Article

NÚÑEZ FRÉ, F.R.[1,2]
JUAN, V.F.[1]*
SAINT ANDRÉ, H.M.[1]
CHANTRE, G.R.[3,4]

DEMOGRAPHIC AND PHENOLOGICAL STUDIES ON DAVID'S SPURGE (*Euphorbia davidii*) IN THE CENTRAL AREA OF BUENOS AIRES PROVINCE, ARGENTINA

*Estudos Demográficos e fenológicos sobre **Euphorbia davidii** na Região Central da Província de Buenos Aires, Argentina*

ABSTRACT - David's Spurge is an spring-summer annual weed, present in the central area of Buenos Aires Province, Argentina. Field studies were carried out during 2011/12 and 2013/14 to assess demography and population dynamics and determine a thermal time scale of this species. At the experimental site, 1 m² quadrants were established as observational plots, four per cohort. The number of individuals at each phenological stage and from each cohort was recorded weekly. At the end of the experiment, all plots were harvested, and seed production was determined. A thermal time scale was established to identify the occurrence of the different phenological events. Three cohorts were detected, the first one emerged in mid-October, the second one in early November, and the last cohort varied from late November till early January, totalling an average of 1,500 m⁻². Over 80% of the evaluated emergences belonged to the first and second cohorts in both periods. Thermal time requirements calculated to reach the 2-4 leaves, 6-8 leaves, branching, and flowering stages, were 192, 370, 515 and 1,155 °Cd, respectively. Average seed production in the first, second and third cohort was 5,700, 6,400 and 1,900 seeds m⁻², respectively. However, the total number of propagules from the sum of the three cohorts was similar in both years, about 14,000 seeds m⁻². Results from this study will foster a better understanding of the ecophysiology of *Euphorbia davidii* in the study area, and it may be a valuable contribution from an integrated weed management perspective.

RESUMO - O eufórbio lactífero (em inglês, "David's Spurge") é uma planta daninha anual de primavera-verão presente na região central da província de Buenos Aires, Argentina. Estudos de campo foram realizados durante os anos de 2011/12 e 2013/14 para avaliar a demografia e a dinâmica de população, bem como para estabelecer uma escala de tempo térmico para essa espécie. No local do experimento, quatro parcelas de 1 m² foram marcadas para cada coorte de indivíduos. O número de indivíduos de cada coorte, em cada estado fenológico, foi registrado semanalmente. Ao final do experimento, todas as parcelas foram colhidas, e a produção de sementes foi determinada. Uma escala de acumulação de tempo térmico foi estabelecida para identificar a ocorrência de diferentes eventos fenológicos. Foram detectadas três coortes: a primeira surgiu em meados de outubro; a segunda, no início de novembro; e a última, entre o final de novembro e o início de janeiro, totalizando uma média de 1.500 plantas m⁻². Mais de 80% das emergências registradas pertenciam à primeira e segunda coortes nos dois períodos de estudo. Os requisitos de tempo térmico calculados para atingir os estádios de 2-4 folhas,

* Corresponding author:
<vjuan@faa.unicen.edu.ar>

[1] Facultad de Agronomía de la Universidad Nacional del Centro de la Provincia de Buenos Aires (FAA-UNCPBA), Argentina; [2] Becario Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (CIC-PBA), Argentina; [3] Universidad Nacional del Sur, Bahia Blanca, Argentina; [4] Centro de Recursos Naturales Renovables de la Zona Semiarida (UNS - CONICET), Bahia Blanca, Argentina.

6-8 folhas, ramificação e floração foram de 192, 370, 515 e 1.155 ºCd, respectivamente. O rendimento médio na primeira, segunda e terceira coortes foi de 5.700, 6.400 e 1.900 sementes m⁻², respectivamente, determinando um número total de mudas de aproximadamente 14.000 sementes m⁻², com a soma das três coortes. Os resultados deste estudo permitirão uma melhor compreensão da ecofisiologia de Euphorbia davidii na área de estudo e representarão uma valiosa contribuição para a gestão integrada desta espécie.

Palavras-chave: coorte, EUDA5, tabela de vida, planta daninha, tempo térmico, Euphorbiaceae.

INTRODUCTION

Euphorbia davidii Subils is a weed belonging to the botanical family Euphorbiaceae Juss., represented worldwide by more than 8,000 species (Govaerts et al., 2000). While in Argentina the presence of approximately 70 species of the genus *Euphorbia* L. is mentioned, only four of them are described as weeds: *Euphorbia serpens* Kunth, usually known as "matted sandmat" (or "hierba meona" in Spanish), *Euphorbia heterophylla* L., *Euphorbia dentata* Michaux and *Euphorbia davidii* Subils, which are commonly referred to as "Spurges" ("lecherón" in Spanish), due to the milky latex sap they contain.

Euphorbia davidii is a species native to the Northern Hemisphere (Mexico, United States and Canada), which has been recently introduced in South America (Argentina), Australia and Europe (Vladimirov and Petrova, 2009). It is a summer annual weed that causes significant yield reductions on soybean crops in Central and Southeastern sections of Buenos Aires Province (Juan et al., 2011). In this region, an increasing incidence, density and geographical distribution of *E. davidii* has been observed in the last two decades.

The presence of this weed is currently reported in Europe and Asia, distributed in Russia, Ukraine, Moldova, Romania, Bulgaria, Hungary, Italy, Belgium, Switzerland, Serbia and France (Barina et al., 2013; Purger et al., 2015). Similar to data recorded in Argentina, an increase in population size and geographic distribution has been observed in several of these countries (Purger et al., 2015).

The survival of a population is one of the most important factors to consider in a demographic study. In order to determine this parameter, it is necessary to carry out both laboratory and field studies (Win et al., 2009).

Survival can be expressed in the form of curves and, according to their general form, these can be classified into three main types. Type I (convex curves) describe situations in which mortality is concentrated at the extreme end of the life span (e.g., animals in a zoo or the leaves of a plant). Type II curves (straight lines) indicate that the probability of death remains constant at each age, and can be correctly applied to the seed banks of many plant populations. Finally, type III (concave curves) indicate significant early mortality rates, followed by a high survival rate at later stages (Pearl, 1928; Deevey, 1947).

Subsequently, survival data are incorporated as part of the demographic processes in consonance with the structure of a life table or a dynamic multi-state model (González-Andújar and Fernández-Quintanilla, 1991). This diagrammatic model represents in a synoptic and synthetic way the variables and demographic processes in quantitative (numerical) terms (Deevey, 1947; Fazle Rabbi, 2013).

