



Altering native community assembly history influences the performance of an annual invader

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Abstract

Understanding the determinants of early invasion resistance is a major challenge for designing plant communities that efficiently repel invaders. Recent evidence highlighted the significant role of priority effects in early community assembly as they affect species composition, structure and functional properties, but the consequences of native community assembly history on the success of subsequent invasions has not been elucidated yet. In a greenhouse experiment, we investigated how (1) the identity of the first native colonizing species (one of two grasses: *Dactylis glomerata* and *Lolium perenne*, or two legumes: *Onobrychis viciifolia* and *Trifolium repens*), each introduced four weeks before the rest of the native community, and (2) timing of species establishment (synchronous vs. sequential sowing), influenced early establishment success of *Ambrosia artemisiifolia*, an annual noxious weed in Europe. First colonizer identity and establishment timing both affected early biomass production and composition of the community, and had implications for *A. artemisiifolia* early invasion success. Invasion success decreased when all native individuals were sown simultaneously, quickly generating a high biomass production, while it increased when the productive N-fixing legume *T. repens* was sown first. These findings support that native species assembly history matters to invasion resistance in the early growth stages, thus opening the way to more effective invasive species management strategies in restoration.

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Keywords: Priority effects; Historical contingencies; Revegetation; Restoration; Competition; *Ambrosia artemisiifolia*

Introduction

An increasing number of invasive species is causing major detrimental effects on the environment (Brondizio et al., 2019), human well-being and economy (Charles & Dukes, 2008), and this increase is expected to

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intensify (Sala et al., 2000). Invasions are also often a serious impediment to the successful restoration of damaged environments (Norton, 2009; Rowe, 2010; Stromberg et al., 2007). Restorative activities, including soil disturbance and vegetation clearing, increase resource availability and decrease competition from neighbors, and can promote plant invasion (Cherwin et al., 2009; Davis et al., 2000; Jauni et al., 2015; McIntyre & Lavorel, 1994). Susceptibility to invasion is expected to decrease over time as the restored community establishes and displays a more complete use of available space and resources (Vitousek & Walker, 1987). Reducing invasive species establishment success in the early, vulnerable stages of community growth is therefore critical. Restoring a rapidly competitive native plant cover has been advocated as a method to reduce invasions (Byun & Lee, 2017; Larson et al., 2013; Middleton et al., 2010; Yannelli, 2021). However, the mechanisms generating rapid invasion resistance are still poorly known.

Recent advances in community ecology have highlighted the defining role of historical contingencies (i.e., the effect of the order and timing of past events, being either abiotic or biotic) in community assembly and invasibility (Fukami, 2015; Švamberková et al., 2019; Werner et al., 2016; Young et al., 2016). Priority effects, the ability of an early-arriving species to either inhibit or facilitate the establishment, growth or reproductive success of species arriving later (Drake, 1991; Helsen et al., 2016), have recently received particular attention. Although priority effects often do not systematically generate changes persisting in the long term (Collinge & Ray, 2009; Young et al., 2016), numerous studies showed that even small differences in species arrival can induce dramatic changes in composition, structure and functional properties (e.g., productivity) at least for one growing season (e.g., Delory et al., 2009a; Grman & Suding, 2010; Martin & Wilsey, 2012; Plückers et al., 2013; Sarneel et al., 2016; Stevens & Fehmi, 2011; Stuble & Young, 2020; Vaughn & Young, 2015; Weidlich et al., 2018; Werner et al., 2016). Priority effects could therefore affect early invasion resistance (Lang et al., 2017; Stevens & Fehmi, 2011; Vaughn & Young, 2015) and could be manipulated to design invasion resistant restored communities (Hess et al., 2019). In the early stages of community development, we expect priority effects to be particularly impactful by influencing (1) biomass production, since higher biomass production reflects higher competitive ability (Gaudet & Keddy, 1988) and is associated with lower invasibility (e.g., Byun & Lee, 2017; Hess et al., 2020; Lulow, 2006; Weigelt et al., 2002) and/or (2) species composition (the identity of the dominant species or functional group; e.g., Byun et al., 2013; Fargione & Tilman, 2005; Mason et al., 2017; Symstad, 2000).

In the context of invasions, priority effects have usually been examined in terms of the consequences for invasive species to arrive before or after natives (Delory et al., 2019b; Grman & Suding, 2010; Lang et al., 2017; Stevens & Fehmi, 2011; Stuble & Souza, 2016; Vaughn &

Young, 2015). Studies investigating how differences in native assembly history affect subsequent invasion events are scarcer (Mason et al., 2013). In a greenhouse experiment, we established native perennial communities differing by (1) the identity of the first colonizer (either of two grasses: *Dactylis glomerata* and *Lolium perenne*, or two legumes: *Onobrychis viciifolia* and *Trifolium repens*), and (2) timing of species establishment (synchronous vs. sequential sowing), in which we subsequently simulated invasion by introducing seeds of *Ambrosia artemisiifolia*, a noxious weed in Europe (Ozaslan et al., 2016). We sought to examine whether these differences in community assembly influence the success of subsequent invasion, and if so, assess whether invasion success is related to variations in biomass production and/or community composition.

