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Gene flow in forest trees: From empirical estimates to transgenic risk assessment

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ABSTRACT

The extent to which transgene flow from plantations can be effectively predicted, managed, and monitored, will be a critical biological and social factor influencing the adoption of transgenic plantations. Studies of historical and contemporary gene flow levels, via genetic structure surveys and parentage analyses, demonstrate that gene flow is generally extensive in both wind- and animal-pollinated forest tree species. Organelle genome studies have shown that pollen is by far the greatest source of gene dispersal, particularly for tree species with limited seed movement.

Marker studies, however, give little insight into the extent and consequences of gene flow in actual deployment scenarios. For example, despite the potential for extensive gene flow, there appears to be extremely low levels of "genetic pollution" of wild poplar stands by plantations of hybrids. Factors such as dilution by regional seed and pollen clouds, deleterious impacts of genotype backgrounds, engineered sterility genes, and the effects of transgenes on competitiveness in the wild, can greatly influence observed levels. Case-by-case analyses are required for useful predictions.

We introduce a spatial simulation model called STEVE that we have used to estimate the levels of future transgene flow from poplar plantations in the United States Pacific Northwest. It synthesizes data from a variety of ecological and genetic processes, and permits virtual experiments that investigate how diverse genetic, ecological, and management factors might influence the magnitude and variance of gene flow over a 50 to 100 year period. Similar approaches could be used elsewhere to help identify priority research needs, suggest means for mitigation where warranted, and to aid in design of monitoring programs for large-scale research and commercial applications.

INTRODUCTION

Any child who has played outdoors in the temperate zone knows that there is copious pollen production from most species of forest trees. They could probably also tell you, at least if asked, that wind can move pollen considerable distances. Naturalists observing the flights of pollinators have known for centuries that—intermixed with intensive local foraging—most pollinators also engage in long distance flights (Levin and Kerster 1974; Loveless and Hamrick 1984). It is also widely known that for some trees, seeds can move great distances due to wind, water, or animal vectors (Cain et al. 2000; Clark et al. 1998). For example, in western Oregon a "snow" of cottonwood seeds often forms near the rivers in June due to their abundant black cottonwood (*Populus trichocarpa*) populations.

The consequent "genetic unity" of widely dispersed tree populations is therefore no secret and no surprise. However, the magnitude and variation in gene flow is beginning to be well understood, primarily due to extensive molecular marker studies over the last few decades (e.g., Loveless and Hamrick 1984). Most of these studies have employed allozymes, which provide low cost means for studying patterns of genetic differentiation, and by inference, gene flow. However, recent studies, particularly using highly polymorphic DNA markers, have enabled more precise and more direct inferences, particularly of within-population mating patterns and immigration (reviewed below).

Until recently, interest in gene flow was largely restricted to a modest subset of evolutionary and population biologists, and to plant breeders, for whom it was important to interpret patterns of phylogeny, adaptation, and degree of contamination in seed production populations. With the advent of genetic engineering, and the biopolitical and legal controversies it has generated, gene flow has moved onto the public stage (e.g., Ellstrand 2001). "Genetic pollution" due to inadvertent mixing of seeds and pollen flow was the cause of "Tacogate," which caused Star-Link corn to be withdrawn from the market and the responsible company to pay compensatory damages in excess of US $100 million (O'Reilly 2001). The legal and financial repercussions of the case are likely to continue for several years. Likewise, the "genetic pollution" of rural, native stocks of corn in Mexico due to gene flow from genetically engineered corn has caused recent headlines (Quist and Chapela 2001), as have ongoing lawsuits brought by organic farmers due to "contamination" and consequent loss of organic certification as a result of gene flow from nearby genetically engineered crops (Saskatchewan Organic Directorate 2001). Because of the strong sentiments against genetic engineering by some sectors of the public, even small amounts of contamination appear capable of generating great concern (Thompson 2001). Labeling regulations for GMO crops that are under development in many countries appear to be requiring strict limits on the extent of transgene flow and crop mixing. The extent to which we understand, can predict, and can efficiently monitor gene flow may therefore be the most important biological determinant of whether transgenic crops are adopted and publicly accepted.

Because of the extensive gene flow possible from trees, and their very limited history of domestication, it has long been known that genes from intensively bred or engineered trees are highly likely to enter wild populations unless very special measures—such as use of sterile trees—are taken to avoid it (Strauss et al. 1995). In the southern hemisphere, where some of the most intensive plantation forestry in the world occurs, most of the trees grown are exotics, thus greatly reducing concerns over "pollution" of wild populations. However, in many of these places the planted trees have feral, "naturalized" forms, and in some cases these have given rise to invasive weeds that, because of their size, can have substantial impacts on local ecosystems (Richardson 1998). Thus, gene dispersal of exotics may present even more of an ecological hazard than that from native trees—where there is often a large "buffer" provided by wild populations, and where the trees already occupy defined niches (Strauss 1999). Although forestry crops are mostly not consumed as food, trees—even when they are farmed like row crops—tend to be considered symbols of durability and wildness by the public (Thompson 2001). And while it is true that people tend to worry more about the quality of their food than they do about the quality of their paper, it is also true that people are far more passionate about their trees than they are about soybean or broccoli crops. Perceived "genetic adulteration" via gene flow, even at a low level, may thus be a significant impediment to public acceptance of transgenic plantations.

