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CAN FERAL RADISHES BECOME WEEDS?

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1. INTRODUCTION

The title of this chapter - can feral radishes become weeds? - is phrased as a question for three reasons. First, the literature on this topic is incomplete and we expect that further investigations will help elucidate the answer to this question. Second, many feral populations of *Raphanus sativus* have resulted from hybrids between the crop and a closely related weed, *R. raphanistrum*, and it is not known whether this external “trigger” is essential for feral populations to become weedy. Third, the answer depends on one’s definition of a “weed”. Inconsistent use of this term can lead to confusion about the weed status of feral radishes. Agricultural scientists define weeds as plants that reduce the productivity of crops, other managed plantations (e.g., vineyards, orchards, planted pine forests), or pastures and rangeland. A broader definition of weeds includes any plant that causes economic and/or environmental harm - for example in agriculture, lawns, recreational areas, wetlands, and other natural areas. Weedy plants that displace native vegetation often are referred to as “invasives”, and economic losses due to invasive plants can be substantial (e.g., 48). Another category of weeds, which we will not employ here, includes species that occupy disturbed, ruderal habitats without necessarily causing economic or environmental harm.

In this chapter, we ask whether feral *R. sativus* can occur as weedy or invasive populations, as defined above. In particular, we describe how feral radishes evolve and ask whether they interfere with the production of food crops anywhere in the world.

Based on a review of the available literature, our answer to this question is “yes, in some

cases”, but this may require the help of genes from weedy *R. raphanistrum*. Likewise, *Raphanus raphanistrum* could become even more troublesome if it were to acquire fitness-enhancing genes from the crop. Here, we review what is known about ferality in radishes and we explore some human-induced evolutionary changes that could allow feral radishes and their sexually compatible relatives to become “weedier” in the future.

2. EARLY DOMESTICATION

Radish and its feral and wild relatives are insect-pollinated, self-incompatible plants with an annual or biennial life cycle. Radish is an ancient crop that appears to have multiple origins from several wild species (12, 60). It is likely that radishes were domesticated independently in both Eurasia and eastern Asia. Herodotus (c. 484-424 BC) suggested that radish was already an important crop in Egypt nearly 5,000 years ago, having been depicted on the 4,000-year-old walls of the Pyramids. Radish also was cultivated in eastern China more than 2,000 years ago, before the establishment of the “Silk Road” that permitted extensive trade with central Asia. The present diversity of culinary and morphological types of radishes is greatest in Asia, particularly in China and Japan.

Deciphering the origins of cultivated radish is complicated by the crop’s many forms and uses in different parts of the world, and by its long history of dispersal around the globe. Crisp (12) recognized several categories of radishes. “European” radishes have small swollen roots (actually part hypocotyl and part root) and are grown primarily in short-season, temperate regions to be eaten as fresh vegetables. Large-rooted daikon radishes

are grown mostly in Asia in both temperate and tropical regions. Daikon radishes are eaten raw, as a cooked vegetable, canned, or pickled. Two less common types of radishes have been bred for their leaves (fodder radish) or seed pods, and the latter have been selected as either oil-seed crops or vegetables. “Rat-tail” radish has been selected for both its leaves and its edible immature seed pods, which are up to 80 cm long. In modern-day Pakistan, some traditional landraces of radish are grown for both their immature seed pods and their swollen roots (43). Thus, there is a huge variety of ways in which the fruits, seeds, sprouts, leaves, and roots are grown for traditional dishes around the world.

Pistrick (42), followed in Specht (52), divided cultivated radishes (all *Raphanus sativus*) into three main taxonomic groups:

convar. *oleifera* - oilseed and fodder radishes

convar. *caudatus* - “rat-tail” radish, also known as var. *mougri*, grown for their edible immature seed pods

convar. *sativus* - all forms with edible roots, with many different varieties.

Here, we focus mainly on the last group, convar. *sativus*, which is composed of widespread and economically important root crops. The swollen root is the primary commercial crop, but the seeds have economic value for seed supply sales and the consumption of germinated radish sprouts.

An elegant study by Yamagishi and Terachi (60) showed that the most likely ancestors of cultivated radish are *Raphanus raphanistrum*, *R. maritimus*, *R. landra*, or their earlier

progenitors. These investigators compared configurations of two mitochondrial gene regions, *cox1* and *orfB*, among three wild species and cultivated radish from Europe, Asia, and Japan. Mitochondrial genes are useful for tracing phylogenetic histories because they are maternally inherited and they seldom recombine. Five mitochondrial haplotypes were found among accessions of *R. sativus* (Table 1). Cultivated varieties that share haplotypes with wild relatives are likely to be descended from one or more of these wild species, or their progenitors.

Reconstructing the phylogenetic history of a crop is complicated by the fact that wild accessions may include wild or feral relatives that have hybridized with the crop during the past millennia. Also, conclusions from this approach can be influenced by the diversity of wild and crop accessions that are examined. Bearing these caveats in mind, it appears that cultivated radishes have originated multiple times from wild taxa that were very similar to *R. raphanistrum*, *R. maritimus*, and *R. landra*. This is consistent with earlier evidence for independent domestication in Eurasia and eastern Asia.