Materials and methods

Native species selection

Six perennial plant species widely used for revegetation in France were selected to compose the recipient native communities: *Dactylis glomerata* (Poaceae), *Lolium perenne* (Poaceae), *Onobrychis viciifolia* (Fabaceae), *Trifolium repens* (Fabaceae), *Plantago lanceolata* (Plantaginaceae), and *Poterium sanguisorba* (Rosaceae). Commercial seeds were purchased from seed suppliers ZYGENE and SCHEIER France.

Invasive species seed collection and stratification

The common ragweed (*Ambrosia artemisiifolia* L., Asteraceae) is an annual plant native from North America (Heckel, 1906) successfully invading disturbed areas such as roadsides, riverbanks, abandoned and cultivated fields in numerous European countries (Smith et al., 2013). The species can produce up to 14,000 achenes per plant, which are mainly dispersed by human activities (Bassett & Crompton, 1975). Achenes from *A. artemisiifolia* were collected from at least ten individuals from each of three mature populations in South-eastern France in autumn 2018 and pooled (population 1: 43°33'4.5"N, 4°7'40.8"E; population 2: 43°31'2.2"N, 5°19'56.2"E; population 3: 43°34'17.8"N, 4°17'8.8"E). Before starting the experiment, achenes were put between two layers of cotton soaked with distilled water and cold-stratified for 20 weeks (wet, dark stratification at 4 °C) in order to break primary dormancy. After stratification, we assessed the germination capacity of 50 seeds placed in five Petri dishes on cotton soaked in distilled water. Petri dishes were placed in optimum germination conditions (25 °C/12 h day and 15 °C/12 h night; Fumanal, 2007), and germination was recorded every two days until no additional germination was recorded. After ten days, the final germination rate was of 98.0% ± 2.0 (mean ± SE).

Study site and infrastructure

The experiment was conducted over six months (early March 2019 until early September 2019) in a greenhouse at the Research Institute of Tour du Valat, France (43°30'N, 4°40'E, 1 m a.s.l.). Walls and roof of the greenhouse are made of Diatex mesh (500–600 μm) so that similar ambient climate conditions occurred inside but seed dispersal was prevented. The site is subjected to a Mediterranean climate, characterized by warm and dry summers and mild, wet winters, with high variability between years (Lionello et al., 2006). Precipitation and air temperature data were recorded using a meteorological station located close to the experimental site (Appendix A: Fig. 1). We established the artificial plant communities in square plastic pots with an upper width of 30.5 cm and a bottom width 25 cm, 27 cm deep, which were filled with, from bottom to top (1) a 27 cm diameter polyester tissue (© Diatex, 50–70 μm mesh size) to prevent loss of substrate, (2) a 20 cm width \times 10 cm deep polystyrene bloc allowing water to flow at the sides, and (3) a substrate mixture of vermiculite (30 vol%; © Projar, 2.6 kg/m³) and commercial organic fertile topsoil (70 vol%; © Géolia). Pots were watered with equal amounts of water through sprinklers. The amount of supplied water was regularly adjusted to ensure moisture conditions suitable to germination and plant development. We ended the experiment in early September to avoid confounding effects of *A. artemisiifolia* natural senescence (Li et al., 2015).

Experimental design

We designed six types of recipient plant communities differing by the identity of the first species established, but all getting all six species eventually (Fig. 1). We ensured an identical final spatial arrangement of the communities by using cardboard patterns with holes, each hole corresponding to a seeding location. On 6 March, we created four priority treatments by introducing 18 seeds of either (1) *D. glomerata* (treatment name Dactylis_f, with “f” standing for “first”), (2) *L. perenne* (Lolium_f), (3) *O. viciifolia* (Onobrychis_f), or (4) *T. repens* (Trifolium_f) per pot. We also introduced (5) three seeds of each of the six species per pot, for the same number of initial seeds as the priority treatments (Synchronous_{seq}) or (6) 18 seeds of each of the six species per pot, which corresponds to the simultaneous sowing of all individuals at full density (Synchronous). Ungerminated seeds were regularly replaced by individuals sown in separate pots on 6 March to ensure similar age and density of individuals. After four weeks (i.e., on 3 April), we carried out a second sowing (except for Synchronous) by adding the rest of the species so that each pot contained 18 individuals of each of the six species, amounting a total of 108 seeds (corresponding to 1200 seeds/m²). *Plantago lanceolata* and *P. sanguisorba* were added to the four priority-tested species in order to create communities that were more diverse and to

reach the desired density of individuals while keeping an identical spatial pattern. Therefore, Synchronous_{seq} had the same density and sowing timing as Dactylis_f, Lolium_f, Onobrychis_f and Trifolium_f, but did not give priority to any particular species. This assembly type tested the role of sowing density in itself on invasion resistance. Ungerminated seeds were regularly replaced by individuals sown in separate pots on 3 April.

