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Biological Aspects of Hybrid Poplar Cultivation on Floodplains in Western North America:

A Review

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Preface

Cottonwoods—both native and hybrid—are receiving a great deal of ecological and economic attention these days. Historically, native cottonwoods were a vital component of most lowland floodplains and associated riparian ecosystems, particularly in the western United States. Unfortunately, those trees have been largely eliminated, leading to widespread stream degradation. Now, however, increasing pressures for stream restoration are inevitably leading to demands to restore cottonwoods to these critical riparian and floodplain environments.

Today, hybrids derived from those native cottonwoods—referred to as "hybrid poplars"—are being widely introduced into those same floodplain habitats. Timber and agricultural interests are planting large acreages of hybrid poplars for pulp and wood products. Environmental agencies are using these hybrids to cost-effectively treat a variety of contaminated soils and wastewaters. And natural resource agencies, struggling to restore critical salmon and riparian habitats, are replanting stream banks with both native cottonwoods and hybrid poplars.

To some, these hybrids represent an opportunity to cost-effectively improve many degraded floodplain and riparian habitats. For example, they argue that farmers could plant these fast growing, flood tolerant tree crops just outside of critical riparian areas, thus protecting those sensitive areas from damaging tillage and grazing impacts, while also intercepting and neutralizing runoff of nutrients and farm chemicals.

Others, however, fear that such uses of hybrids near riparian areas could genetically contaminate native cottonwoods, or could pose other ecological threats. And a few even oppose the re-introduction of native cottonwoods into riparian ecosystems, citing fears of water depletion.

Unfortunately, the knowledge needed to help the various parties resolve such conflicts is fragmented among many scientific disciplines. But clearly, one of the greatest needs is for all parties to have a better understanding of the basic biology and ecological role of cottonwoods, with particular emphasis on the relative biological distinctions between native cottonwoods and hybrid poplars.

To meet this need, the U.S. Environmental Protection Agency asked Dr. Jeffrey Braatne to compile the existing scientific knowledge on selected issues that have arisen most frequently. This is his report, admirably done on a very limited budget. And to assist those interested in investigating specific issues in greater depth, Dr. Braatne has also included an extensive bibliography.

In reviewing this report, please keep in mind that few studies have been specifically designed to address many of these environmental issues. Thus findings in this report necessarily reflect the synthesis of relevant studies conducted by diverse disciplines. However, several long-term studies are now underway that will provide additional information on several key issues. In addition, Dr. Braatne has also included his recommendations for future research needs.

Thank you

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Abstract

Fast-growing hybrid poplars--the product of selective breeding of native cottonwoods-- are being widely planted to supplement the diminishing supply of natural hardwoods. As effective biofilters, these trees are also being increasingly used to treat agricultural runoff and municipal wastewaters. Given such uses, the cultivation of hybrid poplars in floodplain habitats is expected to increase in the coming years. This report discusses the major biological distinctions between hybrid poplars and native cottonwoods, and explores some of the potential management issues associated with their cultivation near riparian corridors.

The biological differences between hybrid poplars and native cottonwoods are subtle, with varying levels of ecological significance. Such differences arise in the following areas: a) genetic and reproductive properties, b) growth and water-use characteristics, and c) wildlife habitat values. Much of our current knowledge of these factors is derived from comparative studies of parental (native cottonwoods) and hybrid genotypes (F_1, F_2, and backcrosses). Only a limited number of studies have compared the ecological properties of commercial poplar plantations with native habitats, hence the potential outcome of ecological interactions must often be inferred.

Over the years, widespread planting of non-native poplars in the West has had a limited effect upon the genetics and ecology of native riparian cottonwoods. Restricted levels of gene exchange are related to phenological incompatibilities and the reduced pollen and seed viability of hybrid crosses. Although hybrid poplars are noted for rapid growth, their potential impact on groundwater and streamflows is comparable to slightly lower than other agricultural crops. Hybrids are more drought tolerant than native cottonwoods, yet potentially more vulnerable to flooding. These physiological differences may favor hybrids in some riparian settings. Since commercial plantations are not designed to serve as wildlife habitat, lower habitat values relative to native riparian zones are expected. However, their habitat values are greater than traditional row and pasture crops.

Given our current knowledge, numerous research and management opportunities exist for reducing gene exchange and improving the habitat properties of hybrid poplar plantations. Future research needs to focus upon these opportunities, while also promoting the conservation and study of native riparian cottonwood ecosystems.

Keywords

biofilter, cottonwood, ecosystem, floodplain, genetic contamination, habitat, hybridization, hybrid poplar, populus, riparian corridor, transpiration, tree crop, water use.

Contents

I. Introduction ..... Page 1
II. Native poplars and natural zones of hybridization ..... Page 2
III. Domesticated non-native and hybrid poplars ..... Page 5
IV. Reproductive properties of native cottonwoods and hybrid poplars ..... Page 7
V. Natural patterns of seedling recruitment in riparian corridors ..... Page 8
VI. Water-use by hybrid poplars and other agricultural crops ..... Page 9
VII. Drought and flood-tolerance of hybrid poplars and native cottonwoods ..... Page 11
VIII. Clearing of floodplain habitats as a means of conserving water ..... Page 11
IX. Wildlife habitat studies ..... Page 12
X. Conclusions, Recommendations and Reasearch Needs ..... Page 13
XI. Literature cited ..... Page 15

Appendix A: About the Author ..... Page 23
Appendix B: Bibliography on the Biological Aspects of *Populus* Spp. and Ecology of the Riparian Landscapes of Western North America ..... Page 25

Figures and Tables

Table 1, Native *Populus* Species in North America ..... Page 2
Table 2, Reproductive characteristics of diploid and triploid F_1 hybrid poplars ..... Page 8
Table 3, Estimated water use by agricultural crops and hybrid poplars in Eastern Washington ..... Page 10
Figure 1, Distributional range of native riparian cottonwoods in North America ..... Page 3
Figure 2, Black Cottonwood Page2
Figure 3, Eastern Cottonwood ..... Page 4
Figure 4, Natural hybrids of *P. fremontii x P. angustifolia* ..... Page 4
Figure 5, F_1 hybrids and advanced generations ..... Page 4
Figure 6, Lombardy Poplar ..... Page 5
Figure 7, White Poplar ..... Page 5
Figure 8, Common leaf forms ..... Page 6
Figure 9, Harvest of seven-year old hybrid poplars ..... Page 6
Figures 10, Poplars are dioecious ..... Page 7
Figure 11, Cottonwood seedlings ..... Page 8
Figure 12, Physiological studies of ttomatal conductance and photosynthesis ..... Page 9
Figure 13, The upper canopy of a four-year old stand of hybrid poplar in Eastern Washington ..... Page 10
Figure 14, Irrigated cornfields in Eastern Washington ..... Page 10
Figure 15, Seasonal flooding of a natural hybrid zone ..... Page 11
Figure 16, The understory of a five-year old stand of hybrid poplar ..... Page 12
Figure 17, Deer and other cosmopolitan wildlife species commonly use hybrid poplar stands ..... Page 13
Figure 18, Riparian hybrid poplar buffers at Carnation Farms ..... Page 14

I. Introduction

Hybrid poplars are the product of the selective breeding of native cottonwoods (*Populus* spp.). Their rapid growth and capacity to supply a broad range of wood products has led to their widespread cultivation in North America (Dickmann and Stuart 1983, Stettler et al. 1996a). In the West, hybrid poplars are a relatively recent agricultural commodity, and only a small proportion of arable lands has been converted from traditional crops, such as corn, hay or pasture, to commercial poplar plantations (Heilman et al. 1995, Stettler et al. 1996a). These conversions are largely driven by dwindling supplies of natural hardwood fiber (Heilman et al. 1995, Sedjo 1997) and by the impressive yields of hybrid poplar when grown under short-rotation intensive culture (Stettler et al. 1988, Heilman and Xie 1993, 1994). Hybrid poplars are thus becoming a new source of wood and fiber for the pulp and paper industry, and thereby an alternative cash crop for many farmers and ranchers.