Raphanus raphanistrum, *R. maritimus*, and *R. landra* are able to hybridize with each other and with *R. sativus* (all have $2n = 18$ chromosomes (34)), and most recently they have been classified as subspecies of *R. raphanistrum* (8, 30). Because *R. sativus* sometimes hybridizes with *R. raphanistrum* in the field, several authors have suggested that these taxa also should be consolidated into a single species (e.g., 4, 12, 51). In fact, one study involving crop-wild hybrids showed perfect collinearity between genomes in the positions of 144 informative RFLP markers on radish's nine chromosomes (4). Given

the close taxonomic relationships among the putative wild ancestors of radish, we simplify our discussion below by assuming that the progenitors of cultivated radish were wild forms of radish that shared many attributes with weedy *R. raphanistrum* (*R. raphanistrum* subsp. *raphanistrum*).

Domestication of radish from its wild relatives involved selection for a larger and more flavorful root, often with a red or purple skin, along with high seed production for propagating the crop. Selection for a larger root probably resulted in delayed flowering and a tendency to be biennial. As with many other crops, domestication also selected for seeds that are easier to harvest. In weedy *R. raphanistrum*, tough, hard-to-crack fruits protect the seeds from bird predation and other types of damage. Fruits of *R. raphanistrum* are shed gradually as they mature on the maternal plant, and the fruit does not split open to release the seeds. Instead, it breaks into distinct sections, each of which encapsulates a single seed (Figures 1 and 2). In a sense, the fruit wall of *R. raphanistrum* acts as a protective “seed coat” for the seeds, which lack the strong, impervious seed coat found in many other annual species. In domesticated *R. sativus*, however, seeds are contained within indehiscent fruits, but the fruits remain firmly attached to the plant after it has senesced and they are not divided into sections (Figure 2). In many modern varieties of radish, the spongy seed pods crush easily by hand, which allows the seeds to be extracted from the seed pod more efficiently. Conditions needed for “de-domestication” of *R. sativus* and its potential to become an agricultural weed are discussed in a later section.

3. MODERN RADISH VARIETIES WITH EDIBLE ROOTS

Before we evaluate the potential for radishes to revert to a feral condition, perhaps aided by genes from *R. raphanistrum*, it is useful to consider salient features of modern-day radishes. As an open-pollinated crop that is self-incompatible, radishes have been bred for root color, taste, texture, size, and shape, as well as agronomic performance, day-length requirements to prevent premature bolting, seed yield, and other traits (2, 12). As noted above, small-rooted, spherical, red radishes are widely consumed in Europe, North America, and other temperate regions of the world, while the large-rooted daikon radishes have greater commercial importance in Asia. In some mountainside villages in Japan, several hundred landraces of daikon radishes are still grown for traditional dishes, thereby preserving a great deal of genetic and phenotypic diversity (61).

Radishes are fast-growing plants - *raphanos* comes from Greek for “quick appearing”. Varieties grown in temperate climates germinate in the early spring and are tolerant of cool temperatures. The spatial scale at which radishes are grown ranges from small kitchen gardens to large, industrial-scale farms. Like other members of the mustard family, the plants produce glucosinolates that provide a peppery flavor and may aid in herbivore defense and allelopathy (1, 29). Asiatic radishes have been selected for resistance to various pathogens, such as *Fusarium*, *Albugo candida*, *Peronospora parasitica*, and viruses (12). Historically, disease resistance was not a high priority for the small-rooted European varieties, because they were grown in the spring and the roots

were harvested before diseases become prevalent. More recently, European varieties have been selected for multiple plantings per season, involving both annual and biennial lifespans, and breeders have introduced various types of resistance to fungal disease pathogens (e.g., *Fusarium*, *Rhizoctonia* spp.). Chinese and Japanese radishes sometimes have been used as sources of resistance genes (e.g., 58).

The yield and overall performance of radishes have been enhanced by the development of F₁ hybrids. Cytoplasmic male sterility (CMS) was found in many Japanese and Chinese cultivars (40), and it has been used to produce hybrid seed in large-rooted cultivars (12). More recently, the Ogura type of CMS has been used to produce F₁ hybrids of small-rooted European varieties, but open-pollinated seed production without CMS is still common. A great deal of genetic diversity is maintained in open-pollinated radish varieties, relative to wild *Raphanus* populations (15). In regions where landraces are grown (e.g. Japan, Pakistan), genetic diversity is especially high because plants that are grown for seed often cross-pollinate with other cultivated and feral varieties (43, 61). The genetic diversity that is maintained in cultivated radish could facilitate the establishment of feral populations, as we discuss further below.

Conventional breeding in radish is expected to become more sophisticated with the use of genomics-guided strategies. The first genetic map of the *Raphanus sativus* genome was published in 2003 (4), paving the way for the use of marker-assisted breeding and comparative mapping with *Arabidopsis* and *Brassica* species. Radish has been transformed using a floral dip method (13), but transgenic radish has not been an

attractive target for seed companies to date because of a relatively small market. Radish is rarely an important staple crop in the west, and future breeding may be focused on the aesthetic value of its color patterns and shapes, for sale in both novel and traditional food markets (12). Breeders also have focused on transferring a late-flowering trait to commercially important varieties, but conventional breeding techniques have been unsuccessful, producing a hybrid of low quality (33). Curtis et al (14) obtained late-flowering radishes by expressing an antisense GIGANTEA gene fragment from *Arabidopsis*. This trait is a possible candidate for the development of transgenic radishes.