Transgene flow, and means to predict its frequency and consequences, are therefore globally important issues for the future of plantation forestry. Unfortunately, we have a limited

knowledge base for risk assessments. There have been very few studies of gene flow from conventional plantations to wild populations. Due to the long lifespans and generation times of trees, predictions of impacts must consider very large temporal and spatial scales—and thus embrace high levels of uncertainty about future ecological conditions (James et al. 1998). New studies, and new tools, will be needed to make rational inferences about possible impacts of transgenic plantations.

We review in detail what is known about gene flow in forest trees, and then consider landscape simulation methods that might be employed for analyzing, predicting, and monitoring gene flow from tree plantations. As a case study, we focus on a recent analysis we undertook for poplars (genus *Populus*) in the Pacific Northwest United States. We suggest that by the use of simulation models to guide research—and to aid in prediction and monitoring during commercial development—society will be in a better position to make informed choices about the circumstances under which transgenic plantations might be acceptable.

DIRECT TRACKING OF SEED AND POLLEN DISPERSAL

Early studies of gene flow in forest trees focused on the physical dispersal potential of pollen and seeds. As early as 1919, pollen grains of *Pinus sylvestris* had been observed far beyond the range of the species (Lindgren et al. 1995). Later studies confirmed long-distance movements for both pollen and seed (Levin and Kerster 1974). However, tracking of propagules provides estimates of *potential* gene flow; *realized* gene flow also depends on fertilization and establishment success. Factors such as pollen competition, phenological synchrony, and seed predation can result in levels of gene flow far below those predicted by propagule movement alone (Adams 1992). Nonetheless, these studies demonstrated the astonishing mobility of pollen, and to a lesser extent, of light seeds (Di-Giovanni et al. 1996).

MEASURING HISTORICAL LEVELS OF GENE FLOW

The advent of genetic markers revolutionized methods of measuring gene flow. Over the last three decades, rates of migration have typically been inferred from the degree of genetic differentiation among populations as measured by the fixation index F_{ST} (Wright 1931, 1965), or its many extensions and analogs (e.g., G_{ST}, representing the interpopulation component of total gene diversity: Nei 1973). A common approach has been to estimate the fixation index from allele frequency data and then convert this to the mean number of migrants per generation ($N_e m$) using the relationship

$$N_e m \approx \frac{1 - F_{ST}}{4 F_{ST}} \text{ (Wright 1931).}$$

There are many methods for estimating the fixation index, each with strengths and weaknesses (see Cockerham and Weir 1993 and Neigel 1997 for discussion). However, the most common approach in forest trees has been to use allozyme allele frequencies to calculate G_{ST}, and derive $N_e m$ using Crow and Aoki's (1984) correction for the number of populations (or subpopulations) in the sample.

Other approaches for measuring historical gene flow include the "rare allele method" and coalescent methods. The rare allele method is based on the approximately negative linear relationship between the logarithm of $N_e m$ and the average frequency of private alleles in the demes of a genetically subdivided population (Slatkin 1985). The large sample sizes needed for

application of this method and the required availability of rare alleles have limited the use of this approach in tree population studies (see Govindaraju 1989 for comparison of $N_e m$ estimated through F_{ST} and through the rare allele method). Gene coalescence-based methods (reviewed in Neigel 1997) are based on genealogical relationships among alleles. They appear to be superior to other methods when variation within populations exceeds variation among populations (Beerli and Felsenstein 1999). They should therefore be highly suitable to forest trees. However, we are aware of no studies that have applied this method to any forest tree taxa.

All such methods of measuring gene flow are 'indirect', because they apply genetic models (and underlying assumptions) to infer long-term levels of gene flow (Neigel 1997; Sork et al. 1998). For example, the correlation between F_{ST} and $N_e m$ is often unreliable because the assumptions of the underlying population structure models are rarely met in real populations (e.g., equilibrium between genetic drift and migration, negligible selection and mutation, equal contributions of migrants from all populations: Bossart and Prowell 1998; Whitlock and McCauley 1999). Indirect measures reflect the complex interactions of all demographic parameters and evolutionary forces acting on a population, and the resulting gene flow estimates should be taken as long-term averages estimated over a large number of populations (Sork et al 1999).

