

Avena, oats

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1. Taxonomy

(Grebenstein et al., 1998): In accordance with current systematic opinions, the tribe *Aveneae* is closely associated with the tribe *Poeae*. Both tribes can be regarded as monophyletic sistergroups (Fig. 2) with a common, monophyletic origin in the grass subfam. *Pooideae* as already indicated by chloroplast DNA restriction site variation (Soreng et al., 1990), by ITS sequence analysis (Barker et al., 2001; Hsiao et al., 1994, 1995a, b; Hsiao et al., 1998; Hsiao et al., 1999), and, though less extensively sampled, by *rbcL* sequence data (Duvall & Morton, 1996). A completely different systematic view was expressed in the last systematic review of grasses published by (Tsvelev, 1989) who argued that separation of the tribes *Poeae* and *Aveneae* is based on comparatively weak morphological characters and consequently summarised them under a broad tribe *Poeae*. This unconventional suggestion should be kept in mind when further molecular data of phylogenetically critical taxa become available by molecular work. The tribe *Triticeae* (represented here by *Secale cereale*) and the *Bromeae* (*Bromus inermis*) are rather distantly related to *Poeae* and *Aveneae* species as indicated by ITS sequence data (Hsiao et al., 1995a, b), studies based on chloroplast DNA restriction fragment length polymorphisms (Soreng, 1990), (Kellogg, 1992), and by morphological evidence (Clayton & Renvoize, 1986).

