Survival of buried seeds of interspecific hybrids between oilseed rape, hoary mustard and wild radish

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Abstract

Two experiments were designed to assess seed survival in the soil of rape (\textit{Brassica napus} L.), hoary mustard, interspecific hybrids between rape and hoary mustard (\textit{Hirschfeldia incana} (L.) Lagreze-Fossat) as well as between rape and wild radish (\textit{Raphanus raphanistrum} L.). The first experiment dealt with seed survival in undisturbed soil over 41 months. It showed a slow decrease in viability of the seeds of hoary mustard, a quick drop to a constant 1% viability of rape, and intermediary behaviour of hybrids. The second experiment was conducted at two field sites in eastern and southern France, with normal cultivation and crop growth during 3 years. Quantitative differences were observed between the two sites, although the relative behaviour of each seed type was similar. Hoary mustard had the greatest seed viability, on average 14% after 3 years, while total seedling emergence in the field was 1.9% after 3 years. The decrease of the viability of rape seed was slower than in the undisturbed experiment, with more than 1% viable seeds remaining after 3 years. Total emergence of rape was up to 4%. Hybrids showed lower seed viability than rape. Total seedling emergence over 3 years was less than 1%. These results are discussed together with the consequences of commercial release of transgenic crops. Transgenes can escape via seeds and volunteer rape, and seeds of interspecific hybrids between rape and wild relatives can survive and germinate after several years, ensuring genetic and spatial spread of transgenes. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Oilseed rape; Interspecific hybrids; Seed survival; Transgenic crops

1. Introduction

Agronomic and ecological consequences of releasing genetically modified crop plants are recent concerns in agriculture (Rissler and Mellon, 1993). One of the main issues is the possibility of transgene escape, either through seed dispersal or sexual crossing between the crop and wild or weedy relatives. Oilseed rape, \textit{Brassica napus} L., produces pollen and seed in such large amounts that it is likely to disperse transgenes. Notably, huge amounts of seed from 1% to 10% of the grain are lost at harvest, resulting in volunteer rape within fields and feral rape populations in field borders (Bowerman, 1984; Lutman, 1993; Price et al., 1996). Volunteer rape is a troublesome weed when growing in other crops as it reduces crop yield (Lutman, 1993). Seed production of volunteer rape grow-
ing within different cultivars of rape could also affect grain purity and quality. Engineering herbicide resistant cultivars may cause additional difficulties to control volunteers. However, to date few studies have been devoted to the biology and survival of rape seed in the soil (Masden, 1962; Crawley et al., 1993; Pekrun et al., 1997). At the same time, crucifer species which are present as weeds within fields or along field borders can cross with rape, thus producing hybrid seeds (Eber et al., 1994; Jorgensen and Andersen, 1994; Darmency et al., 1995; Lefol et al., 1996). Since the survival of seeds in the soil is an important factor for the success of annual species such as weeds (Roberts and Boddrell, 1983), it is likely that hybrids will display greater longevity than rape. Indeed, it has been shown that hybrid seeds between rape and a wild relative, *B. rapa*, show intermediary behaviour between those of the two parent species (Adler et al., 1993; Linder and Schmitt, 1994, 1995). Conceivably, this could result in transgene escape throughout a longer time period in foreign genome backgrounds other than in rape. In particular, if the transgene encodes for herbicide resistance, this could be the origin of troublesome herbicide resistant weed control problems for the farmer. Learning more about seed behaviour, therefore, can bring more insight into predicting the fate of transgene escape and may help in managing herbicide resistance in weeds and volunteers. Here, we report on the comparative survival and germination of seed of rape, hoary mustard (*Hirschfeldia incana* (L.) Lagreze-Fossat), rape × hoary mustard and rape × wild radish (*Raphanus raphanistrum* L.) hybrids buried in soil. Seeds of wild radish have not been included in this study because they produce a hard-coated pod protecting them against soil conditions. Conversely, this is not the case with other species and hybrids obtained with rape as the seed parent. We present the results of experiments in undisturbed garden soil and cultivated field conditions.