On 18 April, six weeks after the first sowing event and two weeks after the second sowing event, we introduced in each pot nine seeds of *A. artemisiifolia* at fixed positions, 8 cm apart from each other (Fig. 1). There were 12 replicates of each assembly type (Dactylis_f, Lolium_f, Onobrychis_f, Trifolium_f, Synchronous_{seq} and Synchronous), totaling 72 pots. Pot distribution in the greenhouse followed a randomized design and pots were randomized every two weeks.

Data collection

Invasive species early establishment success

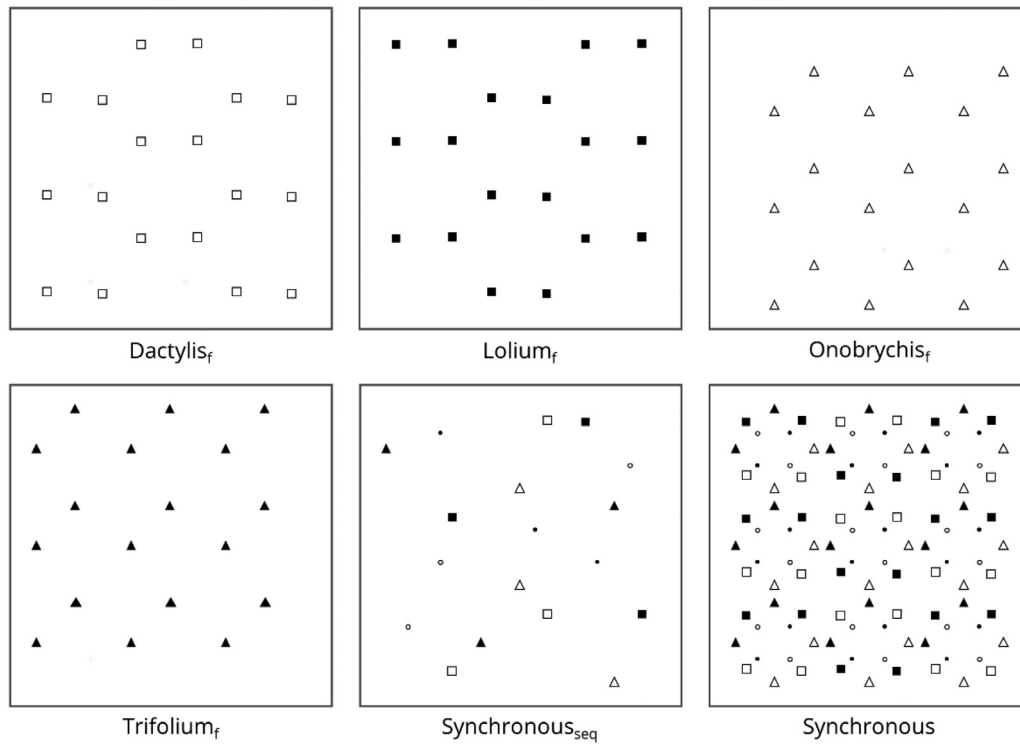
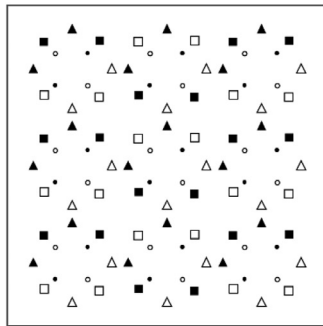
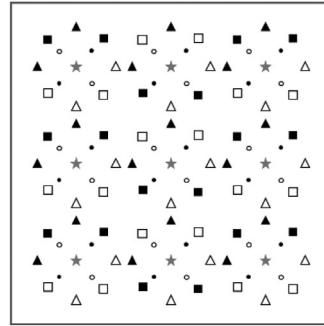
We assessed early establishment success of *A. artemisiifolia* by monitoring seedling emergence and survival visually each week from 30 April to 2 September and final aboveground biomass (2 September). Aboveground biomass of each individual was collected 0.5 cm above ground level, dried at 60 °C for 72 h and weighed.

Recipient communities

We measured aboveground and belowground biomass of the communities three times during the experiment. For this purpose we harvested (1) three pots per assembly type when *A. artemisiifolia*'s seeds were introduced (hereafter ‘initial’ – on 18 April), (2) three pots per assembly type midway through the experiment, on 13 June (hereafter ‘intermediate’), and (3) six pots per assembly type at the end of the experiment (hereafter ‘final’ – 2 September). For each pot, aboveground biomass was harvested, sorted by species and dried at 60 °C for 72 h until weighed. Belowground biomass was measured by collecting one soil core (12 cm diameter \times 16 cm deep) at the center of each pot. Since we were not able to identify and sort the roots of the different species, we measured total belowground dry biomass including native species and *A. artemisiifolia* roots. Roots were isolated from soil, washed and sieved with a 250 μm mesh, dried at 60 °C for 72 h, and weighed.