Despite these shortcomings for estimating contemporary gene flow, indirect approaches have provided a number of valuable insights about historical forces shaping forest tree genetic structure. There have been a large number of studies of allozyme gene diversity, geographic structure, and gene flow among populations of forest trees (reviewed in Govindaraju 1989; El-Kassaby 1991; Hamrick et al. 1992; Müller-Starck et al. 1992; Hamrick and Nason 2000), and a few generalizations have emerged:

1. *Trees are characterized by higher genetic diversity and lower levels of differentiation compared to other plant groups (Hamrick et al. 1992).* The interpopulation component of total gene diversity (based on the fixation index) of woody species rarely exceeds 10-15% (Table 1). This low differentiation suggests extensive gene flow among tree populations. However, some authors have hypothesized that the observed patterns of genetic variation may also be due to the long pre-reproductive phase of most tree species mitigating founder effects, and trees' long generation span retarding differentiation through genetic drift (e.g., Kremer 1994; Austerliz et al. 2000).
2. *Wind-pollinated tree species typically have interpopulation differentiation levels of less than 10%, which translates to more than 2 successfully established migrants per population in each generation.* Hamrick et al. (1992) reported an average interpopulation differentiation of 8% for wind-pollinated trees based on 146 data sets. In species with large and continuous ranges, interpopulation differentiation is often below 3% (e.g., *Pinus sylvestris*, *Picea abies, Quercus petraea, Fagus sylvatica*: Müller-Starck et al. 1992; *Pinus ponderosa, P. contorta*: El-Kassaby 1991; *Quercus chrysolepis*: Montalvo et al. 1997). On the opposite extreme, species with small and fragmented populations can have interpopulation differentiation in the range of 15 to 30%. (e.g., *Pinus cembra, P. halepensis, P. nigra*, *Castanea sativa*: Müller-Starck et al. 1992; *Pinus torreyana, P. muricata*: Hamrick et al. 1992). This observation suggests that even though long-distance pollen dispersal is possible, its effect may be insufficient for genetic homogenization of spatially isolated populations.
3. *Outcrossed animal-pollinated tree species have a detectably (but not significantly) higher degree of interpopulation genetic differentiation compared to wind-pollinated trees.* The

average interpopulation differentiation for animal-pollinated trees with mixed mating systems was 10% based on 37 data sets (Hamrick et al. 1992). As in wind-pollinated species, spatial distribution seemed to be a good predictor of the degree of differentiation. Moran (1992) reviewed interpopulation differentiation in Australian eucalypts and cited values in the range of 8 to 12% for widespread species (e.g., *Eucalyptus saligna*, *E. cloeziana*, *E. delegatensis*); 30% for the highly disjunct *E. nitens* (widespread, but with a highly discontinuous distribution); and 61% for isolated populations of *E. caesia*. However, 67 scattered and putatively isolated low-density populations of the insect-pollinated, and presumably bird-dispersed, *Sorbus torminalis* had interpopulation differentiation of only 15% (Demesure et al. 2000), suggesting that gene flow rates can in some cases be high among spatially isolated populations (but see Austerlitz et al. 2000).

DIRECT METHODS OF MEASURING GENE FLOW THROUGH PARENTAGE ANALYSIS

Direct observations of gene dispersal obviate the need for tenuous assumptions about historical conditions. Instead, they provide short-term "immigration snapshots." Generally, direct methods require the genotyping of all potential parents in a population and estimation of the proportion of progeny that could *not* have been produced by within-population mating. One approach employs simple paternity exclusion, feasible where the maternal genotype can be readily determined (Smith and Adams 1983; Devlin and Ellstrand 1990). However, the low variability of allozyme markers greatly limits the ability to distinguish between local and immigrant genotypes (Adams 1992). To help overcome this problem, a number of methods employ maximum likelihood to either assign parentage (Meagher 1986; Adams et al. 1992; Smouse and Meagher 1994; Kaufman et al. 1998), or to estimate mating parameters that provide the best fit to observed progeny genotypes (Devlin et al. 1988; Roeder et al. 1989; Adams and Birkes 1991).

In the early 1990s, highly variable DNA-based markers began to become affordable for parentage analyses. The high genetic resolution provided by microsatellite and AFLP data allowed scientists to conduct paternity analyses based on genotypic exclusion with acceptable levels of discrimination (Dow and Ashley 1998; Streiff et al. 1999; Lian et al. 2001), as well as to apply maximum likelihood assignments with higher confidence (Gerber et al. 2000; Kameyama et al. 2000).

Seed orchards. There have been a number of studies of genetic contamination of forestry "seed orchards." Seed orchards are plantations in which selected genotypes are placed to allow cross-pollination for production of seeds to be used for reforestation. Most of these orchards are within the range of native or planted populations, and distinct orchard blocks (that service distinct ecogeographic regions) are in many cases planted in proximity for management efficiency. Thus, there are often high levels of unwanted pollen immigration into the orchard blocks. This can result in substantial loss of genetic gain compared to expectations based on selection theory, and can compromise adaptation of seed orchard crops to their intended plantation environments (Adams and Burczyk 2000).

The tracking of rare allozyme alleles has been used to measure orchard contamination (Friedman and Adams 1982), and to study mating patterns within seed orchards (Prat 1995). However, such alleles are often difficult to identify, and force inferences to be based on a very limited number of genotypes. Instead, pollen contamination of seed orchards is usually estimated via simple paternity exclusion, adjusting the observed proportion of immigrants by the probability that an immigrant gamete will be distinguishable from the potential orchard

gamete pool (Adams and Burczyk 2000). Other statistical procedures have also been implemented (El-Kassaby and Ritland 1986; Plomion et al. 2001). These studies have revealed great variation in pollen contamination, even when the same analytical approaches and tree species are considered (Table 2; Adams and Burczyk 2000). Nonetheless, it is clear that pollen contamination is often very large, commonly exceeding 40%, even when the closest stands of the same species are several hundred meters away.