4. DE-DOMESTICATION AND WEED EVOLUTION IN RADISHES

4.1 CHARACTERISTICS OF WEEDY *RAPHANUS RAPHANISTRUM*

To understand which characteristics may prevent feral radish from becoming a serious agricultural weed, it is useful to compare it to *R. raphanistrum*. Known as jointed charlock or wild radish, *R. raphanistrum* has entered the ranks of the 180 worst weeds worldwide (5, 26, 35, 39, 57). This species occurs in agricultural fields, especially where small grains and alfalfa are cultivated, in waste places, and along sheltered beaches in many cool/temperate areas of the world. It is found in North America, South America, Australia, Africa, and Eurasia, but has only recently colonized eastern Asia (28).

Worldwide, *R. raphanistrum* has been reported as a weed problem in more than 45 crop species in at least 65 countries (26). In North America, *R. raphanistrum* is a common

agricultural weed in the northeastern and central USA, eastern and western coastal regions of Canada, and the Pacific Northwest (36). *Raphanus raphanistrum* is especially troublesome in wheat, oat, and barley (11, 20, 57), and it is considered to be one of the most serious agricultural dicot weeds in Australia (9). In Australia and South Africa, *R. raphanistrum* has evolved resistance to several acetolactate synthase (ALS)-inhibiting herbicides (23, 49, 62). Its current prominence in Australian wheat fields is related to the fact that it has become resistant to multiple modes of herbicide action, including ALS-inhibitors, an auxin analog (2,4D), photosystem II-inhibitors (atrazine, metribuzin), and a phytoene desaturase-inhibiting herbicide (diflufenican) (55). A thorough description of the ecology and weed status of *R. raphanistrum* is provided by Warwick and Francis (56).

Raphanus raphanistrum has three essential features of successful agricultural weeds:

- 1) the ability to disperse its seeds widely,
- 2) the ability to produce a large population of dormant seeds in farmers' fields,
- 3) the ability to compete with crop plants.

For example, the tough, woody fruits fall from the plant as soon as they mature, and they later break apart into small segments that are difficult to clean from grain crop seed supplies (26). This allows the seeds to spread wherever contaminated grain seed has been shipped. In the early 1800's, *R. raphanistrum* was cited as one of the worst weeds of arable fields in England (26), and this weed undoubtedly dispersed to other countries along with grain shipments. In the early 1980's, *R. raphanistrum* was a major contaminant of grain seed that was transported throughout Australia during a four-year

drought (53). Even with modern methods of cleaning certified grain seed, there are many other routes by which the seeds can disperse. The silique segments pass through livestock intact, and they can be dispersed with manure and hay. In Iran, for example, *R. raphanistrum* seeds are dispersed in sheep manure, as well as by contamination of farmer-saved seed (26). Once the weed becomes established, it can build up a prodigious seed bank that can last for up to 15-20 years (7, 26, 45, 46, 47). With its long-lived seed bank, early emergence after tilling, and rapid life cycle, *R. raphanistrum* is often a difficult-to-manage weed. Without proper attention to the problem, the plants can produce thousands of seeds per square meter and can drastically reduce wheat yields (5, 26, S. Powles, pers. comm.).

4.2 “WEEDY” TRAITS AND ENDO-FERALITY

4.2.1. General considerations

As discussed in the Introduction to this book, endo-ferality refers to de-domestication of the crop without the aid of gene flow from wild or weedy populations. New mutations and inherent variation within the crop gene pool, including crop-derived off-types, provide the raw material on which selection can act. For cultivated radishes to become feral and evolve into agricultural weeds, strong selection is needed to remove deleterious crop traits and to increase the frequencies of “weedy” traits. We are not aware of any published studies of endo-ferality in radishes, although our ongoing research in Michigan, USA, will begin to fill this apparent gap (see below). In this section, we

speculate about which traits are likely to be most important in the de-domestication of radish. The next section focuses on exo-ferality, which involves progeny from hybrids between the crop and its weedy relatives, and is well documented in radishes.

In some cases, what looks like endo-ferality may actually involve genes from other taxa. It is possible that *weed-to-crop* gene flow has occurred in seed production fields, allowing low levels of weed genes to enter seed supplies. While this may be rare in industrialized countries, especially those with strictly enforced standards for certified seeds, it is probably quite common where landraces co-occur with *R. raphanistrum* (or feral *R. sativus*). Thus, it is difficult to be sure of the source of “de-domestication” genes in the crop. Nonetheless, the concept of endo-ferality still can be useful. Crop seeds are shipped and planted repeatedly over vast geographic areas, and it is important to know whether the crop has an inherent tendency to produce volunteer and feral populations. Some crops are able to spawn new weed populations *de novo*, as discussed elsewhere in this book. Others will do so only when aided by genes from a wild or weedy relative, resulting in exo-ferality.

To understand genetic changes that can lead to endo-ferality, it is helpful to know whether key domestication traits are controlled by a few genes or many genes, and whether these genes are recessive or dominant in the crop. The genetic basis for specific domestication traits in radishes is known in some cases, and a more thorough survey of agricultural publications, especially in Europe and Japan, would probably uncover relevant information. Here, we examine some of the traits that occur in *R. raphanistrum*

and are needed by feral *R. sativus*, building on an excellent earlier summary by Panetsos and Baker (41). We also discuss initial results from our field experiments in Michigan, where we established four artificial populations of volunteer plants from a common cultivated variety (Red Silk), beginning in 2002 (see Section 5.4.3 for further details about this experiment).

