Poplars (*Populus* spp.): Ecological Role, Applications and Scientific Perspectives in the 21st Century (*Review paper*)

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Abstract

In the few last decades, the genus *Populus* has gained a unique position in ecology, commercial applications and science. The special role of riparian habitats in the maintenance of ecological balance between aquatic and land habitats places poplars, cottonwoods and aspens at the center of efforts for their protection and restoration as one of the most important tree participants of riparian forests. Although the urban role of poplars has been reduced, their economic importance has been increasing rapidly as a result of improved methods of cultivation, the introduction of many new hybrids with desirable features, political guidelines for biomass production and their potential for phytoremediation. Successful sequencing of the *Populus trichocarpa* genome became the driving force for further wide-ranging research on poplars and made *P. trichocarpa* a model tree for plant biology (especially genetics). However, ecological actions require financial support, profitability of plantations established for bioenergy production or for bioremediation of contaminated sites is highly dependent on the proper selection of suitable cultivars for specific tasks and local environment, and the use of poplar to produce proteins is indefinite future because of the controversy that in society raise genetically modified organisms. This article reviews the current data on poplars from ecological, functional and scientific perspectives, showing that it is necessary to combine all these aspects to usability poplar possible to maximize profits (not just financial), and reduce risk.

Key words: poplar, cottonwood, *Populus* spp., riparian forest, model tree

Introduction

According to Eckenwalder's (1996) classification, the genus *Populus* includes 29 species growing in Europe, Asia, North America and East Africa and is divided into six sections (Table 1). However, the taxonomy remains unclear and other classifications have been proposed with a range of 25–35 species. The most important problem is easy interspecific hybridization into genus. A well-known example of a natural hybrid is the grey poplar (*P.* × *canescens*). However there is genetic evidence from cpDNA that *P. nigra* and *P. szechuanica* should also be considered as species of hybrid origin (Hamzeh and Dayanandan 2004).

The natural habitats for most poplars are frequently flooded forested stands next to a flowing or non-flowing body of water (exceptions are aspens and some Asian mountain balsam poplars) (Bugała 1973). The most characteristic are riparian forests originally growing along all major rivers in Europe, Asia and North America. Poplars are usually dominant and pioneer species in these ecosystems due to their tolerance for complete even flooding (Cao and Conner 1999, Glenz 2005). However, the riparian forests of industrialized countries in the Northern Hemisphere have been devastated as a result of intensive logging, conversion of fertile riparian areas to croplands, heavy industry and other human activities including large-scale regulation of rivers (Décamps et al. 1988, Sedjo 1997, Chhabra et al. 2006). Riparian forests perform a wide range of important ecological tasks such as: filtering runoff, limitation prevent of soil erosion, reducing the damaging effects of flooding, moderating of water tem-

Table 1. Taxonomic classification of the genus *Populus* – the division into sections

Section	Comments
Aigeiros Duby	black poplars (Europe, western Asia, North America – temperate)
Leuce Duby or *Populus*	true white poplars and aspens (Europe, Asia, North America – circumpolar, subarctic and cool temperate, mountains, *P. alba* warm temperate)
Leucoides Spach	bigleaf poplars (eastern North America, eastern Asia – warm temperate)
Tacamahaca Spach	balsam poplars (North America, Asia – cool temperate)
Turanga Bge	subtropical Asian poplars (southwest Asia, east Africa – subtropical to tropical)
Abaso	endemic Mexican poplars (subtropical to tropical)