Less is known about pollen contamination in seed orchards of animal-pollinated tree species such as eucalypts compared to that of the wind-pollinated conifers. However, these studies also suggest that contamination can be considerable, implying that pollinators can travel long distances from outside orchards (Campinhos et al. 1998; Junghans et al. 1998)—as well as move pollen extensively within orchards (Burczyk, unpublished data).

Commercial plantations. We know of very few studies of the effects of gene flow from forest plantations on wild populations. The best-studied cases are from interspecific hybrids in the genus *Populus*, which are often planted in proximity to wild populations. In Europe, most of the planted cottonwood hybrids include the native *Populus nigra* as a parent. These hybrids are interfertile with wild populations of *Populus nigra*, whose populations are greatly reduced in extent due to destruction of riparian habitat by farming and human habitations. Nonetheless, several studies have reported extremely low levels of gene flow to wild *P. nigra* stands (Benetka *et* al. 1999; Legionnet and Lefevre 1996). Likewise, in the Pacific Northwest United States gene flow from hybrid poplar plantations into wild black cottonwood populations was extremely low, despite the presence of large male plantations in close proximity to native female trees (DiFazio 2002).

Wild populations. Due to restrictions on marker resolution and the high cost of genotyping, spatially distinct forest stands are usually chosen for study, and parentage analysis then applied to a sample of progeny. Typically, seeds are collected from mother trees of known genotype, and paternity estimated by comparing inferred paternal genotypes with those of all potential fathers in the analyzed population (Schnabel and Hamrick 1995; Kaufman et al. 1998; Dow and Ashley 1998; Streiff et al. 1999; Schuster and Mitton 2000). Some researchers have also sampled seedlings and/or saplings, attempting to estimate both pollen- and seed-mediated gene flow (Dow and Ashley 1996; Isagi et al 2000; Konuma et al. 2000). However, such analyses require considerably more exclusion power than paternity analysis (Marshall et al. 1998).

Results from paternity analyses in wind-pollinated species generally agree with predictions from studies of genetic structure (Table 3). In most cases, the frequency of immigrant pollinations was over 30% (e.g., 31% in *Pinus densiflora*, Lian et al. 2001; 57% in *Quercus macrocarpa*, Dow and Ashley 1998; 65% in *Q. robur* and 69% in *Q. petraea,* Streiff et al. 1999), but appeared rather low (6.5%) in a spatially isolated population of *Pinus flexilis* (Schuster and Mitton 2000). Remarkably, Kaufman et al. (1998) reported extensive pollen-mediated gene flow (a minimum of 37%) in a population of the tropical pioneer *Cecropia obtusifolia*, even though the closest population of the same species was at least 1 km away. Kaufman et al. (1998) suggested that successful pollen traveled as far as 10 km. Similarly, Leonardi, et al. (unpublished) observed extensive pollen immigration into stands of *Populus trichocarpa* that were isolated by up to 16 km from the nearest ungenotyped pollen source (Table 4).

As with indirect methods, gene flow estimates based on parentage analysis in animal-pollinated tree species were somewhat lower, but generally similar to immigration rates in wind-pollinated trees (e.g., 17 to 30% in *Gleditsia triacanthos*, Schnabel and Hamrick 1995; 20 to 30% in *Rhododendron metternichii,* Kameyama et al. 2000; 74% in *Magnolia obovata*, Isagi et

al. 2000; and 21 to 69% in *Neobalanocarpus heimii*, Konuma et al. 2000). These results support the notion that animals can be effective agents of long-distance pollen and seed dispersal. However, there is also considerable variance in pollen immigration between species, even when isolation distances are similar (Stacy et al. 1996), cautioning against broad generalizations.

Although paternity analysis based on highly variable markers appears to be the most effective current method for measuring gene dispersal in ecological time, estimates can be greatly affected by the presence of null alleles, and the misgenotyping of complex microsatellite and AFLP phenotypes. Both of these types of errors will cause overestimates of gene flow (Marshall et al. 1998). Despite high reported exclusion probabilities, it is therefore important to treat many of the published estimates with caution; their accuracy will improve over the next several years as applications of molecular technology for gene flow studies mature.

THE PROMISE OF ORGANELLE DNA MARKERS

One of the limitations of parentage analysis using nuclear loci is that it is often difficult to distinguish the contributions from the different agents of gene flow. The predominant uniparental inheritance of organelle DNA (Corriveau and Coleman 1988; Birky 1995), however, provides a means to differentiate pollen- from seed-mediated migration. Chloroplasts are inherited maternally in most angiosperms, and paternally inherited in most gymnosperms. Plant mitochondria are generally passed on maternally, except for some gymnosperms (see Wagner 1992 for a review of organelle genome inheritance in trees). The high amounts of length variability detected in some regions of the chloroplast genome (reviewed in Provan et al. 2001) facilitate its use for gene flow studies. Chloroplast microsatellites can increase efficiency of paternity analysis (Ziegenhagen et al. 1998), and aid the estimation of pollen contamination in conifer seed orchards (Stoehr et al. 1998, Plomion et al. 2001).

