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Phenology, growth, and seed production of junglerice (*Echinochloa colona*) in response to its emergence time and populations

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Research Article

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Abstract

Junglerice [*Echinochloa colona* (L.) Link.] is the most important grass weed species in Australian summer cropping systems. Although it is mainly a spring- and summer-emerging weed species, field observations suggest that *E. colona* is expanding its seasonality. A common garden experiment was conducted at the University of Queensland farm to examine the effect of planting dates on phenology, growth, and fecundity of eight populations of *E. colona*. All populations were planted every second month from September to July in 2019 to 2020 and 2020 to 2021. *Echinochloa colona* took the shortest time (4 to 6 d) to emerge when planted in November or January. However, the November population took the longest number of growing degree days to exhibit panicle emergence. In both years, populations differed in height and leaf, tiller, panicle, and seed production in response to planting times. Plants produced significantly greater biomass for the November planting (123 to 147 g plant^{-1}) followed by the January planting and then the September planting. The March planting produced the lowest biomass. In the first year, the lowest number of seeds (3,500 seeds plant^{-1}) was produced by the March planting; however, in the second year, similar numbers of seeds were produced by the March and July plantings. In the first year, seed production (51,000 seeds plant^{-1}) was greatest for the November planting; however, some populations also produced a similar number of seeds for the January planting. In the second year, significantly greater seed production (111,000 seeds plant^{-1}) was observed for the January planting compared with other planting dates. The aboveground biomass and seed production of *E. colona* were positively correlated. This study reveals variations among *E. colona* populations and suggests that although greater emphasis must be placed on controlling spring- and summer-emerging plants, management practices need to be extended throughout the year to control *E. colona* in southeastern Australia.

Introduction

Weeds are one of the most important biological constraints to Australian grain and cotton (*Gossypium hirsutum* L.) production systems. They cost more than AU\$3 billion yr^{-1} to the Australian grain industry (Llewellyn et al. 2016). Junglerice [*Echinochloa colona* (L.) Link] is the most important grass weed species in summer crops and fallows. *Echinochloa colona* ranks first among summer grass weed species in terms of causing yield and revenue losses to Australian grain growers (Llewellyn et al. 2016). It is an annual C_4 species that infests 35 crops grown in 60 countries (Holm et al. 1977). In Australia, *E. colona* is present in all states and territories (AVH 2022), and in the eastern region, it is a problematic weed in cotton, mung bean [*Vigna radiata* (L.) R. Wilczek], corn (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench], sugarcane (*Saccharum officinarum* L.), and rice (*Oryza sativa* L.) (Osten et al. 2007; Pratley et al. 2008; Shabbir et al. 2019). In an aerobic rice system, *E. colona* at a density of 40 plants m^{-2} was reported to reduce grain yield by 35% (Chauhan and Johnson 2010). In a recent study conducted in the eastern cropping system of Australia, 4 plants m^{-2} of *E. colona* reduced mung bean grain yield by 20% (Mahajan and Chauhan 2022). A survey covering 135 fields in the cotton-growing regions of the eastern part of Australia revealed *E. colona* to be the most common grass weed species, occurring in 67% of the surveyed fields (Manalil et al. 2017).

In the eastern cropping system, a fallow phase that lasts for 12 mo or more is common (Thomas et al. 1997; Webb et al. 1997). Weeds growing in fallow fields can consume a significant amount of soil moisture and nutrients. Therefore, Australian grain growers spend about AU \$500 million yr^{-1} to control weeds during the fallow phase. In fallow conditions in the eastern grain region of Australia, *E. colona* can produce more than 20,000 seeds plant^{-1} (Squires et al. 2021). This weed can also produce a significant number of seeds when in competition with a crop. A recent study, for example, observed about 9,000 seeds m^{-2} of *E. colona* when 16 plants m^{-2} competed with a mung bean crop (Mahajan and Chauhan 2022). Seeds of *E. colona* may remain viable for up to 6 yr in the soil seedbank (Walker et al. 2010). Seed germination of this weed is stimulated by light, and the greatest germination occurs for seeds on the surface (Mutti et al. 2019a), suggesting that *E. colona* will remain a dominant weed species in no-till cropping systems. Because of several benefits of no-till farming systems, growers rely on herbicides for weed control. However, overreliance on herbicides has resulted in the evolution of herbicide resistance in *E. colona*. This weed has evolved resistance to several herbicides, including glyphosate (Storrie et al. 2008). A study conducted in Queensland suggested that there was no fitness penalty in a glyphosate-resistant population (Mutti et al. 2019b).