## 2. Material and methods

### 2.1. Seed survival in undisturbed soil

A male-sterile rapeseed cv. ‘Brutor Fu 27’ produced by the National Institute for Agronomic Research (INRA) of Rennes, France, was grown in alternate rows (0.33 m row spacing) with hoary mustard (population collected at Rennes) in a 1370 m² plot at INRA of Dijon in April 1991. Seed from each species was harvested separately using a combine harvester at the end of August. Seed from the male sterile rape was passed through a 1.4 mm sieve into big-seed and small-seed fractions as it has already been shown that all hybrids have smaller seed size (Eber et al., 1994). A baseline germination rate of four replicates of 100 seeds of each seed type was measured. Seeds were germinated on a Whatman No.1 paper moistened through capillary action from a water tank, in Petri dishes, in a growth cabinet with alternating temperature (between 20°C and 25°C) and a 12 h photoperiod. Germination rates were measured after 2 weeks, following which 0.1 g l⁻¹ gibberelic acid (GA₃) was sprayed on the ungerminated seeds in order to break potential dormancy. The morphology of one hundred plants from each seed type was analysed. Electrophoresis of leaf esterases and acidic phosphatases was done as described previously (Lefol et al., 1996) in order to check hybrid seed purity and calculate the frequency of rape and hoary mustard contaminants.

A total of 28 000 seeds of each type were divided into 28 groups of 1000 seeds. Each group was mixed with 200 g soil and 100 g sand, and then placed in an openwork woven nylon bag (hole diameter=0.2 mm). The 84 bags were buried in the experimental garden of INRA at Dijon in November 1991, at the bottom of a 0.30 m deep trench. The soil (0.5-0.7 m deep clayey calcic brown) was then put back into the trench. The design was completely randomized. Thereafter the garden was left undisturbed except for hand or hoe weeding to keep the surface free from plants. The mesh of the nylon bag allowed the passage of water and soil pathogens, gas exchange, and full contact with soil. From November 1991 until April 1995, four bags of each seed type were chosen randomly and dug out twice a year. Their contents were spread over sterilized sand in a growth cabinet with alternating temperature (between 15°C and 25°C) and a 12 h photoperiod. After 3 weeks, when there was no further germination, seedlings were dug out and counted. Thereafter the sand was sprayed, using the laboratory sprayer facility, with 100 ml m⁻² of a 0.1 g l⁻¹ gibberelic acid solution. New seedlings were counted over a period of 6 weeks. Following this, the remain-
ing soil sample was observed under a magnifying glass in order to detect any dormant seeds. Data were given as a percentage of the initial seed germination rate. As samples of hybrid seeds contained known proportions of contaminants, estimated germination scores of rape and hoary mustard contaminants were discounted from hybrid data. Then the hybrid score was given as a percentage of the initial germination rate of pure hybrid seeds. Each bag was treated separately, thus allowing calculation of mean values and standard deviation.

2.2. Seed survival and seedling emergence in a cultivated field

A male sterile F1 rapeseed ‘Westar×Wesroona’ produced by INRA at Rennes was grown in alternate strips (3 m wide, 0.33 m row spacing) with hoary mustard in a 3500 m² plot, or with wild radish (population collected at Rennes) in a 2200 m² plot at INRA Rennes in Spring 1993. The two plots were separated by 1 km. The immediate proximity of all the plots were weeded, removing all Brassiceae. Seed harvested from the male sterile rape was sieved (diameter 1.6 mm) to obtain the small seed fraction containing the hybrids. Hybrid seed purity was determined by morphological analysis and electrophoresis of leaf esterases and phosphatases (Eber et al., 1994; Damnecy et al., 1995; Lefol et al., 1996). Bulk seed of several spring cultivars harvested in 1993 was also used in the study. Baseline germination of four replicates of 100 seeds of each type was measured in Petri dishes in a growth cabinet with alternating temperature (between 20°C and 25°C) and a 12 h photoperiod. After 3 weeks, 0.1 g l⁻¹ gibberelic acid was sprayed on ungerminated seeds to induce the germination of remaining dormant seeds.

