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REVIEW

Reflections on the contributions of *Populus* research at Rhinelander, Wisconsin, USA[1]

J.G. Isebrands and R.S. Zalesny Jr.

Abstract: The United States Department of Agriculture Forest Service established three regional Institutes of Forest Genetics in the United States in the 1950s to improve trees for reforestation and improve the management of forests. The institute in Rhinelander, Wisconsin, started in 1956 as part of the Lake States Forest Experiment Station. Since that time, the "Rhinelander Lab" has undergone changes in research priorities, organizational changes, and name changes while becoming an international center of forest scientific excellence. Many of the researchers' key findings over the years were published in the *Canadian Journal of Forest Research*. In this paper, for the 50th anniversary edition of the Journal, we reflect upon one part of those accomplishments: the history of the contributions of *Populus* L. research at Rhinelander. We discuss major research programs and the scientists conducting this work, including (*i*) physiology of wood formation, (*ii*) short rotation intensive culture and short rotation woody crops, (*iii*) intensively cultured plantations, (*iv*) physiology and utilization of short rotation poplar yields, (*v*) breeding and selection, (*vi*) biotechnology and molecular genetics, (*vii*) atmospheric pollution and climate change, (*viii*) phytotechnologies, and (*ix*) ecosystem services. Also, we describe four major international conferences held in Rhinelander and (or) hosted by Rhinelander researchers.

Key words: Aspen FACE, bioenergy, biofuels, biomass, carbon allocation, carbon dioxide, hybrid poplar, tropospheric ozone, photosynthesis, phyto-recurrent selection, phytoremediation, poplar silviculture, water use efficiency.

Résumé : Dans les années 1950, le Service des forêts du département de l'Agriculture des États-Unis a créé trois instituts régionaux de génétique forestière aux États-Unis pour l'amélioration des arbres destinés au reboisement et pour améliorer l'aménagement des forêts. L'institut situé à Rhinelander, au Wisconsin, a été mis sur pied en 1956 en tant qu'organisme affilié au Lake States Forest Experiment Station. Depuis ce temps, le laboratoire de Rhinelander a connu des changements dans ses priorités de recherche, des changements organisationnels et des changements de nom tout en devenant un centre international d'excellence scientifique en foresterie. Au cours des années plusieurs résultats clés des chercheurs ont été publiés dans la *Revue canadienne de recherche forestière*. À l'occasion du 50e anniversaire de publication de la Revue, nous nous penchons dans cet article sur une facette de ces accomplissements : l'histoire des contributions à la recherche sur *Populus* L. à Rhinelander. Nous traitons des principaux programmes de recherche et des scientifiques qui effectuent ce travail, incluant : (*i*) la physiologie de la formation du bois, (*ii*) la culture intensive à courte rotation et la ligniculture à rotation courte, (*iii*) les plantations en culture intensive, (*iv*) la physiologie et l'utilisation de la production de peuplier à courte rotation, (*v*) la reproduction et la sélection, (*vi*) la biotechnologie et la génétique moléculaire, (*vii*) la pollution atmosphérique et le changement climatique, (*viii*) les phytotechnologies, et (*ix*) les services de l'écosystème. De plus, nous décrivons quatre conférences internationales majeures tenues à Rhinelander et organisées par les chercheurs de Rhinelander. [Traduit par la Rédaction]

Mots-clés : système expérimental d'enrichissement en dioxyde de carbone à l'air libre, bioénergie, biocarburant, biomasse, allocation du carbone, dioxyde de carbone, peuplier hybride, ozone troposphérique, photosynthèse, sélection phytorécurrente, phytoremédiation, sylviculture du peuplier, efficacité de l'utilisation de l'eau.

Introduction

At the end of the 19th century and beginning of the 20th century, the forests of the northern Lake States of the United States were heavily logged for lumber for rapidly expanding eastern cities (Rudolf 1985). World War I interrupted reforestation that took place in the beginning of the century. Additional reforestation began in the 1930s during the economic depression but was interrupted by World War II. During the postwar era, a second and third wave of cutting occurred to support the paper industry, leaving a massive denuded forest landscape (Rudolf 1985). After the wars, there was a major emphasis on fighting hunger in the world through plant genetics called the Green Revolution, led by Nobel laureate N.E. Borlaug (Borlaug 2007). His success soon carried over to forestry, with an emphasis on improving trees and forests for reforestation and forest management (Wheeler et al. 2015).

Successes in agriculture led the United States Department of Agriculture Forest Service (USDA FS) to establish three new regional Institutes of Forest Genetics in the United States in the 1950s. These institutes were in Placerville, California; Gulfport, Mississippi; and Rhinelander, Wisconsin. The mission of these institutes was to conduct studies to improve trees for reforestation

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Table 1. Timeline of major milestones at the United States Department of Agriculture Forest Service (USDA FS), Forestry Sciences Laboratory in Rhinelander, Wisconsin, organized by *Populus* research programs, projects, or lines of science and scientist(s) (as highlighted in this paper).

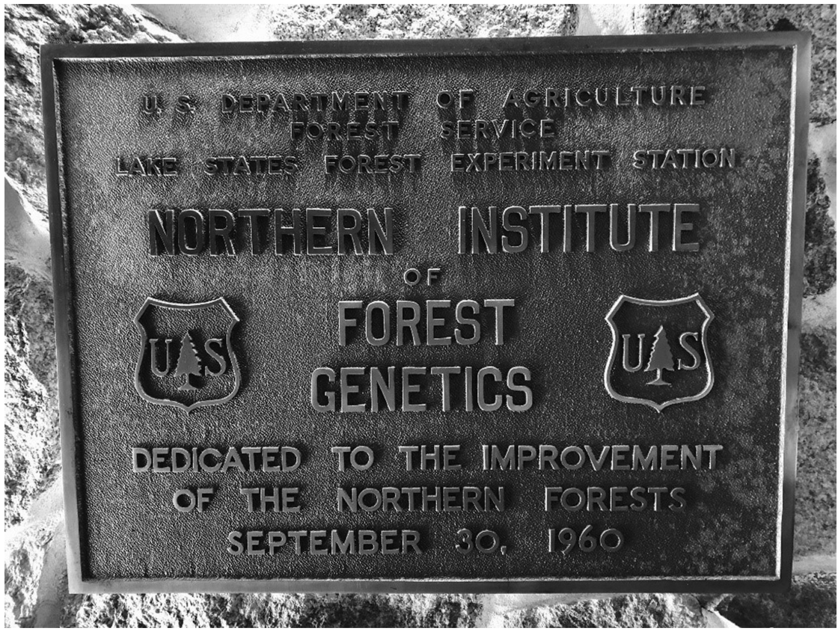
Year	Milestone	Scientist(s)
Project: Genetics of Northern Forest Trees		
1956	Institute of Forest Genetics (IFG) established in Rhinelander, Wisconsin	H. Nienstaedt, P.R. Larson
1957	Greenhouse (headhouse) erected at current site	H. Nienstaedt, P.R. Larson
1960	Main laboratory building erected	H. Nienstaedt, P.R. Larson
1964	B.E. Haissig joined H. Nienstaedt's genetics project	B.E. Haissig
1966	USDA FS reorganized Forest Experiment Stations; Rhinelander IFG became part of North Central Forest Experiment Station; renamed Forestry Sciences Laboratory	
Project: Physiology of Wood Formation		
1962	P.R. Larson awarded first Pioneering Scientist status; new wood formation project established	P.R. Larson
1965	J.C. Gordon joined P.R. Larson's wood formation project	J.C. Gordon
1968	J.G. Isebrands joined P.R. Larson's wood formation project	J.G. Isebrands
1969	D.I. Dickmann joined P.R. Larson's wood formation project	D.I. Dickmann
1970	R.E. Dickson replaced J.C. Gordon and joined P.R. Larson's wood formation project	R.E. Dickson
1971	P.R. Larson and J.G. Isebrands published first-ever paper in the *Canadian Journal of Forest Research* (Larson and Isebrands 1971)	P.R. Larson, J.G. Isebrands
Program: Maximum Yield and Intensive Culture of Planted Stands		
1971	D.H. Dawson became Program Manager of new maximum yield program	D.H. Dawson
1971	J. Zavitkovski joined D.H. Dawson's maximum yield program	J. Zavitkovski
1972	US Department of Energy (USDOE) partnered with USDA FS on short rotation woody crop (SRWC) development; Harshaw Experimental Farm purchased in Harshaw, Wisconsin	D.H. Dawson
1977	Two new projects added to D.H. Dawson's maximum yield program: (*i*) Intensively Cultured Plantations for Fiber and Energy led by J. Zavitkovski and (*ii*) Physiology and Raw Material Evaluation of Intensively Cultured Plantations led by J.G. Isebrands	D.H. Dawson, J. Zavitkovski, J.G. Isebrands
1983	USDA FS poplar research projects closed or temporarily phased out; poplar research continued with USDOE funding	D.H. Dawson
Project: Intensively Cultured Plantations for Fiber and Energy		
1983	E.A. Hansen assumed leadership of J. Zavitkovski's fiber and energy project	E.A. Hansen
Late 1980s – early 1990s	E.A. Hansen and D.A. Netzer established regional field testing network	E.A. Hansen, D.A. Netzer
Project: Physiology and Raw Material Evaluation of Intensively Cultured Plantations		
1982	North American Poplar Council Meeting held in Rhinelander (Table 2)	J.G. Isebrands
Late 1970s – early 1980s	N.D. Nelson, J.B. Crist, and J.E. Phelps joined J.G. Isebrands' physiology and raw material project	N.D. Nelson, J.B. Crist, J.E. Phelps
1985–1986	J.G. Isebrands went on sabbatical at University of Washington; collaborated with world-renowned poplar researchers and graduate students who become world leaders in poplar development; later applied information learned to the North Central region	J.G. Isebrands, R.F. Stettler, P.E. Heilman, R. Ceulemans, G.E. Scarascia-Mugnozza, A.L. Friend, T.M. Hinckley
Program: Biotechnology		
1983	N.D. Nelson left J.G. Isebrands' physiology and raw material project and became Program Manager of new biotechnology program	N.D. Nelson
1983	B.E. Haissig joined N.D. Nelson's biotechnology program as the Project Leader and lead scientist	B.E. Haissig
1983–1984	D.E. Riemenschneider and C.H. Michler joined N.D. Nelson's biotechnology program	D.E. Riemenschneider, C.H. Michler
1992	R.A. Donahue joined N.D. Nelson's biotechnology program	R.A. Donahue
2000	Biotechnology research ended at Rhinelander	
Project: Ecophysiological Processes of Northern Forest Ecosystems		
1986	J.G. Isebrands became Project Leader of new project on the establishment and early growth of northern forest species (at the time, no poplar focus)	J.G. Isebrands
1986	R.E. Dickson joined J.G. Isebrands' ecophysiological processes project	R.E. Dickson
1989	IUFRO Canopy Processes Working Party 20.010.12 Meeting held in Rhinelander (Table 2)	J.G. Isebrands
1990	M.D. Coleman joined J.G. Isebrands' ecophysiological processes project	M.D. Coleman

