788	0.65325751	0.19597518	0.30	1.76				
Seeds	0.4	88052	0.45728233	0.42070058	0.92	1.08				
Germinable seeds	0.0	7044	0.03658176	0.03644673	1.00	1.01				
Adults (m^2): < 0.5	4.0	26	0.00013503	0.00005713	0.42	2.77	226.2	0.03054296	0.1222	3386.75
0.5 - 1	12.0	15	0.00007790	0.00002077	0.27	3.07	692.3	0.05393005	0.6472	5478.29
1 - 2	28.0	11	0.00005713	0.00000519	0.09	2.82	1354.5	0.07737789	2.1666	6526.35
2 - 3	42.0	10	0.00005193	0.00001558	0.30	2.00	2257.5	0.11723923	4.9240	5689.03
3 - 4	56.0	7	0.00003635	0.00002077	0.57	1.43	3160.6	0.11489808	6.4343	4902.19
4 - 5	68.0	3	0.00001558	0.00001558	1.00	1.00	4063.7	0.06331230	4.3052	4063.70
5 - 10	0.0	0	-	-	-	-	-	-	-	-

$R_0 = 0.457$ $T = 40.67$ $r = -0.019$

Appendix 2: Life table and fecundity schedule calculated for *Limoniastrum monopetalum* from data on naturally growing population in the polluted site at Al-Hamra, Al-Alamein, Egypt. x = estimated age in years, N_x = number per stage (age class), l_x = proportion of original cohort surviving to the start of each stage, d_x = proportion of original cohort dying during each stage, q_x = stage-specific mortality rate, e_x = expectation of future life, b_x = average number of seeds per individual, v_x = reproductive value, R_0 = net reproductive rate, T = generation time, and r = intrinsic rate of increase

Stage	X (years)	N_x	l_x	d_x	q_x	e_x	b_x	$l_x b_x$	$x l_x b_x$	V_x
Flower buds	0.35	3917210	1.00000000	0.12552199	0.13	2.73				
Flowers	0.25	3425514	0.87447801	0.26057883	0.30	1.98				
Fruits	0.66	2404772	0.61389918	0.37855540	0.62	1.40				
Seeds	0.40	921891	0.23534378	0.22797706	0.97	1.03				
Germinable seeds	0.00	28857	0.00736672	0.00736672	1.00	1.00				
Adults (m^2): < 0.5	0.00	0	0.00000000	-0.00000102	-	-	-	-	-	-
0.5 - 1	8.00	4	0.00000102	-0.00000051	-0.50	10.50	3998.5	0.00408301	0.0327	240477.40
1 - 2	22.0	6	0.00000153	-0.00000026	-0.17	6.33	7996.8	0.01224872	0.2695	157652.60
2 - 3	34.0	7	0.00000179	-0.00000026	-0.14	4.57	13288.9	0.02374708	0.8074	128276.40
3 - 4	48.0	8	0.00000204	0.00000077	0.38	3.13	18454.4	0.03768887	1.8091	100614.06
4 - 5	55.0	5	0.00000128	-0.00000102	-0.80	3.40	23710.4	0.03026440	1.6645	131455.46
5 - 10	62.0	9	0.00000230	0.00000153	0.67	1.33	39748.8	0.09132500	5.6621	59858.37
> 10	72.0	3	0.00000077	--	--	1.00	60328.7	0.04620281	3.3266	60328.70

$R_0 = 0.246$ $T = 55.27$ $r = -0.025$