Seeds were spread on 6 m×9 m plots at the rate of 12000 seeds m⁻² using an Oyord seeder with the heads up in order to disperse seeds homogeneously. Plots were 5 m apart. Deep ploughing, using a classical plough to invert the soil to a 25–30 cm depth, followed by harrowing to a 10–15 cm depth were carried out to bury the seeds in the soil. The experiment was carried out at two locations, each with two randomized replicates. One site was at the INRA experimental station in Dijon (eastern France, clayey calcic brown soil), the other at the ENSAM experimental station in Montpellier (southern France, clayey silty calcic soil). Neither field had been used to grow rape for at least 5 years. A total of 2.6 million seeds of each type was used. After harrowing again, spring barley (Hordeum vulgare L.) and durum wheat (Triticum durum Desf.) were sown at Dijon and Montpellier, respectively, at the conventional rate (300 pl m⁻²). Thereafter, the field plots were used as in a conventional farming system, with winter wheat (Triticum aestivum L.) at Dijon and durum wheat at Montpellier. The main cultural practices from 1993 to 1996 are listed in Table 1. Following the last counts of emerged seedlings, a non-persistent hormonal herbicide was sprayed to avoid weed infestation and rape seed production in the field.

Seedling emergence counts and soil core sampling were carried out in the 4 m×6 m central part of all plots in which seeds were buried to avoid problems with border effects and seed dispersal by cultivation. Emerged seedlings were counted once a month in 17 permanent quadrats located at random over the plot.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Dijon</th>
<th>Montpellier</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed burial</td>
<td>Nov. 93</td>
<td>Jan. 94</td>
</tr>
<tr>
<td>Ploughing</td>
<td>Nov. 93</td>
<td>Jan. 94</td>
</tr>
<tr>
<td>Sowing</td>
<td>Mar. 94</td>
<td>Jan. 94</td>
</tr>
<tr>
<td></td>
<td>(spring barley)</td>
<td>(durum wheat)</td>
</tr>
<tr>
<td>Emergence counts</td>
<td>Dec. 93–May 94</td>
<td>Feb. 94–June 94</td>
</tr>
<tr>
<td>Weed control (2,4-D)</td>
<td>May 94</td>
<td>May 94</td>
</tr>
<tr>
<td>Harvest</td>
<td>July 94</td>
<td>June 94</td>
</tr>
<tr>
<td>Core sampling</td>
<td>Aug. 94</td>
<td>Sept. 94</td>
</tr>
<tr>
<td>Ploughing</td>
<td>Sept. 94</td>
<td>Sept. 94</td>
</tr>
<tr>
<td>Sowing</td>
<td>Oct. 94</td>
<td>Dec. 94</td>
</tr>
<tr>
<td></td>
<td>(winter wheat)</td>
<td>(durum wheat)</td>
</tr>
<tr>
<td>Emergence counts</td>
<td>Nov. 94–Mar. 95</td>
<td>Jan. 95–April 95</td>
</tr>
<tr>
<td>Weed control (2,4-D)</td>
<td>April 95</td>
<td>May 95</td>
</tr>
<tr>
<td>Harvest</td>
<td>July 95</td>
<td>July 95</td>
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<tr>
<td>Sowing</td>
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</tr>
<tr>
<td>Core sampling</td>
<td>July 96</td>
<td>Sept. 96</td>
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</tbody>
</table>
representing a total of 1 m² for each plot. Seedlings in the quadrats were destroyed after each count. Between harvesting and ploughing, to prepare sowing of winter cereals, 45 soil core samples were taken at random in each plot. The cores were 30 cm deep with a 4.6 cm diameter, thus representing a total area of 0.075 m² and a soil volume of 0.025 m³ in each plot. The soil was spread on plastic sheets in the greenhouse and sprayed with water as frequently as necessary to maintain it moist. Seedlings were counted. When no more seedlings emerged, the soil was treated with successive dry and moist periods and finally watered with 0.1 g l⁻¹ gibberelic acid to induce germination of dormant seeds. Results are expressed as a percentage of the baseline germination rate estimated before burial. Since quantities of hybrid seeds were not large, only two replicates could be set at each location and, therefore, no statistical test was undertaken.