Applied in combination with nuclear loci, plastid DNA markers are also valuable for inferring historical levels of gene flow. For example, Ennos (1994) compared F_{ST} values calculated over nuclear and organelle DNA markers and concluded that pollen-mediated gene flow in wind-pollinated species may exceed seed-mediated gene flow by a factor of 18 to 68 (in the light-seeded pines), and up to 196-fold in the acorn-bearing oaks. Similar studies have been conducted in other tree species (El Mousadik and Petit 1996; Latta et al. 1998; Oddou-Muratorio et al. 2001). Analysis of the spatial structure of cpDNA enabled estimates of postglacial seed dispersal rates, and recolonization routes, of European oaks (Petit et al. 1997). However, because of the lack of independence of polymorphic loci in organelle genomes, differences in mutation rates among genomes, and difficulties in assuming homology among repeat "alleles," organelle-based inferences should be treated cautiously (cf. Hong et al. 1993; Strauss et al. 1993).

SPATIAL SIMULATION MODELING

Extrapolation of short-term or historical gene flow observations to spatial and temporal scales that are relevant for management and ecological policy remains a major challenge (Levin 1992; Turner et al. 2001). Because of the time and expense required for a typical parentage analysis study, only a limited number of populations and years can be examined (Ouborg et al. 1999; Cain et al. 2000). However, ecologically significant levels of establishment may occur only once or twice per generation (i.e., on a decadal scale) (James et al. 1998), and in particular habitats. An emerging solution is the use of spatial simulation models to extrapolate

results of short-term gene flow studies with knowledge of ecological processes (Dunning et al. 1995; King 1991). They provide an extensible framework for integrating data from disparate demographic and genetic field studies with landscape-scale analyses of ecosystem dynamics (Sork et al. 1998; Higgins et al. 2000). In addition, such models allow 'virtual experiments' through sensitivity analyses in which selected components of the system are manipulated to determine their importance in determining long-term outcomes (Turner et al. 2001).

CASE STUDY: GENE FLOW IN POPLAR

We analyzed gene flow in wild black cottonwood populations, and from hybrid poplar plantations, in the northwestern United States. The primary objective of these studies was to provide data for assessing the extent of transgene dispersal that is likely to occur should transgenic hybrid poplars be cultivated in the region. We studied gene flow using parentage analysis in three wild populations with contrasting ecological characteristics (Leonardi et al., unpublished), and gathered data on seedling establishment and survival in experimental plots and in the wild (DiFazio et al. 1999). We also inferred landscape-level spatial and temporal dynamics of black cottonwood establishment from a chronosequence of GIS layers encompassing some of the same populations included in the field studies (Figure 1).

The model, called STEVE (Simulation of Transgene Effects in a Variable Environment—but also named to reflect that four Steves contributed to its development!), provides a spatially explicit representation of gene flow (DiFazio 2002; Figure 2). It operates on a landscape grid (23 km x 37 km, 100 m^2 cells) containing information about elevation, habitat type, and poplar populations. The simulation has an annual time step, with modules to simulate creation and conversion of poplar patches, growth, reproduction, dispersal, and competition within poplar cohorts. The simulations track two genotypes, transgenic and conventional. Transgenic trees originate in plantations and may spread to the wild through pollen, seed, and/or vegetative propagules. The relative amounts of propagules produced in each location are proportional to basal area (i.e., trunk cross-sectional area) of each genotype, modulated by a fecundity factor.

We structured and parameterized the model based on results of our field studies of gene flow. They indicated that long-distance dispersal is considerable for *Populus* (Table 4; Leonardi et al., unpublished), with the tail of the distribution quite 'fat' (*sensu* Kot et al. 1996). We therefore chose to model gene dispersal as a two-stage process, with local dispersal modeled explicitly by a negative exponential distribution, and long-distance dispersal modeled as if a portion of the pollen and seeds were panmictic at the landscape scale. This is analogous to a mixed model approach (Clark et al. 1996). The biological basis for this approach is that locally dispersed pollen and seed is subject to local air flows and eddies, and follows predictable patterns of dispersal in which probability of deposition declines exponentially with distance from the source (e.g., Di-Giovanni et al. 1996). However, a portion of the pollen can be caught in updrafts and escape from local air flows, potentially traveling great distances (e.g., Lanner 1965). Seed dispersal was modeled in the same way, though based on more limited field studies of movement, and assumed much less local and long-distance movement than for pollen. *Populus* seeds are very light and contain cotton appendages that facilitate wind and water dispersal; therefore, a portion of the seeds is expected to attain stochastic long-distance dispersal (Wright 1952).