Seeds of *E. colona* can germinate at temperatures ranging from 20/10 to 35/25 C (alternate day/night [12/12 h]) (Mutti et al. 2019a). While these results suggest that *E. colona* can emerge in spring, summer, and autumn in the eastern cropping region of Australia, there is no information available as to whether the emerged seedlings would survive and produce seeds. Weed emergence time can greatly affect phenology, growth, and fecundity. For example, a population of Palmer amaranth (*Amaranthus palmeri* S. Watson) produced about 50 seeds plant^{-1} when it emerged in the late season (July planting) in Purdue, USA (Spaunhorst et al. 2018). The same population produced about 19,000 seeds plant^{-1} when it emerged in the early season (May planting). In a similar study conducted in Australia, the seed production of sterile oat [*Avena sterilis* L. ssp. *ludoviciana* (Durieu) Gillet & Magne; syn.: *Avena ludoviciana* Durieu) was reduced by >80% for late planting (July) compared with early (May) planting (Mahajan and Chauhan 2021). Similarly, populations of weed species may differ in their growth and seed production. For example, a population of *A. palmeri* from Arkansas, USA, produced about 15,700 seeds plant^{-1}, whereas, a population from Indiana, USA, produced about 48,400 seeds plant^{-1} (Spaunhorst et al. 2018). In another study, seed production of different populations of waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer] varied from 470,000 to 1,286,000 plant^{-1} (Heneghan and Johnson 2017).

A better understanding of the effect of emergence time and population on weed phenology, growth, and seed production could help manage weeds efficiently. However, such information is not available for *E. colona*, especially in Australian farming systems. Therefore, a common garden study was conducted to evaluate the phenology, growth, and seed production of eight populations of *E. colona* in response to different planting times. Such a common garden experiment can help demonstrate inherent differences between populations by allowing the comparison of different populations of interest in a single location (Dorman et al. 2009; Heneghan and Johnson 2017).

Material and Methods

Seed Collection and Planting

Seeds of eight populations of *E. colona* were collected in 2017 from different crop situations in Queensland and New South Wales (Table 1). Seeds of each population were collected from 40 to 50 plants spread across a >1-ha area. Only mature plants were chosen, and seeds were collected by shaking the plants over a tray. Seeds were cleaned and stored in plastic containers at room temperature (25 ± 2 C). In September 2018, these populations were planted separately in plastic pots (24-cm diameter and 30-cm height) filled with a commercial potting mix (Centenary landscape, Brisbane, QLD, Australia). Pots were placed outdoors at the Gatton Farms of the University of Queensland, QLD, Australia. Seeds from these populations were collected and used in the phenology study.

An outdoor pot study was conducted in 2019 to 2020 and 2020 to 2021 at the Gatton research farm. Plastic pots (24-cm diameter and 30-cm height) were filled with potting mix and 3 to 4 seeds of each population were planted at 0.5 cm in the center of each pot. Immediately after emergence, seedlings were thinned to keep only one plant per pot. No nutritional deficiency symptoms were observed throughout the experimental duration, therefore, fertilizer was not added. Pots were placed in trays (30 cm by 25 cm) filled with water and placed on benches. Seeds were planted on the 14th of every second month starting from September 2019 to July 2020. The experiment was repeated from September 2020 to July 2021. Each year, there were six replications of each treatment.

Observations

Dates of seedling emergence, panicle emergence, and maturity were noted. Plants were harvested when 25% of the panicles had started seed shattering. At harvest, plant height was measured from the surface to the tip of the uppermost leaf or panicle. Leaf, tiller, and panicle numbers were also measured at maturity. From each plant, five intact panicles were selected, and seeds present on each panicle were counted. Average seed production per panicle was calculated and multiplied by the total number of panicles to estimate seed production per plant. Plants from individual pots were harvested and oven-dried at 70 C for at least 72 h, after which aboveground biomass was measured. Daily maximum and minimum temperatures (Figure 1) and photoperiod hours (Figure 2) were obtained from the Gatton Bureau of Meteorology Weather Station situated within 500 m of the experimental site. Cumulative growing degree days (GDD) on each day after planting were calculated as:

$$\mathrm{GDD} = [(\text{daily maximum temperature} + \text{daily minimum temperature})/2 - T_b]$$

where the base temperature (T_b) was considered to be 10 C for summer weeds (Squires et al. 2021).