Multi-state life tables are constructed to track, from birth to death of the last individual, the survival and age fecundity rates of a cohort of individuals that are part of a population (Ricklefs, 1990). The basic bioecological information provided by these models is of considerable agronomic value for designing sustainable weed management programs (Rabinovich, 1980; Begon et al., 1988). Clearly, life tables represent one of the main means for conceptualizing population structure and analyzing its dynamics.

Although many phenological changes or events occurring in plants can be defined using numerical scales (for example, based on calendar days), interferences may appear in the data

obtained due to environmental and ecophysiological factors. In contrast, thermal time expressed in degree-days has been shown to be an adequate measure of "physiological time" to evaluate plant growth (Aitken, 1974; Trudgill et al., 2005), as temperature is considered the most important climatic factor that influences the occurence of phenological events (Russelle et al., 1984; Gadioli et al., 2000).

Knowledge on thermal time requirements of a given weed species allows predicting its response to different environmental conditions, agroecological scenarios, or even assessing the effect of cultivation practices (e.g. sowing dates) on different stages of growth and development of the life cycle.

Euphorbia davidii is considered a highly competitive species difficult to control due to the low efficacy of most chemical treatments, combined with a strong dependence on the weed phenological state at control moments (Juan and Saint André, 1997; Juan et al., 2000). Reductions in growth parameters of soybean cultivars, determined in semi-controlled laboratory conditions, range from 35 to 45% for a weed density of 100 plants m^{-2} in comparison with the free-competition control (Juan and Saint André, 1995).

At a global level, far too little is known about management strategies to control this species (Storrie and Cook, 1996), and in Argentina, the most recent studies by Juan et al. (2011) have demonstrated the increasing difficulty to control *E. davidii* using glyphosate as the only herbicide in transgenic glyphosate-resistant soybeans (GRS).

The aim of this work was to study different aspects of the population dynamics of *E. davidii* through the analysis and constant monitoring of field cohorts in the central area of Buenos Aires Province. It was also sought to establish a thermal time scale to characterize each phenological stage, in order to provide basic ecophysiological information about the life cycle of the species.

MATERIALS AND METHODS

The experiments were carried out during the 2011/12 and 2013/14 cropping seasons, in a field located in Sierras Bayas, Olavarría, Buenos Aires Province, Argentina (36°58'4.30" S; 60°11'45.35" W). The experimental site was under direct seeding during the last 10 years. The soil used in this experiment was a Typic Argiudoll containing 5% of organic matter. *Euphorbia davidii* presence at the study site dates back to 2006, with repeated patches showing signs of high infestation (> 500 seedlings m^{-2}). The previous crop to the two-year experiment was RR soybean cultivated under direct drilling.

Daily meteorological reports were provided by the Olavarría Weather Station, located 8.5 km far from the experimental field (36°53'20" S; 60°13'40" W).

In the experimental site, sixteen 1 m² quadrants were established as observation plots. The plots were located in a highly infested area, in order to monitor each cohort throughout the growing cycle. Monitoring was performed without crop competition in both seasons. Sampling started in September, and the quadrants were assigned to each cohort by order of emergence.

Each cohort was defined as the set of seedlings that emerged simultaneously over two consecutive weeks. The number of individuals from each cohort was recorded weekly with four replicates, identifying the following phenological growth stages: cotyledon emergence (CE), 2 to 4 true leaves (2-4 Lv), 6 to 8 true leaves (6-8 Lv), branching (B) and reproductive (flowering and fruit-bearing) (F).

The mortality rate was calculated as the difference in the number of individuals between two successive samples. Emerging individuals belonging to other cohorts and other weed species were manually removed during the growing season.

The monitoring of all cohorts finished when the great majority of individuals reached the reproductive stage, with no additional phenological changes observed in the counts. All plots were harvested just before the natural dehiscence of the fruits (early March) and the number of individuals in the fruit-bearing stage and the seed production per plot were determined.

Thermal time was calculated as the sum of the average daily temperature over a given basal temperature, where the growth rate is close to zero (Monteith and Moss, 1977). Thermal time requirement to reach the 2-4 Lv, 6-8 Lv, B, and F stages was determined as the sum of the thermal time required for at least 50% of the plants to reach each phenological phase. All information obtained during the the two-year study was grouped to calculate thermal time, since no statistical differences between them were observed.

Thermal time (TT) was calculated according to equation 1:

$$TT = \sum [Tx - Tb] \qquad \text{(eq. 1)}$$

where Tx is the average daily temperature, Tb is the base temperature (estimated at 8 ^oC according to Marchessi et al., 2011).

Thermal time accumulation for three cohorts and two years was analyzed using ANOVA. Means comparisons were performed using Fisher's LSD test ($p < 0.05$) with InfoStat software v. 2012 (National University of Cordoba, Argentina).

Results obtained from seed production and density per cohort were analyzed by ANOVA. Means comparisons were performed using Fisher's LSD test ($p < 0.05$) with InfoStat software v. 2012 (National University of Cordoba, Argentina). The total seed production for each cohort and year was analyzed by ANOVA in a factorial design.

Non-linear regressions were established between *Euphorbia davidii* seed production (seeds m^{-2}) and density (plants m^{-2}), and also between individual seed production (number of seeds per plant) and density, using Graph Pad Prism software v. 6.01.

$$Y = S \times \log(X) + B$$

where Y is the seed production (seeds m^{-2}) or the individual seed production (seeds per plant), respectively, X is the population density (plants m^{-2}), S is the slope, and B is the intercept of the model with the Y axis.

RESULTS AND DISCUSSION

A summary of the monthly climate information recorded during the study periods is shown in Table 1.

During the two periods assessed, the emergence of *E. davidii* under field conditions generated three cohorts. As no additional seedlings were observed after the establishment of the third cohort, the fourth set of plots that had been initially established remained empty until the end of the experiment, that is, of the 16 originally established plots, 12 were used (three cohorts of four replicates each).