Soil analyses

Established community composition and biomass production can influence subsequent colonizing species success through modification of soil resource availability (Fargione

(A) First sowing (6 March)**(B) Second sowing (3 April)****(C) Invasion by *A. artemisiifolia* (* , 18 April)**

□ *D. glomerata* ■ *L. perenne* △ *O. viciifolia* ▲ *T. repens* ○ *P. lanceolata* ● *P. sanguisorba*

Fig. 1. Experimental design. Spatial arrangement of individuals in pots (represented by squares) is depicted depending on assembly type. In the second sowing, all communities were completed to achieve same species abundance and spatial pattern (no seed was added for Synchronous).

& Tilman, 2005; MacLaren et al., 2019; Scherer-Lorenzen et al., 2003; Temperton et al., 2007). We therefore analyzed organic carbon, nitrogen, nitrates, ammonium and available phosphorus on soil samples collected from each pot at the end of the experiment. For each assembly type, we collected 24 soil cores of 10 mm diameter × 100 mm deep (four per pot), which were pooled and dried for 48 h at 40 °C and sieved (<2 mm) to remove roots and rocks. Control soil (i.e., soil before recipient community establishment) was also added to the analyses. Samples were

analyzed for organic carbon by sulfochromic oxidation (NF ISO 14235, 1998), total nitrogen by the modified Kjeldhal method (NF ISO 112361, 1995), nitrate NO_3^- and ammonium NH_4^+ (NF ISO 14259-2, 2007), and available phosphorus P_2O_5 by the Dyer method (NF X31-160, 1999). Standard French method AFNOR or standard international method ISO were used to determine soil parameters. Analyses were performed by the accredited soil analysis laboratory Teyssier (Bourdeaux, France), following standard protocols.

Statistical analyses

Invasive species early establishment success

We used generalized linear mixed models (GLMMs) with Laplace approximation ('glmer' function in the 'lme4' package; Bates et al., 2013) for maximum likelihood estimation of the parameters (Bolker et al., 2009) to analyze variations in cumulative final seedling emergence (until 4 June; no new emergence was recorded after this date) and survival (2 September) of *A. artemisiifolia* seedlings, with a binomial error distribution and a logit-link function. We analyzed variations in final aboveground biomass (i.e., 2 September) of *A. artemisiifolia* using a linear mixed model with Gaussian error distribution (data was log transformed to fit into a Gaussian distribution; 'lmer' function of the 'lme4' package; Bates et al., 2013). Analyses of seedling emergence, survival and final aboveground biomass included assembly type (Dactylis_f, Lolium_f, Onobrychis_f, Trifolium_f, Synchronous_{seq}, Synchronous) as fixed predictor variable and pot as random factor. Upon finding a significant effect of the fixed effect assembly type (significance tested using type II sums of squares using the 'Anova' function in 'car' package; Fox et al., 2020), we conducted *post-hoc* pairwise contrasts comparisons with a Tukey adjustment ('emmeans' package; Lenth et al., 2019).

Analyses of invasive species seedling emergence was based on the 81 seeds sown per assembly type. Analyses of survival included emerged individuals in six pots per assembly type (from 50 to 54 individuals; Appendix A: Table 1). Final aboveground biomass considered all individuals surviving until the end of the experiment in six pots per assembly type (from 40 to 53 individuals; Appendix A: Table 1).

Recipient communities

We analyzed the effect of assembly type on (1) total recipient species aboveground biomass and (2) total belowground (native and invasive) biomass for the three harvests using a one-way ANOVA. When a significant effect was found, we performed pairwise comparisons on the least-squares means (LSM) with a Tukey adjustment ('emmeans' package; Lenth et al., 2019). When residuals did not satisfy normality and/or homoscedasticity assumptions, we performed Welch's heteroscedastic *F* tests with trimmed means and Winsorized variances ('welch.test' function in 'onewaytests' package; Dag et al., 2018; Welch, 1951), which are relatively insensitive to the combined effects of non-normality and heteroscedasticity (Keselman et al., 2008). When a significant effect was found, *post-hoc* multiple pairwise comparison tests were performed with a BH adjustment ('paircomp' function in 'onewaytests' package; Dag et al., 2018). All analyses of biomass were conducted on three pots per assembly type, except final aboveground biomass for which six pots were available per assembly type. We also calculated the contribution of legumes and grasses by

summing aboveground biomass of *O. viciifolia* and *T. repens*, and *D. glomerata* and *L. perenne*, respectively.

All analyses were performed using R software (ver. 3.6.2; R Development Core Team, 2020). The *p*-values lower than 0.05 were considered as statistically significant.