perature, stimulating of biodiversity through creation specific habitats, keeping stability of riverbanks and making a buffer zone between agricultural or industrial areas and rivers or streams (Welsch 1991, Malanson 1993, Palone and Todd 1997). Therefore, in recent decades, strong efforts have been made to preserve and regenerate riparian forests and this problem has been perceived not only by the scientific community but also at governmental and political levels (Holmes et al. 2005, Annear et al. 2009). The example is International Instream Flow Program Initiative established in order to protect and restore rivers and lakes in North America (source: http://www.instreamflowcouncil.org/). In Strasbourg Resolution 2, which refers to genetic resources (1990) (signed during the Ministerial Conference for the Protection of Forests with the participation of 32 European countries), *P. nigra* was recognized as an endangered species in Europe (Arbez and Lefèvre 1997). Strategies for the conservation of *P. nigra* in Europe and its restoration in riparian ecosystems were developed on the basis of measurements of the genetic diversity in wild populations in a project funded by the European Union: "Genetic diversity in the river populations of the European black poplar for evaluation of biodiversity, conservation strategies, nature development and genetic improvement", 1998–2001 (Dam 2002, Smulders et al. 2008). It was found that in many European countries, black poplar (*P. nigra*) has been displaced from its natural habitat by numerous hybrids (Fossati et al. 2003, Vanden Broeck et al. 2004). *P. nigra* is also included in the IUCN Red List of Threatened Species (available online: http://www.iucnredlist.org) with some other poplars (Figure 1). Some American species are also regionally imperiled: *P. deltoides* in Texas (Taylor 2001). On the other hand, white poplar (*P. alba*) is considered as a minor invasive alien species in Canada (White et al. 1993).

The history of usage of poplar cultivars started in 1700–1720 when the first cultivar of *P. nigra* 'Italica' (Lombardy Poplar) was selected in Italy and rapidly spread in Europe and beyond (in 1784 it appeared in North America) (Jobling 1990, Wood 1994, Braatne et al. 1996, Gordon 2001). In the mid-18th century, was *P.* × *canescens* 'Serotina' (*P. nigra* × *P. deltoides* var. *monilifera*) was one of the first commonly cultivated hybrid poplars (White 1993). The main features of poplar wood are low density (0.35–0.5 g/cm^3; source: http://www.engineeringtoolbox.com/) and low heating value nearly two times lower than values established for oak, beech or hornbeam (Battaglia et al. 1980), thus the first poplar plantations aimed at wood production appeared at the turn of the 19th and 20th centuries with the growing demand for plywood and pulpwood (FAO 1979). The first artificial regeneration program in United States started in 1893 when the Willamette Pulp and Paper Company planted 400 hectares of *P. trichocarpa* in the vicinity of West Linn, Oregon over a twenty-year period (Berguson et al. 2010). There was a rapid increase in interest in poplars after World War II, when Europe was extremely devastated, due to high demand for quickly available wood as building and fuel materials. In 1947, the International Poplar Commission (IPC) was established as an FAO technical statutory body to promote cultivation, conservation and utilization, monitoring of national and international policies, and maintenance of national registries of poplar clones and willows. In several European countries such as Italy, Belgium, France and Spain, advanced poplar programs were initiated during the 40's and 50's, focusing on intensive poplar cultivation, selection of the most promising cultivars, as well as finding new ones. However, this post-war peak of popularity in poplars was not successful everywhere. In Poland, over 12 000 ha of poplar plantations were established in 1954–1965, but only two-thirds had

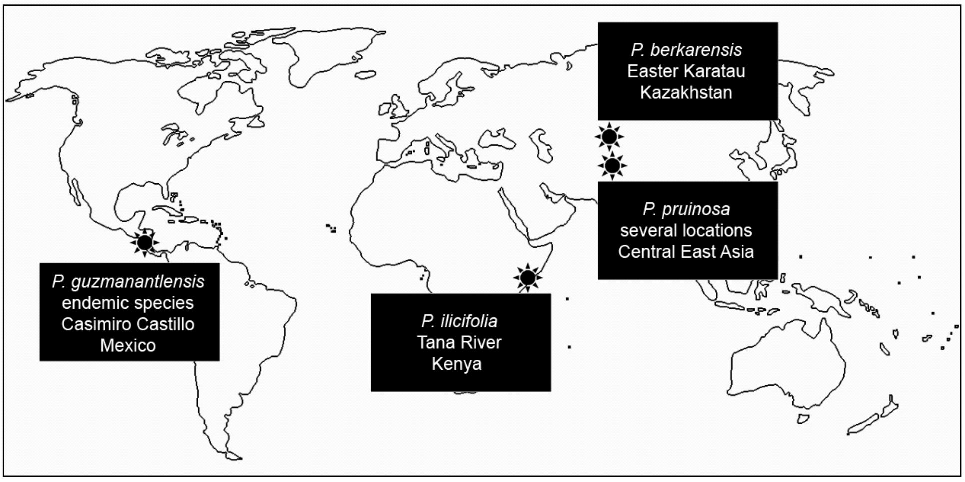

Figure 1. Endangered poplar species in the IUCN Red List of Threatened Species (available online: http://www.iucnredlist.org)

survived in bad condition at the end of this period due to wrong selection, insufficient nurturing, pests and diseases. The polish poplar program collapsed in the 1980s (Zajączkowski 2013).