4.2.2. Earlier flowering and a less swollen root

The evolution of early flowering may be one of the first traits needed for the establishment of volunteer and feral radish populations. Early flowering is advantageous in arable fields because plants often can complete their life cycle before being harvested with crop plants or killed by cold or drought, and this is possible even when germination is induced later in the growing season. Also, since most fields are tilled in early spring, the combination of rapid germination and a short life cycle can allow the plants to avoid herbivores, diseases, and other weeds that appear later in the season (e.g., 50).

Early flowering and a less swollen root are positively correlated in segregating populations of crop-wild hybrids, perhaps because of resource allocation trade-offs that occur during early root growth (41; Campbell and Snow, unpubl. data). Radish is considered to be a long-day species that delays flowering until the next year, although this varies among varieties (2). Earliness in days to bolting and to flowering appears to be a highly heritable, dominant trait that is controlled by a few major genes (63). Bolting and induction of flowering are also influenced by two environmental cues, low

temperatures and long day lengths (14, 33). In North America, when small-rooted radishes are planted in the spring and then remain unharvested, they frequently bolt and produce copious amounts of seeds by late summer. Volunteers of large-rooted radishes are more likely to have a biennial life cycle than small-rooted ones (e.g., 2, 43, 61). Because of heritable variability within and among cultivated varieties, we hypothesize that radishes are able to evolve to have wild-type roots and earlier flowering, allowing them to become short-lived annuals. This transition probably occurs more easily in small-rooted “European” varieties than in large-rooted daikon radishes.

4.2.3 Early abscission of mature fruits

In contrast to *R. raphanistrum*, fruits of cultivated and feral *R. sativus* are retained on the parent plant long after the plant has senesced. This makes the fruits more susceptible to predation and limits the temporal and spatial scales of seed dispersal. Lack of fruit abscission in feral plants could be a major deterrent to the build-up of a seed bank in the soil. We have observed that fruit abscission is not essential for maintenance of feral population at our experimental sites, but it could contribute to their relatively small population sizes. Whether the lack of early abscission persists over the long term in feral populations is unknown.

4.2.4. Thicker and woodier fruits

One obstacle to the establishment of feral populations may be seed predation, especially by birds, because the crop has thin, easily punctured fruit capsules (41). Tougher fruits also aid in the persistence of seeds in the soil. In weedy *R. raphanistrum*, the presence of a thick, impervious fruit capsule prevents seeds from germinating in the fall, thereby enforcing a certain degree of dormancy and allowing deeply buried seeds to remain viable for several years (7, 26, 45, 46, 47). Thus, the evolution of tougher fruit capsules is expected to promote ferality. The extent to which this occurs spontaneously is not known. In our experimental populations in Michigan, the fruits of feral radishes have thinner walls than *R. raphanistrum* and their seeds often germinate within the fruit and die in late summer. Nonetheless, two of our original four populations have persisted over the course of two years in local field conditions.

4.2.5. Segmented fruit capsules that break into single-seeded sections

Weedy *R. raphanistrum* fruits typically have constrictions between the seeds (Figures 1 and 2), although many weedy populations also have individuals that lack this characteristic (AAS and LGC, personal observation). Single-seeded fruit segments are more difficult to remove from seed supplies of small grains than whole fruits, and as such they may represent an example of crop seed “mimicry” (3). This trait could also aid in local seed dispersal and avoidance of predators. However, intact, non-segmented, corky fruits may stay buoyant in water for a longer period of time, which could be important for coastal populations of *R. raphanistrum*. In any case, we have not seen segmented fruits

in cultivated radishes or their early generation descendants (Figure 2). We hypothesize that genes conferring segmented fruits are lacking in the crop.

4.2.6. Staggered seed germination

Crop plants are strongly selected for rapid and synchronous seed germination, while weedy species often exhibit great variability in germination dates, making them more difficult to eradicate. Cultivated and volunteer radish populations lack two characteristics that promote staggered germination dates. First, they lack the tough, segmented fruit capsules that must crack and begin to decompose before the seed can germinate (Figure 2). Second, we have observed that, in the greenhouse, extracted seeds from weedy *R. raphanistrum* germinate over a wider time period (about one to three weeks) than seeds from early-generation feral radishes (< one week) (Campbell and Snow, unpublished data). If feral plants lack staggered seed germination, they could be more susceptible to being killed by extreme weather, weed control methods, and other types of disturbances.

4.2.7 Resistance to insect herbivores and pathogens

The complex effects of insect herbivores and diseases on weedy populations of *R. raphanistrum* are not well known, but these factors may limit population growth rates in some years and locations (e.g., 1). It is conceivable that domestication and selection for flavor and appearance has reduced the ability of volunteer and feral plants to withstand these pressures. However, some cultivars have been bred for resistance to fungal

pathogens (*Fusarium*, *Rhizoctonia*, *Plasmodiophora*, *Telaviopsis* spp., (10), and many have probably acquired some tolerance of abiotic stress from centuries of selective breeding. Herbivore and disease pressures may be relatively unimportant in the evolution of endo-ferality, but this assumption should be investigated further, especially if transgenes for insect and pathogen resistance are introduced into cultivated radishes. Hypothetically, resistance to fungal pathogens, if expressed in the fruit or seed coat, might lead to greater seed longevity, perhaps allowing feral populations to become established in agricultural fields. Mature fungal-resistant plants might also prosper in fields where disease pressure is high.