Statistical Analyses

The experiment (factorial arrangement of planting date by population) was arranged in a randomized complete block design, and each treatment was replicated six times. There were six planting dates (September, D1; November, D2; January, D3; March, D4; and July, D6) but only a few plants, irrespective of population, survived from the May-planted cohorts. Therefore, data from the May-planted cohort were excluded from the analyses. Experimental data were subjected to ANOVA using the statistical software Genstat (Genstat 2021). Years and planting dates were considered to be random effects, and populations were considered to be fixed effects in mixed-model analysis. Before ANOVA, data were validated for meeting the assumptions of normality and equal variance. Year effects were significant; therefore, data were analyzed separately for each year. The biomass data were subjected to square-root transformation $[\sqrt{(x+0.5)}]$ to homogenize the variation. Data transformation was not needed for the other growth parameters. Means were compared using Fisher's protected LSD at 5%. To determine the effect of aboveground biomass on seed production, a linear model ($S = B + bx$; S is seed production plant^{-1} at aboveground plant biomass B, and b is the slope) was fit using SigmaPlot v. 14.5 (Systat Software, San Jose, CA, USA). For each year, data from all populations were included.

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Table 1. Seed collection details of *Echinochloa colona* populations.

Population	Latitude and longitude	Location	Crop situation
B17/7	27.50000000° S,151.69666667°E	Dalby	Wheat–fallow
B17/12	30.268508°S,149.80481°E	Narrabri	Wheat–fallow
B17/13	30.306499°S,149.811438°E	Narrabri	Wheat–fallow
B17/16	30.09099349°S,149.64890°E	Narrabri	Lathyrus–wheat/chick pea[a]
B17/17	30.38230°S,149.59679°E	Narrabri	Fallow
B17/34	28.58305556° S,150.36888889°E	Moree	Wheat–fallow
B17/35	29.95805°S,149.8339°E	Moree	Cotton–fallow
B17/37	27.5514°S,152.3428°E	Gatton	Wheat–fallow

[a]Chick pea (*Cicer arietinum* L.); angled pea (*Lathyrus angulatus* L.).

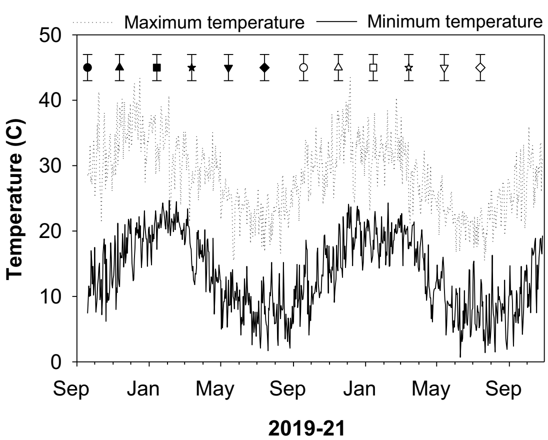

Figure 1. The minimum and maximum temperatures during the duration of the experiment (2019–2021) at the University of Queensland, Gatton, QLD. The error bars and symbols (solid, first run; open, second run) show planting dates.

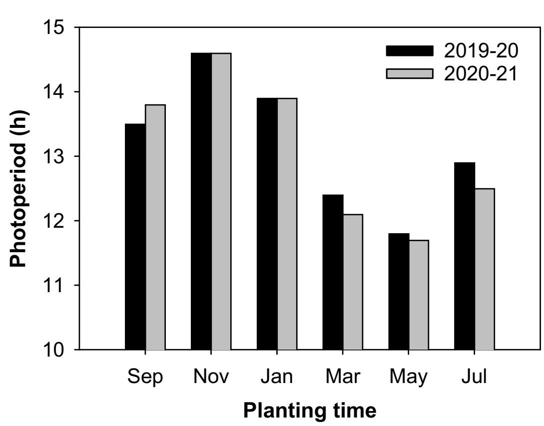

Figure 2. The average photoperiod (hours) during the growth period (sowing to harvest) of *Echinochloa colona* when planted in different months at the University of Queensland, Gatton, QLD.

Results and Discussion

Phenology Dates

In both years, *E. colona* took the shortest time (4 to 6 d; 65 to 96 GDD) to emerge when planted in November or January (Table 2). Although seeds for the July planting took the longest time (13 to 18 d) to emerge, the required number of GDD was 61 to 66. *Echinochloa colona* is mainly a weed in spring and summer crops, and July is a midwinter month in Australia, which explains the extended emergence time.