During the season 2011/12, the first emergence event occurred in October, reaching a maximum number of 180 m^{-2} in the cotyledon (CE) stage (Figure 1A). The second event occurred

Table 1 - Climate information obtained at the Olavarría Weather Station (36°53'20" S; 60°13'40" W)

| Month | 2011/12 | | | | | | | 2013/14 | | | | | | |
| | Temperature (^oC) | | RH | | | | Precip. | Temperature (^oC) | | RH | | | | Precip. |
	Max.	Min.	Average	Absol. Max	Absol. Min	%	(mm)	Max.	Min.	Average	Absol. Max.	Absol. Min.	%	(mm)
September	18.9	4.2	12.5	24.9	-3.4	61	49.7	15.8	4.3	10.7	25.5	-3.5	71	71.8
October	19.2	6.1	13.2	25.5	0.5	74	29.2	20.7	8.2	15.6	27.1	1.2	72	79.1
November	25.2	11.6	19.9	31.3	5.2	68	161	24.4	10.8	18.7	31.5	5.9	68	92.1
December	28.9	11.7	22.6	36.2	2.5	54	12.8	30.9	14.4	23.9	37.6	2.0	49	43.8
January	30.6	14.6	24.5	38.4	7.5	53	140.7	30.9	14.1	23.2	39.7	5.1	67	89.1
February	26.9	14.2	21.5	33.8	6.9	66	141	25.2	13.6	19.4	31.5	5.4	69	87.2

in early November with an initial number of 390 seedlings m^{-2} (Figure 1B), and the last cohort was observed in early January, with about 90 plants m^{-2} (Figure 1C). In this season, a total of 660 individuals, 27, 60 and 13% of the seedlings belonged to the first, second and third cohort, respectively (Figures 1A, B, C).

During 2013/2014, the first cohort was observed in early October with an initial population of 1,400 seedlings m^{-2} (Figure 2A). The second one was detected in the first week of November, with a density of 630 individuals m^{-2} in the CE stage (Figure 2B), while the last cohort was recorded at the end of November with a total of 350 seedlings m^{-2} (Figure 2C). From a total of 2,400 individuals assessed during the period, 60, 25 and 15% corresponded to the first, second and third cohorts, respectively (Figures 2A, B, C).

The number of individuals that emerged in each cohort varied between 2011/12 and 2013/14, that could be associated with variations on the levels of seed dormancy in the soil seed bank (Núñez Fré et al., 2014). However, it should be noted that the first two cohorts were very stable in terms of chronological emergence, as well as regarding the proportion of individuals that emerged in relation to the total annual rate. In both study periods, the emergence of the first and second cohorts occurred within the months of October and November and accounted for 80% of the total annual emergence rate of the species (Figures 1 and 2).

As shown in Figures 1 and 2, regardless of the initial number of established seedlings and the contribution of each cohort, in total only about 250 plants reached reproductive stages (F).

The carrying capacity (*k*) is defined as the maximum population size that the environment's resources can sustain indefinitely (Begon et al., 2006). From the above, it can be concluded that the *k* value, under the agroecological conditions established for these trials, would range between 200 and 300 plants m^{-2}. Nonetheless, further studies should be carried out in order to validate this information.

Table 2 presents the relationship between thermal time accumulation and the phenological states of *E. davidii* using the data pooled across the two years, since they did not present significant differences between them. The estimated thermal time requirements were on average 192, 370, 515 and 1,155 °Cd for 2-4 Lv, 6-8 Lv, branching (B) and reproductive (F) stages, respectively. The second cohort showed a tendency to have higher thermal time values, calculated for all phenological stages. However, only the first cohort showed significant differences in the 6-8 Lv stage. These observations may imply that there is an influence of the photoperiod in the thermal time accumulation of the different cohorts. Nonetheless, more research is needed to clarify this issue. In addition, it is emphasized that field observations were recorded weekly and individual emergences do not occur exactly the same calendar day, maybe there is thus a distinct accumulation of thermal time in individual plants within the same observation plot.

On the other hand, among the environmental factors that influence the variability of the data (Table 2), it could be mentioned the temporary thermal and water stress, a characteristic of the summer season in the central region of Buenos Aires Province. Such events could affect the growth stages of the species, potentially retarding a certain phenological state, even if the required thermal sum had been reached. Finally, it should be noted that *E. davidii* is forms a persistent seed bank (Núñez Fré et al., 2014) containing seeds of different years adapted to distinct environmental conditions, and these factors may contribute to an intrinsic variability in thermal time requirements within the population.