Poplars were planted extensively along motorways, in towns and in urban areas revealing another important and useful feature: high tolerance to urban and industrial pollution (Wang and Jia 2010, Wu et al. 2010). To maintain healthy trees, selective felling/pollarding works need to be carried out and trees in remote or inaccessible areas need to deteriorate naturally in order to encourage biodiversity.

The usage of poplar plantations changed a few decades ago with the development of short rotation coppice (SRC) principles and adapting them for poplars (generally, SRC consists of densely planted, high-yielding varieties of either willow or poplar, harvested on a 2–7 year cycle), the appearance of new cultivars and strong political pressure for new sources of renewable energy (Benetka et al. 2002, Tharakan et al. 2003, Labrecque and Teodorescu 2005, Tullus et al. 2012). In addition, it was found that fast-growing poplars can be used for phytoremediation (Laureysens et al. 2005). It was discovered relatively early that they can be successfully used for the purification of organically polluted soils (Burken and Schnoor 1999). Moreover, although they are not hyperaccumulators, they can also survive on land highly contaminated with heavy metals (Stobrawa and Lorenc-Plucińska 2008). More importantly, these applications (bioenergy production and phytoremediation) can be combined (Licht and Isebrands 2005).

At the beginning of the 21st century, it was suggested that poplars can be considered as model trees for forestry (Bradshow et al. 2000, Taylor 2002). However, a true breakthrough in plant biology was the choice of a cottonwood (*Populus trichocarpa*) as the first tree species in the genome sequencing project due to the compact size of its genome (50 times smaller than pine; source: http://www.phytozome.net/poplar) and other appropriate features. In 2005, the project realized by the International *Populus* Genome Consortium was successfully completed and the results are available (Tuskan et al. 2006). This breakthrough led to a stream of studies on poplars, including numerous genome-wide and systemic studies, resulting in an increase in the number of publications appearing after 2005. Moreover, other genetic databases have been constructed (i.e. EST or miRNA) and are freely available. As a result of free access to genetic sources, poplar is now a model species in plant biology and is a powerful tool in further studies not only on the field of molecular biology.

Poplars as key participants in riparian forests

A typical community for European rivers is a willow–poplar riparian forest (*Salici–Populetum*) with black and white poplars (*P. nigra* L. and *P. alba*); their American equivalents are varieties of cottonwoods (*P. angustifolia* James, *P. balsamifera* L., *P. deltoides* Marsh., *P. fremontii* S. Watson and *P. trichocarpa* T. & G.). Stands of species from *Turanga* sections are typical in arid and semi-arid areas located along main rivers in central Asia and Asia Minor (Bugała 1973).

The most advanced impoverishment and extinction of riparian forests are observed in Europe and North America, in countries with the most degraded landscapes. In Poland (considered as one of the richest natural habitats in Europe; source: http://www.eea.europa.eu/soer/countries/pl/soertopic_view?topic=biodiversity), only sparse and tiny fragments remain along the biggest rivers (Vistula, Oder, Warta and Bug) (Bugała 2000).