Results

Invasive species early establishment success

Seedling emergence and survival of *A. artemisiifolia* were high across all assembly types (i.e., 97.3% ± 1.0 and 93.3% ± 3.1, mean ± SE, respectively; Appendix A: Table 1). Assembly type did not significantly affect *A. artemisiifolia* seedling emergence (Wald $\chi^2 = 3.70$, df = 5, *p* = 0.59) or survival (Wald $\chi^2 = 4.48$, df = 5, *p* = 0.48). Assembly type significantly affected final aboveground biomass (Anova Type II: Wald $\chi^2 = 59.056$, df = 5, *p* < 0.001), which was significantly lower in Synchronous than in all other assembly types except Lolium_f (Fig. 2), and (2) significantly higher in Trifolium_f than in Lolium_f, Synchronous_{seq} or Synchronous.

Recipient community biomass

Assembly type significantly affected recipient communities above- and belowground biomass, at all harvest times (Fig. 3; Appendix A: Table 2). For the initial harvest, aboveground biomass was significantly higher in Synchronous

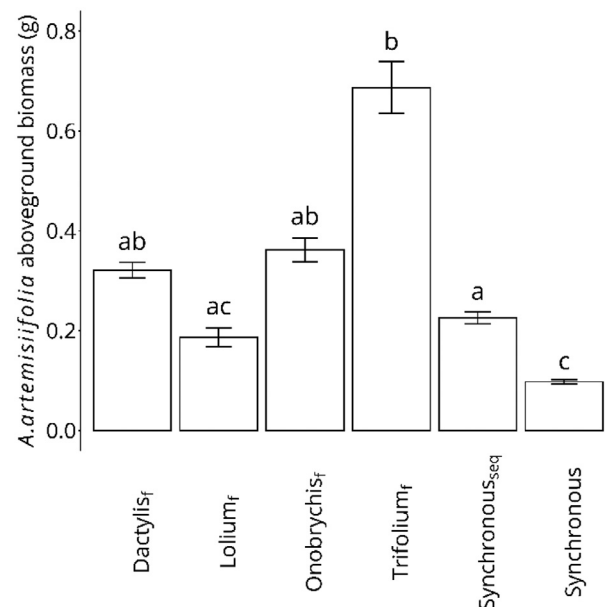


Fig. 2. *Ambrosia artemisiifolia* final aboveground biomass depending on assembly type (mean per individual ± SE, $n_{\text{tot}}=324$). Assembly types with no letter in common are significantly different (pairwise contrasts comparisons with Tukey adjustment; *p* < 0.05).