The number of GDD needed for panicle emergence varied among populations. The time to panicle emergence was different in different years for each planting time. In the first year, September-planted cohorts required the lowest number of GDD (263 to 354) for panicle emergence, whereas in the second year, July-planted cohorts required the lowest number of GDD (342 to 458) for panicle emergence (Table 2). In both years, November-planted cohorts required the greatest number of GDD (550 to 693 in 2019 to 2020 and 466 to 622 in 2020 to 2021) for panicle emergence. Similar responses were found for *E. colona* maturity (i.e., harvest).

Temperature and photoperiod are the two most important factors affecting phenological stages (Hatfield et al. 2011; Hatfield and Prueger 2015). In a previous study in Queensland, the growth period and flowering initiation in redroot pigweed (*Amaranthus retroflexus* L.) and slender amaranth (*Amaranthus viridis* L.) were reduced when planting was delayed to January in comparison with October (Khan et al. 2021). The authors suggested that shorter daylight hours experienced by the January-sown plants resulted in shorter time to flowering. A similar response to temperature and photoperiod was found in *A. palmeri* in the United States (Spaunhorst et al. 2018). In another study, barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.], a species closely related to *E. colona*, under 11-h daylengths produced seeds within 52 d compared with 84 d under 16-h daylengths (Vengris et al. 1966). In the current study, *E. colona* plants sown in spring (September and November), summer (January), and autumn (March) months took 24 to 46 d for panicle emergence, whereas plants sown in winter (July) months took 62 to 83 d for panicle emergence.

Height

In both years, the interaction between planting time and population was significant for the plant height of *E. colona* (Table 3). In general, the shortest plants were observed for the March planting and the tallest plants for the November planting. However, height was similar for some populations when comparing March- and July-planted cohorts and November- and January-planted cohorts. Plants sown in September had intermediate plant heights. Plant height among *E. colona* populations was variable across planting dates. For example, B17/34 height was 17.2 cm for the March planting and 84.3 cm for the November planting in the first year. Similarly, in the second year, its height was 34.4 cm for the July planting and 94.8 cm for the November planting. Plants of B17/16 attained the maximum plant height for most planting dates in both years.

In a previous study, an Illinois (USA) population of *A. tuberculatus* had the tallest plants across three planting dates (May, June, and July) (Heneghan and Johnson 2017). Similarly, the plants of *A. retroflexus* and *A. viridis* were taller for the October planting in comparison with plants from November, December, or January planting (Khan et al. 2021). In the current study, although plants were tallest for the November planting and shortest for the March planting, the results were not consistent among populations. Differences in height among populations and planting dates could be due to high genetic diversity among *E. colona* populations.

Leaf, Tiller, and Panicle Production

In both years, the interactions between planting date and population were significant for leaf (Table 4), tiller (Table 5), and panicle

Table 2. Growing degree days for *Echinochloa colona* seedling emergence, panicle emergence, and harvest when planted in different months in 2019–2020 and 2020–2021.[a]

Planting date (month)	2019–2020			2020–2021		
	Emergence	Panicle emergence	Harvest	Emergence	Panicle emergence	Harvest
	Growing degree days (days)					
D1 (September)	71–106 (7–10)	263–354 (24–31)	634 (54)	90–120 (7–11)	376–514 (35–46)	981 (77)
D2 (November)	66–84 (4–5)	550–693 (31–39)	1145 (67)	68–82 (4–5)	466–622 (28–38)	1202 (75)
D3 (January)	65–96 (4–6)	512–632 (30–37)	963 (59)	69–87 (4–5)	465–541 (30–35)	991 (64)
D4 (March)	87–102 (8–9)	367–411 (29–33)	679 (61)	71–86 (6–7)	353–419 (29–36)	756 (87)
D5 (May)	78–92 (12–14)	507–550 (92–99)	899 (143)	49–55 (9–10)	439–496 (96–107)	670 (130)
D6 (July)	61–66 (13–14)	378–571 (64–83)	799 (103)	61–64 (17–18)	342–458 (62–78)	801 (106)

[a]Values in parentheses are number of days plants took for seedling emergence, panicle emergence, and harvest.

Table 3. The interaction effect of populations and planting dates on the height of *Echinochloa colona* in 2019–2020 and 2020–2021.