Table 1 (*concluded*).

Year	Milestone	Scientist(s)
1991	J.G. Isebrands' northern forest species project was rebranded as the Ecophysiological Processes of Northern Forest Ecosystems to include poplars, atmospheric pollution, and climate change	J.G. Isebrands
1992	D.E. Riemenschneider joined J.G. Isebrands' ecophysiological processes project and led USDA FS contributions to regional tree improvement efforts, including partnerships with regional and national poplar experts (ongoing until 1998, when D.E. Riemenschneider led new project on sustainable intensive forestry)	D.E. Riemenschneider, R.B. Hall, B.G. McMahon, B.J. Stanton
Project: Physiological Mechanisms of Growth and Multiple Stress Responses		
1992	J.G. Isebrands became Project Leader of new project on physiological mechanisms of growth and multiple stress responses	J.G. Isebrands
1992	R.E. Dickson joined J.G. Isebrands' physiological mechanisms project	R.E. Dickson
1992	USDOE began funding research on physiological process modeling of poplars	J.G. Isebrands
1995	R.S. Zalesny Jr. joined J.G. Isebrands' physiological mechanisms project	R.S. Zalesny Jr.
1995	Free-Air Carbon Dioxide Enrichment (aka Aspen FACE) experiment established at the Harshaw Experimental Farm	J.G. Isebrands, R.E. Dickson, M.D. Coleman, D.F. Karnosky
2000	IPC 2000, 21st Session of the International Poplar Commission held in Vancouver, Washington, and hosted by J.G. Isebrands	J.G. Isebrands
Early 2000s	M.E. Kubiske assumed leadership of J.G. Isebrands' physiological mechanisms project	M.E. Kubiske
2004	N.D. Nelson returned to the USDA FS and assumed leadership of M.E. Kubiske's physiological mechanisms project and Aspen FACE experiment	N.D. Nelson
Project: Genetic and Silvicultural Systems for Sustainable Intensive Forestry		
1998	D.E. Riemenschneider became Project Leader of new project on genetics and silvicultural systems for sustainable intensive forestry	D.E. Riemenschneider
1998	R.S. Zalesny Jr. joined D.E. Riemenschneider's intensive forestry project	R.S. Zalesny Jr.
1998–2002	D.E. Riemenschneider continued USDA FS leadership in regional poplar improvement efforts	D.E. Riemenschneider, R.S. Zalesny Jr., R.B. Hall, B.G. McMahon, A.A. Mahama, W. Berguson
Lines of Science: Phytotechnologies and Ecosystem Services		
1999	Phytotechnologies research began at the Lab; collaboration with L.M. Westphal in Chicago, Illinois	J.G. Isebrands, L.M. Westphal
1999	First long-term, field-based phytotechnologies project at Rhinelander (former City of Rhinelander Landfill)	J.G. Isebrands, D.E. Riemenshneider, E.O. Bauer, R.S. Zalesny Jr.
2003	Second long-term, field-based phytotechnologies project at Rhinelander (Oneida County Landfill)	R.S. Zalesny Jr.
2008–present	R.S. Zalesny Jr. assumed leadership of SRWCs lines of science; priorities shifted from biomass production to phytotechnologies and ecosystem services	R.S. Zalesny Jr.
2016–present	With support from the Great Lakes Restoration Initiative (GLRI), R.S. Zalesny Jr. established a regional phytotechnologies network consisting of 16 phytoremediation buffer systems (i.e., phyto buffers) in Lake Superior and Lake Michigan watersheds; this is largest known replicated phytotechnologies field experiment in the world	R.S. Zalesny Jr.
2018	2018 Woody Crops International Conference held in Rhinelander (Table 2)	R.S. Zalesny Jr.
Project: Institute for Applied Ecosystem Studies		
2007	USDA FS North Central and Northeastern Research Stations merged to establish USDA FS Northern Research Station; N.D. Nelson became Project Leader of new integrated project: the Institute for Applied Ecosystem Studies; SRWCs major research line of science within the Institute	D.E. Riemenschneider, N.D. Nelson, D.A. Netzer, R.S. Zalesny Jr.
2009	M.E. Kubiske oversaw full-scale harvest of Aspen FACE experiment	M.E. Kubiske
2010	Aspen FACE experiment ended	M.E. Kubiske
2011–2020	E.J. Gustafson led efforts to scale Aspen FACE results to larger temporal and spatial scales	E.J. Gustafson

and improve the management of forests. In Rhinelander, the locally known Forest Genetics Lab (hereafter referred to as the Lab), which was part of the USDA FS Lake States Forest Experiment Station, was established in 1956 in a single rented office in a local bank building (Table 1). The first staff members were two forest scientists trained at Yale University: H. Nienstaedt, a geneticist from Denmark, and P.R. Larson, a plant physiologist and former World War II Navy fighter pilot from Minnesota. In 1957, a greenhouse (headhouse) was erected on administrative lands of the Nicolet National Forest west of Rhinelander with financial support from the Rhinelander

Fig. 1. Plaque commemorating the establishment of the United States Department of Agriculture Forest Service (USDA FS), Lake States Forest Experiment Station, Northern Institute of Forest Genetics in Rhinelander, Wisconsin, USA, on 30 September 1960. The plaque is still mounted on the wall of the facility. Photograph taken by E.R. Rogers and used with permission.



Paper Company. The main laboratory building was erected in 1960 (Rudolf 1985) (Fig. 1).