4.2.8 Greater genetic diversity

The amount of genetic diversity that is maintained in weed populations can enhance their ability to evolve in step with changing environmental conditions, including various methods of weed management such as tilling and herbicide applications. In some crops, especially those that are propagated vegetatively or by self-pollination, breeders have removed much of the genetic diversity that exists in landraces and wild relatives (e.g., 15). However, radishes have always been bred as open-pollinated, self-incompatible crops (but see 24), and cultivars have retained nearly as much genetic diversity as *R. raphanistrum* (15, 31). Therefore, it is unlikely that inbreeding and other manifestations of low genetic diversity prevent feral radish populations from becoming established. Moreover, seed-mediated gene flow is likely to distribute genetic diversity among

disjunct populations, and recurring gene flow from the crop also could add new alleles to feral radish populations.

5. EXO-FERALITY VIA CROP-WEED HYBRIDIZATION

5.1 General considerations

Spontaneous hybridization between crops and related weeds has the potential to lead to the evolution of more troublesome weeds in some crop-weed systems (6, 16, 17, 18).

Therefore, it is useful to examine the dynamics of hybridization in radishes and to ask whether this process could result in “exo-ferality” and enhanced “weediness”. For convenience, we have drawn a distinction between endo-ferality and exo-ferality, recognizing that a whole spectrum of situations exists in radishes. Feral radishes have acquired genes from *R. raphanistrum*, and *R. raphanistrum* populations have acquired genes from *R. sativus*. Further research involving molecular markers is needed to uncover the varying degrees of cryptic introgression that have occurred in these taxa.

Several lines of evidence suggest that 1) genes from *R. raphanistrum* have introgressed into feral populations of *R. sativus* (41), and 2) genes from the crop have introgressed into weedy populations of *R. raphanistrum* (e.g., 51). Cytological data, flower color polymorphisms, and fruit characteristics have been used as evidence for hybridization and introgression in both directions (i.e., into feral *R. sativus* and into weedy *R. raphanistrum*). As discussed below, it is likely that gene flow from *R. raphanistrum* into

R. sativus has facilitated the establishment of feral populations in California and perhaps Brazil. This has probably occurred repeatedly in other parts of the world where *R. raphanistrum* and the crop co-exist. Thus, radishes appear to show a weak tendency to evolve endo-ferality and a strong tendency for both exo-ferality and the introgression of crop alleles into populations of *R. raphanistrum*. The occurrence of bilateral gene flow means that the distinction between feral *R. sativus* and weedy *R. raphanistrum* can become quite blurred. Nonetheless, these arbitrary taxonomic categories are useful for identifying populations that are more similar to the crop *versus* those that have had little or no influx of crop genes.

Feral radish populations have been reported in Europe (54), North America (19, 37, 41), and South America (21). In Japan and Korea, wild *R. sativus* var. *hortensis* f. *raphanistroides*, a biennial plant, is common along beaches, cliffs, abandoned fields, and other ruderal areas, and sometimes occurs adjacent to cultivated daikon radishes (27, 28, 61). However, a recent study by Yamagishi (60) suggests that these populations are derived mainly from *R. raphanistrum* rather than *R. sativus*. In any case, volunteer and feral populations of daikon radish landraces (*R. sativus* var. *hortensis*) have been observed as ruderal species in mountainside villages in Kyushu, Japan (61), providing clear evidence of ferality. Below, we describe specific case studies of feral *R. sativus* in the Brazil and the US.

5.2. Herbicide-resistant feral *Raphanus sativus* in southern Brazil

Raphanus sativus has become weedy in temperate South America and has evolved resistance to ALS-inhibiting herbicides in southern Brazil (21, 25). Herbicide resistance was reported in Heap (25) by Giovani Theisen (Fundacep Fecotrigo, Cruz Alta, Brazil), who kindly provided us with the following details. In southern Brazil, the main agricultural system has been no-till since about 1980, with soybean and corn grown during the summer and a variety of other crops in the winter, including wheat, barley, white oat (*Avena sativa*), rye, canola, and flax. Before the adoption of no-till methods, *R. raphanistrum* was a common weed in wheat and other winter crops, as has been reported elsewhere (26). After no-till agriculture was adopted, a type of *Raphanus sativus* called “turnip” or “forrageiro” was planted widely as a one of several popular cover crops. This radish cover crop was probably *R. sativus* convar. *oleiferus*, and it started to occur as a volunteer weed in summer crops, where it was treated with various herbicides. Because *R. raphanistrum* was also present in several winter and summer crops, it is possible that crossing occurred between this species and cultivated or volunteer *R. sativus*. By 2001, feral *R. sativus* acquired resistance to several ALS-inhibiting herbicides in the southern state of Rio Grande do Sul. Based on photographs of the flowers and fruits of these plants (see 25), and information provided by G. Theisen, feral *R. sativus* does not appear to have the constricted fruits or yellow flower pigmentation that are common in *R. raphanistrum*. Thus, it is considered to be *R. sativus* even though it may have hybridized with *R. raphanistrum*.