In addition to their commercial value, hybrid poplars are effective in the control of nutrients and toxic compounds found in agricultural runoff and landfill effluents (Haycock and Pinay 1993, Licht 1991, 1993, 1994, Licht and Madison 1995, O'Neill and Gordon 1994, Schultz et al. 1994, 1995, Schnoor et al. 1995, Burken and Schnoor 1997, Chappell 1997, Gordon et al. 1997, Schnoor 1997). For example, a simple four-row buffer of hybrid poplar can reduce nitrates by over 90% and significantly lower pesticide concentrations in agricultural runoff (Licht 1994, Burken and Schnoor 1997). Accordingly, hybrid poplar is being promoted within the agricultural community as a means of improving water quality. New field trials are currently underway in several areas to further assess their efficacy in the treatment of agricultural runoff. As a result of these and other research activities, hybrid poplars may prove to be an economically-attractive approach to the treatment of "non-point" agricultural pollutants (Licht 1994, Sedjo 1997).

Given their emergence as an agricultural commodity and biofilter, the cultivation of hybrid poplars in floodplain habitats is expected to increase significantly. As a result, resource managers and landowners need to have a better understanding of the biology of these trees. On the basis of current research and published findings, this report discusses the major biological distinctions between hybrid poplars and native cottonwoods, and explores some of the potential management issues associated with their cultivation in riparian corridors. The topics addressed include: a) genetic and reproductive properties, b) growth and water-use characteristics, and c) wildlife habitat values. Much of this research is derived from comparative studies of parents (native cottonwoods) and their offspring (F_1, F_2 hybrids), as only a limited number of studies are available from which the ecological properties of native habitats could be compared with commercial plantations. This report highlights research needs and initiates a framework for evaluating the potential role of hybrid poplars in sustaining the natural functions of riparian corridors impacted by agricultural activity.

Those interested in a broader review of the scientific literature should consult a recently published book entitled, "The Biology of *Populus*: implications for management and conservation" (Stettler et al. 1996a). An extensive body of literature is cited directly within this report and an updated bibliography is also provided in Appendix B. A general familiarity with these sources of peer-reviewed literature is critical to understanding the biology of hybrid poplars and the ecology of native riparian forests.

II. Native poplars and natural zones of hybridization

Populus is a large and widespread genus of dioecious woody plants (30 species worldwide), commonly found in temperate regions of the world. In North America, there are eight native species of *Populus* (Table 1, Figure 1), with numerous zones of natural hybridization (Eckenwalder 1977a,b, 1984a,b, c, 1996, Pregitzer and Barnes 1980). Most of these native poplars are riparian cottonwoods (Figures 2 and 3), though two species of aspen are also common in some regions of the continent (Table 1).

The life cycle of native cottonwoods closely follows the seasonal dynamics of streams and rivers, and they are common members of floodplain forest communities (Johnson 1994, Braatne et al. 1996, Scott et al. 1997). Many studies have documented the critical role of cottonwoods and willows in maintaining the integrity of river channels (Beeson and Doyle 1995, Scott et al. 1996) and riparian ecosystems (Stromberg et al. 1991, 1996, Johnson 1994, Rood and Mahoney 1990, Rood et al. 1995, Scott et al. 1996). Cottonwoods and willows growing along river channels and backwaters act to trap sediment and debris and serve as a barrier to the scour and erosion of riverbanks. Native cottonwoods provide critical habitat for a diverse assemblage of amphibians, birds and mammals (Knopf et al. 1988, Finch and Ruggiero 1993, Martinsen and Whitham 1993, Whitham et al. 1996). They are also an important source of carbon for riverine invertebrates, as shredders and decomposers readily breakdown instream woody-debris derived from cottonwoods (R. Naiman, pers. comm.). As such, cottonwoods are integral components of riverine food webs and critical to the ecology of rivers and streams in the West (Braatne et al. 1996).

Natural hybrids between native cottonwoods commonly arise within riparian corridors wherever the distributional ranges of species overlap. As a general rule, cottonwoods are noted for their lack of genetic isolation mechanisms. As species segregate along latitudinal and elevational gradients, hybridization occurs in discrete zones where different species of cottonwood come into contact with one another (Figures 1 and 4). Widespread zones of natural hybridization occur in a) Washington, Oregon, Idaho, Montana , Alberta and British Columbia (*Populus angustifolia, P.*

Figure 2.
Black Cottonwood (*Populus trichocarpa*) is commonly found along riparian corridors throughout the Pacific Northwest. *P. trichocarpa* contributes to the height growth and acute branch angles of interspecific hybrid crosses (F_1 hybrids).
(Photo by R.F. Stettler)

Table 1.
Native *Populus* Species in North America

Section	*Species**	*Common name*	*General distributional range*
Aigeiros	*P. deltoides*	Eastern Cottonwood	Eastern N. America to the Arid West
	P. fremontii	Fremont Cottonwood	Arid Southwest of N. America
Leucoides	*P. heterophylla*	Swamp Cottonwood	Southeastern N. America
Populus	*P. grandidentata*	Bigtooth Aspen	Great Lakes region of N. America
	P. tremuloides	Trembling Aspen	Higher elevations and latitudes
Tacamahaca	*P. angustifolia*	Narrowleaf Cottonwood	Mid-elevations along Rocky Mts.
	*P. balsamifera***	Balsam Cottonwood	Upper latitudes *(Canada and Alaska)*
	*P. trichocarpa***	Black Cottonwood	Pacific Northwest to Alaska

* Nomenclature follows Eckenwalder 1977a,b, 1984a,b,c, 1996, Burns and Honkala 1990.
** Synonymy/taxonomic conflicts: Despite monographs by Eckenwalder (1977a,b, 1984a,b,c), and Brayshaw (1965), the taxonomic status of *P. trichocarpa* remains controversial.