Since 1960, USDA FS research programs have undergone a series of mission changes that reflect budget allocations according to national forestry priorities, as well as politics and economics. For example, there has been a decrease in forest products harvesting and an increase in wilderness, and endangered forest ecosystem preservation along with a major increase in recreational use on National Forests. At the same time, there has been an interrelated change in forest economics as international trade of forest products has increased. The Institute of Forest Genetics in Placerville remains today with the same name and is part of the USDA FS Pacific Southwest Research Station; climate change, biodiversity, and ecosystem services are the Institute's focus. The facility of the Institute of Forest Genetics in Gulfport has been closed because of budget priorities; however, the Institute remains part of the USDA FS Southern Research Station located at the Harrison Experimental Forest north of Gulfport. The Lab in Rhinelander remains today after a series of building additions (Fig. 2), organizational changes, and name changes while becoming known internationally as a center of forest scientific excellence. Much of the early extensive forest science accomplishments produced at the Lab were published in the *Canadian Journal of Forest Research*. In this paper, for the 50th anniversary edition of the Journal, we reflect upon one part of those accomplishments: the history of the contributions of *Populus* L. research and the USDA FS scientists behind this research at Rhinelander.

Physiology of wood formation

In the early years, the primary research program focused on the "Genetics of Northern Forest Trees". That focus began to change over time as tree planting in the North Central region of the United States declined markedly. Few of the improved *Picea* A. Dietr., *Pinus* L., *Larix* Mill., *Betula* L., or *Quercus* L. trees developed by Lab scientists were planted. Nevertheless, Larson's lines of science shifted as his innovative thesis work on the effects of tree crowns on wood formation in southern pines soon became known internationally (Larson 1962, 1963). In recognition of this cutting-edge research, USDA FS Research and Development awarded Larson the first agencywide "pioneering scientist" designation in 1962. This status gave Larson creative liberty to pursue new lines of science, and the "Physiology of Wood Formation" project was born. This project laid the foundation for expanding the Lab's personnel and plant physiology laboratory capabilities. Based on scientific findings from agriculture, Larson's initial research focused on the association between how leaves and the photosynthetic surface area are intimately associated with tree growth and productivity (Milthorpe 1956).

Larson first studied wood formation in naturally occurring and planted larches (*Larix* spp.) and red pine (*Pinus resinosa* Aiton) in the Lake States. In 1965, J.C. Gordon, a biochemistry-trained plant physiologist from Iowa State University, was the first scientist to join the project. They first published on photosynthetic properties of red pine (Gordon and Larson 1968). However, their research focus switched in response to national trends towards planting faster-growing deciduous genera such as *Platanus* L. (planetrees such as American sycamores) and *Populus* (cottonwoods, poplars, aspens, and their hybrids; hereafter referred to as poplars) (McAlpine et al. 1966; Schreiner 1970). They chose the genus *Populus* because of its rapid growth, ease of propagation, and wide natural range. Their first publication on poplars was on leaf development and photosynthesis in eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall) because those physiological properties influenced productivity (Larson and Gordon 1969*a*). That same year, Larson and Gordon published a pivotal paper on how a physiological approach could be used to increase wood yield per hectare (Larson and Gordon 1969*b*). This new approach formed the scientific groundwork for the future establishment of the multiproject research program named "Short Rotation Intensive Culture" at the Lab, discussed in the next section.

In 1968, the "Physiology of Wood Formation" project expanded to include anatomical investigations. At that time, J.G. Isebrands, who was trained on the physiology of wood formation and microscopy at Iowa State University and the USDA FS Forest Products

Fig. 2. USDA FS, Forestry Sciences Laboratory in Rhinelander, Wisconsin, USA, in 1990 (upper photograph) and 2000 (lower photograph). Photographs courtesy of J.G. Isebrands.

Laboratory in Madison, Wisconsin, joined the team. Isebrands and Larson developed a method to standardize trees at different developmental stages across trees and studies and to predict developmental processes nondestructively for poplars. The method, inspired by Erickson and Michelini (1957), was called leaf plastochron index, known as LPI. Around this time, J.L. Farrar of the University of Toronto asked Larson if he had any work ready for publishing in his new scientific journal, the *Canadian Journal of Forest Research*. A description of the LPI method was published as the first article in the Journal (Larson and Isebrands 1971), and poplar scientists have continued to use the index extensively around the world ever since.

One of the initial scientists to use the LPI for poplar study was Larson's first postdoctoral scientist, D.I. Dickmann from the University of Wisconsin – Madison. Dickmann conducted worked on photosynthesis of the developing leaf zone of cottonwood (Dickmann 1971*a*, 1971*b*) during his tenure at the Lab from 1969 to 1970. After leaving the Lab, he devoted his career to the study of poplar physiology and culture at Iowa State University and then at Michigan State University. He authored two books on poplar culture (Dickmann and Stuart 1983; Dickmann et al. 2001) and a major review of the silviculture and biology of short rotation woody crops (SRWCs) (Dickmann 2006) and became a worldwide authority on poplar taxonomy (Dickmann and Kuzovkina 2014).

In 1970, the Lab's physiology research expanded to investigations of source–sink (Dickson and Larson 1975) and carbon–nitrogen (Dickson 1987) relations in poplar with the addition of R.E. Dickson, a biochemistry-trained physiologist from the University of California – Berkeley, who replaced Gordon. At that time, Gordon left the USDA FS to pursue an academic career at Iowa State University, Oregon State University, and Yale University, where he eventually became the Dean of the Yale School of Forestry. Gordon continued to publish about poplar physiology and culture throughout his career (Gordon 1975, 2001). Dickson was in Larson's project until 1984. Over the years, Isebrands and Larson published extensively on the anatomy of the primary–secondary word formation in stems of cottonwood (Larson and Isebrands 1974) and the ontogeny of vascular traces in cottonwood leaves in relation to the stem (Isebrands and Larson 1980). Isebrands left in 1977 to establish a new project at the Lab on the "Physiology of Yield in Poplars".

In his remaining years with the USDA FS, Larson studied the establishment of the early vascular system in cottonwood seedlings (Larson 1979) and the interrelations of phyllotaxis of leaf development to the primary–secondary transition zone in cottonwood (Isebrands and Larson 1980). He also mentored numerous postdoctoral scientists studying the vascularization of other plant species, with emphasis on the relationships of leaf development to wood formation (Larson 1985). After retirement in 1986, Larson spent a number of years writing a treatise on the vascular cambium and its development and structure (Larson 1994). The book remains the most comprehensive review on the cambium to date and summarizes his lifelong research on the subject.

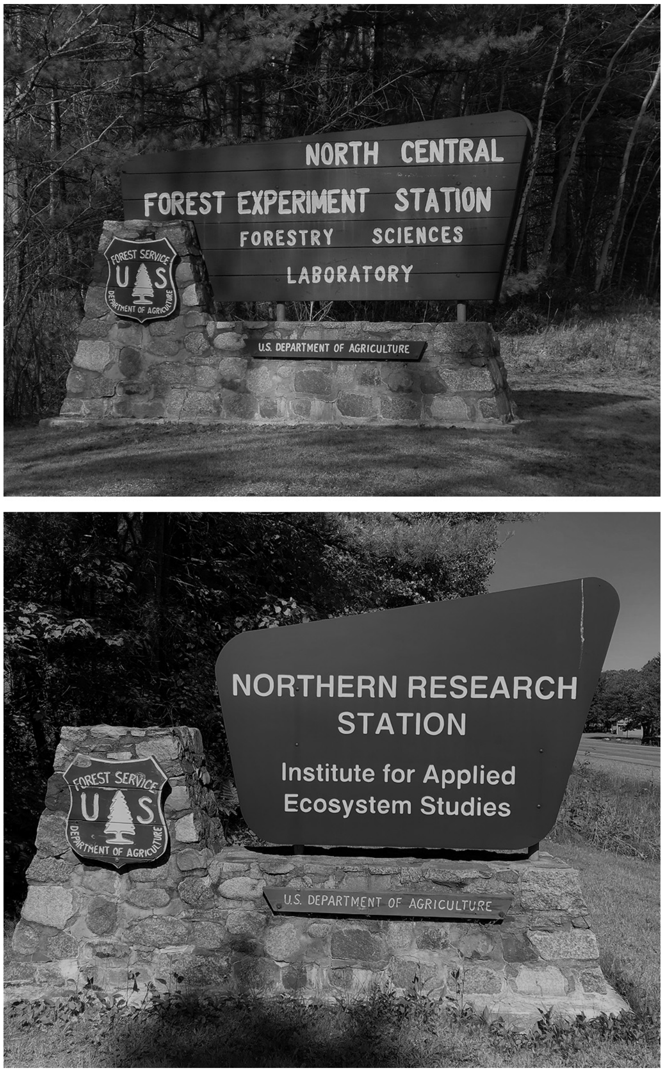
Short rotation intensive culture and short rotation woody crops

