

Research Article

Cite this article: Somerville GJ and Ashworth MB (2024) Adaptations in wild radish (*Raphanus raphanistrum*) flowering time, Part 2: Harvest weed seed control shortens flowering by twelve days. *Weed Sci.* **72**: 143–150. doi: [10.1017/wsc.2024.4](https://doi.org/10.1017/wsc.2024.4)

Received: 10 May 2023

Revised: 22 November 2023

Accepted: 23 January 2024

First published online: 29 January 2024

Associate Editor:

Prashant Jha, Louisiana State University

Keywords:

Adaptation; integrated spatial model; integrated weed management; SOMEF model

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Adaptations in wild radish (*Raphanus raphanistrum*) flowering time, Part 2: Harvest weed seed control shortens flowering by twelve days

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Abstract

Harvest weed seed control (HWSC) is an effective technique for managing wild radish (*Raphanus raphanistrum* L.), a weed that retains its seed until harvest. However, earlier flowering time (leading to increased seed shedding before harvest) is a risk to HWSC effectiveness. This study investigated the effects of repeated HWSC on the evolution of *R. raphanistrum* flowering dates, using two methods: an adaptation of the SOMER model that included flowering genes (called SOMEF); and a mathematical calculation of the endpoints of flowering date evolution utilizing the relevant life-history equations. In weed management systems with highly effective herbicides, the additional use of HWSC predicted *R. raphanistrum* population extinction. Low weed numbers and rapid extinction meant that any gradual evolution in days to first flower (DFF) was insufficient to lead to HWSC evasion. In alternative management systems with less vigorous herbicide control and using HWSC, modeling predicted a maximum 2- to 3-d reduction in DFF. In contrast, mathematical calculations of the phenotypes maximizing seeds returned to the seedbank predicted an endpoint to evolution of 12-d earlier flowering, which matched field observations. However, genetic change postulated by the mathematical calculations was not hampered by a restriction to changing DFF allele frequencies. Unknown accompanying genetic changes could affect germination dates or flowering triggers.

Simulation modeling that included only flowering genes failed to predict the magnitude of an observed 12-d reduction in DFF. Differences between the 12 d observed in the field (and predicted using mathematical calculations) and the modest changes demonstrated in this field-based modeling study are postulated to be due to unaccounted evolutionary changes in *R. raphanistrum*.

Introduction

The rate of discovery of new herbicides is declining, while the rate of loss of effective herbicides is increasing (Duke et al. 2019). Herbicides are being lost both to increasingly rigid legislative requirements and the widespread increase in herbicide-resistant weed biotypes (Heap 2023). As a result, farmers and land managers face an ever-increasing challenge in maintaining cost-effective and efficient weed management systems.

Maintaining a low weed seedbank is considered vital in limiting the evolutionary selection for weeds that can resist or evade weed control (Davis 2006). Herbicides are the single most effective weed control tool currently available, followed closely by a range of harvest weed seed control (HWSC) techniques that intercept and destroy weed seeds at harvest (Burgess et al. 2007; Friesen and Hall 2004; Lacoste and Powles 2014). HWSC is designed to limit weed seedbank recharge and thereby reduce weed population abundance (Somerville et al. 2018; Walsh et al. 2017). The use of HWSC in combination with effective herbicide use and crop competition has been demonstrated to cause rapid decline of agricultural weeds such as rigid ryegrass (*Lolium rigidum* Gaudin) and wild radish (*Raphanus raphanistrum* L.) (Walsh et al. 2013). However, it must be cautioned that the repetitive and predictable application of these highly effective non-herbicide weed management tactics may also eventually select for individuals in a population that can survive or evade control (Bararpour et al. 2017; Mortimer 1997).

Raphanus raphanistrum is one of the most problematic weeds in global agriculture and is rated as the second most economically damaging weed species in Australia (Llewellyn et al. 2016). It is an annual dicotyledonous species that competes strongly within dryland and horticultural crops (Cheam and Code 1995; Monjardino et al. 2003) to produce a large number

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of seeds that remain dormant in the soil (Cheam 1986). In a wheat (*Triticum aestivum* L.) crop, a density of 50 plants m^{-2} has been found to annually contribute in excess of 17,000 seeds m^{-2} to the soil seedbank (Reeves et al. 1981). In addition to having a protracted germination period, *R. raphanistrum* seed can remain dormant in the soil seedbank for up to 7 yr, making eradication difficult (Cheam 1986; Young 2001). The high fecundity and genetic diversity of *R. raphanistrum* populations have facilitated the evolution of herbicide resistance to multiple modes of action (Owen et al. 2015).