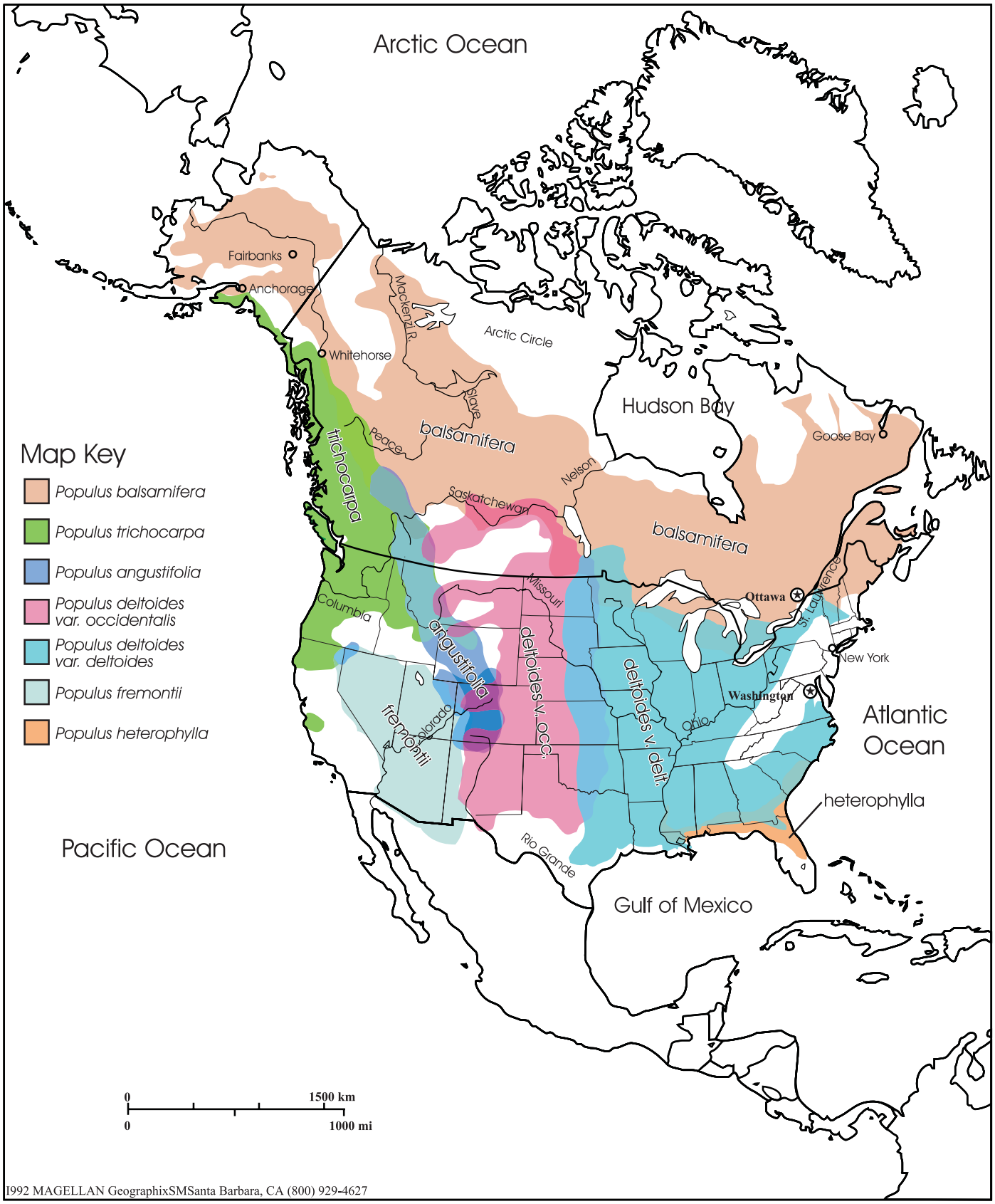

Figure 1.
Distributional range of native riparian cottonwoods in North America. Natural hybrids commonly arise where the distributional range of species overlaps.

balsamifera, P. deltoides and *P. trichocarpa*), and b) throughout the intermountain region of Arizona, Colorado, Utah, and Nevada (*P. angustifolia, P. deltoides,* and *P. fremontii*).

Natural hybrid zones are usually not very broad (10-15 km), and contain not only of F_1 crosses, but also many advanced-generation hybrids (i.e., F_2's and backcrosses, See Figure 5). As such these hybrid zones serve as bridges for the introgression of genes (i.e. genetic exchange between species) and thus are of evolutionary significance not only for cottonwoods, but also for pathogens and invertebrates that rely upon cottonwoods as their host and food source (Paige and Capman 1993, Whitham et al. 1996, 1999, Floate et al. 1998). Natural hybrid zones are further noted for their diverse assemblage of other plants, insects and wildlife species (Martinsen and Whitham 1994, Whitham et al. 1996, 1999, Floate et al. 1998). These natural zones of hybridization are unique and worthy of special efforts to promote their conservation and protection (Whitham et al. 1991, 1996, 1999, Floate et al. 1998).

Figure 3.
Eastern Cottonwood (*Populus deltoides*) is a common riparian species throughout eastern and western regions of temperate North America. Given its widespread distribution, there are several recognized varieties/subspecies, including: a) Plains Cottonwood (*P. deltoides var. occidentalis*) found throughout the Great Plains, and b) Rio Grande Cottonwood (*P. deltoides var. wislizenii*) extends northward from the Rio Grande River along the western slopes of the Rocky Mountains to the southern border of Wyoming. *P. deltoides* contributes to the radial stem growth of interspecific hybrid crosses (F_1 hybrids). *(Photo by J.H. Braatne)*

Figure 4.
Natural hybrids of *P. fremontii x P. angustifolia* in Northern Utah. These areas of natural hybridization are noted for their high biotic diversity. In particular, avian nesting success is promoted by the diverse range of canopy architecture found among parental species and hybrid crosses. *(Photo by R.F. Stettler)*

Figure 5.
F_1 hybrids and advanced generations (F_2 & backcrosses) are characteristic of natural hybrid zones. This photo shows the range of leaf morphology that is characteristic of natural hybrid crosses. *(Photo by R.F. Stettler)*

III. Domesticated non-native and hybrid poplars

Non-native and hybrid poplars have been planted throughout temperate regions of North America. The most common non-native poplars include: Lombardy poplar (*P. nigra* var. *italica*, Figure 6) and white poplar (*P. alba*, Figure 7). Both of these species are indigenous to Eurasia, yet widely cultivated in urban, suburban and agricultural landscapes. In the West, both species have long been planted as shade trees and windbreaks on agricultural landscapes (Burns and Honkala 1990). Occasionally, non-native poplars colonize adjacent riparian corridors via asexual propagation (J.H. Braatne, P.E. Heilman and R.F Stettler, pers. observations), yet there are no reports of these species displacing native cottonwood populations.

Figure 6.
Lombardy Poplar (*Populus nigra* var. *italica*), a desirable columnar cultivar arose from selective breeding and propagation in southern Europe. This male clone is planted as either an ornamental or windbreak throughout temperate regions of the world. Pollen release from Lombary Poplar is noted to give rise to interspecific crosses with *Aigeiros* and *Tacamahaca* poplars (See Table 1).
(Photo by J.H. Braatne)

The domestication of poplar has largely been a process of interspecific hybridization and the selection and propagation of desirable genotypes. Domestication has spanned several centuries, beginning in Eurasia and extending more recently to North America (Stettler et al. 1996b, Zsuffa et al. 1996). The most common interspecific hybrids arise from crosses between members of the Aigeiros and Tacamahaca sections of *Populus* (Table 1, Figure 8). Selective crosses between Asian and North American species are known as Asian-american hybrids, between Asian and European species as Eurasian hybrids, between European and North America species as Euramerican hybrids, and between North American species as Intra-american hybrids. The most common interspecific crosses include:

Asian-american:	*P. trichocarpa* x *P. maximowiczii* (TM Clones)
Eurasian:	*P. maximowiczii* x *P. nigra* (MN Clones)
Euramerican:	*P. deltoides* x *P. nigra* (DN Clones)
	P. trichocarpa x *P. nigra* (TN Clones)
Intra-american:	*P. balsamifera* x *P. deltoides* (BD Clones)
	P. trichocarpa x *P. deltoides* (TD Clones)

Plant breeders are now developing an array of hybrid poplars on the basis of these types of interspecific crosses (Bisoffi and Gullberg 1996, Bradshaw 1996, Stanton and Villar 1996, Stettler et al. 1996b, Zsuffa et al. 1996).