In 1966, the USDA FS reorganized their Forest Experiment Stations, and the Rhinelander Institute of Forest Genetics became part of the North Central Forest Experiment Station (USDA FS NCFES) and was later renamed the Forestry Sciences Laboratory (Fig. 3) to reflect its broader national mission. In the early 1970s, there was a projected wood shortage in the United States because demand for wood was greater than what was being produced in forests, and more forest lands were being set aside for other uses. As a result, in 1971, the USDA FS NCFES created a multiproject research program named "Maximum Yield and Intensive Culture of Planted Stands" at the Lab. The program's mission was to explore the potential of short rotation intensively managed tree plantings for maximum commercial wood production per hectare. Scientists from multiple disciplines were involved, including genetics, physiology, silviculture, pathology, economics, and mensuration. The program mission was based upon the concept of improving the efficiency of wood formation through physiology and genetics principles as in agronomic crops outlined by Larson and Gordon (1969*b*). This approach was also being tested in other parts of the United States and Canada (McAlpine et al. 1966; Smith and Blom 1966; Schreiner 1970; Heilman et al. 1972).

D.H. Dawson, a tree geneticist from the "Genetics of Northern Forest Trees" project at the Lab who was trained at Michigan State University, became the program manager. The objectives of the early studies were to test if selected woody species could be grown under optimum conditions of water, nutrients, and weed control at close spacing to produce more wood per hectare over time than traditional forest management systems (USDA FS 1976). The first species tested were jack pine (*Pinus banksiana* Lamb.), tamarack (*Larix laricina* (Du Roi) K. Koch), and hybrid poplars. The conifers were from local improved seed sources, and the hybrid poplars were imported from poplar programs in Saskatchewan and Ontario, Canada (Richardson et al. 2007). The first experimental plantings were established in small plots in the nearby Hugo Sauer Nursery in Rhinelander. The first scientist assigned to the project was J. Zavitkovski, a plant ecologist from the former Czechoslovakia.

In 1972 and 1973, there was a worldwide oil embargo that increased the need for producing woody biomass from SRWCs for wood and energy. The shortage of oil during this time led

Fig. 3. Signs of the USDA FS, North Central Forest Experiment Station, Forestry Sciences Laboratory (upper photograph; taken by R.S. Zalesny Jr.) and Northern Research Station, Institute for Applied Ecosystem Studies (lower photograph; taken by E.R. Rogers and used with permission) in Rhinelander, Wisconsin, USA.



multiple government agencies to initiate new research on alternative energy sources from woody biomass. Thus, the United States Department of Energy (USDOE) became involved with the ongoing USDA FS research program on SRWCs at the Lab. With USDOE's support, in 1972, the USDA FS purchased the Harshaw Experimental Farm (currently the West Unit of the Rhinelander Experimental Forest) located 20 km west of the Lab to establish larger experimental plantings. This cooperative venture was the beginning of a long-term partnership with USDOE in the study of SRWCs. The USDOE SRWCs program was initially administered by the Biomass Production Program, which was later renamed as the Biomass Feedstock Development Program at Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Wood production was promising based on small plot trials in the first 5 years, and poplars were the most productive (USDA FS 1976; Zavitkovski et al. 1976). However, there were many questions yet to be answered, including the choice of which poplar genotypes to plant, tree spacing, insect and disease issues, utilization of juvenile woody material, and economics. To address these knowledge gaps, in 1977, the USDA FS NCFES established two cooperating research projects at the Lab under the direction of Program Manager Dawson. The projects were "Intensively Cultured Plantations for Fiber and Energy" directed by Zavitkovski and "Physiology and Raw Material Evaluation of Intensively Cultured Plantations" directed by Isebrands.

Intensively cultured plantations

The new "Intensively Cultured Plantations" project was established to identify silvicultural prescriptions that would increase yield of poplars grown for fiber and energy. Early work of the project focused on optimal spacing, vegetation management, fertilization, and managing for pests and insects, under the direction of Zavitkovski. His findings on the extent of "edge effects" of small poplar research trials are still used to inform research and applications (Zavitkovski 1981). In 1983, E.A. Hansen, a research forester at the Lab, took over leadership of the project and, starting in 1987, expanded Zavitkovski's foundational research. In particular, Hansen and D.A. Netzer, a research forester at the Lab, established regional field testing networks throughout Minnesota, Iowa, Wisconsin, and Michigan, which took place through the early 1990s. Many poplar researchers from the Lab reported field performance from these plantings at various stages of development (Hansen 1991, 1992; Hansen et al. 1994; Netzer et al. 2002). These biomass systems, originally established to test their potential as bioenergy feedstocks, were later sampled for evaluations of ecosystem services (see Ecosystem services). In addition to continuing assessments of edge effects (Hansen 1981), optimal spacing (Strong and Hansen 1993), harvest cycles (Strong 1989; Tolsted and Hansen 1992), and other silvicultural prescriptions at field scale (Hansen et al. 1993; Hansen 1994), Hansen's work also focused on genotype × environment interactions and the identification of geographically robust genotypes versus those that were better adapted to particular supplysheds. Coupled with existing poplar breeding programs at the University of Illinois (led by J. Jokela) and the University of Minnesota (led by C. Mohn), information on the regional performance of poplar clones provided by these institutions formed the basis of future poplar breeding and selection that is described in the Breeding and selection section of this paper.

Physiology and utilization of short rotation poplar yields

The goals of the new project on "Physiology and Raw Material Evaluation of Intensively Cultured Plantations" were based on the premise that understanding how poplars grow would allow researchers to improve their yield (Kramer 1956). Another objective was to maximize the harvestable yields into useable end products. These objectives were a major focus of the North American Poplar Council Meeting held in Rhinelander in 1982, which was one of four major international conferences hosted by Lab scientists (Table 2).

The project began with a focus on understanding the relationship of poplar leaf production and photosynthetic processes to wood yields outlined by Larson and Isebrands (1972). The first scientist to join the project was N.D. Nelson, a plant physiologist who trained at the University of Wisconsin – Madison and transferred from the USDA FS Forest Products Laboratory. Soon after, J.B. Crist, a wood scientist who trained at Virginia Tech University and transferred from the Economics Unit at the USDA FS NCFES in Duluth, Minnesota, joined the team, followed by a postdoctoral wood scientist, J.E. Phelps from the University of Missouri.

Nelson's work focused on photosynthesis, photosynthate production, and leaf area development under controlled environments and field conditions. He demonstrated important differences in photosynthetic processes across these controlled and natural settings (Nelson and Ehlers 1984). Nelson and Isebrands also studied crown architecture of poplars in relation to productivity (Nelson

Table 2. Scientific conferences that had substantial leadership from the USDA FS, Forestry Sciences Laboratory in Rhinelander, Wisconsin.