While known for its ability to evolve resistance to multiple groups of herbicides, *R. raphanistrum* is considered to be highly susceptible to HWSC, because this species retains up to 95% of seed at harvest (Walsh et al. 2013; Walsh and Powles 2014), with the majority of seeds located above the combine cutting height. Due to the effectiveness of HWSC, its recurrent use may pose a significant anthropogenic selection pressure for any evasion trait. As the effectiveness of HWSC is contingent upon weed seeds being captured by the combine harvester, seed retention at harvest is essential (Walsh et al. 2016). Earlier-flowering *R. raphanistrum* ecotypes have more mature pods, with pod maturity linked to increased seed abscission before harvest (Walsh et al. 2018). *Raphanus raphanistrum* flowering time has evolved to maximize fecundity. However, significant phenotypic variability in flowering time exists within and among populations (Conner and Via 1993; Kercher and Conner 1996; Madhou et al. 2005). Previous studies have shown that plants can rapidly adapt their flowering time in response to selection (Chuine 2010; Elzinga et al. 2007). It has been speculated that the repeated capture and destruction of *R. raphanistrum* seeds at harvest will likely impose a selection for traits that enable increased fruit abscission before harvest, which may include early flowering (Panetsos and Baker 1967; Panetta et al. 1988). Recurrent glasshouse selection studies have demonstrated the evolutionary capacity of a small *R. raphanistrum* population to adapt life-cycle traits such as flowering time (Ashworth et al. 2016).

This study uses a newly adapted model Spatially Orientated Model for Evolutionary Flowering (SOMEF) that has been parameterized for this study, using *R. raphanistrum* flowering genes (Somerville and Ashworth 2024). This study simulates a theoretical finite population of *R. raphanistrum* living within a wheat field. We investigate whether a wheat field-based population will adapt its time to flowering when repeatedly exposed to seed capture and destruction using HWSC techniques.

Materials and Methods

Modeling of *Raphanus raphanistrum*'s biological characteristics

A list of biological characteristics used in the modeling are included in Table 1. Previous work showed that a newly adapted model (SOMEF) could replicate large amounts of genetic change in *R. raphanistrum* under strong artificial selection (Somerville and Ashworth 2024). The contrived flowering genes developed within SOMEF were found here to also be capable of simulating a steady-state wild population (without selection pressure) of *R. raphanistrum* growing within a wheat crop (Supplementary Figure S1).

Within these field-based SOMEF simulations, germination of the *R. raphanistrum* plants was assumed to occur into seven distinct cohorts, with each cohort germinating over 10 d (Table 2). No genetic links between germination and flowering were included.

Flowering duration and fecundity affected genetic exchange. The window for pollination between *R. raphanistrum* plants with different days to first flower (DFF) were based on a relatively intensive 30-d flowering period (Ashworth et al. 2016) (Table 3). Fecundity was fit to a quasi-Poisson function (Equation 1):

$$\frac{\text{Seeds}}{\text{Plant}} = \exp(-5.117 + 0.299\text{DFF} - 0.002\text{DFF}^2) \quad [1]$$

Fruit abscission before harvest is dependent on the flowering date. Fruit abscission was parameterized by fitting data from Taghizadeh et al. (2012) to a Weibull function using least-squares multiple regression (Equation 2):

$$\text{Fruit abscission} = c + (d - c) (1 - \exp(-\exp(b(\log(\text{days}) - \log(I_{0.5})))))) \quad [2]$$

where b (-3.05) is the slope of the curve around $I_{0.5}$; c (0.350%) is the lower limit of the fruit abscission rate; d (37.14%) is the upper limit of the fruit abscission rate; and $I_{0.5}$ (26.83 d) is the delay in emergence after seeding with an abscission rate of $d/2$. Adjustments to the data from Taghizadeh et al. (2012) to enable the use of flowering date were accounted for by assuming that a minimal DFF of 35 d corresponded with maximum seed dispersal. Later-emerging weeds exhibit shorter DFF (with the same genotype) due to increasing growing degree days (GDD) later in the season (Cheam 1986). Accordingly, fruit abscission rates for later-emerging cohorts were delayed by 7 d (vs. a 10-d delay in emergence) for each sequential cohort (Cheam 1986).

Pollen and fruit dispersal (natural and anthropogenic) were unchanged from those in the original SOMER model, which were initially set for *L. rigidum* weeds growing within a wheat crop. Both *L. rigidum* and *R. raphanistrum* are self-incompatible for pollination. They naturally spread most of their pollen and seeds within 1 m^2 when growing within a crop, where most seed is spread anthropogenically (Ellstrand and Marshall 1985; Sampson 1964). *Raphanus raphanistrum* seeds can be collected and destroyed during harvest (using HWSC) at a rate similar to *L. rigidum* (Walsh et al. 2013).

Simulations and Analysis

Part A. Simulation Model Design—Field-based Study

The *R. raphanistrum* study area was confined to 10 ha within a wheat field and simulated using 100,000 subpopulations (each growing within 1 m^2). This 10-ha area was assumed to be located within a part of a larger field growing in the Western Australia grainbelt. A spatial model was used due to the influence of dispersal on multi-gene studies of weed populations (Somerville et al. 2017b). The SOMER model was developed in R v. 3.1.2 (R Core Team 2008). The species-specific field-based biological characteristics of dormancy, sequential emergence, relative fitness penalty (for later-emerging weeds), pollen and seed production, and crop productivity are listed in Tables 1–3.