During the season 2011/12, the first cohort showed the highest mortality rate between the fourth week of October and the third week of November, which led to a 45% reduction in the number of individuals in comparison with the initial population (Table 3). During this period, individuals were mainly found in cotyledon emergence and 2-4 leaves stages (Figure 1A). In the second cohort, mortality events were more homogeneous between the fourth week of November and the first week of January, when the majority of individuals transited between 2-4 leaves and branching stages (Figure 1B), with a reduction of 58% in the number of individuals. The majority of deaths observed in this cohort were probably due to individuals emerging in very high densities and exhibiting lower growth rates as a consequence of intraspecific competition. In the last cohort, none of the individuals reached the reproductive stage.
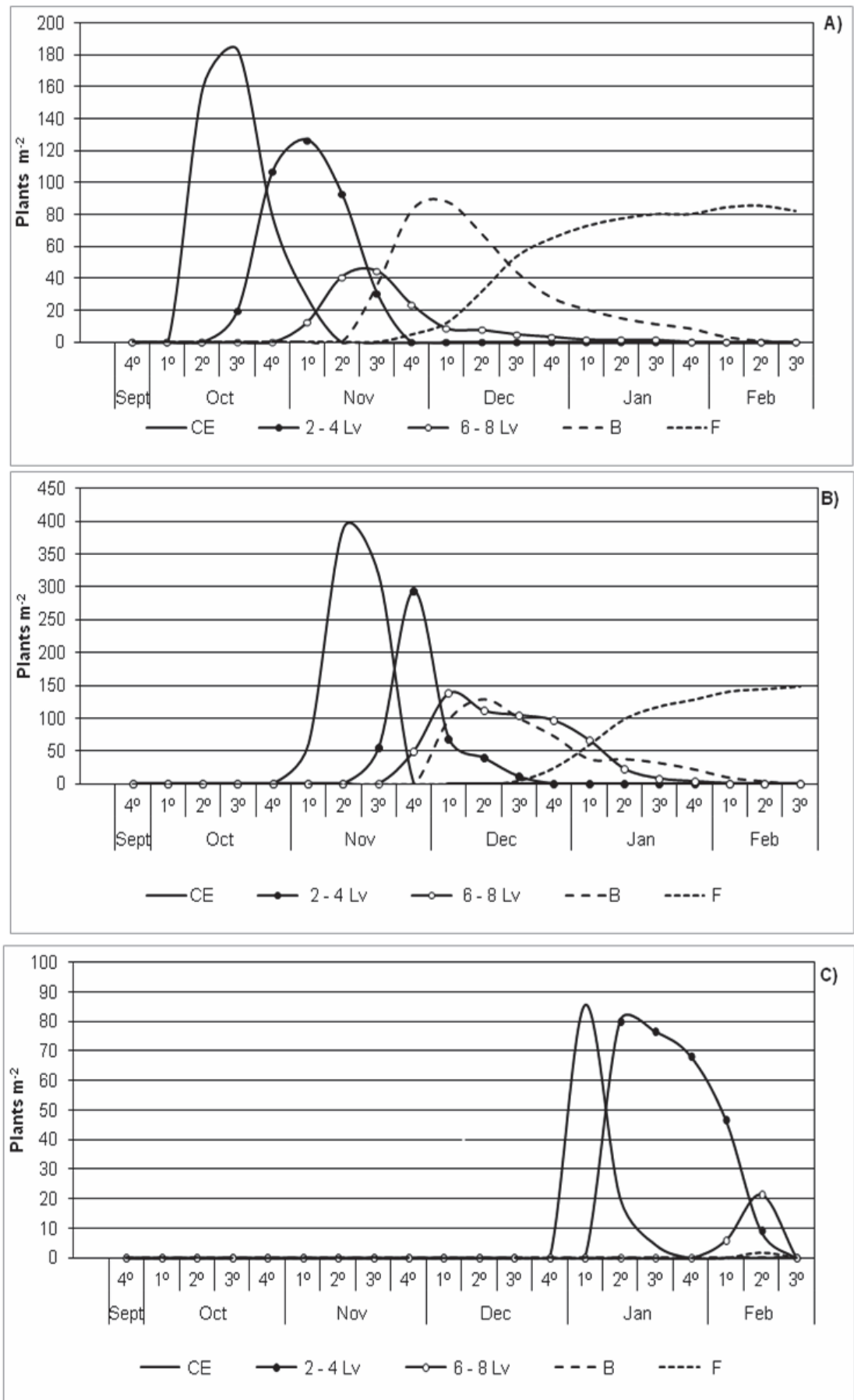
Figure 1 - *E. davidii* population, through different phenological stages in 2011/12. 1st, 2nd and 3rd cohort (A, B, C respectively).
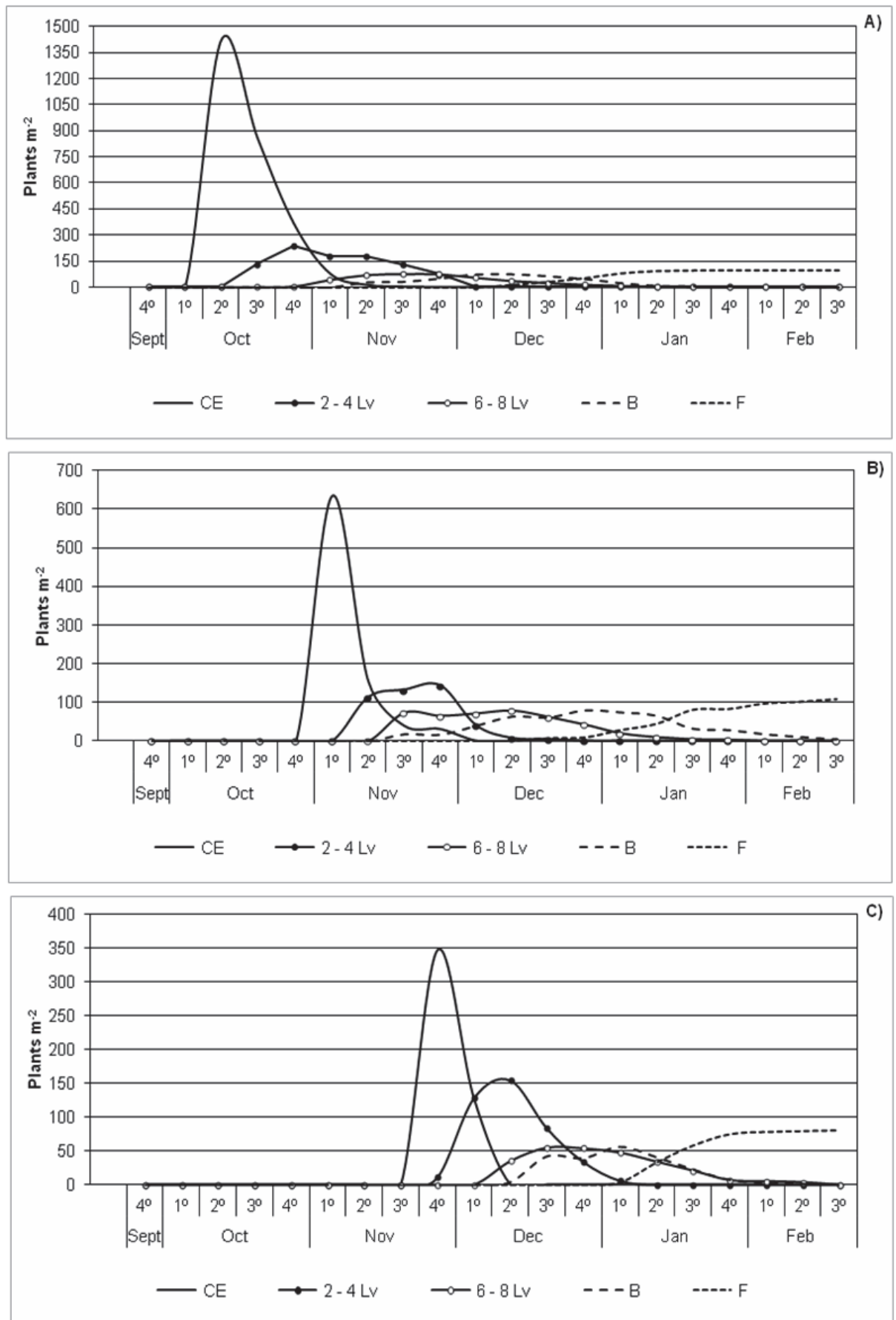
Figure 2 - *E. davidii* population*,* through different phenological stages in 2013/14. 1st, 2nd and 3rd cohort (A, B, C respectively).