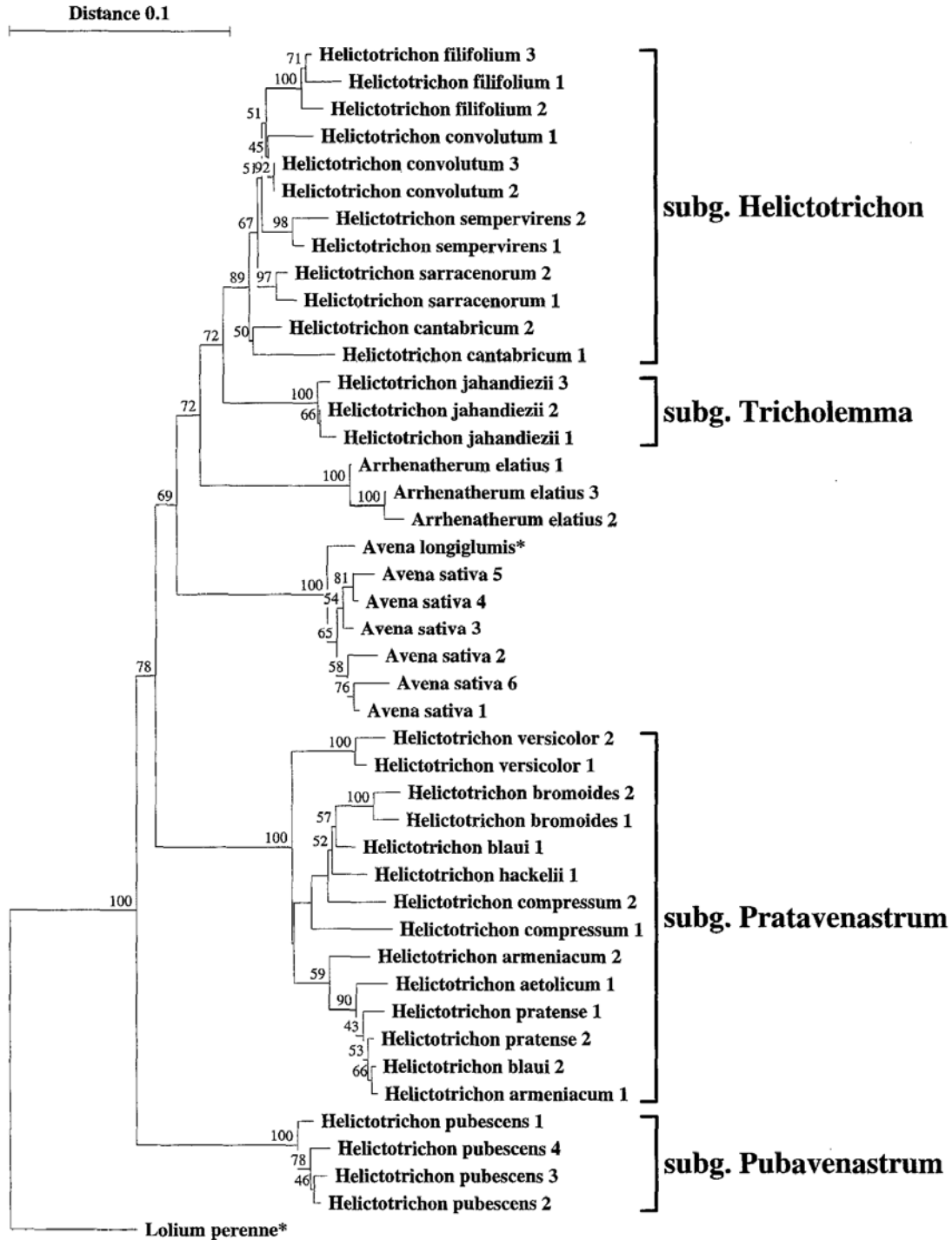


Fig. 1 Neighbor-joining tree inferred from rDNA ITS sequences in 'core genera' of *Aveneae* subtribe *Aveninae* analysed with the distance matrix method. Numbers above branches are bootstrap values. Branch lengths are proportional to distance. Outgroup: *Lolium perenne* (*Poeae*). Asterisk designates sequence data taken from (Hsiao et al., 1994, 1995a, b), out of (Greibenstein et al., 1998).