North American Poplar Council Meeting, 20–22 July 1982, Rhinelander, Wisconsin, USA	
Sponsors	Poplar Council of North America (Canada, United States); USDA FS, North Central Forest Experiment Station
Goal	Provide a forum for North American poplar researchers to share their latest research results
Theme	Improving Cottonwood and Hybrid Poplar Plantings for Wood and Energy
Technical sessions	(*i*) Planting poplars, (*ii*) maintaining poplars, (*iii*) growth and yield, (*iv*) coppicing, (*v*) insect and disease problems, (*vi*) harvesting, (*vii*) utilization potential, (*viii*) biomass and energy, and (*ix*) economics of energy plantings
Fast facts	25 presentations
Published outputs	Zavitkovski and Hansen (1982)
IUFRO Canopy Processes Working Party Meeting, 25–29 September 1989, Rhinelander, Wisconsin, USA	
Sponsors	International Union of Forest Research Organizations (IUFRO) Working Party 20.010.12 (Canopy Processes); USDA FS, North Central Forest Experiment Station
Goal	Review research on structure–functional relationships in tree crowns and canopies to better understand processes of tree and forest growth
Theme	Dynamics of Ecophysiological Processes in Tree Crowns and Forest Canopies
Technical sessions	(*i*) Crown architecture and canopy structure, (*ii*) structure–functional relationships of branches, (*iii*) photosynthesis and respiration of tree crowns, (*iv*) carbon allocation and budgets, (*v*) carbon and nitrogen interactions in tree crowns, and (*vi*) stress effects on crown processes (including pests)
Fast facts	27 conference papers published as 7th volume of *Tree Physiology*; 3-day field tour of Wisconsin forest ecotypes
Published outputs	Isebrands et al. (1990)
IPC 2000, 21st Session of the International Poplar Commission, 24–28 September 2000, Vancouver, Washington, USA (hosted by the Rhinelander Lab)	
Sponsors	International Poplar Commission (IPC) of the Food and Agriculture Organization (FAO) of the United Nations; Poplar Council of the United States; Poplar Council of Canada; Canadian Forest Service; USDA FS
Goal	Disseminate research results and highlight research activities on poplar and willow breeding, diseases, insects, production, and utilization
Theme	Poplar and Willow Culture: Meeting the Needs of Society and the Environment
Technical sessions	(*i*) Poplar and willow genetics, conservation, and improvement; (*ii*) poplar and willow diseases; (*iii*) poplar and willow insect and animal pests; (*iv*) production systems and environmental applications for poplars and willows; and (*v*) logging and utilization of poplar and willow wood
Fast facts	220 presentations; 250 participants from 31 countries; 12 papers published in special issue of *The Forestry Chronicle*; two books published
Published outputs	Isebrands and Richardson (2000, 2001, 2014); Dickmann et al. (2001)
2018 Woody Crops International Conference, 22–27 July 2018, Rhinelander, Wisconsin, USA	
Sponsors	Short Rotation Woody Crops Operations Working Group; Poplar and Willow Council of Canada (led by R.Y. Soolanayakanahally (Saskatoon Research and Development Centre, Saskatoon, Saskatchewan, Canada) and J. Richardson (Poplar and Willow Council of Canada, Ottawa, Ontario, Canada)); IUFRO Working Party 20.080.04 (Physiology and Genetics of Poplars and Willows); IUFRO Working Party 10.030.00 (Short Rotation Forestry); International Energy Agency Task 43 (Biomass Feedstocks for Energy Markets); IPC FAO Environmental and Ecosystem Services Working Party (WP5); USDA FS, Northern Research Station
Goal	Unite world-leading SRWC researchers at a forum designed to enhance information exchange while also building a platform for developing future collaboration around SRWC production systems
Theme	Short Rotation Woody Crop Production Systems for Ecosystem Services and Phytotechnologies
Technical sessions	(*i*) Genetics and physiology; (*ii*) phytotechnologies; (*iii*) stakeholders, bioproducts, harvesting, and logistics; (*iv*) biomass production; and (*v*) ecosystem services
Fast facts	38 presentations; 80 participants from nine countries; 38 abstracts and 16 papers published in special issue of *Forests* (as manuscripts and compiled into a book); technical plenary presentations from four international speakers (B.R. Thomas (University of Alberta, Alberta, Edmonton, Canada); A. Pilipović (University of Novi Sad, Novi Sad, Serbia); J. Van Acker (University of Ghent, Ghent, Belgium); B. Kulišić (Energy Institute Hrvoje Požar, Zagreb, Croatia)); dinner keynote on the history of *Populus* at the Rhinelander Lab (i.e., the basis of this current paper) (J.G. Isebrands, Environmental Forestry Consultants, New London, Wisconsin, USA); 2-day poplar tree improvement preconference tour in Minnesota; 3-day phytotechnologies postconference tour in Wisconsin
Published outputs	Zalesny et al. (2020); Gardiner et al. (2018)

et al. 1981; Isebrands and Nelson 1982). High growth rate in poplars was attributed to elevated photosynthetic rates, leaf area index, and late-season leaf retention resulting in high annual whole-tree photosynthesis (Nelson and Isebrands 1983). An important development during this work was adapting laboratory radiotracer methods for field studies of photosynthate distribution in poplars. A synopsis of their work on yield physiology in short rotation poplars was published (Isebrands et al. 1983). Nelson left the project in 1983 to pursue biotechnology leadership opportunities at the Lab (see Biotechnology and molecular genetics).

The forest products industry at the time was concerned that wood produced from short rotation poplar systems would not be acceptable for many traditional products because of the high percentage of juvenile wood and bark of the harvested material. Industrial specialists also were concerned that piece size was too small for those products, which was not as important for those using the wood for alternative energy uses. However, bark content, moisture content, and density of the wood were still a concern. Isebrands et al. (1979) outlined alternatives for the integrated utilization of short rotation poplar raw materials, including biomass for energy. Phelps (1983) reviewed the potential of biomass products from short rotation poplars for energy, chemical, and nutritional feedstocks. Crist (1983) gave a synopsis of the overall suitability of short rotation-grown poplar material for industry, and he determined that wood from these plantings was suitable for most reconstituted end products. Short rotation poplar raw materials had promising potential as alternative biomass products, but they were not yet economical. Isebrands later reviewed the worldwide potential of poplar bioenergy systems (Rockwood et al. 2012).

In 1983, USDA FS poplar research projects closed or were temporarily phased out because of budgetary constraints. However, research on short rotation poplars continued at the Lab with USDOE funding. During this time, Isebrands joined the USDOE-funded poplar program headed by R.F. Stettler and P.E. Heilman at the University of Washington and Washington State University in the Pacific Northwest while on sabbatical leave from the USDA FS. During this time, his research focused on the physiological genetics of poplar genotypes produced by the Stettler–Heilman team that proved to be very productive when grown under short-rotation intensive culture (Stettler et al. 1988). Isebrands brought this knowledge to the Lab to help develop similar production systems in the North Central region.

The first studies investigated genetic variation of photosynthetic traits among poplar clones in relation to yield, which Isebrands conducted with visiting scientist R. Ceulemans from Belgium (Isebrands et al. 1988). Studies expanded into carbon allocation patterns in the Stettler–Heilman poplar clones by using field radiotracer methods developed at the Lab (Isebrands and Dickson 1991). Genetic variation in crown architecture and photosynthetic processes in the clones made them amenable to selection and breeding for specific applications (Ceulemans et al. 1992; Ceulemans and Isebrands 1996). Field studies of photosynthate distribution from sylleptic branches in poplar clones were also conducted with G.E. Scarascia-Mugnozza, a PhD student from Italy. This research showed that clones with high numbers of sylleptics were more productive than others because sylleptics exported more carbon to the stem and roots (Scarascia-Mugnozza et al. 1997, 1999). A.L. Friend, who is the current Deputy Chief of USDA FS Research and Development, used the same field radiotracer methods to quantify distribution to roots in poplar clones (Friend et al. 1991). T.M. Hinckley published a synopsis of the basis for the poplar physiology studies being conducted by the University of Washington and Washington State University scientists and colleagues (Hinckley et al. 1989).

Poplar research continued collaboratively with the Washington colleagues after Isebrands returned to the Lab in 1986 (Isebrands et al. 1990; Scarascia-Mugnozza et al. 1994). Isebrands continued these partnerships throughout his career, after Ceulemans returned to Belgium where he became Professor at the University of Antwerp and Scarascia-Mugnozza returned to Italy and became Professor at the University of Tuscia – Viterbo; both have worked on European poplar physiology and culture throughout their careers. In particular, Scarascia-Mugnozza was the lead investigator on Italy's short rotation poplar program, which included poplar genetics, biomass production, climate change, and phytoremediation. Likewise, Ceulemans became one of the European Union's lead scientists on using short rotation poplars for biomass production and ecosystem services.

In the early 1990s, the USDOE funded research on physiological process modeling of poplars based upon the understanding of how young poplar trees grew in the field. Ecophysiologists were using process-based models at the time to make quantitative predictions about the behavior of forest ecosystems in response to environmental changes (Landsberg 1986). One such ecophysiological growth model for poplar (i.e., ECOPHYS) was developed and validated by a team of cooperating forest scientists based on the physiological work done at the Lab. At the time, it was the first of its kind for forest trees (Host et al. 1990; Host and Isebrands 1994; Rauscher et al. 1990).