This method of modeling pollen and seed dispersal had major implications for gene flow from transgenic plantations. Modeled gene flow was highly sensitive to changes in the proportion of pollen and seed dispersed long-distances (Figures 3A and B), but relatively insensitive to the slope of local dispersal curves (Figures 3C and D). This was primarily because

poplars require very intense disturbance, abundant moisture, and freedom from most competition by other plants for successful establishment. These conditions are rarely met in space and time. The majority of establishment sites therefore occurred beyond the local seed and pollen shadows of the plantations (Figure 3E). Also, because long-distance dispersal was insensitive to wind in this model (pollen and seed were assumed to be panmictic at the landscape scale), wind speed had no detectable effect on gene flow from plantations (Figure 3F). Long-distance dispersal ensured that a proportion of plantation-derived propagules would encounter stochastic establishment sites regardless of distance from plantations, which explains why this portion of the dispersal function was overwhelmingly important in determining gene flow. One implication of this result is that future research on gene flow in *Populus* would benefit most from better definition of the dynamics of long-distance dispersal, rather from studies of local pollen movement and mating between trees within stands.

Sensitivity analyses allowed us to study the consequences for gene flow of many ecological conditions and transgenic deployment scenarios over a 50 to 100 year time frame. For example, we studied (DiFazio 2002) the consequences of:

1. Transgenes that imparted herbicide resistance with respect to various scenarios of herbicide use and disturbance on the landscape
2. Transgenic trees with insect resistance, with varying levels of insect attack in wild populations
3. Reductions in fertility due to transgenic or other sources, and implications of various levels of efficiency and stability
4. The effects of transgenes with positive or negative effects under natural selection
5. Effects of transgenic vs. non-transgenic plantation area, plantation gender, and rotation length (time to harvest)

Most of these simulations also included stochastic variation, so that natural environmental variances, and uncertainty in parameter estimates, could be reflected in model outputs. Ideally, the model structure and parameters would be continually revised based on research results, and by results of monitoring programs during commercial deployment. The most important contribution of spatial simulation models such as STEVE is that they provide a comprehensive, explicit logical framework for thinking about the long-term consequences of different options for deploying transgenic, as well as conventionally bred, plants. It therefore helps to reduce the immense ecological complexity of tree gene flow to a set of specific, testable predictions that can guide further research, and inform business plans, regulatory decisions, and ultimately public views about transgenic technology in plantation forestry.

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Table 1. Neighborhood sizes and per-generation migration events estimated by two indirect methods for some tree genera.

Genus	G_{ST}	N_em	N_em*	N_a
Abies	0.063	3.72	8.71	260
Picea	0.055	4.30	-	133-260
Pseudotsuga	0.074	3.13	-	-
Pinus	0.065	3.60	1.51-21.83	158-534
Quercus	0.107	2.09	2.24-6.74	-
Populus	0.041	5.85	-	-
Eucalyptus	0.169	1.23	0.76-6.51	-

G_{ST} - averages from Hamrick et al. (1992)
N_em - estimated based on the G_{ST} values
N_em*- estimated for some species using the method of Slatkin (1985); from Govindaraju (1989)
N_a - neighborhood area in m² (area from which the parents of some central individual may be treated as randomly drawn) estimated for some species; from Govindaraju (1988)

Table 2. Estimated pollen contamination in clonal seed orchards of forest trees.

Tree species	S	Di	b	m
Picea abies	13.2	none	-	0.55-0.81 [1]
		-	0.10-0.17	
Picea glauca	-	1000	-	0.01
Pseudotsuga menziesii	1.8-3.3	none	-	0.29-0.91
	20	500	-	0.11
Pinus sylvestris	22.9	2000	-	0.48
	3	1000	0.15	-
	6	500	0.38	-
	12.5	>100	-	0.72
Pinus taeda	2	100	-	0.36
Pinus maritima	-	none	0.36 [2]	-
Eucalyptus grandis x *E. urophylla*	7.4	400	0.14 [3]	-
	8	800	0.03 [4]	-

S - area in which all potential parents have been genotyped (ha)

D_i - distance to the nearest population or tree of the same species (m)

b - observed proportion of immigrant pollen gametes

m - pollen contamination adjusted for the probability to distinguish local and migrant gametes

References from Adams and Burczyk 2000, unless otherwise indicated:

[1] Pakkanen et al. 2000

[2] Plomion et al. 2001

[3] Campinhos et al. 1998

[4] Junghans et al. 1998

Table 3. Mean pollination distance and gene flow estimates from parentage analyses in wind- and animal-pollinated trees.

Tree species	S	D_i	d_{wp}	d_{op}	m	Reference
A. Wind-pollinated						
Pinus flexilis	-	>2000	133-140	155-265	0.07	Schuster and Mitton 2000
Pinus densiflora	9.1	N/A	68	-	0.31	Lian et al. 2001
Quercus macrocarpa	5	>100	75	-	0.57	Dow and Ashley 1998
Quercus robur	5.8	>100	22-58	333	0.65	Streiff et al. 1999
Quercus petraea	5.8	>100	18-65	287	0.69	Streiff et al. 1999
Cecropia obtusifolia	8.6	>1000	-	-	0.37	Kaufman et al. 1998
B. Animal-pollinated						
Gleditsia triacanthos	3	>85	-	-	0.17-0.30	Schnabel and Hamrick 1995
Ficus (from 3 diff. species)	-	>1000	-	-	>0.90	from Hamrick and Nason 2000
Rhododendron metternichii	1	>50	-	-	0.20-0.30	Kameyama et al. 2000
Magnolia obovata	69	N/A	131	-	0.74*	Isagi et al. 2000
Neobalanocarpus heimii	42	None	188-196	-	0.21-0.69*	Konuma et al. 2000