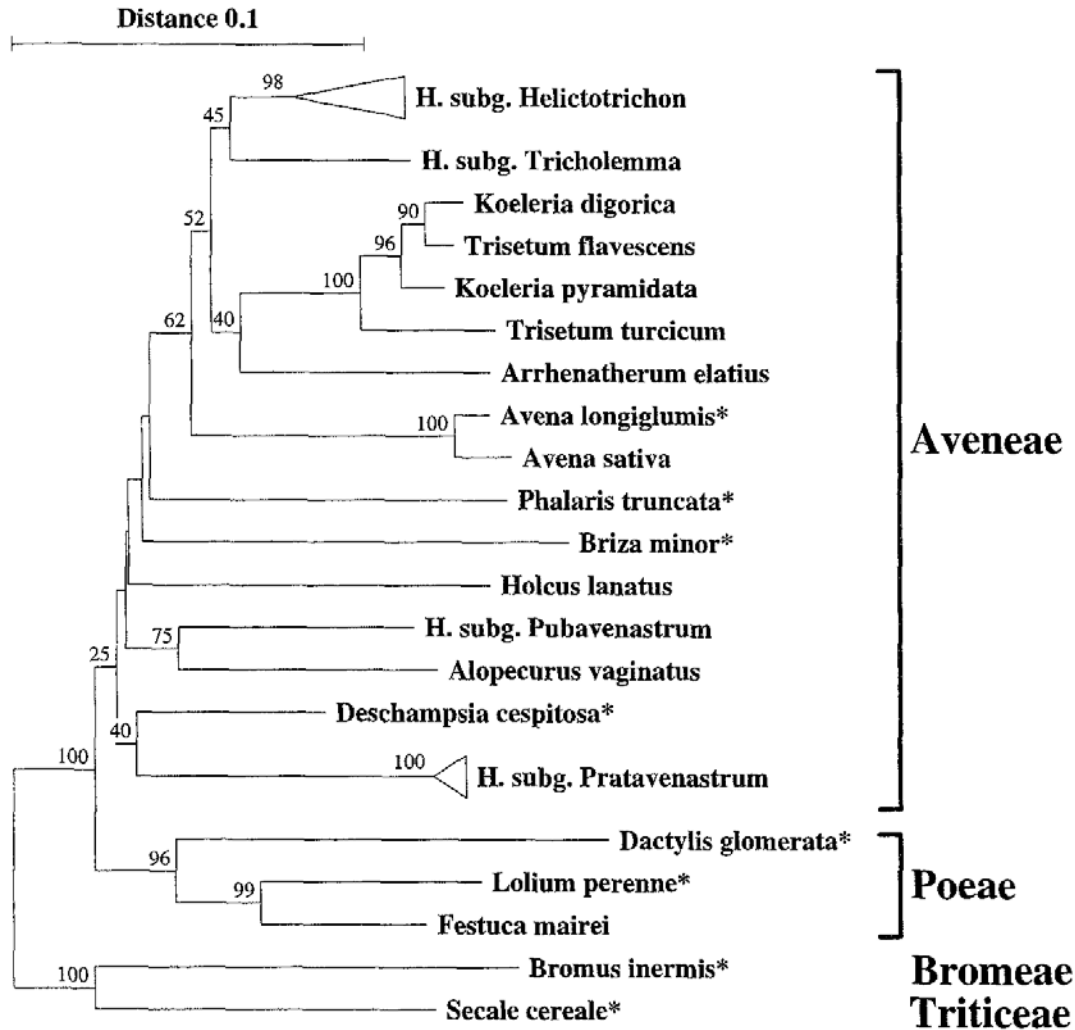


Fig. 2 Phylogenetic tree inferred from ITS sequences of 15 genera of tribes *Aveneae* and *Poeae* generated by the neighbor-joining distance matrix method. Numbers above branches are bootstrap values. Branch lengths are proportional to distance. Outgroups: *Bromeae* (*Bromus inermis*) and *Triticeae* (*Secale cereale*). Asterisk designates sequence data taken from (Hsiao et al., 1994, 1995a, b)

In conclusion, the molecular analysis of ITS sequences of several taxa of the *Aveneae* suggests that (i) the ancestry of the agronomically important genus *Avena* has to be sought within comparatively small-flowered *Aveneae* taxa, (ii) genus *Arrhenatherum* and small-flowered subgenera of *Helictotrichon* are close extant relatives of *Avena*, (iii) genus *Helictotrichon* is para- if not polyphyletic, (iv) genera *Trisetum*, *Koeleria* and probably others form a separate lineage characterised by a particular 9-bp deletion, (v) the delineation of some genera and subtribes of *Aveneae*, and perhaps tribes of subfam. *Pooideae* needs to be reevaluated by including phylogenetically critical taxa and combining morphological, anatomical and molecular datasets.

(Beer et al., 1993) demonstrate, that genetic patterns revealed by proximity coefficients may be affected by choice of traits, method of scoring, any subsequent transformations of scores, and choice of proximity coefficient. Their objective was to compare restriction

fragment length polymorphism (RFLP), isozyme polymorphism, and variation in qualitative and quantitative morphological traits in a geographically stratified set of 177 accessions of a hexaploid wild oat, *Avena sterilis* L. Jaccard similarity coefficients (SJ) and Russell and Rao similarity coefficients (SRR) were calculated for all pairs of genotypes from restriction fragments and, separately, from isozymes. Standard taxonomic (DSZ), Mahalanobis, and Good mean distances were calculated from 26 morphological trait scores. Clustering of mean DSZ values or mean SJ(RFLP) values between pairs of countries produced similar dendrograms while SRR(isozymes) values resulted in different subgroups. Rankings of within-country diversity were similar for different types of traits but were unrelated to geographic proximity of provenances of the accessions. Proximity coefficients based on the same type of trait (either RFLP, isozyme, or morphology) were highly correlated (Mantel statistic) (0.6-0.9), while correlations for proximities based on different types of traits were less than or equal to 0.35. Isozyme and RFLP-based proximities were poorly correlated, and both were poor predictors of morphological relationships with the highest correlation being -0.35 between SJ(RFLP) and DSZ. While broad patterns of variation revealed by different types of traits were similar in this sample of *A. sterilis*, differences in pairwise estimates of relationship were sufficiently great to question the exclusive use of one type of trait for sampling and management of plant germplasm collections.

2. Biosafety considerations

Outcrossing in *Avena sativa* L. have been reported to range from 0 to 9.8%) but mostly it was less than 17, (Jensen, 1966). (Thurmann & Womak, 1961) and (Grindeland & Froberg, 1966) obtained up to 10.4 and 6.0% outcrossing, respectively, following mutagen treatments of *A. sativa*, although (McKenzie et al., 1975) found less than 1.0% outcrossing following such treatments. Outcrossing in *Avena sterilis* L. - *Avena fatua* L. natural mixed populations, measured by the number of plants having an *A. sterilis* phenotype among plants derived from the *A. fatua* parent, was 4.8 and 1.2% in 2 consecutive years. Herein, the authors estimated the degree of outcrossing in selfed progeny of the F1 and successive backcross generations in four *A. sativa* x *A. sterilis* matings. They also considered effects of various natural crossing rates on maintenance of heterozygosity.