Globalization in the last two centuries has led to significant migration of plants and animals, which has changed native ecosystems including the remains of riparian forests (Uowolo et al. 2005). Among other factors, poplars seem to be very sensitive to decline in groundwater levels, which can be directly related to human activities; for example, regulation of rivers or open-pit mining essentially disturbs groundwater balance (Mahoney and Rood 1991, Scott et al. 1999, Rood et al. 2003).. For example, introgression of genetically pure native European black poplar (*P. nigra*) populations has occurred; they are rare in natural habitats due to hybridization with American cottonwood (*P. deltoides*) introduced into Europe (Fossati et al. 2003, Vanden Broeck et al. 2004). There is a fear that these spontaneous hybrids between *P. nigra* males and *P. deltoides* females (*P. x canadensis* Moench.) could be a source of serious problems in attempts to restore *P. nigra* stands in Europe, as competitors in riparian habitats (Smulders et al. 2008). On the other hand, recent reports from Switzerland show that *P. nigra* is more abundant in this country than has hitherto been thought and there is little evidence of hybridization of *P.* x *canadensis* males with *P. nigra* females, which is good news for restoration of *P. nigra* (Csencsics et al. 2009). However, this problem still exists and other cultivars (e.g. Lombardy poplar, *P. nigra* var. *italica*) can produce hybrids with black poplars (Chenault et al. 2011).

The need for preservation and restoration of riparian forests arose when it became clear that they fulfil important functions as a buffer between terrestrial and aquatic ecosystems. There has been a rapid increase of the number of studies focused on various aspects as a result (Watanabe et al. 2005, Rodewald and Bakermans 2006). The main ecological functions of riparian forest buffers are as follows: (1) infiltration of rainwater from sediments, nutrients, pesticides and other pollutants before they reach a stream; (2) uptake of nutrients and pollution; (3) moderating water temperature through canopy shadows; (4) providing food and tremendous diversity of habitats for a wide range of animals; (5) stabilization of river banks (Palone and Todd 1997, Saab 1999).

In practice, the most advanced work, including transformations of whole areas, has taken place in the United States and Canada, where a great number of well-funded projects to rebuilding river environments have been initiated in the last decades of the 20th century (Hunter et al. 1999, Poulin et al. 2000). The importance of restoration of totally devastated European riparian forests has been more and more appreciated in scientific studies since the end of the 20th century (Hughes and Rood 2003, Glenz 2005, Hughes et al. 2005). Some the most important actions are listed in the Table 2.

Table 2. The list of most important actions related with restoration of rivers and riparian forests

Project	Area	Comments
Restoration of Chesapeake Bay	USA	One of the most extensive projects; since 1983
Dam removal on the Elwhra River	USA	Largest dam removal in the history of United States; since 2011
Natura 2000 Project	European Union	Among other, many actions on riverside areas, wetlands and riparian forests http://natura2000.eea.europa.eu/
The London Wetland Center	UK	Example of successful restoration of an urban riverside area; http://www.wwt.org.uk/
Living Rivers for Europe	Europe	WWF's program funded by the European Union, the Global Environment Facility and the World Bank has included more than 65 actions in 25 European countries since 1999, with main aim of preservation and restoration of the most important European rivers. It is a part of a global Living Rivers project by WWF.
The European Centre for River Restoration Project	Europe	The aim ECRR project is to gather river restoration projects in order to share knowledge and experiences and to assess trends in techniques, costs, monitoring and effectiveness of these projects. The ECRR database contains about 50 projects and is available online: http://www.ecrr.org/
RESTORE River Wiki	Europe	Another project of The European Centre for River Restoration with 500 river restoration case studies from all over Europe (available online: http://riverwiki.restorerivers.eu). This data base contains detailed information about river restoration projects, links per country to relevant organizations, networks and other sources of knowledge and expertise.

Biomass production and phytoremediation applications

Due to poor quality of the wood and numerous mistakes made in cultivation, many poplar programs undertaken in the 20th century in different countries have failed. A new opportunity for poplar applications has arisen with public demand for renewable energy production. Therefore, SRCs have a fundamental advantage over traditional forest cultivation with a short harvesting cycle, such that SRCs are a viable source of renewable energy on an industrial scale. Poplars are among the most promising tree species for SRC cultivation due to very fast growth, easy and efficient propagation and a high level of genetic variation, providing good possibilities for hybridization and cultivation of new hybrids with desirable properties (Klasnja et al. 2002). Profitability of poplars in modern plantations is dependent on the choosing of cultivars and plantation rules adapted to the local environmental conditions (Jain and Singh 2000, Dhillon et al. 2001, Dķaz and Romero 2001). Detailed calculations on the adequacy of the selected methods for investment economic effectiveness appraisal in poplar plantations were done based on of the analysis of poplar plantation production and economic investment models in Serbia (Keča et al. 2011). Another modelling system from Canada indicate that additional efforts are necessary including refinement of yield estimates and lowering of establishment, management and harvesting costs in order to increase of competitiveness of SRC plantations against conventional energy systems (Mc Kenney et al. 2011). Moreover, fast-growing *Populus* species and hybrids can be successfully grown in relatively cold climates; for example, aspens and aspen hybrids in northern Europe (Tullus et al. 2012).