Population	Height				
	D1 (Sep)	D2 (Nov)	D3 (Jan)	D4 (Mar)	D6 (Jul)
			—cm—		
			2019–2020		
B17/7	41.5	85.2	82.8	18.7	46.3
B17/12	40.0	83.8	84.0	25.3	48.3
B17/13	44.7	80.7	75.8	24.3	39.7
B17/16	45.7	97.8	87.2	26.5	40.0
B17/17	41.8	90.8	83.0	22.7	34.0
B17/34	43.5	84.3	66.0	17.2	33.0
B17/35	43.3	91.7	73.7	25.5	33.2
B17/37	43.7	88.0	85.2	23.2	34.0
LSD[a]			7.74		
			2020–2021		
B17/7	59.0	85.2	80.3	42.0	46.3
B17/12	51.8	96.5	74.8	39.2	37.3
B17/13	52.3	97.2	77.7	41.8	40.2
B17/16	55.7	100.8	89.1	46.7	44.3
B17/17	48.8	99.8	77.2	43.0	35.5
B17/34	54.2	94.8	72.5	41.7	34.4
B17/35	55.0	78.2	75.8	42.3	36.6
B17/37	53.3	89.7	76.2	40.8	37.0
LSD[a]			6.04		

[a]LSD at a 5% level of difference.

Table 4. The interaction effect of populations and planting dates on leaf production of *Echinochloa colona* in 2019–2020 and 2020–2021.

Population	Leaf production				
	D1 (Sep)	D2 (Nov)	D3 (Jan)	D4 (Mar)	D6 (Jul)
			—no. plant^{-1}—		
			2019–2020		
B17/7	96	704	134	40	528
B17/12	125	630	164	49	551
B17/13	109	769	129	41	266
B17/16	104	553	138	32	145
B17/17	118	394	204	39	284
B17/34	127	409	203	34	518
B17/35	128	384	184	51	366
B17/37	157	379	203	65	462
LSD[a]			102		
			2020–2021		
B17/7	546	490	653	255	232
B17/12	581	358	712	301	280
B17/13	447	392	693	264	233
B17/16	459	405	543	159	287
B17/17	525	350	613	300	312
B17/34	690	375	738	258	301
B17/35	668	529	1,085	378	227
B17/37	396	505	816	284	211
LSD[a]			123		

[a]LSD at a 5% level of difference.

numbers (Table 6). The responses of different populations varied between years and planting dates. In general, plants from March planting produced the lowest number of leaves and tillers. In 2019 to 2020, September- and January-planted cohorts produced a similar number of leaves and tillers. Similar results were found in 2020 to 2021, but some populations varied in their response. The maximum numbers of leaves and tillers were observed for the November planting in 2019 to 2020 but for the January planting in 2020 to 2021. In 2019 to 2020, leaf production among populations was similar for September, January, and March plantings, whereas in 2020 to 2021, similar leaf production among populations was obtained for only the July planting. For tiller production, similar responses among populations were obtained for the March planting in both years and the September planting in 2019 to 2020. At other planting dates, populations varied in their tiller production.

In general, March-sown plants produced the lowest number of panicles in both years (Table 6). Depending on the year, November- or January-sown plants produced the maximum number of panicles; however, some populations had similar numbers of panicles across September, November, January, or July planting dates. Not a single population responded consistently to different planting dates.

In a similar study in Queensland, the maximum number of leaves in *A. retroflexus* and *A. viridis* were produced in plants sown in October, and leaf production rates were reduced by delaying the planting dates (Khan et al. 2021). In another study at the same location, six populations of *A. sterilis*, a winter weed species, had a similar number of panicles across their planting dates (early, mid, and late) and a greater number of panicles per plant was observed for early planting compared with mid- or late planting (Mahajan and Chauhan 2021). In the United States, *E. crus-galli* produced a greater number of panicles for the May planting compared with the late plantings from June to September (Keeley and Thullen 1989). In a field study in the United States, *A. palmeri* was planted at monthly intervals from March through October (Keeley et al. 1987). The authors observed that flowering of the earlier plantings was initially delayed, but the larger plants for the March through June plantings eventually produced significantly more inflorescences than

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Table 5. The interaction effect of populations and planting dates on tiller production of *Echinochloa colona* in 2019–2020 and 2020–2021.