Breeding and selection

One of the primary outcomes of Dawson's management of the "Intensive Culture" and "Physiology and Raw Materials" projects was a commitment from USDOE to support breeding and selection of superior poplar clones for the North Central region. Building on the poplar tree improvement work of Jokela and Mohn, two additional regional centers of poplar breeding were established in the early 1990s. While there were no active breeding activities at the Lab, D.E. Riemenschneider, a quantitative forest geneticist trained at the University of Minnesota, assumed leadership for USDA FS contributions to the regional tree improvement efforts, including partnerships with poplar breeders R.B. Hall at Iowa State University and B.G. McMahon at the University of Minnesota – Duluth, Natural Resources Research Institute (NRRI). At the time, Riemenschneider was a scientist within Isebrands' "Ecophysiological Processes of Northern Forest Ecosystems" work unit.

The expansion of the Lab's poplar research during the 1990s and beyond was largely due to experimental material developed by Hall and McMahon, of which many genotypes serve as the foundation of current phytotechnologies and ecosystem services research at the Lab. Notably, McMahon was and continues to be a common denominator for poplar breeding throughout the North Central region. He began his poplar breeding career while getting his master's degree under the tutelage of Jokela at the University of Illinois, then came to the Lab to work with Riemenschneider on selection strategies for balsam poplar (*Populus balsamifera* L.) (Riemenschneider et al. 1992; Riemenschneider and McMahon 1993) and black cottonwood (*Populus trichocarpa* Torr. & A. Gray ex Hook.) (Riemenschneider et al. 1994) before going to Iowa State University to become the first breeder for Hall's program (Hall and Hanna 1995). When McMahon left Iowa State University to be the breeder at the NRRI center under the direction of W. Berguson, Hall hired A.A. Mahama, a postdoctoral scientist trained in agronomic crop improvement methods at Iowa State University, who conducted extensive breeding along with research on pollen viability, grafting success, and breeding incompatibilities — for the latter, he published a detailed account of incompatibility mechanisms in cottonwood, European black poplar (*Populus nigra* L.), and Japanese poplar (*Populus maximowiczii* A. Henry) (Mahama et al. 2011). It was during this time that Hall, Mahama, and Riemenschneider mentored PhD graduate student R.S. Zalesny Jr. on the methods, science, and applications of poplar genetics and tree improvement.

Enhancements of the regional poplar network included robust statistical field designs and the incorporation of quantitative genetics under the leadership of Riemenschneider, who was awarded funding from the USDOE. To do so, Riemenschneider established a clonal testing network in Minnesota, Iowa, Wisconsin, and Michigan. Replicated clonal trials were planted in 1995, 1997, and 2000 to expand on the previous networks of Hansen and Netzer (described in Intensively cultured plantations) by incorporating promising new genotypes from Hall and McMahon. In addition, Riemenschneider collaborated with B.J. Stanton of Greenwood Resources (who was then with James River Corporation) to collect individuals from natural *Populus trichocarpa* populations in the Pacific Northwest that could be tested and used as parents in advanced generation breeding strategies. In particular, through backcross breeding ((*Populus trichocarpa* × *Populus deltoides*) × *Populus deltoides*), they sought to incorporate rooting ability of *Populus trichocarpa* with growth potential, insect and disease resistance, and regional adaptability of *Populus deltoides* (Riemenschneider et al.

2001). This contribution from Riemenschneider was essential to the mapping of the *Populus* genome (Tuskan et al. 2006), which was the first tree genome to be mapped. Since that time, genotypes within this backcross family have been phenotyped for a diverse set of traits such as insect and disease resistance (Simon et al. 2020), biomass (Wullschleger et al. 2005), and rooting ability (Ribeiro et al. 2016). Following these backcross breeding efforts, Riemenschneider expended extensive efforts studying the rooting of *Populus trichocarpa* and its hybrids (Riemenschneider and Bauer 1997). Although the backcross hybrids were not the most productive genotypes for biomass applications, they have shown potential for use in phytoremediation and associated phytotechnologies (Zalesny et al. 2016*b*) (see Phytotechnologies). Overall, two reviews were published detailing the gains from clonal selection and genotype × environment interactions of the 1995, 1997, and 2000 regional tests (Riemenschneider et al. 2001; Zalesny et al. 2009).

Based on this research, a new "Genetic and Silvicultural Systems for Sustainable Intensive Forestry" project was created in 1999 and led by Riemenschneider. Despite that the USDOE ended funding for the Biofuels Feedstock Development Program in 2002, much of the research under this project formed the basis of the ecosystem services research described in the Ecosystem services section of this paper. After 2002, Hall continued to breed poplars but on a significantly reduced scale. McMahon's NRRI poplar breeding program, under the current direction of Nelson (who restarted with NRRI in 2012 following his USDA FS retirement), is the only poplar tree improvement program in the North Central region (Nelson et al. 2019*a*, 2019*b*). This project was active until 2007 when the USDA FS North Central and Northeastern Research Stations merged to form what is currently the USDA FS Northern Research Station (USDA FS NRS). At the Lab, three research programs were integrated to form the Institute for Applied Ecosystem Studies (Fig. 3), within which developing SRWCs is a major research line of science.

Biotechnology and molecular genetics

The potential for using tissue culture for forest tree improvement increased in the 1970s (Karnosky 1981). Tissue culture had the advantage of accelerating the propagation phase of conventional poplar breeding approaches. Thus, in 1983, the USDA FS initiated a "Biotechnology" research program for forest trees, including one at the Lab, which focused on tree improvement of poplars, jack pine, red pine, and important Christmas tree species (e.g., balsam fir (*Abies balsamea* (L.) Mill.) and Fraser fir (*Abies fraseri* (Pursh) Poir.)) (Nelson and Haissig 1984). The program's primary objective was to produce high-valued planting stock for the region. B.E. Haissig, a biochemical plant physiologist from the University of Minnesota specializing in the biochemistry of rooting in forest trees and who joined the original "Genetics" project at the Lab in 1964, became the lead scientist. His early work was on rooting of conifers, but he later focused on the rooting of poplars (Davis et al. 1988; Davis and Haissig 1994). In a similar role as Dawson, Nelson was the "Biotechnology" program manager, and Haissig was the first project leader who oversaw specific research studies within the program. Soon after, coming from the "Genetics" project at the Lab, the "Biotechnology" program added Riemenschneider and C.H. Michler, a horticulturist from Ohio State University with expertise in tissue culture of woody plants.

After researching several forest species in tissue culture, the group's effort soon focused on poplars, as they were more amenable than other trees to tissue culture methods needed for genetic engineering. In particular, the poplar clone of choice was a putative hybrid of white poplar and bigtooth aspen (*Populus alba* L. × *Populus grandidentata* Michx.) discovered in Iowa (McComb and Hansen 1954) and successfully grown in tissue culture (Chun and Hall 1984). A team of cooperating scientists employed a gene transfer method utilizing an *Agrobacterium* known to infect poplars. They chose to transfer the candidate gene for resistance to glyphosate, a broad-spectrum herbicide used for controlling weeds, because weed control was an important problem for the establishment of short rotation poplars (Hansen and Netzer 1985). The transformation was successful, and transformed plants were viable. This marked the first successful recovery of genetically transformed plants for a forest tree. It was also the first example of inserting a foreign gene of agronomic importance into a woody plant (Fillatti et al. 1987).

The discovery of the first genetically transformed tree led to a number of seminal publications (Michler 1988; Riemenschneider 1990, 1994; Haissig and Riemenschneider 1993). Further, the discovery led to increased USDOE support for the Lab to develop broad-spectrum herbicide-resistant poplar germplasm for short-rotation poplar culture. Initial objectives were to test whether (*i*) the transformed poplars grew normally in the field and (*ii*) the conferred glyphosate tolerance adversely affected productivity. R.A. Donahue, a postdoctoral scientist at the Lab who was trained at the University of Wyoming, found that transformed poplars grew normally and had normal photosynthetic processes (Donahue et al. 1994). These discoveries were used by other researchers across the country working on genetic transformation of poplars in their regions (Wheeler et al. 2015). Nelson left the program in 1986 to pursue a commercial approach for using biotechnology in poplars and other species.