3. Results

3.1. Seed survival in undisturbed soil

Seeds harvested from the male sterile rape formed two fractions. There were approximately 35,000 ‘big’ seeds with diameter more than 1.4 mm and weighing 3.8 mg. Seeds of this fraction served as the rape reference in the experiment, and were identified as rape × rape hybrids on the basis of electrophoretic patterns (not shown). Their presence was probably due to some volunteer rape growing near the plot providing contaminant pollen and thus producing rape × rape hybrids. There were also about 35,000 ‘small’ seeds (Table 2). Morphological and electrophoretic analysis proved that they consisted of 81% interspecific hybrids, 3% hoary mustard belonging to plants on adjacent rows, and 16% rape × rape hybrids.

A total of 28,400 hybrid seeds were produced in this experiment which represented 20 hybrid seeds per m².

Germination of the three seed types were estimated prior to burying the seeds in the soil. Total germination, after GA₃, was more than 96% for rape (big seeds), 89% for hybrids (small seeds), and 93% for hoary mustard. Germination of seeds of hoary mustard decreased to 50% within 2 years, and then remained constant up to the end of the experiment at 41 months (Fig. 1). In contrast, germination of rape seeds immediately dropped to 1%, remained constant over 3 years, and dropped to 0% at 41 months. Examination of the soil sample after the germination test showed that there were no remaining intact seeds in any bag. There were no dormant seeds which means that all the seeds that did not germinate in our germination test

Table 2

<table>
<thead>
<tr>
<th>Location</th>
<th>Pollen donor</th>
<th>Plot area (ha)</th>
<th>Yield small seeds (g)</th>
<th>Weight of seed (mg)</th>
<th>Hybrid purity (%)</th>
<th>No. of hybrid produced (per plot)</th>
<th>(per m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dijon</td>
<td>Hoary mustard</td>
<td>0.14</td>
<td>42</td>
<td>1.21</td>
<td>80</td>
<td>27,700</td>
<td>20</td>
</tr>
<tr>
<td>Rennes</td>
<td>Hoary mustard</td>
<td>0.35</td>
<td>3400</td>
<td>0.90</td>
<td>94</td>
<td>3.5 × 10⁶</td>
<td>1000</td>
</tr>
<tr>
<td>Rennes</td>
<td>Wild radish</td>
<td>0.22</td>
<td>5000</td>
<td>0.89</td>
<td>100</td>
<td>5.6 × 10⁶</td>
<td>2500</td>
</tr>
</tbody>
</table>

Fig. 1. Proportion of initial viable seeds of hoary mustard (star), rape × rape (triangles) and rape × hoary mustard hybrids (circle) germinating after different times buried in undisturbed soil in experiment 1 at Dijon. Bars indicate standard deviation.
were lost because of predation or germination during burial within the soil. Therefore, half of the hoary mustard seed showed a long viability in the soil while the rape seed completely disappeared after 3 years of burial.

Raw data from hybrid seeds were corrected to take into account the presence, in the small-seed fraction, of 3% hoary mustard seeds that remained more than 50% viable throughout the experiment, and 16% rape seeds that died quickly. Survival of hybrid seeds was intermediate between those of the two parents, with nearly 15% survival the first year which decreased to complete extinction at 41 months. Again, no intact seed was observed in the soil contained in the bags after the germination tests.

3.2. Seed survival and seedling emergence in the cultivated field

Large amounts of seed were collected from the male sterile oilseed rape. The small seed fractions contained 5.6 and 3.5 million seeds when grown with wild radish and hoary mustard, respectively. Morphology and electrophoresis analyses of small seeds showed that they were 100% interspecific hybrids when crossed with wild radish, and 94% when crossed with hoary mustard. Remaining seeds in the last cross were 6% rape×rape hybrids. Therefore, yields were 2500 hybrids m⁻² with wild radish, and 1000 hybrids m⁻² with hoary mustard (Table 2). To account for the presence of rape contaminants together with hybrid seeds, data on viability of hybrid seed samples were corrected as above.

Total germination prior to burying seeds in the soil was more than 97% for rape and the two hybrids, and 89% for hoary mustard. Seeds of hoary mustard had the highest germination rate at both Dijon and Montpellier locations (Fig. 2(a) and (b)). Averaged over the two locations, germination of buried seeds was 29% after 1 year and 14% after 3 years. However, germination was higher at Dijon than at Montpellier. Germination of rape was also higher at Dijon. Average germination of rape seed was 7% after 1 year, and 2% after 3 years. Seeds of interspecific hybrids behaved in the same way as rape seeds and germination decreased to 1% and less after 3 years.