Figure 7.
White Poplar (*Populus alba*) is a drought hardy species that is native to southern Europe. The drought resistance of this species has led to its widespread cultivation in arid agricultural landscapes. Interspecific crossability is limited solely to those species found in the *Populus* section (See Table 1). *(Photo by J.H. Braatne)*

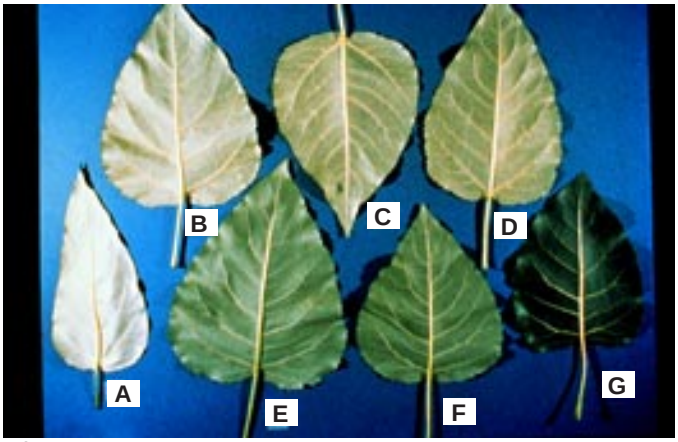

Figure 8.
Common leaf forms associated with interspecific crosses between *P. trichocarpa* (female) and *P. deltoides* (male). Large F_1 hybrid leaves (B-F) are related in part to the large cell size inherited from *P. trichocarpa* (A) and the high cell density from *P. deltoides* (G). The undersurface of aneuploid and triploid hybrid leaves (B-D) is much lighter than diploid hybrid leaves (E and F). This lighter color is correlated with higher stomatal density and rates of water loss. *(Photo by R.F. Stettler)*

The agronomic interest in hybrid poplars arises from their rapid juvenile growth and production of woody biomass (Figure 9, Stettler et al. 1988, Ceulemans et al. 1992, Heilman and Xie 1993, 1994). Emphasis on the early part of their life cycle and on favorable cultural conditions (i.e. high nutrients, irrigation and control of weedy and herbivorous pests) has promoted the selection of rapid-growing genotypes. The ease with which poplars can be propagated vegetatively (i.e. cloned), allows the selection of the best performing genotypes and/or cultivars, such as columnar forms of white poplar and Lombardy poplar. Selective breeding combined with clonal propagation thus enables the widespread cultivation and perpetuation of desirable hybrid cultivars (Stettler et. al 1996b).

The biological consequences arising from the artificial breeding and selection of hybrid poplars are many. Of particular interest to their cultivation in floodplain habitats, are those related to declines in reproductive fitness (Bisoffi and Gullberg 1996, Stanton and Villar 1996, Stettler et al. 1996b, Zsuffa et al. 1996) and reduced resource allocation to defense mechanisms (Newcombe 1996, Floate and Whitham 1993, Floate et al. 1993, Whitham et al. 1996). Defense against insects and pathogens is primarily a function of quantitative and qualitative variation in biochemical traits. Interspecific crosses can result in F_1 genotypes that are more susceptible to insect and pathogen attack than parental species. This reduction in defense mechanisms is known as "hybrid breakdown" and has been observed in hybrids growing in commercial plantations and natural zones of hybridization (Floate and Whitham 1993, 1994, Floate et al. 1996, 1998, Newcombe 1996, Whitham et al. 1996).

Figure 9.
Harvest of seven year old hybrid poplars along the lower Columbia River. The harvest rotation of hybrid poplars is commonly seven to eight years for the purposes of fiber production. The production of veneer logs for solid wood products would require approximately 12 to 18 years in most regions. *(Photo by J.H. Braatne)*

Thus, whereas hybrid poplars have been bred and selected to grow extremely well under managed conditions (i.e. with irrigation, fertilization and pest control), they may face significant challenges from competitive interactions and pathogen attack in natural riparian corridors (Stettler et al. 1996b). Factors related to lower reproductive fitness are discussed below.

IV. Reproductive properties of native cottonwoods and hybrid poplars

Populus species are predominantly dioecious; thus individual trees are either male (Figure 10a) or female (Figure 10b). The age of reproductive maturity varies among native species from five to ten years, yet in some natural populations may not occur until the trees are 15 to 20 years old (Horton et al. 1960, Fenner et al. 1984,

Cooper 1990, Debell 1990, Dewit and Reid 1992, Van Haverbeke 1990, B. Stanton, pers. communication). In contrast, hybrid poplars grown in well-maintained plantations commonly attain reproductive maturity in four years (H.D. Bradshaw, B. Stanton and R.F. Stettler, pers. communication). Pollen is widely dispersed by wind, which in part helps explain the common occurrence of natural hybrids. The dispersal of seeds primarily follows wind vectors, though some seeds are also water dispersed. These dispersal vectors contribute to long-distance gene flow (up to several km) and high levels of genetic diversity within natural populations (Weber and Stettler 1981, Dunlap et al. 1994, 1995, Farmer 1996).

Many researchers report that pollen and seed viability is significantly lower in hybrid poplars (F_1 hybrids) relative to parental species (Stanton and Villar 1996, Stettler et al. 1996b). This pattern of reduced fertility among F_1 hybrids has been widely reported for agronomic crops and other interspecific *Populus* crosses (Henry and Barnes 1977, Pregitzer and Barnes 1980, Spies and Barnes 1982, Gladysz and Ochlewska 1983). Recent studies by the Poplar Molecular Genetic Cooperative (PMGC) and Tree Genetic Engineering Research Cooperative (TGERC) have documented lower reproductive activity among diploid and triploid hybrids (F_1) relative to their parents (Bradshaw and Stettler 1993, Bradshaw 1996). These researchers have studied variation in the reproductive biology of hybrid poplars over several breeding seasons. Some recent findings from TGERC are shown in Table 2.

Although additional large-scale genetic studies are needed, the general trend of lower reproductive effort by F_1 hybrids is evident (Table 2). The causes, inferred or known, for declines in the fertility of hybrids are related to pre- and post-zygotic incompatibility (Bisoffi and Gullberg 1996, Stanton and Villar 1996, Stettler et al. 1996b, Strauss and DiFazio 1997). Incompatibility in the temporal patterns of capsule and embryo maturation is a critical factor regulating fertility. If the capsules and embryos of hybrid females lack synchronous patterns of development, capsules will mature prior to embryos resulting in the production of non-viable seed. In the case of triploidy, it is the imbalance in chromosome number among gametes that contributes to their low fertility. Given the complexity of the reproductive process, the nature and extent of genetic incompatibility among *Populus* spp. warrants further study.