More information on the SOMER model is detailed in Somerville and Renton (2015) and Somerville et al. (2017b), with the HWSC parameterizations within SOMER described in Somerville et al. (2018). New script within the adapted SOMEF model, to enable an accurate portrait of DFF in *R. raphanistrum*, is described in Somerville and Ashworth (2024). For the scenarios described and discussed in this study, all practices are within the

Table 1. Parameter values used to simulate days to flowering adaptation in *Raphanus raphanistrum*.^a

Parameter	Value
Initial weed seed density (number m ⁻²)	70
Probability of weed seedling death	0.02
Probability of winter seed death of ungerminated seeds	0.05
Probability of summer seed death	0.1
Probability of annual seed germination from seedbank	0.3
Probability of plant death from knockdown on cohort 1	0.99
Probability of death of susceptible plants from the postemergence herbicide	0.97
Wheat seeding density (no. m ⁻²)	150
Wheat size/competitiveness parameter	0.0909
Annual <i>R. raphanistrum</i> size/competitiveness	0.1111
Maximum <i>R. raphanistrum</i> seeds produced (no. m ⁻²)	15,000
Probability of an unselected seed joining the seedbank	0
Probability of new gene mutation conferring resistance	10 ⁻⁸

^aSources: Friesen and Hall (2004), Lacoste and Powles (2014), and Monjardino et al. (2003).

same growing season, and weed management is identical each season (year).

Part B. Mathematical Calculations of the Evolutionary Endpoints, where Seedbank Gains Are Maximized

All of the biological processes included in part A of this study were stochastically controlled in SOMEF utilizing specific functions. These same functions were used here, where they were mathematically combined. First, the reproductive functions that control the dates and duration of germination, growth, flowering, fecundity, and fruit abscission were included. In addition, typical farm weed management practices using herbicides (known here as weed management system E) for *R. raphanistrum* in the southern Australian grainbelt was parameterized numerically (Table 2). The reproductive functions, together with the implemented management system, control the relative proportion of seeds that successfully enter the seedbank from each cohort of weeds. In addition, two alternative weed management systems were examined; one with a lower efficiency post-emergence spray (management system D), and one using only a single pre-season spray (management system P) (Table 2). Combining these influences with the data in Table 2 enabled us to mathematically explore the way seed fall/plant changed for different DFFs, for each cohort of weeds (Figure 1). Whichever DFF gave the maximum seed fall/plant was assumed to be the endpoint of DFF evolution.

Results and Discussion

Part A. Investigating the Evolution of Flowering Time Adaptation following HWSC using SOMEF

Genetic Ratios, without HWSC Selection

Multiple replications were run temporally, using the same genetic coding as developed in Somerville and Ashworth (2024) (replicating an earlier glasshouse study). This genetic coding used two types of contrived genes; larger *M1* genes that could cross over and accumulate 10 dominant alleles per plant, and three replicates of smaller effect *M2* genes. In this study growth parameters were changed to reflect field growing conditions (without HWSC). Stochastic flowering genes in the initial population were based on replicating the G₀ population in (Ashworth et al. 2016). More information on the G₀ population

Table 2. Cohort emergence dates measured in calendar days since crop seeding date (where day 1 is the crop seeding date).

Emergence dates ^a	Median relative fitness	Germination (sum = 30%)	Relative seed production with no management (sum = 1) ^b	Relative seed production			Management system P (sum = 1)			Management system D (sum = 1)			Management system E (sum = 1)		
				Single knock-down herbicide efficacy (system P)	Double knock-down (systems D and E)	Good post-emergence efficacy (systems D and P)	Poor post-emergence efficacy (system E)	Management system P (sum = 1)	Management system D (sum = 1)	Management system E (sum = 1)					
-10:-1	1	16	0.551	0.96	0.999	0.5	0.4	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
1:10	1	8	0.275	0	0	0.96	0.9	0.57	0.59	0.37	0.37	0.37	0.37	0.37	0.37
11:20	0.979	5	0.168	0	0	0.96	0.9	0.35	0.36	0.22	0.22	0.22	0.22	0.22	0.22
21:30	0.42	0.25	0.00363	0	0	0.96	0.9	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
31:40	0.060	0.25	0.00052	0	0	0	0	0.04	0.02	0.03	0.03	0.03	0.03	0.03	0.03
41:50	0.023	0.25	0.00020	0	0	0	0	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
51:60	0.018	0.25	0.00016	0	0	0	0	0.01	0.00	0.01	0.00	0.01	0.00	0.01	0.01

^aThe first cohort emerges before crop seeding and is typically treated with pre-seeding knockdown herbicides.

^bThe "relative seed production" considers the relative germination, fitness, and survival probabilities of a weed surviving through to seed set from each cohort.