Table 2 - Thermal time (ºCd) calculated for each phenological stage and each cohort, comprising both years (2011/12 and 2013/14). Standard deviations in parentheses

Phenological stage	1st cohort	2nd cohort	3rd cohort
2-4 leaves	171.5 (42.07) a	216.3 (45.39) a	190.5 (36.89) a
6-8 leaves	335.5 (39.90)a	405.2 (62.89) b	372.0 (58.38) ab
B (branching)	494.0 (35.78) a	549.4 (53.70) a	502.1 (25.81) a
F (flowering and fruit-bearing)	1177.3 (54.26) a	1182.0 (65.94) a	1107.6 (38.40) a

Differences between cohorts sharing a letter are not statistically significant, Fisher's LSD test (p≤0.05).

Table 3 - *E. davidii* mortality, expressed on a weekly basis for each cohort in 2011/2012

Week	1st cohort			2rd cohort			3rd cohort		
	Plants m^{-2}	Mortality (%)	Cumulative mortality (%)	Plants m^{-2}	Mortality (%)	Cumulative mortality (%)	Plants m^{-2}	Mortality (%)	Cumulative mortality (%)
Sept 4º	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 1º	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 2º	159	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 3º	203	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 4º	186	8.4	8.4	0	0.0	0.0	0	0.0	0.0
Nov 1º	168	9.1	17.5	60	0.0	0.0	0	0.0	0.0
Nov 2º	134	16.6	34.1	391	0.0	0.0	0	0.0	0.0
Nov 3º	111	11.3	45.4	373	4.5	4.5	0	0.0	0.0
Nov 4º	111	0.1	45.6	343	7.8	12.3	0	0.0	0.0
Dec 1º	109	1.0	46.6	304	9.9	22.1	0	0.0	0.0
Dec 2º	107	0.7	47.3	279	6.5	28.6	0	0.0	0.0
Dec 3º	102	2.3	49.6	221	15.0	43.6	0	0.0	0.0
Dec 4º	96	3.1	52.7	194	6.8	50.4	0	0.0	0.0
Jan 1º	95	0.7	53.4	164	7.6	58.0	86	0.0	0.0
Jan 2º	94	0.5	53.9	160	1.2	59.1	119	0.0	0.0
Jan 3º	93	0.5	54.4	158	0.4	59.6	81	31.6	31.6
Jan 4º	89	2.0	56.4	155	0.9	60.5	68	10.8	42.4
Feb 1º	87	0.6	57.0	151	0.9	61.4	53	13.1	55.5
Feb 2º	86	0.7	57.8	149	0.5	61.9	32	17.3	72.8
Feb 3º	82	1.8	59.6	148	0.4	62.3	0	27.2	100.0

During the season 2013/14 (Table 4), the mortality rates of the first cohort were similar to those found in the same cohort in 2011/12, with the highest rate occurring between the cotyledon emergence and 2-4 leaves stages. In 2013/14, mortality from birth to the first week of November caused a 79% reduction on the population. The second cohort showed two significant mortality events, the first took place in the second week of November, when most individuals were between cotyledon emergence and 2-4 leaves stages, resulting in a 58% population reduction, and the second mortality event occurred in the first week of December, when most individuals had between 2-4 and 6-8 leaves, with a 76% population reduction in comparison with the initial emergence.

As already mentioned, the initial counts of the first and second cohorts in 2013/14 were much higher than those observed in 2011/12, possibly indicating that the environmental conditions were more favorable for dormancy break and/or seedling establishment.

Unlike 2011/12, when the last cohort was recorded in mid-January, the last cohort of the season 2013/14 was detected at the end of November, with an initial density of 350 seedlings m^{-2} (Figure 2C). In this case, the mortality events were similar to those of the previous cohort, with two major events occurring in December. It was observed that the first mortality event took place between the first and second week of December, when the population was mostly between

Table 4 - *E. davidii* mortality, expressed on a weekly basis for each cohort in 2013/2014

Week	1st cohort			2nd cohort			3rd cohort		
	Plants m⁻²	Mortality (%)	Cumulative mortality (%)	Plants m⁻²	Mortality (%)	Cumulative mortality (%)	Plants m⁻²	Mortality (%)	Cumulative mortality (%)
Sept 4º	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 1º	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 2º	1422	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Oct 3º	988	30.5	30.5	0	0.0	0.0	0	0.0	0.0
Oct 4º	604	27.0	57.5	0	0.0	0.0	0	0.0	0.0
Nov 1º	298	21.5	79.1	634	0.0	0.0	0	0.0	0.0
Nov 2º	288	0.7	79.7	267	57.8	57.8	0	0.0	0.0
Nov 3º	242	3.2	83.0	263	0.7	58.6	0	0.0	0.0
Nov 4º	198	3.1	86.0	256	1.0	59.6	359	0.0	0.0
Dec 1º	131	4.8	90.8	151	16.6	76.1	256	28.5	28.5
Dec 2º	127	0.3	91.1	150	0.2	76.4	195	17.0	45.5
Dec 3º	120	0.4	91.5	135	2.3	78.7	182	3.7	49.2
Dec 4º	114	0.4	92.0	130	0.7	79.5	128	15.0	64.3
Jan 1º	111	0.2	92.2	122	1.3	80.8	114	3.8	68.1
Jan 2º	102	0.6	92.8	119	0.4	81.2	109	1.5	69.6
Jan 3º	102	0.1	92.9	118	0.2	81.4	103	1.6	71.2
Jan 4º	101	0.0	92.9	116	0.3	81.7	91	3.5	74.7
Feb 1º	100	0.1	93.0	115	0.1	81.8	88	0.8	75.5
Feb 2º	98	0.1	93.1	114	0.1	81.9	86	0.4	75.9
Feb 3º	95	0.2	93.3	114	0.1	82	81	1.4	77.3

cotyledon emergence and 2-4 leaves stages, causing a 45% reduction in the number of individuals; the second, for its part, occurred in the fourth week of December, when most individuals were between the 2-4 and 6-8 leaves stages, with a 65% reduction in population compared to the initial population (Table 4). It is noteworthy that the third cohort was able to produce individuals that reached reproductive stages and generated viable offsprings, whereas in the 2011/12 season none of the individuals managed to produce seeds (Table 5).