The lower fertility of F_1 hybrids limits their potential gene exchange with native species. Nevertheless, a few cases of gene exchange between hybrid poplars and native cottonwoods have been reported in the lower Columbia River (Strauss and DiFazio1997). TGERC studies have also shown that crosses between hybrid males and native females yield slightly more viable seed than crosses between native males and hybrid females. This lower seed yield by

Figure 10a.

Figure 10b.

Figure 10.
Poplars are dioecious, thus individual trees are either male or female. Male catkins of *Populus deltoides* (10a) are reddish to purple and rapidly senescence following pollen release. Female catkins of *Populus trichocarpa* (10b) are green and release seed throughout the early months of summer. *(Photos by J.H. Braatne and R.F. Stetter)*

Table 2.
Reproductive characteristics of diploid and triploid F_1 hybrid poplars (TD clones) relative to their maternal species, *Populus trichocarpa*.*

Reproductive Trait	*Diploid Hybrids*	*Triploid Hybrid***	*Populus trichocarpa*
Pollen viability (%)	48	22	98
Seeds per capsule	5 to 25	14 to 17	34 to 38
Capsules per catkin	33 to 38	40 to 46	34 to 36
Catkins per tree	210 to 256	260 to 320	ND
Seed viability (%)	83 to 86	41 to 51	92
Viable seeds per tree	43,000 to 200,000	~98,000	ND

* Data are based on seven-year old border trees from four different clonal blocks, *P. trichocarpa* was growing adjacent to the plantation.
** Only one triploid clone (184-402) was included in this study.
ND = No data taken, however several researchers have reported that native cottonwoods release millions of seed annually, up to 25 million or more per tree (Braatne et al. 1996).

hybrid females is related to their lower number of viable seeds per capsule (Table 2). Given the close spacing of commercial plantations, hybrid females growing as interior trees (i.e. non-border row positions) would be expected to have a much lower number of catkins per tree than those reported in Table 2. In assessing potential avenues for gene exchange, it is also important to remember that there is a high level of variation in the fecundity of native females.

Many researchers have reported cases of spontaneous hybridization when non-native poplars are planted in the vicinity of native populations (Stettler et al.1996b). These instances are relatively easy to identify, as F_1 crosses display intermediacy with their parents in a number of morphological traits (i.e. leaves, branches, buds and bark). In more advanced-generation hybrids, the diagnosis can be more difficult and require the use of molecular genetic tools to confirm hybridization. Some documented examples of gene exchange between non-native and native poplars include: a) 18th Century introduction of eastern cottonwood (*P. deltoides*) to Europe gave rise to euramerican (DN) hybrids (Houtzagers 1937), b) widespread cultivation of euramerican hybrids in Eurasia has compromised the genetic integrity of native stands of black poplar (*P. nigra*) (Frison et al. 1995), c) introduction of white poplar (*P. alba*) to the Midwest gave rise to *P. alba* x *P. grandidentata* clones (D. Dickmann and J. Isebrands, pers. comm.), and d) semi-columnar hybrid poplars may often be found in the vicinity of Lombardy poplar (Stettler et al. 1996b, Eckenwalder pers. comm.). Despite these observations and the widespread planting of non-native poplars throughout the West, it appears that their influence on the genetics and ecology of native cottonwoods has been limited.

Seeds developing from crosses between hybrid poplars and parental species have a significantly lower viability (Table 2), and thusfar their establishment on agricultural floodplains has been extremely limited (Strauss and DiFazio 1997). Low levels of seedling establishment by hybrids appear related to a number of factors including a longer period of seed maturation, and lower seed output and viability. The interaction among

Figure 11.
Cottonwood seedlings growing on moist, exposed substrates along the Elk River in Southeastern British Columbia. Cottonwood seedlings require peak-flows to create nursery sites and a gradual stream stage decline during their first growing season. *(Photo by J.H. Braatne)*

these factors and their role in limiting the recruitment of hybrid seedlings warrants further study. Another important factor is the natural constraints on seedling recruitment within riparian corridors.

V. Natural patterns of seedling recruitment in riparian corridors

The reproductive cycle and natural recruitment patterns of native cottonwoods closely follow the seasonal dynamics of rivers (Johnson 1994, Braatne et al. 1996, Scott et al. 1996, 1997). The progression from pollination to seed dispersal is closely attuned to the seasonal rise and fall of river levels. In general, pollination and fertilization occur before leaf bud-break, either before or during peak springflows. Seeds are dispersed as river levels decline, such that seedlings colonize moist, recently exposed soil along gravel bars and riverbanks within the riparian corridor (Figure 11).

The establishment of cottonwood seedlings is highly dependent upon flooding events (when overbank flows inundate the floodplain). Cottonwood seeds are

small, with little or no endosperm (stored energy) and will not establish in the shade of competitors (Braatne et al. 1996). Under favorable conditions (i.e. moist, barren soil), seeds germinate and their radicle enters the soil within 24 hr of soil contact (Reed 1995). After germination, the roots of young seedlings must keep pace with declining river levels. Several studies have documented that their rate of root growth averages 0.5 to 1.0 cm per day, with rooting depths commonly exceeding one meter by the end of the first growing season (Mahoney and Rood 1991, 1992, 1998, Segelquist et al. 1993, Johnson 1994, Rood et al. 1995). If river levels decline too rapidly, seedlings succumb to drought stress. Seedlings that establish on moist soils at lower river levels are subject to later removal or damage by the scouring of ice and floodwaters. Collectively, these environmental constraints contribute to the infrequent establishment of cottonwood seedlings, on the order of every 10 to 20 years depending on climatic conditions and channel morphology (Bradley and Smith 1986, Baker 1990, Johnson 1994, Rood et al. 1995, Braatne et al. 1996, Mahoney and Rood 1998, Rood and Kalischuk 1998).

Given these environmental constraints to seedling establishment, the delay in seed maturation by hybrid poplars (2-3 weeks longer than native species) may place them at a disadvantage relative to native cottonwoods and willows. Seed dispersal at a later point in the growing season would coincide with lower river levels, hence only lower streambanks would be available for germination. As previously noted, several studies have documented that seedlings establishing along lower streambanks are subject to scour by spring- and storm-related flows (Johnson 1994, Scott et al. 1996, 1997).

After establishment, the continued health and vigor of riparian cottonwoods is closely tied to the seasonal dynamics of fluvial systems and the continuity of water supply throughout their life cycle. The following sections explore water-use patterns, and the relative tolerance of hybrids and native cottonwoods to seasonal drought and flooding.

VI. Water-use by hybrid poplars and other agricultural crops

It is commonly assumed that riparian woody plants, such as cottonwood, transpire large volumes of water relative to agricultural crops and other forest communities. However, recent studies reveal that water-use by hybrid poplars and native cottonwoods is comparable to agricultural crops and some conifer species (Braatne et al. 1992, Hinckely and Braatne 1994, Hinckley et al. 1994).