Table 3. Relative pollination rates due to pollen release through time, governed by “days” (a measure of calendar days from crop seeding until anthesis).^a

Days	16–44	45–75	76–104	105–135	136–164
16–44	2	1	0	0	0
45–75	1	2	1	0	0
76–104	0	1	2	1	0
105–135	0	0	1	2	1
136–164	0	0	0	1	2

^aIn these simulations, ova were twice as likely to be pollinated by weeds entering anthesis within the same 30-d period.

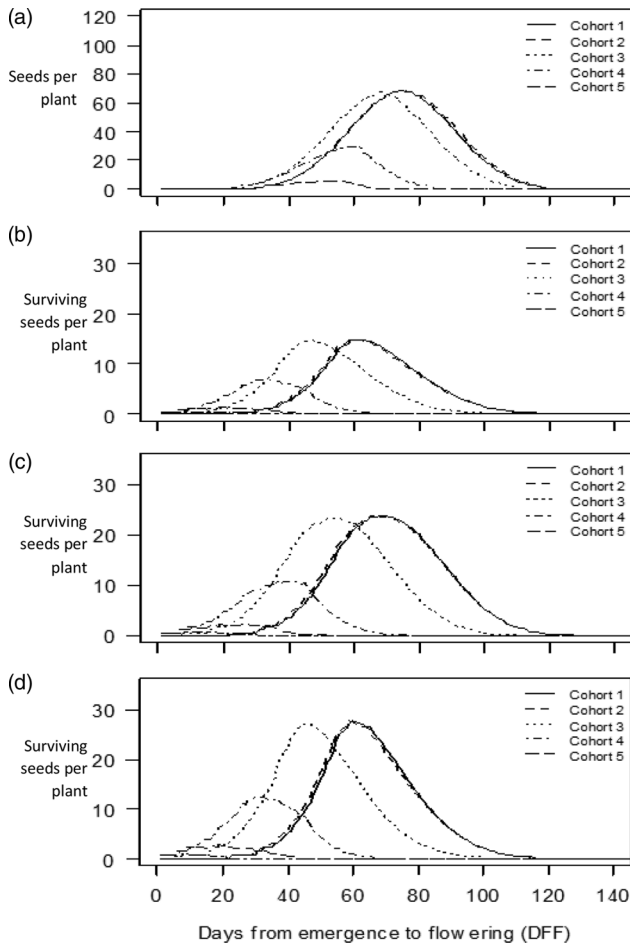


Figure 1. Showing the number of seeds produced by weeds from each cohort (y axis), dependent on the evolved days to first flower (DFF) (x axis). The peak of each curve indicates the ideal DFF, with earlier cohorts taking longer to flower. (A) The standard farming system, before introduction of harvest weed seed control (HWSC). The range in ideal DFF across the different cohorts is approximately 15 d for Figure 1A. (B–D) How the various weed management systems affect the number of live seeds (avoiding HWSC) for weed management systems E (B), D (C), and P (D). In Figure 1B–D, the range in ideal DFF across the different cohorts is approximately 50 d.

is in the Supplementary Material. The values, range and distribution of both the *M1* and the *M2* genes remained remarkably stable from that starting position, over 30 simulated years (Supplementary Figure S1). This stability of the glasshouse-based genes in field-based simulations (without selection pressure) helps support their use in this study. All subsequent studies used the population generated herein (G_{30}) as their initial population.

Genetic Ratios, with HWSC

Time from emergence to flowering was predicted by SOMEF to change from a mean of 74.2 down to 72.5 d due to HWSC (Figure 2F). This is an underestimate of what has been observed in the field by the authors (12 d; see Table 4). This study, however, clearly demonstrates that alterations in seedbank size, HWSC efficiency, and changes in fruit abscission rates do affect these changes in DFF (Figure 3).

Alternative Herbicide Scenarios and Seedbank Size, Both with and without HWSC

Altering the herbicide effectiveness in this study did not alter the *R. raphanistrum* DFF when HWSC was not used (Figure 2C). However, highly effective herbicide control (weed management system E) resulted in fewer seeds being exposed to HWSC capture. When highly effective herbicides were used with HWSC, the *R. raphanistrum* population was in rapid decline (Figure 2D).

In subsequent simulations, less effective weed management systems (systems D and P; Table 2) were used. When herbicidal control was less effective and HWSC was routinely applied, modest reductions in *R. raphanistrum* flowering time (1 to 2 d) were evident (Figure 2F). When HWSC was used with less-effective pre-seeding knockdown herbicides, which killed a smaller proportion of the emerged seedbank, in combination with a more effective postemergence herbicide (comparable to weed management system E), there were more mature *R. raphanistrum* plants at harvest. In contrast, if the knockdown herbicide controls weeds well, and the postemergence herbicide is less effective, there will be more less-mature weeds at harvest. While this younger population of weeds resulted in a small increase in HWSC control (Figure 2E), these changes in herbicide rates were insufficient to alter the rate of change in DFF in the population (Figure 2F).