Two separate field experiments were conducted by (Murray et al., 2002) to quantify the degree of plant-to-plant outcrossing and pollen-mediated gene flow (PMGF) in wild oat. The purpose of the study was to determine the extent to which pollen movement could contribute to the spread of herbicide resistance in this species. In both experiments, an acetyl-CoA carboxylase inhibitor-resistant (R) wild oat genotype (UM1) was used as the pollen donor and a susceptible (S) genotype (UM5) was used as the pollen receptor. Hybrid progeny resulting from a cross between UM1 and UM5 were identified using the herbicide resistance trait as a marker. In the plant-to-plant outcrossing experiment, single UM5 plants were closely surrounded by 20 homozygous R UM1 plants in hills. By screening seed from the S parent for resistance, outcrossing was determined to range from 0 to 12.3%, with a mean of 5.2% over 10 hills. In the PMGF experiment, single

homozygous R UM1 plants were surrounded by UM5 plants arranged in a hexagonal pattern at low and high densities (total of 19 and 37 wild oat plants m^{-2}), growing within spring wheat and flax crops. In the wheat crop, mean wild oat outcrossing was 0.08 and 0.05% at low and high densities, respectively. In the less competitive flax, corresponding outcrossing values were 0.07 and 0.16% at low and high densities, respectively. Distance from the pollen source was a significant factor only for the high-density planting arrangement in flax. Up to 77 R hybrid seeds were recovered from 6 m^2 in the PMGF experiment, indicating that PMGF contributes to the evolution of resistance in wild oat populations. However, the contribution of pollen movement to resistance evolution and the spread of resistance in wild oat populations would be relatively small when compared with R seed production and dispersal from a resistant plant.

3. Transgenic oats

Transgenic *Avena* have already been constructed:

(Leggett et al., 2000) report on *Avena* transformed with *gus* and *bar* transgenes.

Fluorescence in situ hybridization (FISH) was used to localize two transgenes (*gus* and *bar*), carried on plasmids pACT-1F and pUBA, respectively, on mitotic metaphase squashes of T1 plants of the cultivated hexaploid oat *Avena sativa* L. cotransformed by microprojectile bombardment of embryogenic callus. Among the eight progeny analysed by FISH in each of two lines, they detected plants null, hetero- and homozygous for the two genes in one line, and plants null and heterozygous for the two genes in the other line. Their results demonstrated that in the two independent transformation events, the *gus* and *bar* genes had inserted in the same position relative to each other. In each transformation event, the insertions occurred on D satellite (SAT) chromosomes bearing a C genome translocation.

(Perret et al., 2003) transformed by particle bombardment of primary embryogenic callus Two oat varieties, Melys (spring variety) and Bulwark (winter variety) using either a *ubi-bar-ubi-gus* co-integration vector or co-transformed (Melys) with a *ubi-bar* plasmid together with one of three plasmids containing the *-glucuronidase (gus)* gene under the control of either a rice actin promoter, a CaMV35S promoter or a wheat high molecular weight glutenin promoter. Morphologically normal and fertile transgenic plants were regenerated following callus selection with glufosinate ammonium. Evidence for the integration and functioning of the selectable (*bar*) and reporter (*gus*) genes in T0 and T1 plants was confirmed by PCR, Southern hybridisation, fluorescence in situ hybridisation (FISH), histochemical assays, and by progeny analysis. Transformation rates varied from 0.2 to 5.0 lines/plate of callus bombarded, with co-transformation frequencies of 83 to 100 %, and co-expression frequencies of 60 to 100 %. Copy numbers for the *bar* and *gus* gene varied from 3 to 17 and from 2 to 20 respectively. Cell and tissue specific expression of the *gus* gene was evident from the different promoters, with the HMW glutenin promoter showing endosperm specific expression in T1 seed. No expression of the *gus* gene under the CaMV35S promoter was detected in any tissues. Progeny analysis provided evidence of Mendelian inheritance of the introduced genes suggesting either one or two unlinked integration sites. This was confirmed by fluorescence in situ hybridisation to chromosome spread preparations. No segregation of the *gus* gene from the *bar* gene was observed in any of the progeny derived from co-transformation.