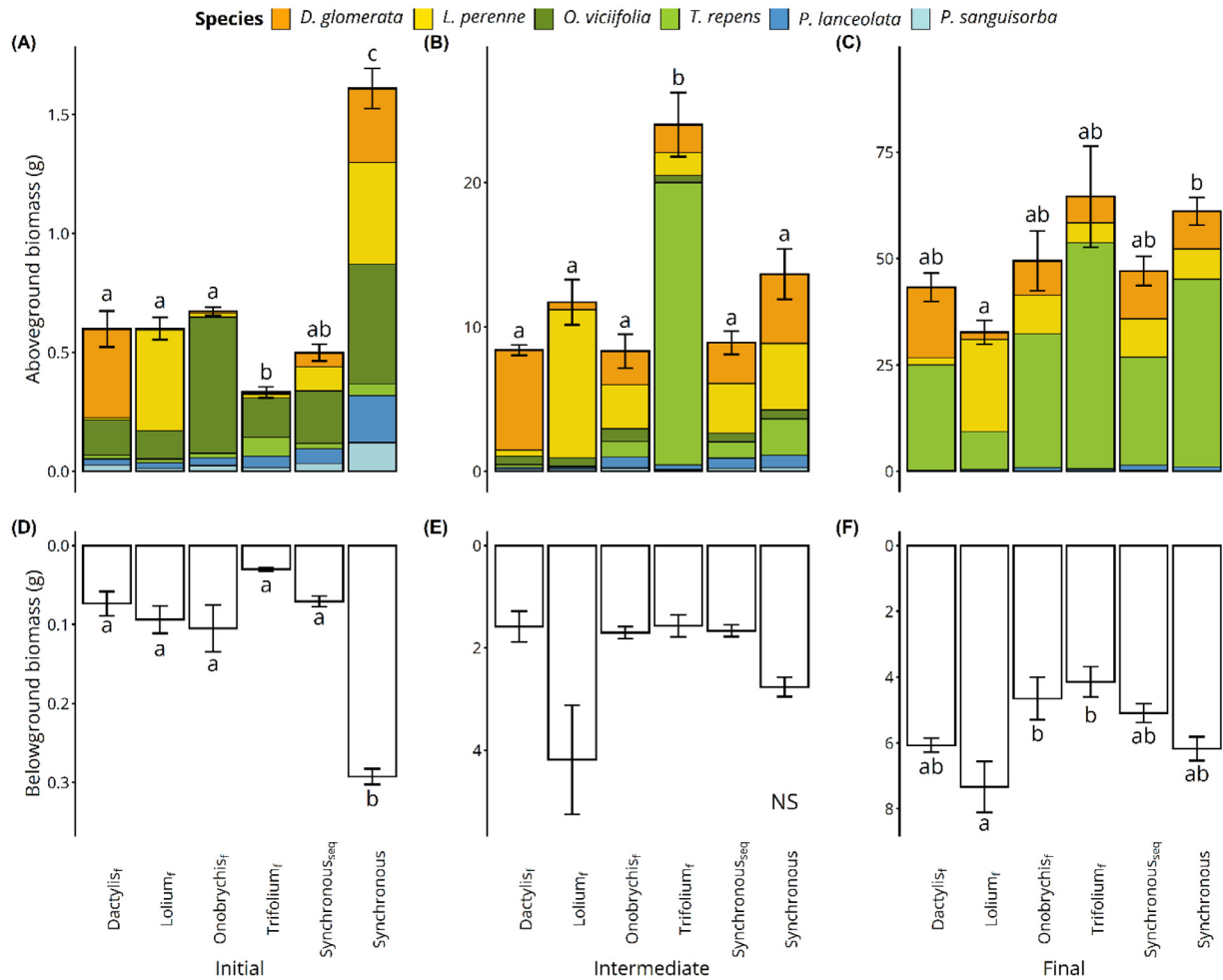


Fig. 3. Above- and belowground biomass of the recipient communities depending on assembly type for (A,D) initial (18 April), (B,E) intermediate (13 June), and (C,F) final (2 September) harvests. Aboveground biomass (A,B,C) represents total biomass per pot (mean±SE) and includes native species only, while belowground biomass (D,E,F) represents sample biomass per pot (mean±SE) and includes both native and invasive species. Treatments with no letter in common are significantly different (pairwise comparisons with Tukey adjustment; $p < 0.05$). ‘NS’ indicates to non-significant *post-hoc* differences between assembly types.

than in all other assembly types and significantly lower in *Trifolium_f* than in all other assembly types except *Synchronou_{sseq}* (Fig. 3A), and belowground biomass was significantly higher in *Synchronous* than in all other assembly types (Fig. 3D). Legumes contributed to aboveground biomass more than grasses in *Onobrychis_f*, *Trifolium_f* and *Synchronou_{sseq}*, and less than grasses in *Dactylis_f*, *Lolium_f* and *Synchronous* (Table 1). For the intermediate harvest, aboveground biomass was significantly higher in *Trifolium_f* than in all other assembly types (Fig. 3B), and belowground biomass was not significantly different between assembly types (Fig. 3E). Legumes contributed to aboveground biomass more than grasses in *Trifolium_f*, and less than grasses in all other assembly types (Table 1). For the final harvest, aboveground biomass was significantly lower in *Dactylis_f* and *Lolium_f* than in *Synchronous* (Fig. 3C), and belowground biomass was significantly higher in *Lolium_f* than in *Onobrychis_f* and *Trifolium_f* (Fig. 3F). Legumes contributed to

aboveground biomass less than grasses in *Lolium_f*, and more than grasses in all other assembly types (Table 1).

Soil analyses

Compared to control soil (i.e., soil before recipient community establishment), all planted treatments depleted the soil of available phosphorus and nitrates (Table 2). *Trifolium_f* communities produced soils with greater concentrations of nitrates and ammonium than any other treatments, including the other legume species. Soil supporting *Lolium_f* communities showed the lowest nitrate content.

Discussion

This study provides evidence for a role of assembly history and priority effects in invasion resistance during the

Table 1. Aboveground biomass of legumes (sum of *O. viciifolia* and *T. repens*, mean±SE) and grasses (sum of *D. glomerata* and *L. perenne*, mean±SE) for each assembly type for initial (18 April, $n = 3$), intermediate (13 June, $n = 3$), and final (2 September, $n = 6$) harvests. Contribution to total biomass (mean±SE), and ratio between mean biomass of legumes and grasses ('Ratio L:G'; mean±SE) are also indicated, with ratios > 1 in bold (i.e. mean biomass of legumes exceeds mean biomass of grasses).