Leaf-level studies of stomatal conductance (Figure 12) suggest that hybrid poplars are capable of transpiring large volumes of water. Maximum rates of stomatal

Figure 12.
Physiological studies of stomatal conductance and photosynthesis. Numerous studies have documented seasonal and diurnal patterns of water-use and growth characteristics. These studies reveal that interspecific F_1 hybrids are often more drought-resistant than their parents.
(Photo by J.H. Braatne)

conductance (g_{max}) for hybrid poplar approach 600 mmol m^{-2} s^{-1}, whereas g_{max} for white oak (*Quercus alba*), Pacific silver fir (*Abies amabilis*), and Douglas fir (*Psedotsuga menziesii*) are 300, 240 and 100 mmol m^{-2} s^{-1}, respectively (Fritchen et al. 1973, Price and Black 1990, Braatne et al. 1992, Hinckley et al. 1992, 1994, Martin et al. 1997). Among agricultural plants, g_{max} typically range from 300 to 500 mmol m^{-2} s^{-1} (Nobel 1991, Korner 1994, Larcher 1995). Based on stomatal conductance values, one might expect large rates of transpiration by hybrid poplar stands relative to other plant canopies. However, transpiration is governed by a number of biophysical and environmental factors, including: a) size and density of stomata, b) degree of stomatal opening, c) hydraulics of water-conducting tissues, d) size, density and distribution of leaves within the canopy, e) environmental conditions, such as solar radiation, temperature, humidity, and soil moisture content, and f) canopy boundary-layer conditions (wind speed, patterns of turbulent airflow, etc.).

Transpirational water loss by a hybrid poplar canopy was recently documented on alluvial soils in Western Washington (Puyallup River Floodplain, Hinckley et al. 1994). In this study, the maximum rate of transpiration for a four-year old hybrid poplar stand was calculated to be 4.92 mm d^{-1} (0.194 inches d^{-1}) over a wide range of atmospheric conditions. This value is slightly more than transpiration rates of Douglas-fir stands (4.2 to 4.8 mm d^{-1}, up to 0.193 inches d^{-1}; Fritschen et al. 1973, 1977, McNaughton and Black 1973, Tan et al. 1978, Price and Black 1990). On the basis of these findings, it appears that hybrid poplars and some conifers have comparable rates of water use.

Similar rates of stand-level transpiration for Douglas-fir and hybrid poplar arise from offsetting differences in the ways these species control

Figure 13.
The upper canopy of a four-year old stand of hybrid poplar in eastern Washington. The upper canopy of hybrid poplars is a complex and highly variable surface from which water fluxes are governed by an interaction of numerous environmental factors, including radiation inputs, turbulent air flows, and temperature gradients. Seasonal rates of water-use by mature poplar stands are comparable to slightly lower than many agricultural crops.
(Photo by J.H. Braatne)

Figure 14.
Irrigated cornfields in eastern Washington. Annual rates of water use by agricultural crops, such as sweet corn, are comparable to slightly lower than hybrid poplars. Differences in the length of growing season and harvest rotation cycles are critical variables in comparing long-term rates of water use by hybrid poplars with agricultural crops.
(Photo by J.H. Braatne)

transpiration. In particular, these species differ in their partitioning of canopy water fluxes between the stomatal and boundary-layer components of water loss. For example, thin conifer needles are directly exposed to wind and solar radiation, and thus readily lose moisture through a high boundary-layer conductance, even though their stomatal conductance is low (i.e. the conifer canopy is tightly coupled with atmospheric conditions). In a poplar stand, stomatal conductance is high, but their large, dense canopy (Figure 13) results in a low boundary-layer conductance (i.e. the poplar canopy is poorly coupled with the atmosphere).

Table 3.
Estimated water use by agricultural crops and hybrid poplars in eastern Washington*.

Crop type	*Estimated Water Use (inches acre^{-1}yr^{-1})*
Alfalfa	28-45[1]
Apples w/ cover crop	34-50 [1]
Onions (dry)	30-36 [1]
Potatoes	28-34 [1]
Sweet corn	24-28 [1]
Winter wheat	25-31 [1]
Hybrid poplar (1st yr)	10-14 [2]
Hybrid poplar (2nd to 3rd yr)	22-26 [2]
Hybrid poplar (4th yr to harvest)	32-36 [2/3]

* Significantly lower water-use values would be expected in cooler, maritime climates.

1) Values are derived from twenty-year water-use records (James et al. 1989).

2) Calculated values based on maximum stand water losses of 0.188-0.194 inches d^{-1} (Hinckley et al. 1994). Note: Evapotranspiration rates can be expected to range from 0.3 to 0.4 inches d^{-1} when mid-day air temps > 35°C (R. Cuenca, unpubl. data), thus water-use may approach 34 inches acre^{-1}yr^{-1} for 3 yr stands and 40-42 inches acre^{-1} yr^{-1} for 4 yr^{+} stands during growing seasons that are hotter and longer than normal (J. Eaton, pers. comm.).

3) The leaf area of a hybrid poplar canopy growing in eastern Washington remains relatively constant from the end of the fourth yr until harvested at 7-8 yr (Kim Brown and Tom Hinckley, unpubl. data), hence annual rates of water use would be comparable during the latter stages of the commercial harvest cycle.

Related physiological studies suggest that a homeostasis between stomatal and boundary-layer conductance results in a relatively constant rate of maximum transpirational water loss across a range of canopy and vegetation types. Meinzer and Grantz (1989, 1991) observed that as leaf area and boundary-layer conductance of a stand change over time, total canopy conductance also changes in a manner that maintains relatively steady rates of water loss (boundary-layer plus stomatal components). Kelliher et al. (1993) also reported similar observations across a range of vegetation types. There are two plausible explanations for these observations. First, the range of maximum stomatal conductance appears to be quite conservative within vegetation types (Nobel 1991, Korner 1994, Larcher 1995). Second, stands with low leaf areas will have a lower canopy conductance, yet the corresponding rate of soil evaporation will increase as higher levels of solar radiation warm the soil surface. The increased rate of soil evaporation compensates for a lower canopy conductance, resulting in relatively steady rates of water loss across a range of canopy and vegetation types.

Similar trends in water use by agricultural crops can be seen in Table 3. Contrary to common misconceptions, water use by agricultural crops is not solely related to the amount of water applied through irrigation (Figure 14). Rather water-use is regulated by solar radiation (McNaughton and Jarvis 1983), whereby inputs of solar energy drive evapotranspirational fluxes from the canopies of agricultural plants.

In viewing the data presented in Table 3, it is important to note that the growing season of hybrid poplars is significantly longer (April to October) than most annual crops. Since hybrid poplars take up to 4 years to reach their maximum transpiration potential, their long-term water-use will also be significantly lower than agricultural crops whose annual water demand is relatively constant from year to year. Detailed models of evapotranspiration by hybrid poplars are currently being developed at Washington State University and Oregon State University. Until these findings are published, the range of values presented in Table 3 can be used to approximate water fluxes from hybrid poplar plantations.

VII. Drought and flood-tolerance of hybrid poplars and native cottonwoods

There have been numerous water relation studies of hybrid poplars (F_1 hybrids) and their parents (native cottonwoods). Although canopy and stand-level comparisons are noticeably absent, whole-plant and leaf-level studies reveal that hybrid poplar rapidly close their stomata in response to atmospheric and soil-water deficits (Schulte et al. 1987, Tschaplinski and Blake 1989a,b, Braatne et al. 1992, Hinckley et al. 1992, Hinckley and Braatne 1994). This type of stomatal behavior typically results in lower transpiration rates and a greater drought resistance among hybrids relative to native species (Tschaplinski and Tuskan 1994, Tschaplinski et al. 1994, Blake et al. 1996). Furthermore, these water relation properties enable hybrids to maintain higher leaf areas for longer periods during a drought-cycle than native species (Braatne et al. 1992).