(Pawlowski et al., 1998) published about an irregular pattern of transgene silencing which they revealed in expression and inheritance studies conducted over multiple generations following transgene introduction by microprojectile bombardment of allohexaploid cultivated oat (*Avena sativa* L.). Expression of two transgenes, *bar* and *uidA*, delivered on the same plasmid was investigated in 23 transgenic oat lines. Twenty-one transgenic lines, each derived from an independently selected transformed tissue culture, showed expression of both *bar* and *uidA* while two lines expressed only *bar*. The relationship of the transgenic phenotypes to the presence of the transgenes in the study was determined using (1) phenotypic scoring combined with Southern blot analyses of progeny, (2) coexpression of the two transgenic phenotypes since the two transgenes always cosegregated, and (3) reactivation of a transgenic phenotype in self-pollinated progenies of transgenic plants that did not exhibit a transgenic phenotype. Transgene silencing was observed in 19 of the 23 transgenic lines and resulted in distorted segregation of transgenic phenotypes in 10 lines. Silencing and inheritance distortions were irregular and unpredictable. They were often reversible in a subsequent generation of self-pollinated progeny and abnormally segregating progenies were as likely to trace back to parents that exhibited normal segregation in a previous generation as to parents showing segregation distortions. Possible causes of the irregular patterns of transgene silencing are discussed.

(Makarevitch et al., 2003) write: A substantial literature exists characterizing transgene locus structure from plants transformed via *Agrobacterium* and direct DNA delivery. However, there is little comprehensive sequence analysis of transgene loci available, especially from plants transformed by direct delivery methods. The goal of this study was to completely sequence transgene loci from two oat lines transformed via microprojectile bombardment that were shown to have simple transgene loci by Southern analysis. In line 3830, transformed with a single plasmid, one major and one of two minor loci were completely sequenced. Both loci exhibited rearranged delivered DNA and flanking genomic sequences. The minor locus contained only 296 bp of two non-contiguous fragments of the delivered DNA flanked by genomic (filler) DNA that did not originate from the integration target site. Predicted recognition sites for topoisomerase II and a MAR region were observed in the transgene integration target site for this non-functional minor locus. Line 11929, co-transformed with two different plasmids, had a single relatively simple transgene locus composed of truncated and rearranged sequences from both delivered DNAs. The transgene loci in both lines exhibited multiple transgene and genomic DNA rearrangements and regions of scrambling characteristic of complex transgene loci. The similar characteristics of recombined fragments and junctions in both transgenic oat lines implicate similar mechanisms of transgene integration and rearrangement regardless of the number of co-transformed plasmids and the level of transgene locus complexity.

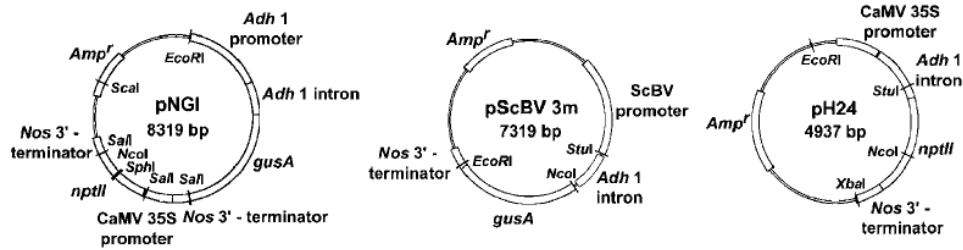


Fig. 3 Maps of plasmids used to produce transgenic oat lines 3830 (pNGI) or 11929 (pH24 and pScBV 3m). Restriction sites used in the analysis are shown. From (Makarevitch et al., 2003)