Both a small (average 70 seeds m^{-2}) and large (average 700 seeds m^{-2}) initial *R. raphanistrum* seedbank size (Figure 2G–I) were simulated. The larger seedbank required a longer period to eliminate (20 vs. 5 yr). However, seedbank size did not affect the percentage of seed captured by HWSC (Figure 2H) or the rate of change in flowering time (Figure 2I). High *R. raphanistrum* weed densities have been linked to an increase in early-season weeds and an increased percentage of early flowering time from early-germinating weeds (Mazer and Schick 1991). However, genetic links between flowering and germination dates were not simulated in this study. Nonetheless, when modeled, the initial large number of seeds led to a more rapid initial decline in the weed seedbank (Figure 2G). These simulations modeled *R. raphanistrum* seeds that can successfully emerge over successive seasons (dormancy up to 7 yr) (Peltzer and Matson 2002). Dormancy will slow evolutionary changes; previously unselected genetics introduced into the emergent *R. raphanistrum* populations will dilute previous genetic selections.

Alternative HWSC Efficiencies and Fruit Abscission Rates

The greatest reduction in *R. raphanistrum* days to flowering occurred when HWSC efficacy was increased from 75% to 95% (Figure 3), indicating that the effective use of HWSC is likely to contribute to flowering time shifts in the field. More seeds were destroyed by the HWSC technique (Figure 3B), thereby reducing seedbank recruitment. This increase in HWSC efficacy increased selection pressure and resulted in a more rapid adaptation to earlier flowering times, although adaptive changes were limited to a 1- to 2-d decrease in *R. raphanistrum* flowering time (Figure 3C).

Table 4. Comparisons of shortened average days to first flower (DFF) in *Raphanus raphanistrum* populations (compared with G_0), across related studies that utilized similar initial populations.

Study environment	Shortening in DFF	Number of generations of selection	Reason for halting selection	Reference
Glasshouse	30 d	5	Population invariant	Ashworth et al. 2016
Stochastic simulations	34 d	5	Replication of Ashworth et al. (2016)	Somerville and Ashworth 2024
Field observations ^a	12 d	>20	Ongoing	M Ashworth and S Powles, unpublished data
Part A (this study, stochastic simulations)	2 d	10–20	Extinction	Somerville and Ashworth 2024
Part B (this study, calculations)	12 d	NA	Nontemporal	Somerville and Ashworth 2024

^aThis is a field observation of a 12-d difference in DFF between population G_0 (Ashworth et al. 2016) and current weed populations. However, G_0 seeds were collected from the field in 1999 (and never exposed to harvest weed seed control [HWSC]); in contrast, current weed populations have been exposed to a drying environment in Western Australia since then (Asseng and Pannell 2013), the result of which may be a shortening of the inherent flowering date even without pressure from HWSC.