Population	Tiller production				
	D1 (Sep)	D2 (Nov)	D3 (Jan)	D4 (Mar)	D6 (Jul)
			—no. plant^{-1}—		
			2019–2020		
B17/7	104	187	88	20	131
B17/12	89	175	86	24	132
B17/13	87	181	83	18	94
B17/16	81	152	58	18	57
B17/17	88	119	99	21	85
B17/34	95	133	68	16	167
B17/35	103	138	99	26	119
B17/37	85	137	100	31	120
LSD[a]			28.2		
			2020–2021		
B17/7	116	120	126	56	162
B17/12	123	94	128	67	148
B17/13	106	128	133	55	128
B17/16	102	115	109	45	104
B17/17	115	116	126	62	100
B17/34	135	130	146	69	104
B17/35	141	139	140	81	83
B17/37	100	126	142	70	171
LSD[a]			27.2		

[a]LSD at a 5% level of difference.

Table 6. The interaction effect of populations and planting dates on panicle production of *Echinochloa colona* in 2019–2020 and 2020–2021.

Population	Panicle production				
	D1 (Sep)	D2 (Nov)	D3 (Jan)	D4 (Mar)	D6 (Jul)
			—no. plant^{-1}—		
			2019–2020		
B17/7	120	201	168	27	241
B17/12	116	186	143	32	244
B17/13	115	220	144	26	193
B17/16	107	167	104	24	94
B17/17	115	131	171	28	192
B17/34	112	143	79	21	232
B17/35	111	169	162	31	247
B17/37	122	139	173	46	216
LSD[a]			44.6		
			2020–2021		
B17/7	216	240	267	103	233
B17/12	237	160	297	129	261
B17/13	200	228	328	95	218
B17/16	180	182	209	71	206
B17/17	209	190	306	130	202
B17/34	283	227	286	138	185
B17/35	270	270	307	148	121
B17/37	142	211	294	128	79
LSD[a]			54.0		

[a]LSD at a 5% level of difference.

later plantings. Such clear responses were not observed in the current study.

Biomass and Seed Production

In both years, the main effect of population and the interaction between planting date and population were nonsignificant for the aboveground biomass of *E. colona*. Biomass, however, was affected by planting date. In both years, plants produced significantly higher biomass for the November planting (147 and 123 g plant^{-1}) followed by the January and then the September planting (Table 7). In the first year, biomass was similar for September and July plantings, but in the second year, biomass was greater for the September planting compared with the July planting. In both years, plants produced the lowest biomass for the March planting.

Table 7. The effect of planting dates (averaged over populations) on aboveground biomass of *Echinochloa colona* in 2019–2020 and 2020–2021.

Planting dates	Aboveground biomass[a]	
	2019–2020	2020–2021
	—g plant^{-1}—	
D1 (Sep)	24.7 c	43.9 c
D2 (Nov)	147.1 a	122.6 a
D3 (Jan)	88.4 b	104.3 b
D4 (Mar)	3.7 d	16.3 e
D6 (July)	30.7 c	34.5 d

[a]Data were back-transformed after analysis. Means with different letters within a column are different at a 5% level of significance.

In the current study, the observed differences in *E. colona* biomass between planting dates could be due to both temperature and photoperiod. Plants experienced the maximum photoperiods for the November planting (an average of 14.6 h during the growing duration in both years) followed by the January planting (an average of 13.9 h during the growing duration in both years) (Figure 2). Plants for these planting dates also experienced the maximum temperatures of the year (Figure 1). Although plants from the September planting received an average of 13.5 to 13.8 h during their growing duration, the average minimum temperature was less than 15 C on most days. Low night temperatures can adversely affect the growth of summer weed species. Plants from the March planting experienced only 12.1- to 12.4-h photoperiods. Most plants from the May planting died (data not shown), because it was too cold for *E. colona* and the photoperiods during their growing durations were 11.8 h in 2019 to 2020 and 11.7 h in 2020 to 2021.

Results are similar to those of a recent field study conducted at Gatton (QLD) and Narrabri (NSW), in which *E. colona* produced greater biomass for the November planting in comparison with the January planting. However, the previous study had only those two common planting times (Squires et al. 2021). For *A. retroflexus* and *A. viridis* (summer broadleaf weeds), shoot biomass was reduced by 70% to 80% as a result of a delay in planting from October to January (Khan et al 2021), suggesting that *Amaranthus* species could be more sensitive to planting time in Queensland compared with *E. colona*. Similarly, in the United States, *A. palmeri* planted early season (May) produced 100% more biomass than *A. palmeri* planted late season (July) (Spaunhorst et al. 2018).