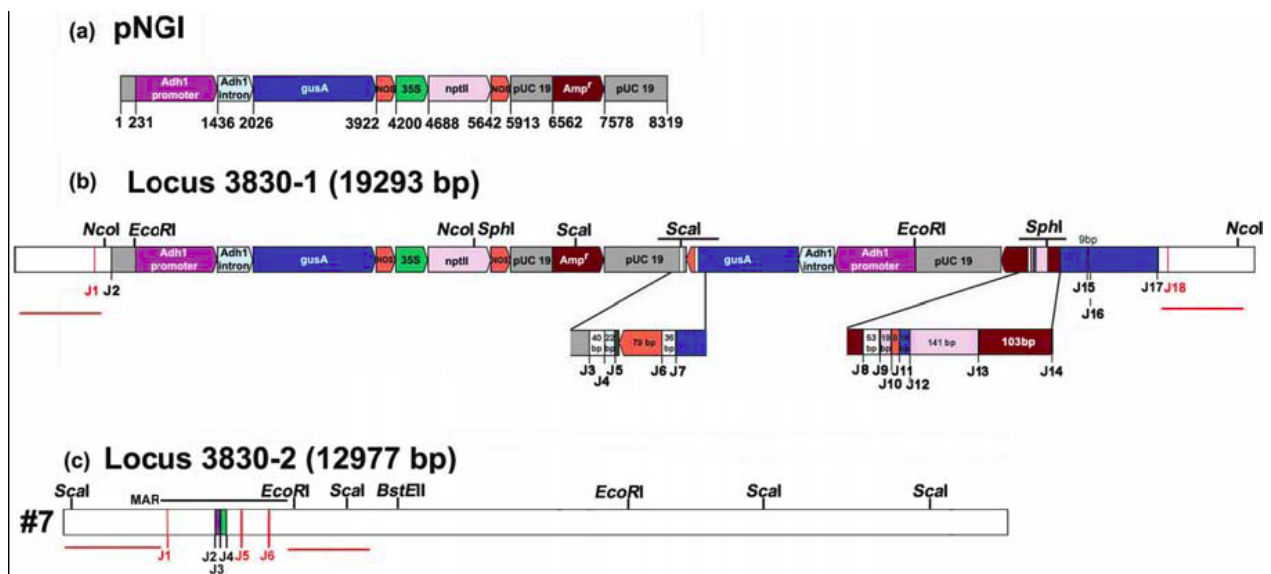


Fig. 4 Summary of sequence analysis of transgene locus clones isolated from transgenic line 3830. a. Linear map and structural components of pNGI used in producing transgenic line 3830. Colors indicate the structural components of pNGI. b. Structures of locus 3830-1 and ten lambda clones isolated from line 3830 corresponding to the main transgene locus 3830-1. Colors indicate transgene sequences that are identical to structural components of pNGI. White boxes indicate unknown sequences that are presumably oat genomic DNA. Black vertical arrows denoted by 'J' indicate junctions between noncontiguous transgene fragments or between transgene and genomic DNA. Red vertical arrows denoted by 'J' indicate the deduced position of junctions between noncontiguous genomic DNA fragments. Black bars above loci represent the regions of extensive scrambling that were PCR-amplified and sequenced from total genomic DNA for the structure verification. Red bars under loci represent regions of genomic DNA that were used as probes for hybridizations. c. The structure of lambda clone 7 isolated from line 3830 and corresponding to one of the minor transgene loci designated as 3830-2. A matrix attachment region is designated as MAR. Colors, bars, and arrows are coded as in b. From (Makarevitch et al., 2003)

4. Management and mitigation of gene flow

(Cavan et al., 2001) studied the case of *Avena fatua* coming up in wheat cultures, and proposed management methods in order to avoid herbicide tolerant wild oat. This paper demonstrates the management problems involved in cultivating transgenic oats, since wild oat is present all over Europe and needs to be taken into account. Consequently, from these management proposals one can learn for cultivation transgenic non-food oats.

A striking feature of the model the authors used is that good weed control is achieved for a number of years, but once this is lost, the resistant population increases very rapidly (Figures 1 and 2). In our model, herbicides act to reduce the seed bank and then maintain populations at 0.02 to 0.07 plants m⁻² (200 to 700 plants ha⁻¹) in the years preceding development of field resistance. In real populations of this density, resistance may be increasing from a low initial frequency for many years before serious infestations are observed. An early warning of resistance evolution could be gained if seed samples from occasional rogued plants are screened. We also can learn that wild oats are very difficult to control as weeds and everything should be avoided to produce wild oat populations with unwelcome transgenes.