In contrast to traditional forest cultivations, there was only a relatively small area of poplar plantations clustered in some countries in 1992 (Heilman 1999). Since then, this has increased substantially. According to an FAO report from 2000 (FAO 2000), the largest total area of poplar plantations was reported in China (about 6 million ha); only 100 000 ha in total were reported in six other countries (France, Hungary, Italy, Spain, Turkey and United States). In 2011, poplar plantations in Europe covered a total area of 940 200 ha (Coaloa and Nervo 2011). The fast increase in total area of poplar plantation is also related to political decisions and strategies; for example, the European Union directives which have forced increases in participation of renewable sources of energy within the national power balance. Most recently, in the Kwidzyn area (Poland), a consortium between International Paper Kwidzyn and GreenWood Resources has initiated the creation of a huge plantation of hybrid poplars for biomass production. This will reach a size of 25 000 ha and is the largest poplar plantation in Europe at the present time. In Oregon, the Boardman Tree Farm is other example of a 25 000-ha plantation of hybrid poplar operated by GreenWood Resources. Even larger plantations have been established in China, the first country in the world where genetically modified poplars have been used in large-scale programmes (Sigaud 1999). In other countries, including the United States and Europe, the use of genetically modified trees is allowed only for scientific purposes.

The possibility of negative environmental effects must also be considered because high water demand is a typical feature of poplars and can be a reason for disturbances at groundwater level (Perry et al. 2001). Moreover, isoprene emission from poplar plantations has been reported, which can have a severe impact on air quality and even regional climate (Kesselmaier and Staudt 1999). Detailed studies suggest that poplars can be particularly useful in buffer zones for wastewaters with high amounts of nitrogen and phosphorus (Guidi et al. 2008, Minogue et al. 2012). Poplars growing in coppices are usually treated as a crop. Thus, only selected cultivars are suitable, with the best ability to adapt to the local environmental conditions, the potential to reach the biggest biomass possible and the best quality of wood (Laureysens et al. 2004, Filat et al. 2010). The hybrids tested include transgenic poplars overexpressing xyloglucanase, which have enhanced growth rate in terms of stem length and diameter and produce wood with a higher specific gravity than the wild type (Yamamoto et al. 2011, Kaku et al. 2012), poplars in which isoprene emission was knocked down by RNA interference technology (*PcISPS*-RNAi plants) without decreasing growth and biomass (Behnke et al. 2012), poplars with suppressed cinnamyl alcohol dehydrogenase suitable for production of improved paper pulp (O'Connell et al. 2002), and poplars carrying insect-resistant genes (Ewald et al. 2006). Methods of poplar transformation are still being optimized (Nishiguchi et al. 2006, Yevtushenko and Misra 2010) in parallel with studies on preventing possible transgene outcrossing (Bialozyt 2012). Due to high tolerance to various toxic factors, poplars can be applied in phytoextraction and phytostabilization projects in areas contaminated by organic compounds or heavy metals (Burken and Schnoor 1999, Komárek et al. 2008). Moreover, phytoremediation by poplars can be enhanced by genetic modifications (Yadav et al. 2010, Dai et al. 2011), mycorrhizal associations (Tacács et al. 2005, Göhre and Paszkowski 2006) or other symbiotic organisms (Kang et al. 2012). A Belgian group has carried out comprehensive investigations on complex heavy metal uptake and accumulation in tissues in several clones of poplars in SRCs as well as their biomass production (Laureysens et al. 2005). Intensive studies are also being conducted to find new cultivars with the best features. In 2011, the Italian Poplar National Commission registered definitively 17 new cultivars and temporarily 11 new cultivars. Eleven other cultivars were being tested before registration (Italian Country Report for 24th session of IPC, Dehradun, India, 2012). An additional advantage of using poplars in remediation projects is that although the demand for water and nutrients is high, they are able to endure deficits better than willows, which is an advantage in polluted environments that are poor and often acidic (Benetka et al. 2002).