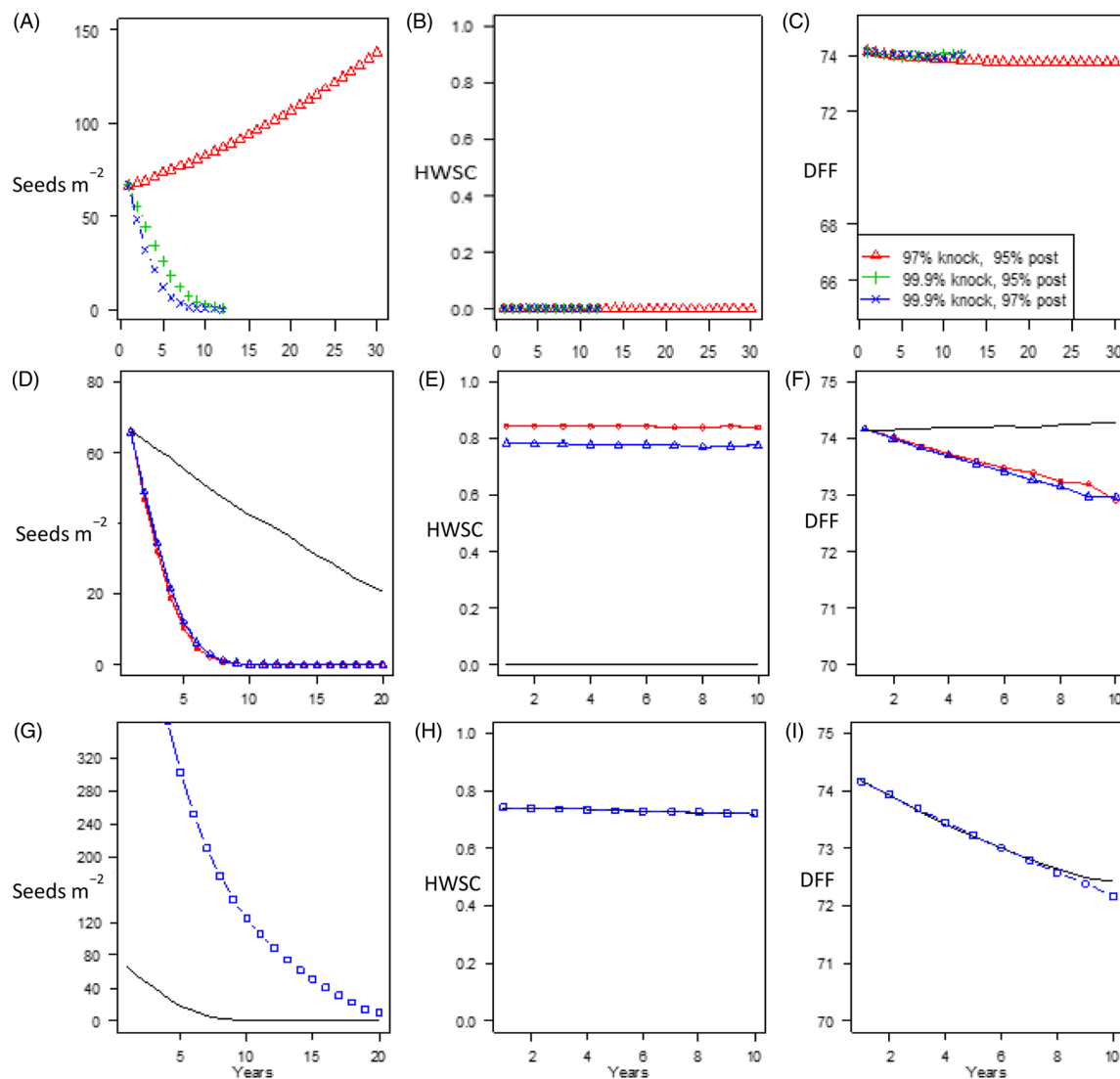


Figure 2. Changes in the number of seeds m^{-2} (A, D, G), the probability of seed capture by harvest weed seed control (HWSC) (B, E, H), and days to first flower (DFF) (C, F, I). (A–C) Varying herbicide efficiencies, in the absence of HWSC, over 30 yr. (D–F) When knockdown herbicide was less effective ($-p$), when postemergence herbicide was less effective ($-o$), and when both herbicides were effective, without HWSC (—) over 20 yr. (G–I) Model used management system P and started with either a smaller seedbank (—) or a larger seedbank ($-o$) over 20 yr.