Giovani Theisen noted that feral *R. sativus* is not as aggressive as many other weeds, but it is common in winter crops (mainly wheat, barley and oat) as well as summer ones (soy, corn, and bean). In this case, it is likely that the evolution of ferality was facilitated by

planting *R. sativus* as a cover crop in regions where it could hybridize with *R. raphanistrum*. It is interesting to note that *R. raphanistrum* has also evolved resistance to ALS-inhibiting herbicides in Australia, but this has not been reported Brazilian populations of *R. raphanistrum*.

5.3. Crop-weed hybridization in California

Raphanus sativus and *R. raphanistrum* first appeared in California in the 19th century (41). These taxa hybridized to such an extent that distinct populations of *R. raphanistrum* have largely disappeared, while *R. sativus* bearing occasional traits from the weed (e.g., yellow petal color) is common (41, 51). California populations, which have the common name of wild radish, can occur as an agricultural weed, especially in cole crops, such as broccoli, cauliflower, and cabbage (59). However, they are most common in ruderal areas (e.g., 37, 41, Steven A. Fennimore, University of California at Davis, pers. comm. to AAS; AAS personal observation). The Nature Conservancy includes feral *R. sativus* on a state list of invasive plants (44) because it is a non-native species that occurs in disturbed natural areas, including coastal dune habitats.

Panetsos and Baker (41) concluded that hybridization between feral *R. sativus* and weedy *R. raphanistrum* “appears to have been a major factor in converting the erstwhile crop plant into a highly successful weed”. Citing Panetsos and Baker (41), Ellstrand and Schierenbeck (16) went a step further to argue that hybridization was a stimulus for the evolution of invasiveness in *R. sativus*. However, their criterion for “invasiveness” was that the hybrid derivative “must replace at least one of its parent taxa or invade a habitat

in which neither parent is present.” In this case, feral *R. sativus* may have displaced weedy *R. raphanistrum*, but it is not clear whether this process caused new problems in natural or agricultural areas. At most, hybridization may have made it easier for *R. sativus* to establish feral populations that sometimes occur as weeds. In terms of agricultural areas, we found some evidence that feral populations of *R. sativus* are regarded as problematic weeds in California (59), but it is not known whether they are “weedier” or more “invasive” than their wild parent, *R. raphanistrum*. In any case, wild radish populations have the potential to become more abundant due to continued gene flow from the crop. This was demonstrated in a fitness experiment by Klinger and Ellstrand (32). Their findings suggest that feral *R. sativus* can benefit from further episodes of hybridization with the crop, perhaps due to heterosis, because F₁ plants produced more seeds per plant than local genotypes of wild *R. sativus*.

5.4. Crop-weed hybridization in experimental populations in Michigan

5.4.1 Overview of experimental populations

Our current research is designed to test the hypothesis that hybridizing populations derived from *R. sativus* and *R. raphanistrum* can evolve into more successful weeds than either of these parental taxa. To address this question, we established two long-term studies at the University of Michigan Biological Station in Pellston, Michigan. The first study, which started in 1996, consists of four artificial hybrid populations in which three

crop-specific genes are being monitored from year to year to evaluate their ability to persist (51, Snow et al. *in prep.*). The second study, which started in 2002, is a replicated experiment that is more relevant to the evolution of ferality. In this experiment, we established four populations of F₁ *R. sativus* (small-rooted Red Silk variety), five populations of F₁ weedy *R. raphanistrum* obtained from a nearby farm, and five populations of F₁ weed-crop hybrids derived from these two parental taxa. All eighteen populations in both experiments are spatially isolated from local populations of *R. raphanistrum* and from each other to prevent gene flow among them. Results from these two studies are useful for understanding the process of introgression in radishes, as well as the evolution of “weediness”.

5.4.2. Fitness of F₁ weed-crop hybrids and persistence of crop alleles

The evolutionary outcome of hybridization is often influenced by how chromosomes and linkage groups of the parental taxa interact. In *R. sativus* and *R. raphanistrum*, the rate at which introgression occurs is likely to be affected by an interesting chromosomal translocation between the crop and the weed. Many investigators found that F₁ hybrids between *R. sativus* and *R. raphanistrum* are heterozygous for a reciprocal translocation (41). A few studies did not detect this heterozygosity, perhaps due to past episodes of gene flow (see 41), but this seems to be unusual. In any case, plants that are heterozygous for the translocation have problems with chromosome pairing: quadrivalents are formed instead of bivalents between homologous pairs. This reduces pollen fertility to ~60% and seed set per fruit to ~50% relative to levels of ~95% for both

traits in either parent (41, 51). Thus, F₁ hybrids have lower fitness than *R. raphanistrum*, which is a locally abundant weed in Michigan. Despite this partial barrier to gene flow, three crop-specific markers remain fairly common in all of the populations that we established in 1996 and have monitored in each subsequent year (51, Snow et al., *in prep*).

Panetsos and Baker (41) found that the reciprocal translocation was linked to genes that influence root structure and flowering time, although their sample sizes were fairly small. If true, the presence of this linkage group has two important implications. Linkage among these genes may have made it easier to maintain important domestication traits during centuries of crop breeding. Conversely, linkage could facilitate the loss of deleterious crop genes following crop-wild hybridization. Because heterozygosity for the translocation reduces plant fitness, hybridizing populations should become fixed for one form or the other, in a positive, frequency-dependent fashion. Thus, when crop-to-weed hybridization is infrequent, *R. raphanistrum* populations should quickly eliminate the fertility-reducing translocation derived from the crop, as well as linked, fitness-reducing genes for swollen roots and delayed flowering. This is precisely what we have observed within a period of 3-4 generations in experimental populations that initially consisted of 25% crop alleles and 75% alleles from *R. raphanistrum* (Figure 3; Snow et al., *in prep*).