(Gonzalezandujar & Fernandezquintanilla, 1993) did similar studies in Spain, and found, that results to fight wild oats were much better without a fallow year inbetween:

A bioeconomic model is described and used to investigate the agronomic and economic consequences of using a range of management strategies for the control of winter wild oats (*Avena sterilis* L.) in cereal cropping systems representative of central Spain. The results of simulations indicated that growing winter wheat continuously with the annual application of herbicides may be the optimum strategy, resulting in acceptable wild oat populations and maximum economic benefits. However, the practice of wheat monoculture was only a valid option as long as herbicides were applied annually: spraying herbicides in alternate years failed to control wild oats adequately and resulted in major economic losses. The rotation of wheat with a fallow year, with no herbicides applied in either of the two years, may be a satisfactory low-cost alternative when wild oat infestation levels are low, but it is not valid when infestation levels are high. The strategy that combines the use of a fallow year with herbicide application in the wheat year resulted in optimum wild oat control and moderate profitability under all conditions. However, the net returns obtained were substantially lower than in the continuous wheat plus herbicide strategy. The sensitivity of the model to variation in various key parameters was tested: wheat yield level and fixed costs were the two parameters that had the largest effect on model output. In general, the effect of changing parameter values was more pronounced in continuous wheat systems than in wheat-fallow rotations

(Murray et al., 1995) documented the fate of another herbicide tolerance in wild oats: Resistance to fenoxaprop-P and other aryloxyphenoxypropionate and cyclohexanedione herbicides in the wild oat population, UM1, is controlled by a single, partially dominant,

nuclear gene, In arriving at this conclusion, parents, F-1 hybrids, and F-2 plants derived from reciprocal crosses between UM1 and a susceptible wild oat line, UM5, were treated with fenoxaprop-P over a wide range of dosages, Based on these experiments, a dosage of 400 g al ha(-1) fenoxaprop-P was selected to discriminate between three response types, At this dosage, susceptible plants were killed and resistant plants were unaffected, whereas plants characterized as intermediate in response were injured but recovered, Treated F-2 plants segregated in a 1:2:1 (R, I, S) ratio, indicative of single nuclear gene inheritance, This was confirmed by selfing F-2 plants and screening several F-3 families, Families derived from intermediate F-2 plants segregated for the three characteristic response types, whereas those derived from resistant F-2 plants were uniformly resistant, Chi-square analysis indicated the F-2 Segregation ratios fit those expected for a single partially dominant nuclear gene system, In addition, F-2 populations from both crosses were screened with a mixture of fenoxaprop-P and sethoxydim, The dosages of both herbicides (150 g al ha(-1) fenoxaprop-P and 100 g ha(-1) sethoxydim) were sufficient to control only susceptible plants. Treated F-2 populations segregated in a 3:1 (R:S) pattern, thereby confirming that resistance to the two chemically unrelated herbicides results from the same gene alteration.

(Page et al., 2006): The spatial and temporal pattern of wild oat emergence in eastern Washington is affected by the steep, rolling hills that dominate this landscape. The objective of this study was to assess the impact of landscape position and crop residue on the emergence phenology of wild oat. Emergence of a natural wild oat infestation was characterized over two growing seasons (2003 and 2004), at two wheat residue levels (0 and 500 g m(-2)), and at five landscape positions differing in slope, aspect, and elevation in a no-till winter wheat field. Wild oat emerged 1 to 2 wk earlier at south-facing landscape positions than at north-facing landscape positions. Crop residue delayed wild oat emergence by 7 to 13 d relative to bare soil at south-facing positions in 2003 and had a reduced effect on emergence at north-facing landscape positions. Therefore, preserving surface residues tended to synchronize emergence across the landscape and may facilitate better timing of weed control where residue is present. Emergence of wild oat was modeled as a function of thermal time adjusted by water potential using a Weibull function. Temperature explained more variation in the model than water potential. This model explained much of the variability in wild oat emergence among landscape positions over these 2 yr and may be useful as a tool to predict the timing of wild oat emergence. Results also indicate that site-specific modeling is a plausible approach to improving prediction of weed seedling emergence.