When analyzing the occurrence of *E. davidii* cohorts in 2011/12 and 2013/14, some similarities were found. In general, the emergence of individuals from the first and second cohorts accounted for more than 80% of the total annual emergence of the species. A significant initial mortality rate (between cotyledon emergence and 2-4 leaves stages) was observed in the first cohorts, with a seedling reduction between 50 and 80% of the initial emergence recorded (Tables 3 and 4).

The second cohort also showed similarities between the two periods, with two significant mortality events; between cotyledon emergence and 2-4 leaves stages, and between 2-4 and 6-8 leaves stages. At the same time, due to the non-occurrence of interspecific competition, one

Table 5 - Individual and population seed production, and population density by cohort during 2011/12 and 2013/14

| Year	Seed production (fecundity)			
	Cohort	Plants m⁻²	Seeds m⁻²	Seeds per plant
2011/12	1st cohort	94.53 c	6610.50 cd	55.20 b
2011/12	2nd cohort	113.68 c	7559.25 d	48.23 b
2011/12	3rd cohort	0 a	0 a	0 a
2013/14	1st cohort	106.25 c	4792.43 bc	63.93 b
2013/14	2nd cohort	183.25 d	5279.28 bc	43.39 b
2013/14	3rd cohort	40.63 b	3925.24 b	96.03 c

Differences sharing a letter are not statistically significant, Fisher's LSD test (p≤0.05).

should take into account that competition with crops and other weed species could surely alter the results of these assessments, increasing and anticipating deaths at each event (Tables 3 and 4). The third cohort showed a different behavior during the study years. In 2011/12, late emergence generated individuals that were incapable of producing propagules (Table 5).

In general, the behavior of *E. davidii* cohorts is similar to that of a *r* strategist species, with a high birth rate and initial mortality, between the cotyledon emergence and 2-4 leaves stages (Tables 3 and 4), followed by lower mortality rates in advanced growth stages, and a significant fraction of the resources allocated for reproduction (Gadgiland and Solbrig, 1972).

Considering both periods of field evaluation, it is concluded that the first cohort contributed more than 50% of the total number of individuals, but also showed the lowest probability of survival in the cotyledon stage since less than 25% of the individuals reached the 2-4 leaves stage and only 10% reached fruit-bearing stage (Figure 3). The main adverse factor limiting the survival of *E. davidii* emerged seedlings was the low temperature recorded during early spring, when minimum temperatures can reach 0 ºC (Table 1). The second cohort accounted for about 30% of the plants and their survival rate was relatively high, with a greater contribution coming from individuals that reached the fruit-bearing stage (approximately 25%), allowing the perpetuation of the species. In this case, November emergences allowed a quick growth of the species, as the risk of frost (<0 ºC) is almost nil and the average daily temperature during this month is usually above 8 ºC. The third cohort showed the highest variability (Figures 1 and 2). Although it took account for approximately 14% of the total number of emerged individuals, only 14% were able to complete the life cycle (Figure 3). In one of the study periods, none of the individuals of the third cohort were able survive due to climatic conditions, such as thermal and water stress, and also because of a higher incidence of attacks by ants, lepidopteran larvae, thrips and grasshoppers that severely affect seed production.

In environments with low predictability on the availability of scarce resources, germination and emergence time are crucial traits that affect survival, growth, flowering phenology and reproductive success (Hartzler et al., 2004). In summary, the highest mortality rates observed between the cotyledon emergence and the 6-8 leaves stages indicate that the transition probability between these early phenological stages for all cohorts is generally less or close to 30%, whereas mortality rates between the 6-8 leaves and the flowering stages were lower than 25% and, in some cases, they were insignificant (Figure 3).
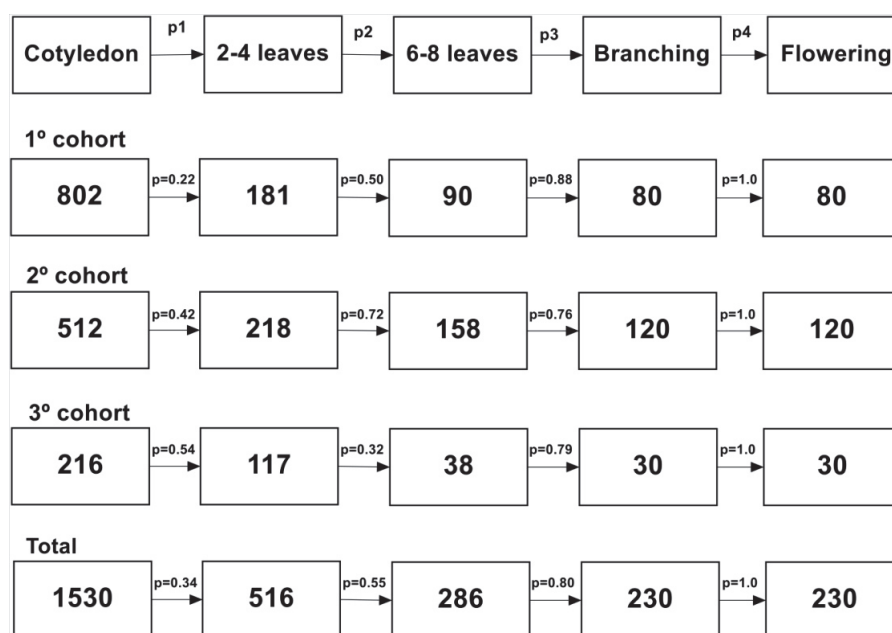
Numbers indicate the amount of individuals m^{-2} and the arrows indicate transition probabilities between different phenological states. On average, approximately 1,500 individuals m^{-2} emerged annually, including the three cohorts.

Figure 3 - Graphical overview of 2011/12 and 2013/14.

Seed production (Table 5) varied between cohorts during both periods. However, during the season 2011/12, no statistically significant differences were observed between the first and second cohorts, but differences were found in the third cohort, which failed to produce offspring. In the season 2013/14, no significant differences in seed production were found between the three cohorts. The third cohort showed a lower seed yield, but reached approximately 4,000 seeds m^{-2} (Table 5).

When grouping together data and information obtained from both study periods, it was observed that the average seed production of the first, second and third cohort was 5,700, 6,400 and 1,900 seeds m^{-2}, respectively. The second cohort in 2011/12 produced a greater number of seeds compared to the same cohort in 2013/14, while the third cohort produced more seeds in the last year of the research. Nonetheless, the total number of propagules, adding up the three cohorts, was similar in both periods (2011/12 and 2013/14), about 14,000 seeds m^{-2}.