The success with genetic transformation of poplar at the Lab had some unintended consequences. Shortly after Haissig gave an invited presentation at a national meeting of the American Association for the Advancement of Science (AAAS), the USDA FS was flooded with adverse reactions to the genetic transformation work. There were concerns from national and international environmental groups and elected United States politicians that the genetically modified trees (i.e., GMOs) would escape into the wild and contaminate the widespread native poplars and aspens in the region, including those growing in urban areas. Their concerns went beyond poplars to include all trees, despite USDA Animal and Plant Health Inspection Service having strict quarantines on field-testing of the transformed poplars. For example, the trees were being tested inside a secure fenced area at a Rhinelander nursery and at Iowa State University under the direction of Hall. Trees were not allowed to flower until further research was done to ensure their environmental safety.

Eventually, given these concerns, project support drastically decreased, and gene transfer work ended at the Lab. Cooperating work was transferred to universities (Wheeler et al. 2015) and offshore private research laboratories. Global debates about the use of GMO trees continue to this day. Haissig retired from the Lab in 1992, at which time Michler became the new biotechnology research project leader. Riemenschneider left the "Biotechnology" project at this time to pursue his quantitative genetics interests on poplars, working in Isebrands' "Ecophysiological Processes of Northern Forest Ecosystems" work unit (see Breeding and selection).

Another major consequence of the work on GMO poplars was an unprovoked attack on the Hugo Sauer Nursery during the night of 20 July 2000 by an ecoterrorist group known as Earth Liberation Front (ELF). They caused over $1 million (United States dollars) of damage to improved forest trees and to vehicles as a protest of the GMO work. Years later, the perpetrators were prosecuted, and evidence collected near Rhinelander was used to convict them of felony offenses. The biotechnology group continued at Rhinelander until 2000 when the project was ended. At that time, some personnel and equipment were moved to West Lafayette, Indiana, and became part of a new research group on hardwood tree improvement.

Atmospheric pollution and climate change

In the 1960s and 1970s, forest scientists noticed significant foliar damage to high-elevation eastern forests that was attributed to

Fig. 4. The Aspen FACE site of the USDA FS, Forestry Sciences Laboratory located in Harshaw, Wisconsin, USA. Some of the Lab's poplar studies are located in the center and bottom areas of the photograph. Currently, the site is part of the West Unit of the Rhinelander Experimental Forest. Photograph courtesy of J.G. Isebrands.

acidic rain caused by air pollutants from industrial activities. The pollutants were identified as sulfur dioxide and nitrogen oxides that reacted with water to produce acid rain. These findings led to a well-funded United States government program called the National Acid Precipitation Assessment Program (NAPAP) in 1980. NAPAP was the precursor of decades of research on air pollution and climate change in forests, including studies on elevated carbon dioxide (CO_2) and tropospheric ozone (O_3) effects on *Populus* conducted at the Lab (Karnosky et al. 2003*a*). The original research that led to those studies was conducted in national parks by Michigan Technological University (MTU) researcher D.F. Karnosky and collaborators, in cooperation with the National Park Service of the United States Department of the Interior. They found differences in trembling aspen (*Populus tremuloides* Michx.) clonal sensitivity to tropospheric O_3 in five national parks across its natural range (Berrang et al. 1986). Soon after, Karnosky et al. (1992) identified aspen clones from the Lake States region ranging in sensitivity to O_3, with certain genotypes falling into low, intermediate, and high O_3 tolerance categories. These clones formed the basis for the next 20 years of air pollution and climate change research at the Lab in cooperation with MTU scientists and other external partners.

In the late 1980s, the United States became concerned with elevated CO_2, ever-changing climate in the world, and its effect on humans and their environment, including forests. Therefore, the United States Global Change Research Program was founded in 1990 (Houghton 1989), and a robust national budget for research on climate change followed. The USDA FS Global Change Research Program was founded as part of this governmentwide program, and the Northern Global Change Program (i.e., a joint effort between the USDA FS North Central and Northeast Forest Experiment Stations) formed, led by R.A. Birdsey (Mickler et al. 2000). This program provided funds to study the effects of elevated O_3 on northern forest species, including poplars, at the Lab and MTU. In the meantime, Dickson transferred from the "Physiology of Wood Formation" project to Isebrands' "Ecophysiological Processes of Northern Forest Ecosystems" project in 1986 and then, in 1992, to Isebrands' newly formed "Physiological Mechanisms of Growth and Multiple Stress Responses" project. Dickson played an important role in the Lab's climate change studies (Dickson and Isebrands 1991), and he worked closely with M.D. Coleman, a plant physiologist from the University of Washington who joined Isebrands' "Ecophysiological Processes of Northern Forest Ecosystems" project in 1990, and Riemenschneider, who provided genetic and statistical expertise, as previously noted.

The Lab's climate change scientists, Coleman, Dickson, and Isebrands, partnered with MTU and Karnosky to conduct research on the effects of elevated O_3 on physiological processes in the aforementioned aspen clones grown in open top chambers in the field. They found that O_3 exposure had a negative effect on the photosynthetic productivity of aspen leaves and had a differing effect on biomass productivity of the clones, depending on their O_3 sensitivity (Coleman et al. 1995*a*, 1995*b*; Karnosky et al. 1996). Also, O_3 exposure negatively affected root growth of the clones (Coleman et al. 1996). Then, Dickson et al. (2001) followed up Coleman's work by exposing the aspen clones to combinations of elevated O_3 and CO_2 in open top chambers, and they found that increased CO_2 counteracted the negative effect of O_3 in some clones and not in others. Dickson et al. (1998) also studied the effects of interacting elevated CO_2 and O_3 on commercially important hybrid poplar clones planted in the United States and Canada. Their results showed significant differences in clonal response to these interacting stresses, with the fastest-growing clones most affected (Dickson et al. 1998). Although these results contributed greatly to our understanding of the effect of air pollution on forests, their applicability from controlled settings to stand-level northern forests were unknown. Nevertheless, these research studies provided preliminary results needed to obtain further funding that was available through competitive research grants on climate effects on forests.

In the mid-1990s, a Free-Air Carbon Dioxide Enrichment system known as FACE (Hendrey and Kimball 1994) was established at the Harshaw Experimental Farm near Rhinelander (now part of the West Unit of the Rhinelander Experimental Forest) (Fig. 4) (Dickson et al. 2000). This major research experiment was a direct result of the group of scientists at the Lab and MTU receiving significant funding from the USDOE Global Change Program to supplement USDA FS funds. Known as Aspen FACE, the study was the first and only free-air experimental system in the world to examine the interacting effects of CO_2 and O_3 on trees in the field. Coleman was the first operating manager for 2 years before joining the USDA FS Southeastern Research Station. For the next 12 years, the steering committee assembled a team of at least 50 cooperating researchers from eight countries and more than 10 graduate students from seven universities to work at the facility. The long-term goal of the Aspen FACE experiment was to examine the interacting effects of elevated CO_2 and O_3 alone and in combination on trembling aspen, sugar maple (*Acer saccharum* Marsh.), and paper birch (*Betula papyrifera* Marshall) (*i*) growth, (*ii*) carbon and nitrogen allocation, (*iii*) competition among genotypes, (*iv*) foliar composition, and (*v*) responses to insect pests and diseases.

Hundreds of scientific papers were published by the Aspen FACE team in a multitude of journals (including the *Canadian Journal of Forest Research*), books (e.g., Karnosky et al. 2003*a*), and proceedings (e.g., Chappelka et al. 2001) over these 12 years. A synthesis of the early molecular- to ecosystem-level results of Aspen FACE were published (Karnosky et al. 2003*b*), along with a complete summary of the experiment that can be found on the websites of MTU (http://www.aspenface.mtu.edu) and USDA FS NRS (https://www.nrs.fs.fed.us/disturbance/climate_change/face/). Dickson and Isebrands retired from the Lab in the early 2000s, and Karnosky died unexpectedly in 2008. In 2004, Nelson returned to the Lab and became the USDA FS project leader in charge of the Aspen FACE experiment, taking over for M.E. Kubiske, a plant physiologist trained at Penn State University who remained on as a project scientist and later published a USDA FS General Technical Report detailing the history, technology, and methods of the Aspen FACE experiment (Kubiske et al. 2015). Kubiske oversaw a full-scale harvest of the Aspen FACE experiment in 2009 to characterize the stand-level above- and belowground carbon storage and biomass production. In 2010, the Aspen FACE experiment ended. From 2011 to 2020, E.J. Gustafson, a scientist at the Lab trained in landscape ecology at Purdue University, led efforts to scale Aspen FACE results to larger spatial and temporal scales by integrating the mechanistic processes into forest landscape succession and disturbance modeling (Gustafson et al. 2013, 2018, 2020).