Seedling emergence was also different between locations (Table 3). Over the 3 years, the sum of emerged seedlings represented 1.2% of the initial viable seed stock for hoary mustard at Dijon, and 2.6% at Montpellier. More emerged seedlings were recorded for rape at Dijon with a total of 4% of the initial seed stock emerging, but only 0.5% at Montpellier. Total emergence of hybrids was lower.
than 1%. At both locations, a higher number of emerged seedlings were recorded during the second year.

4. Discussion

Data from the first experiment provided a direct estimate of the viability of the seeds as no more intact seeds were found in the soil samples. However, soil core samples in the second experiment were not checked for the presence of intact ungerminated seeds following the germination test. The efficiency of the germination procedure, as observed in the first experiment, indicates that the results of the second experiment represent seed viability data, or perhaps just slightly underestimated viability values. Longevity of buried seeds of hoary mustard was far greater than that of rape and interspecific hybrids in the two experiments. About half the seeds remained dormant in undisturbed soil conditions. Disturbed soil conditions which included ploughing, harrowing and crop sowing, affected the longevity of seeds buried in the soil as expected from previous work on other weeds (Roberts and Dawkins, 1967; Chancellor, 1986). Remaining viable seeds in the cultivated field after 3 years were only 21% and 6% at Dijon and Montpellier, respectively. No previous data has been published for hoary mustard. Survival of hoary mustard seed appears to be similar to that of wild mustard (*Sinapis arvensis*, another *Brassicaceae*) the seed of which persists in soil from 6% to 15% after 5 years (Roberts and Bodrell, 1983; Barralis et al., 1988).

Wild radish, the other wild species used to produce interspecific hybrids, was not tested in this study because it shows high innate dormancy associated with the fruit structure (Mekenian and Willemsen, 1975) which is not the case for hoary mustard, rape, and the hybrids. Wild radish has seed pods with up to seven constrictions that form up to eight portions, each containing one seed. Pod tissues are very thick and hard so that they exercise mechanical and chemical restriction to germination. Hence, wild radish has a long duration in the soil, with 18% of seeds being viable after 5 years in cultivated soil (Roberts and Bodrell, 1983).

Seed aging, predation, fungal attack and seed germination presumably account for the degeneration of the viable seed bank. Soil cultivation periodically moved the seeds and, therefore, resulted in more and varied dormancy-breaking stimuli. In the first year, seedling emergence of hoary mustard was very low (0.1%), probably because most of the seed had been buried down in the lowest soil layer by deep ploughing. The next year, cultivation brought some seeds back to the surface (Dessaint et al., 1996), resulting in more seedling emergence. It is generally assumed that 6% of seeds of a homogeneous seed stock gives seedlings under the soil and climate conditions at Dijon (Barralis et al., 1988). Here, the seedlings that emerged in the second and third years were 4% of the hoary mustard seed stock that remained at the end of the first year. However, seedling emergence made no important contribution to the decrease of seed survival (Table 3). Emergence of hoary mustard was double at Montpellier (Mediterranean climate), its natural habitat, than at Dijon (mild Continental climate), although this does not completely explain the seed survival difference between the two locations.

In contrast to hoary mustard, there was only 1% of rape seeds surviving in the undisturbed experiment,
although the survival rate in the cultivated field at Montpellier was also 1% and more than 10% in the first and second years of burial at Dijon. Variability from 0% to 27% survival after 1 year has been observed between studies and, even, between samples in the same study (Lutman, 1993; Linder and Schmitt, 1995). Long-term survival up to 16 years of rape seed buried in undisturbed soil has been reported (Masden, 1962). Light and water conditions before burial can induce secondary dormancy, and genotype response is also varied (Pekrun et al., 1997) which might account for high variability. Different emergence rates might be related to differentially induced dormancy at the two locations. Total seedling emergence of 0.5% at Montpellier and 4% at Dijon represented a small part of the initial soil seed bank. Higher emergence at Dijon was related to 10 times higher seed survival in the soil. There were still up to 10 rape plants emerged per m² in the third year. Such a rate of seedling emergence 3 years after rape in a crop rotation fits well with practical evidence from farmers’ fields (Lutman, 1993). Our experiment corresponds to a situation where 12 000 seeds per m² are lost at harvest, representing around 400 kg per hectare; i.e., about 12% of the rape harvest in normal field conditions. It is clear that reducing seed loss during harvest is an important task both for increasing yield and preventing field infestation by volunteers.