***Populus trichocarpa* as model tree for plant biology**

Studies on trees encounter numerous technical problems associated with specific features of trees: long lifespan, huge size and long period from seed to maturity. The differences between trees and herbaceous plants are so fundamental that it is not possible to use *Arabidopsis*, a commonly accepted model (i.e. a reference organism for all other organisms from a defined group) in plant biology, as a model for studies on trees (Prusinkiewicz 2004). Therefore, at the end of 20th century, it became clear that it would be desirable to choose a suitable tree model for forestry and plant biology. One of the first candidates was poplar with its characteristics features of rapid growth, prolific sexual reproduction, ease of cloning, small genome, facile transgenesis, and tight coupling between physiologic traits and biomass productivity (Bradshaw et al. 2000, Taylor 2002, Jansson and Douglas 2007).

In 2006, black cottonwood (*Populus trichocarpa*) became the first tree with a completely sequenced genome, gaining the status of a model tree species in genetics and molecular biology (Tuskan et al. 2006). It was chosen for its relatively small genome size (about 550 million base pairs, only four times larger than the genome of *Arabidopsis*), fast growth (for a tree) and other features allowing easy cultivation and ease of research with the possibility of mass vegetative reproduction and reaching reproductive maturity in 4–6 years. The project to sequence the poplar genome was a collaborative effort of the International *Populus* Genome Consortium with 34 institutions from around the world. Disclosure of the poplar genome opens new possibilities for a wide spectrum of studies, from genetics and molecular studies, to ecological studies, to investigation of large-scale systems. The number of publications on poplar topics has increased rapidly since the publication of the poplar's genome sequence (Figure 2).

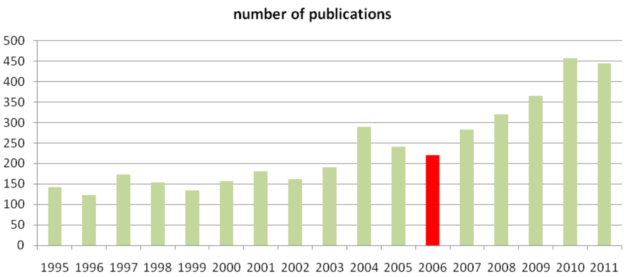

Figure 2. Number of publications with the word "poplar" or "populus" in the title, according to the Web of Knowledge database by Thomson Reuters (1995–2011)

The final version of the *P. trichocarpa* genome database (v3.0) including 73013 protein-coding transcripts is available online (http://www.phytozome.net/poplar/) as part of the Phytozome project performed to facilitate comparative genomic studies amongst green plants. Sequencing of the poplar genome facilitated other genetics studies: numerous genome-wide studies (Migeon et al. 2010, Petre et al. 2011, Liu et al. 2012), studies on characterization of genes with tissue-specific differential expression patterns (Segerman et al. 2007), computational study of the dynamics of long terminal repeat retrotransposons (Cossu et al. 2012) as well advanced genetic studies on poplars' tolerance to heavy metals (Induri et al. 2012).

Recently, some papers with more systemic research on poplars have appeared which could be considered as evidence of the increasing importance of the poplar model in biological sciences. One example is the andromonoecious poplar model used for studying sex-specific flower development in dioecious plants (Song et al. 2012). The reason for conducting this study was the increasing evidence that flower development is regulated epigenetically and especially through DNA methylation. In this study, screening for sex-specific DNA methylation alterations revealed 27 methylation sites. Three candidate regulatory genes were detected and a mechanism of their upregulation by methylation was proposed. The results suggested that DNA methylation sites have the potential to regulate the genes' transcript levels in poplars. Moreover, this can be a valuable starting point for understanding the mechanism of this type of regulation of gene expression. Recently, one of the first large-scale epigenomic studies on DNA cytosine methylation was conducted on poplar and striking differences in methylation between tissues at chromosome level, gene level and transposable elements were found (Vining et al. 2012).