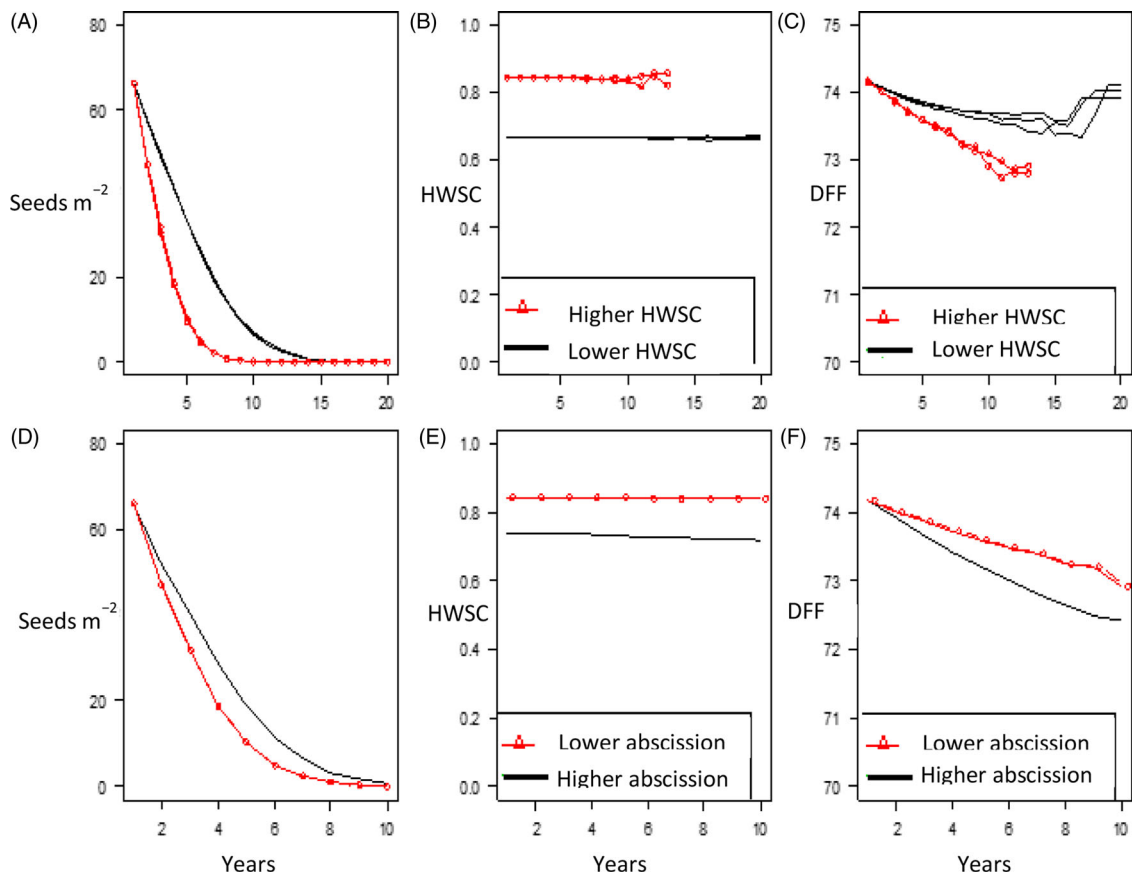


Figure 3. Changes in the number of seeds m^{-2} (A, D), the probability of seed capture by harvest weed seed control (HWSC) (B, E), and changes in days to first flower (DFF) (C, F) under weed management system P; HWSC efficacy (up to 20 yr) was increased from 75% (—) to 95% (-○-) (A-C); the level of fruit abscission (up to 20 yr) was changed from low (37%) (-○-) to high (74%) (—) (D-F). Note the variation between replicates was small as long as seed numbers are above $1 m^{-2}$; below that level, genetic changes in one or two plants had a more significant effect on the results.

Two fruit abscission rates, high (maximum 74%) and standard (maximum 37%), and their effect on flowering date were examined. The seedbank size was more rapidly reduced when using a lower fruit abscission rate, as more seeds were captured. In contrast, an increased fruit abscission rate meant that more seeds avoided HWSC (Figure 3E), resulting in a faster evolution of tolerance to HWSC due to earlier flowering (Figure 3F). Reduced HWSC (Figure 3B) can slow evolution (Figure 3C); however, reduced HWSC (Figure 3E) can also speed evolution (Figure 3F). In Figure 3B, reduced HWSC efficiency causes greater survival of all plants, which reduces selection and slows evolution. In contrast, reduced HWSC that is due to the greater survival of only early-flowering plants (Figure 3E) increases selection and speeds up evolution. These modeling results imply that a reduction in HWSC efficiency (e.g., due to mechanical faults) will reduce evolutionary pressure to evade HWSC, whereas a reduction in HWSC due to evolutionary change will increasingly drive that evolutionary change. Similar results have been seen for herbicides, where the more efficient herbicide spurs resistance evolution (Somerville et al. 2017b).

Part B. Mathematical Calculations of Environmental Selection Pressure for Changes in DFF

For genetic adaptation to occur, there needs to be a fitness advantage to flowering earlier in the presence of HWSC.

Early-flowering individuals under HWSC selection have to add more seeds per plant to the seedbank (relative to larger, later-flowering plants). The range of selection pressure imposed by HWSC could be estimated (without stochastic variability) by combining equations for relative fitness (Table 2), seed production (Equation 1), and fruit abscission (Equation 2) with rates for management control, including HWSC efficacy (Table 2). From this mathematical analysis, flowering dates that maximized additions to the seedbank in the absence of HWSC were 74- to 75-d for cohorts 1 and 2 (Figure 1A); a result that reflects current unselected field populations. However, when HWSC was added, *R. raphanistrum* plants from the same population produced the maximum number of surviving seeds if they exhibited DFF between 60 and 62 d (Figure 3B-D).

The range in ideal DFF of the different cohorts is increased when HWSC is used (Figure 1). The use of HWSC means that later cohorts will select a much shorter DFF (to maximize seed production) compared with earlier cohorts (Figure 1). There was a substantial fitness advantage of being in the early-emerging cohorts (their longer DFF means larger plants and more seeds), which meant that the later-emerging weeds (which produce few seeds) had little effect on the change in population-wide flowering genes (Figure 1). No matter the management system, when HWSC was used, there was stronger selection pressure for all weeds to emerge in the early cohorts and for each of those early cohorts to have a specific DFF.

Multiplying together the relative fitness penalty, germination probabilities, and seed death probabilities of the different weed cohorts (Table 2) resulted in two-thirds of the seeds that enter the seedbank being produced by weeds germinating within the first 40 d after crop seeding (even without the influence of HWSC). This clearly demonstrates the importance of early weed control as part of wider weed control strategy. Early-germinating *R. raphanistrum* have been found to contribute significantly to total seed production (Cheam 1986), increase yield losses through competition (Cheam and Code 1995), and produce more mature seed at harvest, thus likely leading to increased seed abscission before harvest (Ashworth et al. 2016; Walsh and Powles 2014). This research shows that early weed control will become even more important as weeds evolve under pressure from HWSC.

Variability between SOMEF Modeling (Part A) and Mathematical Calculations (Part B)

Different weed management systems (Table 2) had minimal effect on the changes in DFF predicted by SOMEF (Figure 2) or those seen in the mathematical calculations (Figure 1). This may be due to the temporal invariance between these systems; although herbicide and HWSC effectiveness varied between systems, the timings and cohorts affected were unchanged. Greater differences in DFF between different management systems may be generated by significantly altering the seasonal timings of weed management. However, due to the marginal production operating across much of the region (Asseng and Pannell 2013) and the difficulty of controlling larger *R. raphanistrum* plants with herbicides, significant temporal management shifts are not currently realistic and were not investigated here.