	Legumes		Grasses		Ratio L:G
	Biomass (g)	Contribution to biomass (%)	Biomass (g)	Contribution to biomass (%)	
Initial					
Dactylis _f	0.16 ± 0.00	28.2 ± 3.9	0.38 ± 0.09	62.1 ± 8.4	0.42
Lolium _f	0.13 ± 0.01	22.3 ± 1.1	0.43 ± 0.04	71.6 ± 1.7	0.30
Onobrychis_f	0.59 ± 0.02	87.9 ± 0.2	0.02 ± 0.00	3.6 ± 0.1	29.50
Trifolium_f	0.25 ± 0.03	73.1 ± 5.6	0.02 ± 0.00	7.1 ± 0.6	12.50
Synchronous_{seq}	0.24 ± 0.02	48.8 ± 2.7	0.16 ± 0.03	32.0 ± 3.3	1.50
Synchronous	0.55 ± 0.03	34.5 ± 1.4	0.74 ± 0.03	46.0 ± 1.5	0.74
Intermediate					
Dactylis _f	0.81 ± 0.15	9.6 ± 1.6	7.34 ± 0.3	87.5 ± 1.5	0.11
Lolium _f	0.64 ± 0.04	5.6 ± 0.5	10.79 ± 1.56	91.5 ± 1.1	0.06
Onobrychis _f	1.98 ± 0.64	22.6 ± 4.0	5.36 ± 0.52	65.2 ± 2.6	0.37
Trifolium_f	20.05 ± 2.29	83.2 ± 2.1	3.5 ± 0.19	14.9 ± 1.9	5.72
Synchronous _{seq}	1.72 ± 0.24	19.3 ± 2.3	6.28 ± 0.62	70.5 ± 2.1	0.27
Synchronous	3.16 ± 0.77	22.7 ± 3.0	9.40 ± 0.95	69.4 ± 3.0	0.37
Final					
Dactylis_f	24.75 ± 3.18	47.5 ± 3.2	18.23 ± 1.44	35.7 ± 2.6	1.35
Lolium _f	8.90 ± 3.09	20.3 ± 6.0	23.35 ± 1.65	61.5 ± 6.5	0.38
Onobrychis_f	31.38 ± 7.59	49.1 ± 7.0	17.15 ± 1.11	32.8 ± 5.5	1.79
Trifolium_f	53.15 ± 11.73	64.1 ± 4.3	10.91 ± 1.81	14.2 ± 2.5	4.87
Synchronous_{seq}	25.40 ± 4.17	41.8 ± 4.5	20.27 ± 1.40	35.1 ± 3.4	1.25
Synchronous	44.08 ± 3.58	55.3 ± 2.2	15.98 ± 0.98	20.5 ± 1.9	2.75

Table 2. Results of soil analyses performed at the end of the experiment. Control soil refers to soil before recipient community establishment. Since one soil sample was analyzed per treatment, no statistical test was performed.

	Total organic matter (%)	C (g/kg)	N (g/kg)	NO ₃ ⁻ (g/kg)	NH ₄ ⁺ (g/kg)	P ₂ O ₅ (g/kg)
Dactylis _f	11.0	63.6	4.1	0.007	0.012	0.078
Lolium _f	11.1	64.6	4.4	0.003	0.010	0.074
Onobrychis _f	11.3	65.7	5.0	0.005	0.012	0.076
Trifolium _f	11.1	64.3	5.2	0.010	0.015	0.070
Synchronous _{seq}	11.3	65.7	4.6	0.007	0.012	0.070
Synchronous	11.4	66.1	4.4	0.008	0.010	0.083
Control soil	11.2	65.0	4.5	0.011	0.005	0.136

early stages of community development and thus corroborates several recent studies (e.g., Delory et al., 2019; Grman & Suding, 2010; Lang et al., 2017; Stevens & Fehmi, 2011; Stuble & Young, 2020; Vaughn & Young, 2015). The novelty of our results lies in the fact that the history of native species establishment (i.e., timing and order of species arrival) affects the success of the subsequent invasion event (i.e., not only the timing and order of invasive species arrival, as classically addressed). Altering (1) the identity of the first native colonizer, the establishment of which

preceded other species arrival by four weeks, and (2) species establishment timing (i.e., synchronous vs. sequential sowing) both significantly affected the biomass production of the invasive plant species *A. artemisiifolia* (Figs. 2 and 3). Seedling emergence and survival did not significantly differ and were high across all communities (97.3% ± 1.0 and 93.3% ± 3.1, mean ± SE, respectively; Appendix A: Table 1). A high germination success is crucial for annual species, such as *A. artemisiifolia* because they reproduce sexually. The reduction of its biomass goes along with a

decrease in the number of produced seeds (Chauvel & Fumanal, 2009), therefore potentially resulting in a lower invasion success the following season (Gentili et al., 2015). This way, revegetation strategies may help to reduce invasion by annual species. These findings are in accordance with the results of the meta-analysis of Levine et al. (2004) showing that competitive interactions with native species are more likely to reduce the performance of invaders than totally repel invasions.

Differences in assembly history influenced early community composition (i.e., species contribution to biomass), although it tended to converge after six months (Fig. 3). The invasive species exhibited the lowest overall performance in Synchronous, where all recipient individuals were sown at the same time (Fig. 2). Receiving more seeds in the first two weeks allowed Synchronous to reach high biomass more quickly (Fig. 3A,D), which is likely to be responsible for lower invasive species success at the end of the experiment. This assumption is supported by the lower resistance of Synchronous_{seq} (sequential sowing of all six species), since both assembly types differed in initial biomass production while sharing close intermediate and final biomass (Fig. 3B,C), species composition (Fig. 3B,C; Table 1) and soil nutrient contents (Table 2). These results emphasize the importance of an initial quick and high biomass production to counter invasion (Lulow, 2006; Mason et al., 2013, 2017; Rinella et al., 2007; Symstad, 2000). These results also indicate that sequential sowing may increase community vulnerability to invasion (Martin & Wilsey, 2012; Stuble & Young, 2020), challenging the implementation of this sowing technique in invaded restoration sites (e.g., sequential sowing may sometimes be beneficial to promote positive interactions between early and target late-successional species; Weidlich et al., 2021). Additional native species sowings might still improve invasion resistance when environmental conditions at the time of initial sowing are uncertain or not ideal for establishment.