The interaction between planting time and population was significant in both years for the seed production of *E. colona* (Table 8). In both years, *E. colona* populations produced the lowest number of seeds (3,500 plant^{-1}) for the March planting; however, in the second year, plants produced similar numbers of seeds for the March and July plantings. No comparable studies are available in which the growth and fecundity of a summer weed species were evaluated by planting in autumn and winter months. In the first year of the current study, the maximum number of seeds (an average of 51,000 plant^{-1} across populations) was produced for the November planting; however, some populations (B17/7, B17/17,

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Table 8. The interaction effect of populations and planting dates on seed production of *Echinochloa colona* in 2019–2020 and 2020–2021.

Population	Seed production				
	D1 (Sep)	D2 (Nov)	D3 (Jan)	D4 (Mar)	D6 (Jul)
			—no. plant^{-1}—		
			2019–2020		
B17/7	14,206	50,376	46,237	2,723	51,945
B17/12	15,027	50,920	36,907	4,865	52,112
B17/13	14,294	63,161	33,283	2,743	25,386
B17/16	11,644	52,871	31,882	3,235	15,202
B17/17	12,353	42,825	41,732	2,936	21,708
B17/34	11,899	44,835	24,490	2,179	43,345
B17/35	10,293	50,859	44,658	3,759	28,848
B17/37	14,903	52,227	42,295	5,476	27,816
LSD[a]			11,640		
			2020–2021		
B17/7	58,038	56,982	105,308	15,712	24,645
B17/12	59,633	40,340	126,073	17,626	26,437
B17/13	58,065	63,616	150,038	16,911	25,697
B17/16	52,066	45,495	89,622	13,614	18,195
B17/17	56,228	48,133	105,931	21,390	18,817
B17/34	72,043	57,922	99,194	27,105	17,272
B17/35	74,109	72,063	106,213	2,8298	10,423
B17/37	35,797	55,380	104,968	27,337	7,403
LSD[a]			17,941		

[a]LSD at a 5% level of difference.

B17/35, and B17/37) produced a similar number of seeds for the January planting, also. In the second year, a significantly greater number of seeds (an average of 111,000 plant^{-1} across populations) were produced from the January planting compared with other planting dates. Except for some populations, seed production was similar between September and November plantings in the second year. However, in the first year, plants produced a greater number of seeds from the November planting (51,000 plant^{-1}) compared with the September planting (13,100 plant^{-1}). As mentioned earlier, most plants for the May planting died, but some plants survived and produced seeds. Averaged over survived plants across populations, *E. colona* produced 2,855 seeds plant^{-1} in 2019 to 2020 and 4,750 seeds plant^{-1} in 2020 to 2021 for the May planting (data not shown). These results suggest that some plants of *E. colona* could survive the mild winter months of Queensland and produce enough seeds for reinfestations in future cropping systems.

A recent field study, conducted in Queensland and New South Wales, reported that the seed production of *E. colona* was greater for the November planting (16,300 seeds plant^{-1}) compared with the January planting (12,400 seeds plant^{-1}) (Squires et al. 2021). In the United States, April and May plantings of *E. crus-galli* produced a greater number of seeds compared with June, July, or August plantings (Keeley and Thullen 1989). In a recent U.S. study, *A. palmeri* planted early (May) and midseason (June) produced 160% to 220% more seeds than when planted late season (July) (Spaunhorst et al. 2018). In *A. retroflexus* and *A. viridis* grown in Queensland, seed production was greater for the October planting compared with the November, December, and January plantings (Khan et al. 2021). In the same region, *A. sterilis* seed production was reduced by 21% and 84% for mid-planting (June) and late planting (July), respectively, compared with early planting (May; 2,660 seeds plant^{-1}) (Mahajan and Chauhan 2021).

Population B17/13 produced the maximum number of seeds each year (63,200 plant^{-1} in 2019 to 2020 for the November planting and 150,000 plant^{-1} in 2020 to 2021 for the January planting). In Australia, the maximum seed production of *E. colona* has been reported as 29,000 seeds plant^{-1} (Mutti et al. 2019b). The greater number of seeds in the current study could be due to differences between the populations used in this and the previous study. This justification is supported by large differences observed in the current study in seed production between populations within a planting time (e.g., 89,000 seeds plant^{-1} by B17/16 and 150,000 seeds plant^{-1} by B17/13 for the January planting in 2020 to 2021). Differences between the two studies could also be due to differential planting dates, as the current study also observed a large difference in a population's seed production between different planting dates. In addition, the previous study (Mutti et al. 2019b) was conducted in a screen house, but the current study was conducted in an open environment. Differential temperature, light, and humidity conditions between the two study environments may have affected the growth and seed production of *E. colona*. The current study did not evaluate the seed viability of *E. colona*; therefore, the seed numbers represent the potential seed production by *E. colona*.