A study was conducted by (Beckie et al., 2005) at a 64-ha site in western Canada to determine how preventing seed shed from herbicide-resistant wild oat affects patch expansion over a 6-yr period. Seed shed was prevented in two patches and allowed to occur in two patches (nontreated controls). Annual patch expansion was determined by seed bank sampling and mapping. Crop management practices were performed by the grower. Area of treated patches increased by 35% over the 6-yr period, whereas nontreated patches increased by 330%. Patch expansion was attributed mainly to natural seed dispersal (nontreated) or seed movement by equipment at time of seeding (nontreated and treated). Extensive seed shed from plants in nontreated patches before

harvest or control of resistant plants by alternative herbicides minimized seed movement by the combine harvester. Although both treated and nontreated patches were relatively stable over time in this cropping system, preventing seed production and shed in herbicide-resistant wild oat patches can markedly slow the rate of patch expansion.

Final remarks: the problem with transgenic oats to be released in the field is not primarily the outcrossing dynamics, but the fact that the cultivated oats have some really nasty weeds as close relatives, which will be very difficult to control.

Here a bibliography of wild oats scientific literature from the Web of Sciences:

<http://www.botanischergarten.ch/EPOBIO-Avena/Bibliography-wild-oats-20070121.pdf>

Strand Question	Score
CPW <i>Propensity for successful pollen-mediated gene flow between the crop and wild relatives</i>	
CPW1 Do interfertile wild relatives of this crop exist ? (0/1) southern Europe yes, northern Europe no	1
CPW2 Is there a probability that the crop will flower and produce viable pollen during its cultivation? (0/1)	1
CPW3 Upon flowering, is 95% of the crop pollen deposited within 1 m (1), 10 m (2), 50 m (3), 100 m (4), 250 m (5) or 500 m (6)? (1-6)	6
CPW4 If flowering does occur is the wild relative in question rated as an obligate inbreeder (0), a partial inbreeder/outbreeder (1) or an obligate outbreeder (2)? (0-2)	1
CPW5 If fertilization is achieved by the deposited pollen, will a viable F ₁ hybrid individual establish itself? (0/1)	1

Strand Question	Score
CPC <i>Propensity for successful pollen-mediated gene flow between the crop and related commercial varieties</i>	
CPC1 Probability that crop flowers and produce viable pollen during its cultivation? (0/1)	1
CPC2 Upon flowering, is 95% of the crop pollen deposited within 1 m (1), 10 m (2), 50 m (3), 100 m (4), 250 m (5) or 500 m (6)? (1-6)	6
CPC3 If flowering occurs is receptive crop rated as an obligate inbreeder (0), a partial inbreeder/outbreeder (1) or an obligate outbreeder (2)? (0-2)	1
CPC4 If fertilization happens, will a viable F ₁ individual be established itself from hybrid seed in absence of mechanical/chemical control? (0/1)	1

CSV <i>Propensity for successful seed- and tiller mediated gene flow from commercial crop to volunteer</i>	
CSV1 Does the crop produce seed during its cultivation? (0/1)	1

CSV2	Post-harvest, will the seed survive and germinate within the confines of a managed field? (0/1)	1
CSV3	Will the volunteer develop into a viable individual? (0/1)	1
CSF	<i>Propensity for successful seed- and tiller mediated gene flow from commercial crop to feral</i>	
CSF1	Does the crop produce seed during its cultivation? (0/1)	1
CSF2	Following transfer from cultivation site: will wayward seed survive and germinate? (0/1)	1
CSF3	Will the resulting individuals establish into a viable feral population? (0/1)	1
CGC	<i>Consequences of Gene Flow</i>	
CGC1	Does crop mix with related crop traits and jeopardize harvest value ? (0/1)	1
CGC2	Does crop mix with wild relatives or feral traits and pose an biodiversity threat ? (0/1)	1
CGC3	Does crop produce volunteers and/or seed deposits and pose an environmental threat ? (0/1)	1
CMG	<i>Mitigation Gene Flow crop to crop, crop to wild relative and crop to feral</i>	
CMG1	Mitigation with safety distances possible (J/N) 1 m (1), 10 m (2), 50 m (3), 100 m (4), 250 m (5) or 500 m (6)? (J/N) (1-6)	4 (J)
CMG2	Mitigation with molecular safety measures apomixis AP, cytoplasmatic sterility CS, tandem construc TA, gene switching GS AP, TA, GS, (0/1)	AP, CS, TA, GS, 1

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