Given current trends in climatic warming, these research findings may be significant as streamside plantings of hybrid poplar could potentially compensate for the adaptive limitations of some native species (notably black cottonwood, *P. trichocarpa*). The fact that *P. trichocarpa* x *P. deltoides* hybrids could provide more shade to moderate stream temperatures than native species is not a minor point, especially in a warming climate with periodic drought. Hybrids are thus not only suitable for short-rotation fiber plantations, but may also hold some promise as supplemental plantings with native species in the restoration of riparian corridors. New research is needed to explore the potential ecological role of hybrid poplar in light of changing riparian landscapes.

Seasonal flooding is a common feature of riparian landscapes (Figure 15), and the flood tolerance of native cottonwoods and hybrid poplars has been subject of several recent studies (Lui and Dickmann 1992a,b, 1993, Neuman et al. 1996). The general symptoms associated with flooding include: a) yellowed leaves, b) leaf curl (i.e. epinasty), c) formation of adventitious roots, and d) wilting (reviewed by Kozlowski 1984, 1997). Cottonwoods are considered to be fairly tolerant of excess soil moisture (Harrington 1987), yet flooded soils reduce growth and survival in many species (Smit et al. 1989, Lui and Dickmann 1992a). Some cottonwoods appear to be more flood tolerant than others, yet there are some disparities among research findings. For example, Harrington (1987) has shown that 20 d of flooding did not affect the growth and survival of black cottonwood (*P. trichocarpa*). These results contradict the findings of Smit et al. (1989), where flooding was observed to significantly reduce leaf growth in this species. These observations suggest that there is a high level of genetic variability in flooding responses within and between species. In fact, Smit (1988) found that flooding tolerance was more variable within populations of black cottonwood than between populations. Overall, native cottonwoods appear to be more flood tolerant than hybrid poplars, yet both are significantly more flood tolerant than the agricultural crops commonly planted in floodplain habitats (Kozlowski 1984, 1997, Neuman et al. 1996, D.I. Dickmann, pers. communication). Additional research is needed to assess the physiological and morphological relationships between flooding and drought-tolerance in hybrids and native species.

Figure 15.
Seasonal flooding of a natural hybrid zone (*P. angustifolia x P. trichocarpa*) along the upper Yellowstone River, Montana. The life cycle of riparian cottonwoods is highly dependent upon seasonal flooding to create nursery sites for the seedling recruitment. Periodic flooding is thus critical to sustaining native riparian cottonwood populations. Native cottonwoods and hybrid poplars are very flood-tolerant relative to other natives and invasive eurasian species as well as most of the agricultural crops typically planted on floodplain habitats.
(Photo by J.H. Braatne)

VIII. Clearing of floodplain habitats as a means of conserving water

On the basis of the misconception that riparian trees transpire excessive amounts of water, agronomists

and hydrologic engineers widely promoted their removal from floodplain habitats during the late 1940's to the early 1980's (Robinson 1952, 1958, US. Congress 1960, Horton 1966, Culler 1970, Ritzi et al. 1985, Welder 1973, 1988). The removal of riparian vegetation was justified in part on poorly conceived physiological studies of water-use and overly simplistic hydrologic models of fluvial systems (Gatewood et al. 1950, Robinson 1958, Bowie and Kam 1968, Van Hylckama 1974, Horton et al. 1976, Culler et al. 1982, Weeks et al. 1987, Welder 1973, 1988). While many of these programs were undertaken in the arid southwest to conserve water for crops and municipalities, it is useful to review what we know about how these fluvial systems and how they responded to the removal of riparian woody vegetation.

Government-sponsored programs for the removal of phreatophytes (i.e. deep-rooted plants that absorb water from the water table or the soil above it) were primarily directed at rapidly expanding populations of salt cedar (*Tamarix* spp.), though cottonwoods were also cleared from many riparian corridors (Horton 1966, 1976, Bowie and Kam 1968). Unfortunately, there is only a limited database on the hydrologic responses of streams to these vegetation removal programs. Most of the studies were limited to short-term measurements of scattered river reaches and/or isolated watersheds (Robinson 1952, 1958, Bowie and Kam 1968, Welder 1973, 1988). In these studies, summer baseflows appeared to increase on the order 10 to 15% in the year following vegetation clearing (Robinson 1958, Bowie and Kam 1968, Culler 1982, Ritzi et al. 1985, Welder 1973, 1988). These gains in baseflow were attributed to phreatophyte removal, however, some alternative explanations include: a) large-scale spatial and temporal variation in precipitation patterns across arid landscapes, and b) increased drainage and dewatering of shallow aquifers lacking vegetative cover. As only moderate gains were reported, these studies suggest that there were significant increases in evaporative water loss from exposed floodplain surfaces.

Today, the general condition of many of these riparian corridors reveals that the increases in baseflow following phreatophyte removal were not sustained. Rather, removal of riparian vegetation contributed to increased rates of evaporative water loss and localized streambank erosion. In some cases (primarily low to mid-order riverine environments), stream channels were downcut or abraided through a series of erosive events. Downcutting and streambank erosion further diminished ground-water recharge and aquifer storage capacity. The expansion of salt cedar populations has also not diminished over time (Everitt 1980, Shafroth et al. 1995).

The long-term response of riparian corridors to phreatophyte control and stream channelization from the 1940's to 1980's still requires systematic documentation, particularly in light of our current understanding of evapotranspirational fluxes from plant canopies. Nevertheless, our knowledge of fluvial responses to vegetation removal reveals a critical role for riparian woody plants in maintaining stream channel morphology and sustaining seasonal baseflows (Scott et al. 1996, Braatne et al. 1996, Beeson and Doyle 1997, Naiman and Decamps 1997, Poff et al. 1997, Rood and Kalischuk 1998).

IX. Wildlife habitat studies

A common observation upon entering a poplar plantation following canopy closure is the lack of understory vegetation and wildlife activity (Figure 16). Given the deciduous nature of these trees, low species

Figure 16.
The understory of a five-year old stand of hybrid poplar. After canopy closure, a sparse understory is a common characteristic of hybrid poplar stands. The general lack of structural diversity in commercial stands contributes to lower wildlife usage relative to native riparian plant communities.
(Photo by J.H. Braatne)

Figure 17.
Deer and other cosmopolitan wildlife species commonly use hybrid poplar stands for seasonal cover and resting habitat. *(Photo by J.H. Braatne)*

diversity and lack of avian activity is striking in comparison to natural riparian cottonwood forests.

To date, only a few studies have compared patterns of wildlife activity in poplar plantations with adjacent agricultural row-crop and small-grain fields. In these studies, only minor differences were reported in the abundance and diversity of wildlife species (Hoffman et al. 1993, Christian et al. 1997, Hanowski et al. 1997). In grasslands and areas with limited forest cover, plantations are commonly used for resting and cover by deer, rodents, upland game birds and raptors (Figure 17). Wildlife abundance in many plantations appears to be significantly lower than native forests (Christian et al. 1997). On the other hand, wildlife data from the Columbia River Basin show higher summer bird densities along the edges of young plantations than surrounding native shrub-steppe habitat. Use of plantations by raptors during winter months is also greater than adjacent cover types (Pat Heglund and Brian Moser, unpubl. data). Additional research is needed to further clarify localized and regional patterns of wildlife activity within plantations relative to natural riparian corridors and other native habitats.