Also, in a separate selection experiment that was conducted in a greenhouse, we found that flowering time is highly heritable in F₂ crop-weed hybrids, as expected (Campbell and Snow, *in prep*). This heritable variation can allow the hybrids to evolve earlier

flowering times very easily. In California, where *R. sativus* appears to have “displaced” *R. raphanistrum*, and where heterozygosity for the translocation subsequently remained fairly common (41), it is not known how these dynamics have played out. California populations have non-swollen roots and early flowering, similar to *R. raphanistrum*. Further research involving mapped molecular markers (e.g. 4) would help elucidate patterns of introgression involving various crop-specific and weed-specific genes and their linkage groups.

5.4.3. Persistence of feral populations

Our efforts to establish feral experimental populations in Michigan have been partially successful, in that two out of four field populations that were started in 2002 persisted to the summer of 2004 (this study is ongoing). At the same time, it has been much easier to establish vigorous experimental populations of crop-weed hybrids as opposed to volunteer plants from the crop, as predicted by Panetsos and Baker (41). Many plants in our second-generation feral radish populations had swollen roots and failed to flower and set seed before winter, while others flowered only 3-16 days later than the wild populations that serve as controls. In a milder climate, such biennial individuals would be able to tolerate winter conditions and persist (it is possible that mild winters could facilitate the evolution of ferality in radishes). To summarize our initial findings to date, this experiment suggests that endo-ferality is possible in radishes. We also expect that progeny from the hybridizing populations will have greater fecundity and greater

population growth rates than those from control populations of *R. raphanistrum*, but this remains to be seen.

6. CONCLUSIONS

Radishes are capable of establishing volunteer and feral populations, as either annuals or biennials, but they do not appear to be serious agricultural weeds in most areas. Rather, non-weedy feral radish populations may be regarded as “incipient” weeds - we expect that some populations could evolve into worse weeds given the right combination of selection pressures and sufficient genetic diversity, as occurred in no-till rotations in Brazil (25). New genes from crop breeding or from weedy *R. raphanistrum* have the potential to accelerate this process, especially if there is a great deal of gene flow into feral populations.

Weed scientists are familiar with the potential of weed populations to shrink or expand rapidly in response to tilling, herbicide use, biological control, crop rotations, cover crops, annual variations in the weather, and other factors, such as the use of clean, certified crop seeds. For example, intermittent low-till practices often favor increases in the abundances of biennial weeds. Therefore, it is worth recognizing that weeds that are relatively harmless at present, such as feral *R. sativus*, could be propelled into greater dominance in the future by specific types of changes. Also, a more thorough search of the literature on feral *R. sativus* may reveal other cases in which this has already occurred.

The economic and environmental harm that weeds cause also depends on where they occur. For example, weedy *R. raphanistrum* is not a great concern in potato, alfalfa, or corn in north-central Michigan (AAS and LGC, personal observation) or along the New England coast, where it occurs in low frequencies above the storm-tide level on sheltered, cobble beaches. In contrast, this plant is one of the worst weeds in Australian wheat fields; it is a “nemesis” of grain crops in general (26), and it has recently spread to eastern Asia. In the future, it is conceivable that feral populations of *R. sativus* could also disperse over great distances and encounter favorable conditions for “invasion”.

Because *R. raphanistrum* is already an economically important weed, great care will be needed to decide which types of novel transgenic traits will be introduced into cultivated radishes, if any (32, 51). Single-gene traits for enhanced resistance to herbicides, diseases, herbivores, and abiotic stress are very likely to spread to weedy populations by means of pollen flow and seed dispersal, and this has the potential to lead to worse weed problems. Traits that do not offer fitness-related benefits are unlikely to pose risks, nor is the intentional use of fitness-reducing transgenes as a means of biological confinement (e.g., 22, Gressel and Al-Ahmad, this volume). However, no method of biological confinement is likely to be 100% effective (38). In our view, this method of reining in questionable transgenes should be used very cautiously, and only when possible risks are offset by significant economic or environmental benefits.

In any case, it does not seem likely that new varieties of transgenic radishes will be developed in the near future. The crop is not essential for food security, it is not a widely traded commodity, which would make it attractive to large seed companies, and it is already quite well adapted for commercial production. In the future, weedy *R. raphanistrum* and feral populations of the crop will continue to evolve in response to natural and human-induced factors. The most immediate threat that they pose for crop productivity is probably the recent and increasingly common evolution of herbicide resistance in both *R. raphanistrum* and feral *R. sativus*.

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Table 1 Evidence for multiple origins of cultivated radish based on mitochondrial DNA haplotypes in radish and its putative wild ancestors (*R. raphanistrum*, *R. maritimus*, and *R. landra*; from 60). Numbers of accessions with each haplotype are shown.