The aboveground biomass and seed production of *E. colona* were positively correlated (r = 0.75 and 0.64 in 2019 to 2020 and 2020 to 2021, respectively) in both years (Figure 3). These results suggest that irrespective of population, plants of *E. colona* with greater aboveground biomass will produce a greater number of seeds than plants with less aboveground biomass. A positive correlation between biomass and seed production was also reported in *A. palmeri* and *A. tuberculatus* (Schwartz et al. 2016; Spaunhorst et al. 2018). A field study in Queensland also reported a linear correlation between aboveground biomass and seed production of *E. colona* (Mahajan et al. 2020). The results from the current study and previous studies (Mahajan et al. 2020; Schwartz et al. 2016) suggest that plants with large amounts of biomass will produce a large number of seeds for the next generation and replenish the soil seedbank. Failure to control these plants will result in the formation of a large seedbank of *E. colona*, and it will be difficult to manage this weed, especially if the population has evolved herbicide resistance.

Implications for Management

The current study revealed that there were no differences in biomass production between *E. colona* populations; however, there were differences in other growth parameters and seed production. Differences could be due to genetic makeup or maternal environments during plant growth and seed production. In the current study, the effect of maternal environments was removed by growing all populations in a single environment. Therefore, the observed differences in growth parameters indicate inherent genetic differences between populations and the variable growth potential of *E. colona* (Heneghan and Johnson 2017; Khan et al. 2021). A recent study identified that *E. colona* populations from Queensland and New South Wales had high genetic diversity, which was indicative of free gene flow (Chauhan et al. 2022). Although the greatest seed production was observed for the November and/or January plantings, *E. colona* produced a considerable number of seeds at all planting times. These results suggest that although greater emphasis must be placed on controlling spring- and summer-emerging plants, close monitoring of *E. colona* emergence throughout the year is needed. While most plants from the May planting of *E. colona* died due to cold temperatures, some plants survived and produced seeds. These results

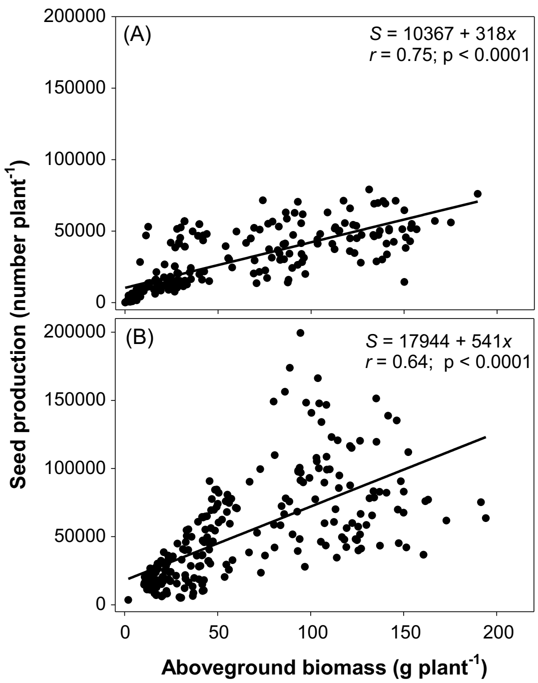

Figure 3. Correlation between *Echinochloa colona* aboveground biomass and total seed production in 2019–2020 (A) and 2020–2021 (B). For each year, data from all populations were included.

suggest that this weed species has the potential to expand its seasonality. Seasonal expansion is also being observed in another summer weed, feather fingergrass (*Chloris virgata* Sw.), in the southeastern cropping region of Australia (unpublished data). The dormancy status of *E. colona* was not evaluated in the current study; however, fresh seeds are known to have a high level of dormancy in Australian conditions (G Mahajan and BS Chauhan, unpublished data). These results suggest that any surviving plant will contribute to a persistent weed seedbank. Therefore, the most important management practice is to prevent *E. colona* introduction and seed spread to clean fields (Spaunhorst et al. 2018). Integrated weed management options, including preventive measures and the use of competitive crops, could be the best approach for the successful management of *E. colona*. Field studies need to be conducted to evaluate the effect of planting dates on the growth and reproduction of *E. colona* in different crop situations (fallows as well as in summer and winter crops).

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