Seed production (seeds m^{-2}) is influenced by population density (Figure 4A). Seed production increased with density, however, there was no significant increase in seed production when the population reached 150 individuals m^{-2}. Possibly the addition of a new individual would be offset by a lower fecundity of each individual plant.

On the other hand, individual fecundity (seeds per plant) is even more strongly influenced by population density (Figure 4B). High population densities can cause strong intraspecific competition by significantly reducing the reproductive success of the plant (Cordes et al., 2004)

Population seed production (seeds m^{-2}), according to studies conducted in 2011/12 and 2013/14, seems to be mainly influenced by the emergence timing of cohorts and the environmental conditions during the year (Table 5), while fecundity per plant was more affected by population density (Figure 4).

Considering that the maximum annual emergence observed in the development conditions of the present study was less than 2,500 individuals m^{-2}, and that the average seed yield was 14,000 seeds m^{-2}, one might infer that, although the carrying capacity of the system can be easily reached in a delimited space (plot), *E. davidii* would be able to colonize new niches and, consequently, to exploit the system's available resources.

As noted in both periods, regardless of the cohort or the initial number of seedlings, the total number of individuals that actually managed to bear fruit and produce viable seeds was always lower than 300 plants m^{-2}. Therefore, a small number of uncontrolled individuals (escapes from chemical treatments) of successive cohorts may be sufficient to produce a large number of seeds. This may generate a trend towards the accumulation of a greater number of *E. davidii* propagules in the soil seed bank and, consequently, an increase in emergence densities in the following years.

The role of the third cohort of *E. davidii* in the agroecosystems of the central area of Buenos Aires Province should be highlighted, as it showed great flexibility in terms of emergence time and an ability to adapt to environmental variability in comparison with the first and second
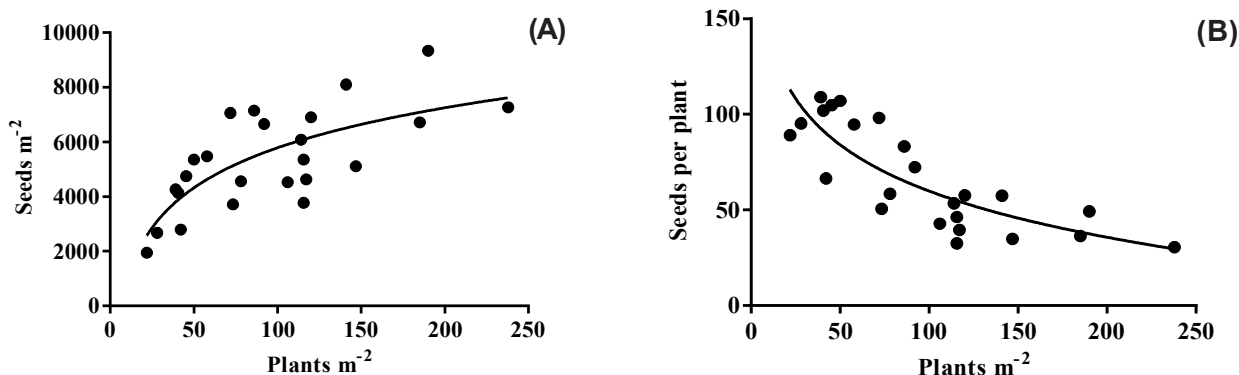

Figure 4 - (A) Population seed production (2011/12 and 2013/14) according to *E. davidii* density ($Y = 4870 ´ \log (X) - 2952$) R^2 = 0,54. (B) Fecundity (2011/12 and 2013/14) according to *E. davidii* density ($Y = 80.37 ´ \log (X) - 220.6$) R^2 = 0,66.

cohorts. In addition, in production lots, this cohort, possibly due to its density and emergence period, is not controlled, as it may be below the economic threshold. This fact would represent an opportunity for replenishment of the seed bank and, thus, increased levels of infestation.

According to studies carried out by Juan et al. (2003), an infestation rate of 100 *E. davidii* plants m^{-2} would lead to a 30% reduction in soybean yield, manifesting itself through a decrease in the number of pods per plant, and to a lesser extent, the weight of 1,000 seeds. Juan and Saint-André (1995) showed that a density of 60 plants m^{-2} may produce a significant competitive effect with soybean crops, and that would affect the amount of trifoliate leaves, leaf area and dry weight of the plant.

On the basis of the information obtained from previous studies, there are several issues that should be considered. First, *E. davidii* infestation levels have significantly increased, since surveys carried out during the summer months in October 2000 considered <100 plants m^{-2} to be a common density level for this weed, while in 2011/12, the maximum emergence was about 700 plants m^{-2} and, in 2013/14, density levels were higher than 2,000 plants m^{-2}.

According to Juan et al. (2002), for the density levels previously observed (<100 plants m^{-2}), control rates of 75% were acceptable, since the remaining uncontrolled plants did not cause reductions in production levels in comparison with free-weed control plots. Currently, however, due to a significant increase in the initial densities, control techniques (including efficiencies > 95%) may prove to be insufficient, as the remnants of uncontrolled plants exceed the economic damage thresholds, requiring more than one application of herbicide or the implementation of other complementary and alternative management techniques.

On the other hand, a greater number of individuals, combined with the need for more herbicide applications, could significantly increase the risk of developing resistance, especially if most post-emergence chemical controls in RR crops of the central area of Buenos Aires Province use glyphosate as the main herbicide.

Chemical control is the world's most frequently used weed control strategy (Christoffoleti, 2004), and glyphosate is currently the most commonly used herbicide in RR soybean and maize crops. In the case of *E. davidii* control using glyphosate, it is well known that the most sensitive phase occurs between the 2-4 leaves stage and the beginning of branching; in addition, the beginning of flowering is a crucial point, as control doses increase substantially and field controls become more erratic (Juan et al., 2011).

Considering the established thermal time scale, the best moment for field control ranges from 200 to 500 ^{o}C, which includes the phenological states of 2-4 leaves and branching.

Based on the information presented in this paper, the thermal time accumulation of 500 ^{o}C could be considered the limit for an acceptable control. Such value is expected to occur in the eighth week after emergence for the first cohort, in the sixth week for the second cohort, and between the fourth and sixth week for the third cohort. It should be noted that, in calendar days, the late cohorts will have a narrower window for an effective herbicide application, because when temperatures increase, thermal accumulation and, consequently, phenological states occur early.