A prior establishment of the productive N-fixing legume *T. repens* boosted *A. artemisiifolia* biomass (Figs. 2 and 3C, D), which is consistent with previous studies (Mwangi et al., 2007; Scherber et al., 2006). The facilitative effect of legumes has been attributed to their ability to fix atmospheric nitrogen, directly transferring it to neighbors via root exudation and mycorrhizal links (Govindarajulu et al., 2005; Paynel et al., 2001), or releasing it into the soil by decomposition (Tomm et al., 1995). In addition, nitrogen-fixing legumes display a small root system and preempt little soil nitrogen, leaving more opportunities for root and nutrient foraging by later arriving species ('N sparing'; Temperton et al., 2007; von Felten et al., 2009). In our study, the reduced invasion resistance of *Trifolium*_f may result from a lower competition for root space and below-ground resources arising from (1) a low initial biomass production of the community (Fig. 3A,D), (2) a greater response of *A. artemisiifolia* to elevated soil N level, which is more likely to result from N sparing (Table 2;

Govindarajulu et al., 2005; Paynel et al., 2001; Temperton et al., 2007; von Felten et al., 2009), and/or (3) a low grass content (Table 1), since perennial grass dominance has been associated with higher invasion resistance via a strong competition for belowground resources, as seems to be the case here for *L. perenne* (Fargione et al., 2003; Frankow-Lindberg, 2012; Scherber et al., 2010; Scherer-Lorezen et al., 2003).

Our study focused on exploring the influence of immigration history in a perennial native community on *A. artemisiifolia* establishment success during early community assembly. The few existing long term experiments highlight long-lasting consequences of early differences in species arrival on invasibility and community structure (i.e., several years; Švamberková et al., 2019; Vaughn & Young, 2015; Werner et al., 2016), acknowledging the importance of studying mechanisms driving early community assembly. For instance, Vaughn and Young (2015) showed that giving a two-week advance to perennial native species favored those species over annual invasives for four years. In ecosystems characterized by seasonal rainfall and a high proportion of annual species, phenological gaps between native and invasive species might particularly matter to invasion success (Wolkovich & Cleland, 2011). In these environments, repeated invasive species management actions might be required (Wainwright et al., 2012).

Although the direction, strength and persistence of priority effects appear dependent on biotic and abiotic site conditions (Young et al., 2015) such as soil biota (Reinhart & Callaway, 2006), the identity (or traits) of interacting species (Cleland et al., 2015; Delory, Weidlich et al., 2019; Hess et al., 2020; Stuble & Souza, 2016) and resource availability (Kardol et al., 2013), there is growing evidence that priority effect-based management strategies help decreasing plant invasions across many systems (e.g., Grman & Suding, 2010; Vaughn & Young, 2015; Yannelli et al., 2020; Young et al., 2016). A successful application of priority effect-based strategies requires the identification of the main drivers underlying site effects. Notably, understanding how phenological, morphological and physiological traits of early and later colonizers interact and how both affect priority effects would help building strategies adapted to specific species.

Conclusions

Overall, our study supports that native species colonization history matters to invasion success of the annual invader *A. artemisiifolia* when invasion occurs in the early stages of community assembly. Altering the timing of species establishment (all together or sequential sowing) and the identity of the first native colonizer affected early biomass production and composition of the community, which influenced invader performance. Notably, communities reached a higher invasion resistance when quickly displaying a high

native biomass. Thus, when immediate invasion risk is high in a restored site, establishing productive, densely sown native perennial communities and avoiding an early planting of highly productive N-fixing legumes may help decrease invasion success of *A. artemisiifolia* in the first stages of community assembly. Our results are in line with Gentili et al. (2015) who showed that establishing a dense, competitive vegetation cover in autumn helps reducing *A. artemisiifolia*'s success the following spring. Whether variations in community assembly might influence longer-term invasion success of *A. artemisiifolia* remains however uncertain. In the study of Gentili et al. (2017), passive and active (seeding of hayseed or a commercial seed mixture) revegetation resulted in *A. artemisiifolia* suppression over three years, whatever initial species compositions and vegetation percent covers. According to these results and to ours, showing biomass convergence for the various community types within six months (Fig. 3), we expect the decline of *A. artemisiifolia* in perennial communities over time, resulting in few or no long-lasting consequences of initial conditions on invader success. Further real-world studies are needed to evaluate whether such priority effect-based management strategies (i.e., altering native species colonization history) are efficient to limit various invasive species across systems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2022.01.004](https://doi.org/10.1016/j.baae.2022.01.004).

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