In some studies, avian and mammalian diversity was higher in isolated patches within plantations where small groups of trees had died or weed control was less effective (Christian et al. 1997, Hanowski et al. 1997). This type of finding suggests that plantations could be designed to incorporate spatial heterogeneity as a means of increasing habitat quality. Some possible options include: a) multi-age clonal rotations, such that large plantations contain a mosaic of differing stand ages, patch sizes and canopy structure, and b) restoring native willows and cottonwoods along streambanks adjacent to commercial plantations. Additional research is needed to explore the efficacy of these options.

X. Conclusions, Recommendations and Research Needs

Native cottonwoods are critical elements in the structure and function of riparian corridors. As such, remnant stands of native cottonwood need to be inventoried, ecological studies initiated and long-term efforts directed towards their conservation and restoration. Native germ plasm should be collected from remnant stands and used to establish ex-situ collections in designated arboreta throughout the West. Research should also be initiated that develop options for promoting the natural recruitment of cottonwoods and other riparian plants through controlled flow-modifications of dams and agricultural diversions (Mahoney and Rood 1998, Rood and Kalischuk 1998), and other cost-effective practices for large-scale restoration of riparian forests (Friedman et al. 1995, Braatne and Rood 1998).

A. Gene exchange between commercial hybrid plantations and native populations:

If hybrid poplar plantations are established near native populations, preference toward the use of triploids or genetically-engineered sterile clones would strongly limit gene exchange. Unfortunately, triploids have lower growth rates than other hybrids, which limits their commercial value and biofiltration capacity. Other options to reduce gene flow include: a) limited planting of triploids in border rows to deter pollen and seed dispersal, and b) preferential planting of hybrid females to limit long-distance pollen release to native females.

Future research needs include exploring: a) the nature and extent of genetic incompatibility among Populus spp., b) the development of sterile clones with comparable growth rates to existing hybrids, c) patterns of long-distance gene flow within and between populations using molecular genetic tools, and d) phenological barriers to the establishment of hybrid seedlings within natural riparian corridors.

B. Growth and water-use characteristics: hybrid poplars vs. agricultural crops

The growth and vigor of hybrid poplars is dependent on adequate weed control, fertilization, and irrigation. Since poplar stands take several years to reach their maximum transpiration potential, water-use by hybrid poplars will be lower than that of many annual crops. Canopy-level studies of evapotranspiration are needed to clarify

seasonal and long-term trends in water-use and stand-water balance. Research is also needed to compare water-use by poplar plantations with native stands of riparian cottonwood.

C. Drought and flood-tolerance of hybrid poplars and native cottonwoods:

Native cottonwoods appear to be less drought-tolerant, yet more flood-tolerant than hybrid poplars. Agricultural crops traditionally planted in floodplain habitats are significantly less flood-tolerant than either hybrid poplar or native cottonwoods and willows. Additional research is needed to explore the physiological and morphological relationships between flooding and drought-tolerance in hybrids and native species.

D. Clearing of floodplain habitats to conserve water:

Removal of riparian trees and shrubs from streambanks increases erosion, channel downcutting, sediment loading and localized dewatering of shallow aquifers. Clearing of vegetation may give an initial impression of water conservation, but streamflow increases are spatially and temporally limited. Additional research is needed to assess the role of vegetation in maintaining the functional integrity of river channels and riparian corridors.

B. Wildlife habitat studies:

Minor differences in the abundance and diversity of wildlife have been observed between hybrid plantations and adjacent row-crop or small-grain fields. In arid grasslands or areas with limited forest cover, plantations provide habitat for deer, upland game birds, raptors and rodents. In some plantations, mammalian and avian diversity were higher in localized patches where hybrid clones had died, suggesting that plantation designs could be developed that incorporate spatial and temporal heterogeneity as an approach to increase habitat quality.

Additional research is required to understand the relationships between stand structure, plantation design and wildlife utilization. Comparative ecological studies of poplar plantations and native stands of riparian cottonwood are needed to assess spatial and temporal variation in habitat value and utilization. Studies of silvicultural practices and harvesting regimes are also needed to determine how hybrid poplars can be integrated into agricultural floodplains in a manner that promotes the natural functions of riparian corridors (Figure 18).

Figure 18.
Riparian hybrid poplar buffers at Carnation Farms near Carnation, WA. Floodplain plantings of hybrid poplar can be used to intercept excess nutrients associated with the surface runoff from hayfields, pastures and agricultural crops.
(Photo by J.H. Braatne)

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Appendix A: About the Author

Dr. Jeffrey H. Braatne

Education:

1989	Ph.D. Department of Botany, University of Washington, Seattle
1978	B.A. Departments of Biology & Botany, University of Montana, Missoula

Additional training (94-98): Applied Fluvial Geomorphology I & II, River Restoration & Natural Channel Design (Wildland Hydrology w/ D. Rosgen, Pagosa Springs, CO); Stable Isotope Ecology (BIO581, University of Utah, Salt Lake City); Federal, State and Local Clean Water and Wetland Regulations I & II (Seattle Law Review Board).

Background: Dr. Braatne is a physiological plant ecologist with expertise in the ecology of riparian landscapes and the physiological ecology of riparian plants. Over the last ten years, he has been an active participant in the University of Washington/Washington State University Black Cottonwood Research Program. His research and teaching interests focus on the physiology and ecology of riparian cottonwoods and willows in western North America. Some recent research topics include: a) physiological and morphological responses of willows and cottonwoods to drought and flooding, b) fluvial/ecological modeling of the riparian plant communities, and c) impacts of stream-flow modifications on riparian plant communities and landscapes. Recent studies have focused upon the ecology of riparian plant communities along the lower Snake (Hells Canyon) and Salmon River Corridors. Dr. Braatne teaches graduate courses on riparian landscape ecology at the Universities of Washington and Montana.

Employment History (90-99)**:**

Assistant Research Professor: Biology Dept., University of Lethbridge, Alberta 1997-Present

Affiliate Assistant Professor: Forestry Dept., University of Washington, Seattle, WA 1994-Present

Independent Environmental Consultant: Seattle, WA 1995-Present

Senior Ecologist: National Wetland Science Training Cooperative;
L.C. Lee & Associates, Inc.; Springwood Associates, Inc., Seattle, WA 1993-96

Postdoctoral Fellow: Forestry Dept., University of Washington, Seattle, WA 1990-93

Selected Publications (96-99)**:**

Braatne, J.H., W.C. Johnson, and S.B. Rood. Riparian ecosystems: biophysical processes influencing plant and animal diversity. In: R.C. Wissmar and P.A. Bisson (eds.), Strategies for Renewing River Ecosystems: variability and uncertainty of biophysical processes and their ecological consequences. American Fisheries Society (In prep)

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Appendix B: Bibliography on the Biological Aspects of *Populus* Spp. and Ecology of the Riparian Landscapes of Western North America

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