S - area in which all potential parents have been genotyped (ha)
D_i - distance to the nearest population of the same species (m)
d_{wp} - average pollination distance within the reference stand (m)
d_{op} - mean pollination distance from assumed dispersal curve (m)
m - proportion of offspring with immigrant paternal gametes
* Offspring having one or both parents located outside the reference stand

Table 4. Population and gene flow statistics from three microsatellite-based studies of pollen dispersal in Oregon, USA (Leonardi, et al., unpublished).

Site	r[1]	Mothers[2]	Fathers[3]	N[4]	D_i *	d_{wp} *	d_{op}*	P[5]	M[6]	G[7]
Willamette	0.25	5	221	235	100-300	138	809	103	32	43
Luckiamute	1	5	57	423	1000-1100	128	-	98	5	76
Vinson	10	28	54	849	2680-9760	1093	4157	355	29	58

[1] Radius of sampled area (km)
[2] Number of trees from which seeds were collected
[3] Number of reproductively mature male trees within sampled area
[4] Number of progeny genotyped
[5] Number of seeds for which a single putative father was compatible within the sampled area
[6] Number of seeds for which multiple putative fathers were compatible within the sampled area.
[7] Percentage of seeds for which no compatible fathers were identified within the sampled area
*Defined in Table 3

Figure 1. GIS representation of modeled area in northwestern Oregon (37 km x 23 km: 845 km^2). White shows main channels of the Columbia River, black, areas of hybrid cottonwood plantations, dark grey, wild black cottonwood stands, and light grey is non-poplar land (mostly farms, coniferous uplands, and wetlands; DiFazio et al. 2002).

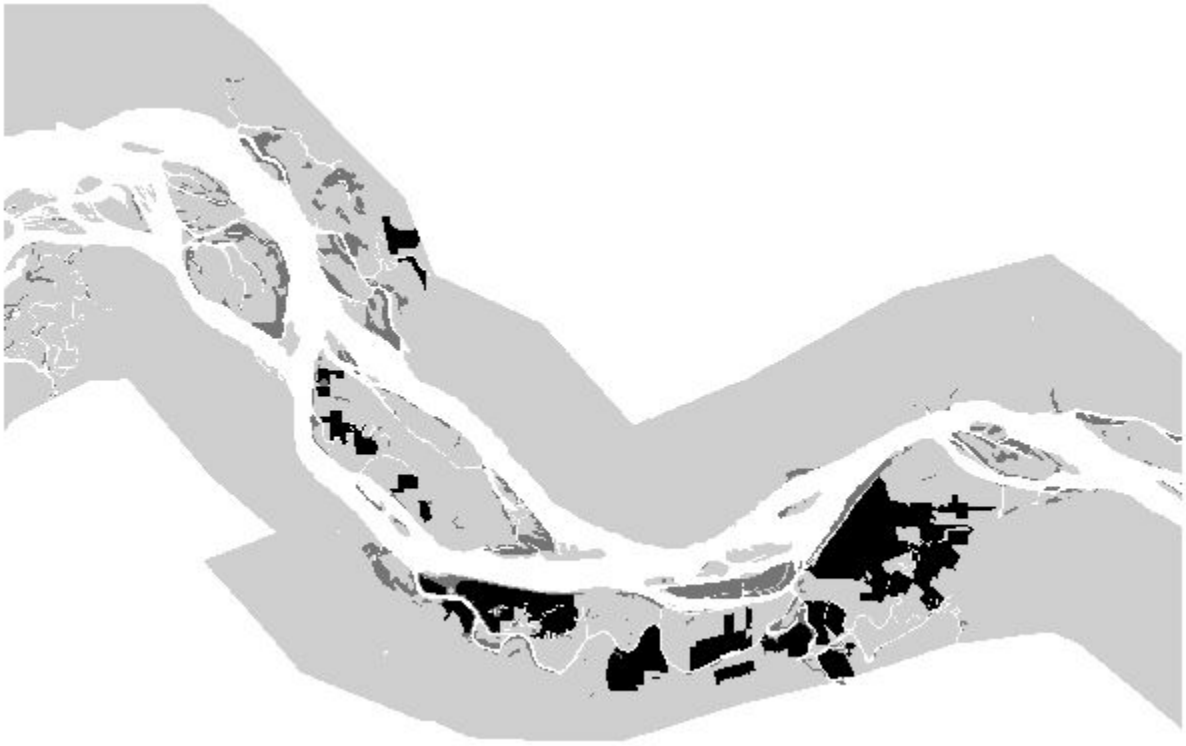

Figure 2. The STEVE model. Model begins with preprocessing of GIS layers representing initial simulation conditions. Data are stored in a spatial database containing information about elevation, cover type, poplar populations, plantations, and agricultural fields. Simulation begins with management activities such as plantation harvesting and herbicide spraying. Poplar establishment and mortality is simulated in the disturbance function. Seed, pollen, and vegetative propagules are produced proportional to basal area of each genotype, followed by dispersal, establishment, growth and mortality. Outputs are text files and spatial data layers**.**