Interspecific hybrids appeared to be easy to obtain between male sterile oilseed rape and hoary mustard and wild radish. The lower yield recorded at Dijon is probably due to the fact that hoary mustard is not native nor adapted to the Dijon region. The hybrid yields recorded at Rennes are the highest ones published up to date with more than 1000 hybrid seeds per m². Of course, these results were due to the absence of rape pollen leading to non-competitive conditions for foreign pollen germination and fertilization of rape ovules. It is likely that far fewer hybrids would be obtained in farmers’ fields growing fertile or composite varieties (mixture of male and fertile plants). Field studies on this topic are currently being developed at INRA. However, hybrid seeds are small and are consequently sieved out by the combine harvester and returned to the soil. In the reciprocal cross direction, no more than 0.1 hybrid seeds per m² have been recorded in field conditions (Darmency et al., 1995; Lefol et al., 1996).

The amount of hybrid seed used to constitute the artificial soil seed bank was much greater than that expected in the field: 12 000 in contrast to 0.1; i.e., 10⁵ times greater. This artificial abundance raised for experimental purposes facilitated the observation that interspecific hybrids seeds have an intermediate survival rate in undisturbed soil, as reported in a 1-year experiment with canola (Linder and Schmitt, 1994). However, in cultivated soil conditions in fields at two different locations with different types of climate, hybrids behaved in the same way as rape seeds and had an even lower survival. As the hybrids tested here were obtained from male sterile rape, one may surmise that the reciprocal hybrids should result in higher dormancy. Indeed, hybrid cross direction has been shown to affect germination and dormancy in canola×wild Brassica rapa hybrids because of the effect of maternal tissues and seed-coat characters (Adler et al., 1993; Linder and Schmitt, 1994). Unfortunately, the rate of hybrid production with hoary mustard as the female was too low to provide enough seed to study the effect of cross-direction. Finally, less than 1% of rape×wild radish and rape×hoary mustard hybrid seeds gave emerged seedlings, especially in the second year after burial. In a 2-year rape-wheat rotation, for instance, this would mean that most hybrid seedlings produced in the rape rotation would emerge during the second year after burial, that is during rape again, so that they could experience good conditions for growth. In addition, if herbicide-resistant rape varieties were repetitively grown on the same field, interspecific hybrids would exhibit herbicide-resistance inherited from rape, therefore, displaying a tremendous selective advantage.

5. Conclusion

This work shows that the persistence of transgenes via dormant seeds of genetically modified rape buried in the soil may be an important source of temporal dispersal of these transgenes. The huge amount of seed loss at harvest, a 1% seed survival in cultivated fields, and a seedling emergence rate close to 0.01% of the initial soil seed bank after 3 years, make the likelihood of volunteer transgenic rape occurring in fields every year very possible. These plants could be detrimental volunteers in other crops, especially if they display
resistance against the herbicide used in those crops, or if they were genetically modified for enhanced resistance to stress, etc. They could reproduce and release seeds of which a part would be shed onto the soil again. They could exchange pollen with wild relatives even at a time when no rape crop is grown in the area. Interspecific hybridization creates a way for the dispersal of transgenes into various genome backgrounds. Hybrid seeds, although rare in proportion to the total soil seed bank, can survive as well as rape seeds. They can germinate and produce seedlings. If there are 0.1 hybrids produced per m², a rate of hybrid emergence up to 0.8% as at Dijon in the second year would result in 8 hybrids per hectare. As hundreds of thousands of hectare of rape are grown each year, this makes transgene escape through interspecific hybridization unavoidable. These hybrids grow as well as their wild progenitor (Lefol et al., 1995) and could have progeny and backcross with wild Brassicaceae populations (Lefol et al., 1996; Chèvre et al., 1997). The impact of such a transgene transfer remains to be determined according to the advantages associated with each type of transgene.

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References