Another interesting study on gene regulatory mechanisms focused on identification of *cis*-regulatory modules (CRMs) in *Arabidopsis* and *P. trichocarpa* as two model plant species with completely sequenced genomes (Ding et al. 2012). CRMs are short DNA sequences that contain multiple binding sites for transcription factors (TFs); there are known CRMs with binding sites for more than three TFs. Using the pattern mining-based approach, this work is the first extensive study on CRMs in plants. Previous CRM studies were limited to only a few families of TFs and considered only co-occurrence of binding sites of one or two TFs. Investigators have found over 18,000 combinations of two to six *cis*-regulatory sequences that are shared by *Arabidopsis* and cottonwood.

Among plant species, poplar currently has one of the best recognized miRNAs, small regulatory RNA molecules (20–24 nt) discovered in plants at the beginning of the 21st century (Sun et al. 2012). miRNAs can regulate a wide range of features of plants including development, metabolism, adaptation and evolution. The mechanism involves mediating post-transcriptional gene silencing and chromatin modification. There are 369 known mature miRNAs for *P. trichocarpa* (and 323 precursors) and five mature miRNAs for *P. euphratica* (and five precursors) in release 19 of miRBase (a searchable database of all published miRNA sequences and annotation; http://www.mirbase.org/). It is striking that many miRNA families from poplar are identical or very similar to *Arabidopsis* miRNAs, which shows their high conservatism (Lu et al. 2008).

Easy online access to poplar genome databases has led to fast progress in studies using other approaches based on genetics, such as advanced proteomic studies (Abraham et al. 2012) and metabolomics studies (Bylesjö et al. 2009, Robinson and Mansfield 2011). In addition to the genome of *P. trichocarpa*, EST databases from other poplars are available online, including ESTs from *P. nigra*, *P. tremula*, *P. trichocarpa × deltoides*, *P. tremula × deltoides*, *P. alba × tremula*, and *P. euphratica*. Also a poplar co-expression database for the genome-wide prediction of gene function based on poplar co-expression analysis was constructed and has been made available online (Ogata et al. 2009).

Somatic mosaicism of black cottonwood is the most recently exciting discovery, highly important for evolutionary studies. It was shown that in 11 clumps (clonal colonies propagated vegetatively and joined by roots) of *P. trichocarpa*, there are essential genetic differences between individuals as well as between roots, stems and leaves from a single tree (Olds et al. 2012). They found that the variation within a tree was the same as variation between trees. Thus, this changes a classic paradigm of evolutionary biology, which states that evolution happens only in populations and never at an individual level. The uniqueness of poplar as a model arises from the availability its genome sequence as well as long distances between tissues of the same individual, both in space (tree height) and time (long lifespan).

Perspectives

Poplars have played an increasing role in environmental, commercial and research projects in the past few decades. In addition to extremely rapid growth, the driving force for this phenomenon remains the great plasticity of poplars, understood as easy creation of hybrid clones with the desired properties and adaptations to the specific conditions. However, although ecologists', foresters' and scientists' focus on poplars has been independent so far, it seems that new challenges will force them to combine efforts. For example, poplar plantations can fall into the three-zone concept of riparian buffers (Welsch 1991).. Another example of functional diversification are poplar plantations established for phytostabilization of polluted soils unsuitable for agricultural production, where wood can be used for bioenergy/biofuel production. A major limitation here is the need to use clones, which have no pollutant translocation to the aboveground organs. As a result of scientific discovery and genetic engineering, other commercial opportunities will appear. The first sign is a report in which hybrid poplar is considered to be a suitable organism for large-scale and low-cost production of commercially important recombinant proteins, for example, xylanase from *Trichoderma reesei* (Kim et al. 2012). Perhaps we are close to realizing the vision whereby we will be able to establish riverside hybrid poplar forests (safe for native species) with combined functions of ecological buffer, recreational area, a source of high-performance green fuel and bioreactors producing proteins for the pharmacy or agriculture?

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