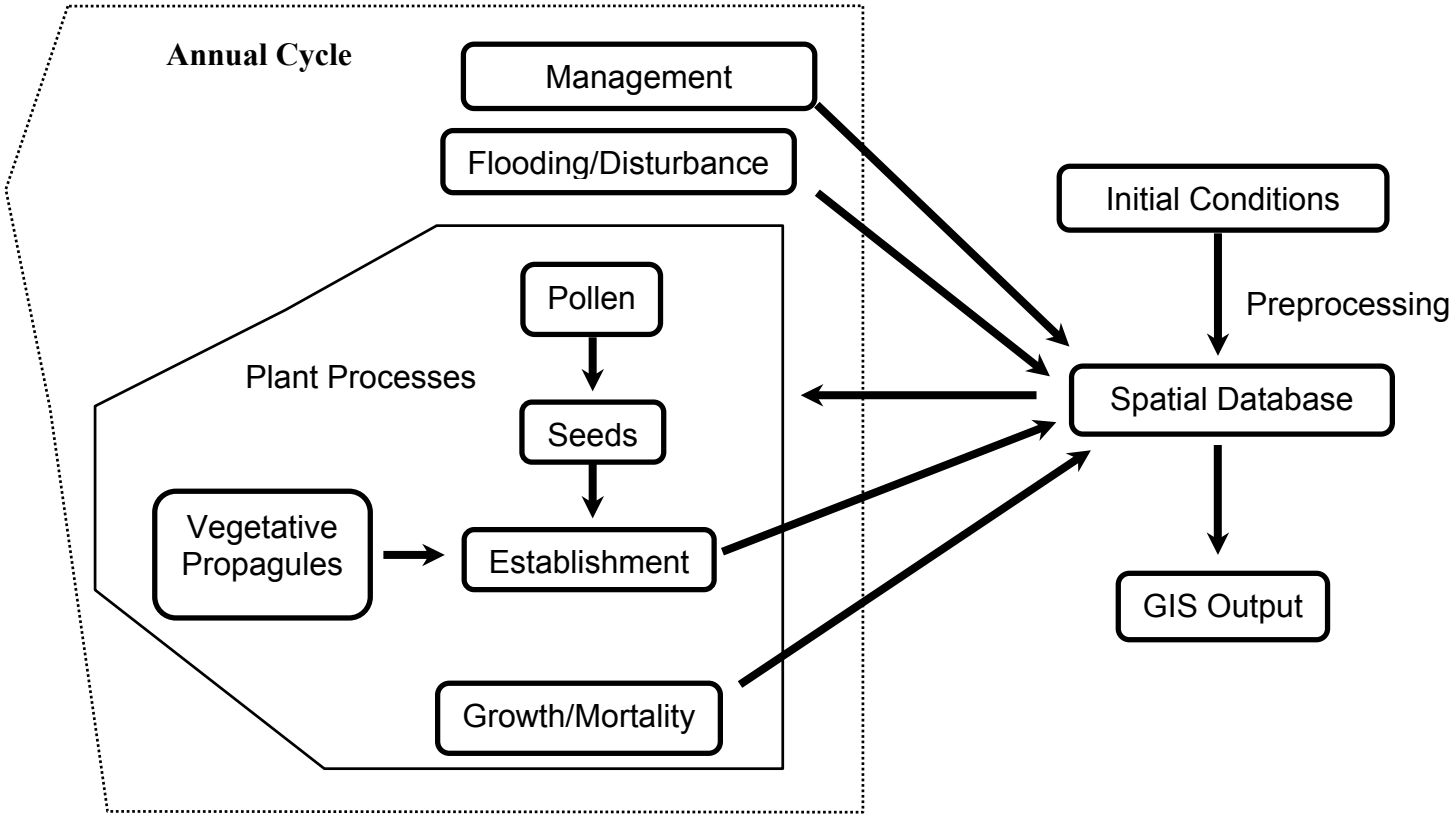

Figure 3. Effects of dispersal and wind on simulated gene flow. Error bars are 1 standard error from 10 repetitions with each set of parameter values.
A. Effects of distant pollination on transgene flow. Distant pollination is the proportion of seeds that are fathered by trees that do not occur in the local population. This parameter has a strong effect on transgene flow, reflecting the importance of long distance pollen dispersal.
B. Effects of distant seed establishment on transgene flow. Distant seed establishment had minor effects except at very low levels.
C and **D.** Effects of varying the slope of the negative exponential distributions depicting local pollen and seed dispersal, respectively. Varying this slope had little effect on gene flow.
E. Effect of relative wind speed, with wind direction set at 90 degrees.
F. Distance of transgenic cohorts from mature transgenic plantations. The local pollen and seed shadows end at 440 m and 220 m respectively.