Haplotypes:	1	2	3	4	5
Wild Species					
- <i>R. raphanistrum</i>	5	6	4	1	1
- <i>R. maritimus</i>	4	1	1	1	0
- <i>R. landra</i>	1	0	0	0	0
Cultivated Varieties					
- Japan	10	1	10	2	1
- Asia	1	2	9	3	0
- Europe	0	7	0	0	0

Figure 1. The habit and reproductive structures of weedy *Raphanus raphanistrum* L.
Note the woody, segmented fruits (siliques) with constrictions between individual seeds.
1. habit, 2. seedling, 3. flower, 4. open flower, 5. fruit, 6. seed. (*Source*: Holm LG et al.
1997. *World weeds: natural histories and distributions*. NY: John Wiley and Sons, Inc.
With permission.)

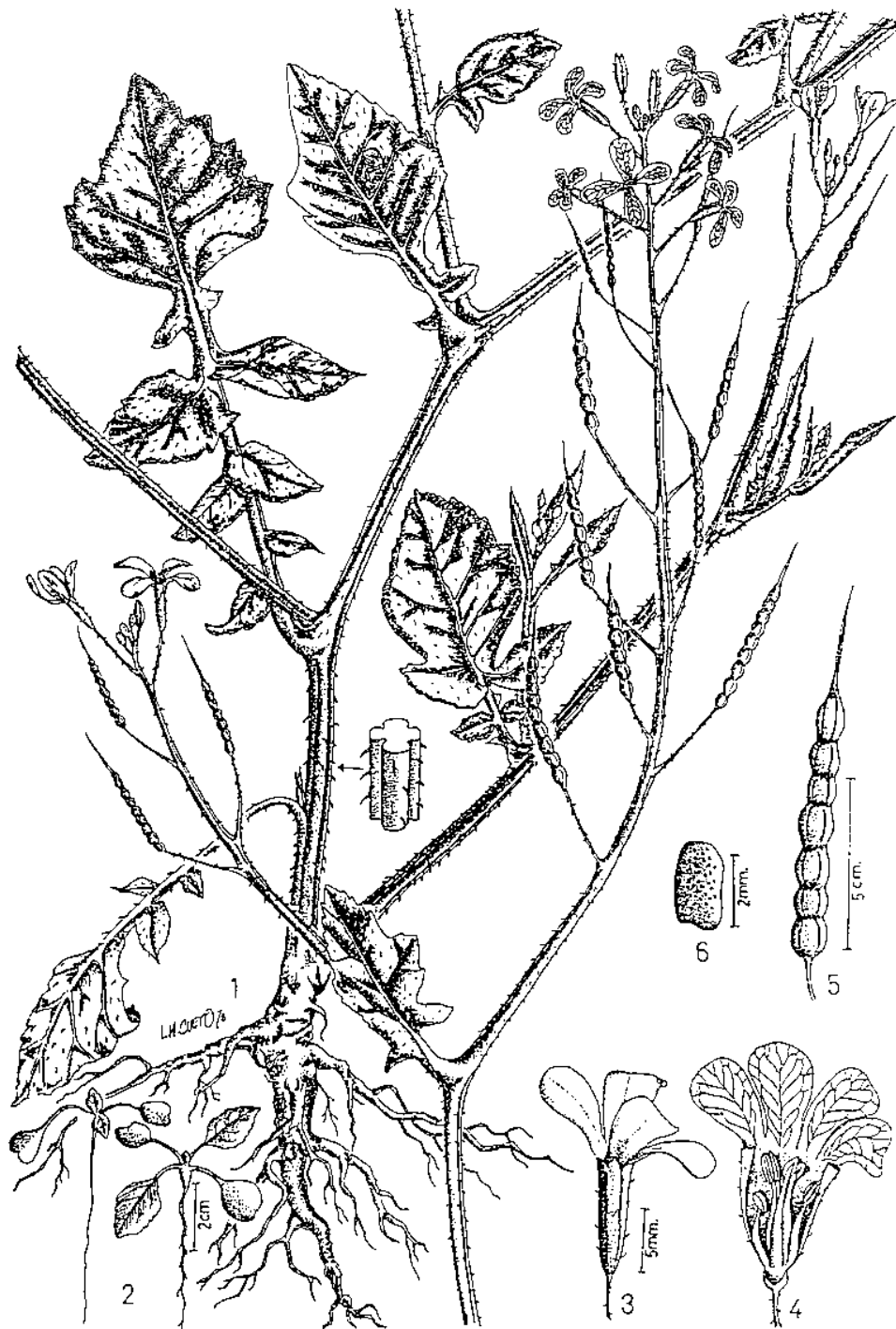


Figure 2. Morphological differences among fruits of cultivated, feral, hybrid, and weedy *Raphanus* taxa. From left to right: one fruit from cultivated *R. sativus* (Red Silk variety), two from F₂ feral radish plants, two from F₂ wild-crop hybrids, and one from *R. raphanistrum*, which typically has constrictions between individual seeds. Note that two fruits remain attached to the pedicel. All fruits except the Red Silk variety were collected from experimental field populations in Michigan in 2003 (see text); digital photographs were converted to high-contrast images; for scale, the wild fruit is 4 cm long.



Figure 3. Rapid restoration of male fertility in hybrid radish populations. Changes in the frequencies of plants with normal pollen (>70% viable) in four experimental populations in Michigan are shown (see text). Plants that are heterozygous for a reciprocal translocation are likely to have <70% viable pollen. In 1996, half of the plants were *R. raphanistrum* and half were F₁ wild-crop hybrids that were heterozygous for the translocation. No data were collected in 2000 or 2002.