Taking into account that the control threshold was set at 500 ^{o}C under field conditions, herbicide treatments should be applied near that limit, calculated from the emergence of the first cohort. Thus, the second cohort would also have emerged and would use the density-dependent mortality phenomena that could naturally reduce the number of individuals (Tables 3 and 4). According to the findings of this study, if this type of treatment is applied using post-emergent herbicides, which correspond to the eighth week from the emergence of the first cohort; the third cohort would had not emerged yet, thus it will require further treatments or other additionals control techniques to prevent individuals from providing seeds to the seed bank and increasing problems related to weed control in future years.

It is expected that the present findings would contribute as a valuable basis for improving decision-making processes and control interventions within the scope of integrated weed management programs.

REFERENCES

Aitken Y. **Flowering time, climate and genotype**. Melbourne: Melbourne University Press, 1974. 193p.

Barina Z. et al. Current distribution and spreading of *Euphorbia davidii* (*E. dentata* agg.) in Europe. Central. **Eur J Biol.** 2013;8:87-95.

Begon M. et al. **Ecología:** individuos, poblaciones y comunidades. Barcelona: Omega, 1988. 883p.

Begon M. et al. **Ecology**: from individuals to ecosystems. 4th. ed. Oxford: Wiley-Blackwell, 2006. 752p.

Christoffoleti P.J. **Aspectos de resistência de plantas daninhas a herbicidas**. Campinas: HRAC-BR, 2004. 100p.

Cordes J.C. et al. Late-emerging common waterhemp (*Amaranthus rudis*) interference in conventional tillage corn. **Weed Technol.** 2004;18:999-1005.

Deevey E.S. Life tables for natural populations of animals. **Quart Rev Biol.** 1947;22:283-314.

Fazle Rabbi A.M. Imbalance in life table: Effect of infantmortality on lower life expectancy at birth. **J Sci Res.** 2013;5:479-88.

Gadgil M., Solbrig O. The concept of r and K selection: evidence from wildflowers and some theoretical considerations. **Am Nat.** 1972;106(947):14-31.

Gadioli J.L.et al. Temperatura do ar, rendimento de grãos de milho e caracterização fenológica associada à soma calórica. **Sci Agr.** 2000;57:377-83.

González-Andújar J.L., Fernández-Quintanilla C. Modeling the population dynamics of *Avena sterilis* under dry land cereal cropping systems. **J Appl Ecol.** 1991;28:16-27.

Govaerts R., Frodín D.G., Radclife Smith A. **World checklist and bibliography of Euphorbiaceae**. Kew: Royal Botanic Gardens, 2000. 1620p.

Hartzler R.G., Battels B.A., Nordby D. Effect of common waterhemp emergence date on growth and fecundity in soybean. **Weed Sci.** 2004;52:242-5.

Juan V.F., Saint-Andre H.M. Comportamiento de *Euphorbia dentata* en la zona centro de la provincia de Buenos Aires: Biología de la germinación y sus efectos competitivos sobre el crecimiento de soja. XII Congreso Latinoamericano de Malezas, Montevideo (Uruguay). **Rev INIA Serie Técn.** 1995;56:174-8.

Juan V.F., Saint André H.M. Control de "Lecherón" (*Euphorbia dentata*) en soja con imazethapyr aplicado en distintos estados fenológicos. In: Actas del Trabajo completo en las 23º Congreso Latinoamericano de Malezas. Buenos Aires: 1997.Tomo II p.128-32.

Juan V.F. et al. Control de *Euphorbia dentata* en soja con herbicidas post-emergentes. **Rev Bras Herb.** 2000;1:147-51.

Juan V.F. et al. Control de *Euphorbia dentata* con diferentes formulaciones de glifosato en soja transgénica resistente a glifosato. **Rev Bras Herb.** 2002;3(1):29-32.

Juan V.F., Saint-Andre H.M., Fernandez R.R. Competencia de Lecherón (*Euphorbia dentata*) en Soja. **Planta Daninha**. 2003;21:175-80.

Juan V.F., Marchessi J.E., Nuñez Fre F.R. Control de *Euphorbia davidii* (Lecherón) con Glifosato. **Rev Esp Malezas – Aapresid**. 2011:61-7.

Marchessi J. et al. Efecto de la temperatura sobre la germinación de *Euphorbia davidii* Subilis. 2ª Reunión Conjunta de Sociedades de Biología de la República Argentina. XIII Jornadas de la Sociedad Argentina de Biología, XXIX Reunión Anual de la Sociedad de Biología de Cuyo and XVIII Jornadas Científicas de la Sociedad de Biología de Córdoba, held in San Juan City from 17 to 19 Aug. 2011. **Rev Biocell**. 2011;3(35):A 237-EB33.

Monteith J.L., Moss C.J. Climate and the efficiency of crop production in Britain. **Phil Trans Royal Soc.** 1977;281:277-94.

Nuñez Fré F.R., Juan V.F., Chantre G. Distribución vertical del banco de semillas de *Euphorbia davidii* Subils, en lotes agrícolas de la zona centro de la provincia de Buenos Aires, Argentina. **Planta Daninha**. 2014;32:709-18.

Pearl R. **The rate of living**. New York: Knopf, 1928.

Purger D. et al. *Euphorbia davidii* Subils (Euphorbiaceae), a new alien species in the flora of Serbia. **Bot Serbica**. 2015;39:49-52.

Rabinovich J.E. **Introducción a la ecología de poblaciones animales**. México: Compañía Editorial Continental, 1980. 313p.

Ricklefs R.E. **Ecology**. 3rd. ed New York: WH Freeman and Co, 1990.

Russelle M.P. et al. Growth analysis based on degree days. **Crop Sci.** 1984;24:28-32.

Storrie A.M., Cook A.S. Distribution and herbicide options for the management of *Euphorbia davidii* Subils. In: Proceedings of the 11th. Australian Weeds Conference: where in the world is weed science going. 1996. v.30. p.93-6.

Trudgill D.L.et al. Thermal time-concepts and utility. **An Appl Biol.** 2005;146:1-14..

Vladimirov V., Petrova A. A new alien species of Euphorbia (Euphorbiaceae) to the Bulgarian Flora. **Phytol Balc.** 2009;15:343-5.

Win S.S. et al. Life table and population parameter of *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae) on rice. **J Biol Sci.** 2009;9:904-8.