Differences between replicates (in part A) were very small (Figure 2B and 2C), except when seed numbers fell below 1 m^{-2} . This similarity between replicates was at least partly due to the use of identical run-in populations at the beginning of each simulation. The similarity between replicates persisted until seed numbers were very low, despite the stochastic nature of the tabled parameters (Tables 1–3). Therefore, Figures 1 and 2 typically show only average results to simplify the presentations.

Comparisons of DFF across the Different Studies

On initial examination, the magnitude and speed of reductions in DFF in various related studies into Western Australian *R. raphanistrum* populations exposed to HWSC are variable (Table 4).

However, closer examination yields surprising similarities that hint at helpful conclusions. First, the mathematical calculations in Part B (giving an ideal time of 12 d shorter to flowering [DFF] than without HWSC) exactly replicated field-collected *R. raphanistrum* populations that have adapted to flower (DFF) an average of 12 d earlier than ecologically appropriate control populations collected from ruderal locations (M Ashworth and S Powles, unpublished data). This mathematical analysis showed the most favorable endpoint (under evolutionary pressure applied by these weed management systems) and implies that no further adaptations would occur in the field, unless alternative selection pressure was applied. However, these populations were gathered 20 yr apart (Table 4), and flowering time changes in the field are likely to be exacerbated by seasonal changes in moisture scarcity and heat stress (Asseng and Pannell 2013), resulting in the need of weed populations to flower earlier to maintain fecundity.

The stochastic simulations in part A (using SOMEF) showed only a small change (<2 d) in DFF, despite SOMEF incorporating the same equations used in part B and using the same parameterizations in Somerville and Ashworth (2024) that were able to accurately replicate the large genetic changes in Ashworth et al. (2016). Moreover, alternative uses of the spatial stochastic-related SOMER model (Somerville et al. 2017a, 2018) have accurately predicted field-verified temporal evolution of herbicide resistance. The slower rate of change in DFF in this SOMEF adaptation of SOMER, when compared with field-observed changes, could be due to additional field-based adaptations in seed dormancy (Burgess et al. 2007), crop competition (Mazer and Schick 1991), or plant fitness. The evolutionary pressure for a link between flowering dates and germination is strong (Figure 1), which may guide further research. If earlier-flowering weeds also germinated earlier, or if short life cycle weeds were relatively more competitive (thereby producing more seeds), this is predicted to enhance early flowering evolution.

Strong evolutionary pressure was shown for greater fruit abscission rates, as it both increases survival against HWSC and promotes more rapid shortening of DFF (Figure 2D–F). In addition, variable dormancy is under genetic control (Cheam 1986). Complex genetic changes are likely to be operating to increase the fitness of plants with shorter DFF, thereby increasing evolutionary pressure for shorter DFF in field-based populations that were not encompassed in this modeling study.

Notwithstanding the degree of change indicated in these simulations, this study nevertheless identified possible important factors affecting the evolution of early flowering in *R. raphanistrum* as an adaptive strategy to avoid HWSC. Escapes from early weed control treatments (before crop seeding) are more important in evolving earlier DFF than weeds that escaped herbicides used later in the season. If there are greater numbers of weeds in the field when HWSC is used, this results in more rapid evolution of tolerance to HWSC via earlier flowering. Additionally, higher inherent rates of fruit abscission resulted in a more rapid reduction in DFF. Moreover, simulations indicated that increased seedbank deposition from plants with later DFF will slow the evolutionary pressure of HWSC toward early DFF.

In conclusion, with the widespread increase of multiple herbicide-resistant *R. raphanistrum* populations, HWSC has become very important to maintain crop productivity. Investigating life-cycle adaptation to HWSC is important for predicting the evolutionary responses to HWSC use in order to maintain the effectiveness of this transformational non-herbicidal weed management technique. This study clearly demonstrated that while *R. raphanistrum* contains the genetic diversity required to adapt its flowering time, the anthropogenic selection for early flowering in the field as modeled with this SOMEF adaptation of the SOMER model was less and far slower than expected. A better genetic picture may be gained by investigating additional genetic changes, in addition to adaptations in flowering genes.

Deterministic mathematical analysis yielded accurate results, indicating its potential usefulness to explore alternative management systems. However, mathematical analysis determined only the endpoint and yielded no information about genetic or temporal changes.

Recommendations gleaned from this study indicate that HWSC should be used within a diverse weed control system that includes a highly competitive crop plus effective and diversified herbicide use to control early-emerging cohorts. It is recommended that growers maintain vigilance to identify the causes of any HWSC failures and

identify opportunities to further control any weeds flowering too early for effective HWSC.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/wsc.2024.4>

Acknowledgments. This study was supported in part by the Grains Research and Development Corporation grant UWA2007-002RTX. No conflict of interest is declared.

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