Key findings of the Aspen FACE experiment were as follows.

1. Whereas CO_2 increased growth of aspen without the influence of elevated tropospheric O_3, moderate levels of O_3 offset elevated CO_2 growth responses in aspen. But there were clonal differences in that response, resulting in dieback (Isebrands et al. 2001; Percy et al. 2007).
2. Competition status of aspen clones was affected by interacting elevated CO_2 and O_3 leading to some disadvantaged clones in an aggrading stand (McDonald et al. 2002; Kubiske et al. 2007; Moran and Kubiske 2013).
3. Soil carbon accumulation in aspen stands decreased when elevated tropospheric O_3 occurred in an elevated CO_2 environment (Loya et al. 2003).
4. Pests and foliar diseases in aspen increased under interacting elevated CO_2 and O_3 (Percy et al. 2002; Holton et al. 2003).

These results provided a window into the future and implied the following effects of future climate conditions on aspen:

1. elevated CO_2 may delay autumnal senescence in aspen and cause increases in winter dieback in the future,
2. future climate scenarios may overestimate the growth of aspen in a high CO_2 atmosphere,
3. soil carbon formation in aspen stands may decrease in future climates,
4. aspen pests and diseases may increase in future climates,
5. Aspen FACE results may be extrapolated to project forest dynamics under future environmental conditions (Gustafson et al. 2013, 2018), and
6. Aspen FACE results are used by the United States Environmental Protection Agency (USEPA) to develop O_3 standards for forests.

Phytotechnologies

Building on the rich history of poplar silviculture, genetics, and physiology from previous decades, phytotechnologies introduced a logical way to expand poplar research across multiple research programs at the Lab in the late 1990s. In particular, phreatophytic traits such as extensive root systems, fast growth, and elevated hydraulic control potential make poplars ideal for phytotechnologies, and the diverse set of genotypes developed for traditional biomass applications offered a means by which to test different varieties of poplars for phytoremediation and other environmental applications (Rockwood et al. 2004; Licht and Isebrands 2005). As a result, phytotechnologies research at the Lab started in 1999, continued through the retirements of Isebrands (2002), Nelson (2009), and Riemenschneider (2008), and is currently the primary focus of Zalesny's SRWCs research.

Isebrands was involved in the initial phytoremediation study involving a researcher from the Lab, which took place in Chicago in collaboration with L.M. Westphal, a social scientist with the USDA FS NRS (Westphal and Isebrands 2001). However, the first long-term, field-based phytotechnologies application took place in Rhinelander. Based on Wisconsin Department of Natural Resources data, water from a creek located adjacent to the closed Rhinelander municipal landfill was showing levels of nitrates and other potential pollutants that were above regulatory thresholds. Mitigation measures were necessary. Along with Isebrands and Riemenschneider, E.O. Bauer, a biological laboratory technician at the Lab, developed a partnership with Sand Creek Consultants, the City of Rhinelander, and a group of industrial representatives to test whether the creek water could be used to irrigate field-planted poplars and willows (species of *Salix* L.) without adverse impacts on tree physiology and growth nor soil conditions. In addition to this wastewater recycling, the group sought to determine whether the trees could reduce runoff and filter subsurface water flow before it reached the creek. The initial phytoremediation efforts involved a set of experiments in which selected poplar and willow clones were grown in tanks in the landfill soil and were irrigated with the creek water. Starting in 2003 during his postdoctoral appointment under Riemenschneider at the Lab, Zalesny analyzed these tank experiment data and concluded that both genera exhibited elevated phytoremediation potential that was clone specific for certain contaminants (Zalesny and Bauer 2007*a*, 2007*b*). In addition, sap flow testing results showed that the trees were capable of reducing the volume of water reaching the creek (Zalesny et al. 2006).

The next major phytotechnologies field application for the Lab began in 2003 and involved collaborations between Zalesny and B. Sexton, Solid Waste Director of the Oneida County Solid Waste Department (currently of Sound County Environmental, previously known as Sand Creek Consultants). Sexton had an applied need to treat landfill leachate, and the research question was whether the leachate could be used as irrigation and fertilization for poplar trees, thereby potentially reducing off-site hauling and treatment costs. To test this, Zalesny, Bauer, and others developed phyto-recurrent selection, a method involving multiple testing cycles to choose superior poplar (and willow) clones for phytoremediation and associated phytotechnologies (Zalesny and Bauer 2007*c*; Zalesny et al. 2007*a*). Testing duration and data complexity increase with subsequent cycles, whereas the number of genotypes decreases. Development of phyto-recurrent selection proved to be the most important milestone for the Lab's phytotechnologies research, as the method has been used in North America and globally to match genera and genotypes with pollutants and the specific tissues (roots, leaves, and stems) that are involved with application-specific remediation processes. For the Oneida County Landfill project, once the greenhouse phyto-recurrent selection was completed, trees were established in replicated trials at the landfill and irrigated with the leachate until crown closure (Zalesny et al. 2007*b*).

Dating back two decades, these two landfill projects served as the foundation for the Lab to become a worldwide leader in phytotechnologies. Since that time, Zalesny and others have published dozens of manuscripts involving both inorganic and organic contaminants across the rural to urban continuum. Examples of applications include phytoremediation, wastewater or groundwater recycling, mine reclamation, anthropogenic succession, and vegetative forest buffers (i.e., riparian buffers used to reduce wind and water erosion from waterways via sediment trapping and water infiltration). In recent years, one of the most notable accomplishments includes establishment of a regional phytotechnologies network consisting of 16 phytoremediation buffer systems (i.e., phyto buffers) to reduce potential surface runoff and subsurface water flow at landfills in the Lake Superior and Lake Michigan watersheds. To date, with support from the Great Lakes Restoration Initiative (GLRI), over 20 000 poplar and willow trees have been planted. Results of this GLRI network and many other phytotechnology projects have been summarized in three major review articles (Zalesny et al. 2016*b*, 2019*a*, 2019*b*).

Ecosystem services

The timeline of poplar ecosystem services research at the Lab mirrors the evolution of research programs during the last two decades. In particular, the focus of the "Sustainable Intensive Forestry" project was to increase productivity of poplar production systems in the region through enhanced vegetation management techniques, breeding for improved rooting and insect and disease resistance, and optimizing genotype × environment interactions for biomass across the landscape. From 2003 to 2008, Riemenschneider and Zalesny focused substantial efforts on understanding the influences of edaphic factors such as soil temperature and moisture on the establishment potential of poplars grown for biomass, bioenergy, and bioproducts, which resulted in a paper describing the quantitative genetics of poplar rooting (Zalesny et al. 2005*a*), as well as a thermal-based index used for determining when to plant poplars to enhance rooting (Zalesny et al. 2004, 2005*b*). The merger of multiple Rhinelander research programs in 2007 created broader-based research priorities. After the retirements of Riemenschneider and Nelson, Zalesny became the sole remaining poplar scientist at the Lab. Since that time, Zalesny has refocused poplar ecosystem services research on linkages among energy, carbon, and climate. For example, using the previous Hansen–Netzer and Riemenschneider regional field testing networks as a source of testing material and long-term information, ecosystem services studied include biomass productivity, carbon sequestration (in trees and soils), water use efficiency and drought tolerance, biofuels recalcitrance, and wood properties (e.g., fiber composition, ash content, and specific gravity). These ecosystem services are also investigated during the phytotechnologies activities previously described. The collective efforts have been published in two review articles (Zalesny and Headlee 2015; Zalesny et al. 2016*a*) and a comprehensive database of North American poplar literature published from 1989 to 2011 (Zalesny and Coyle 2013).

Summary

Contributions of *Populus* research at the Lab spanned decades and mirrored USDA FS priorities at the national level. When we reflect on the history of poplar research at Rhinelander and our successes, we have lessons learned to share with others to assist them with their future challenges. Specifically,

1. stay up-to-date on the latest priorities in national and regional forest science issues;
2. be flexible and adaptable when priorities change;
3. stay in contact with community, state (provincial), and national leaders;
4. inform political leaders of key mission and findings;
5. keep the media informed of activities and visitors;
6. engage in cooperative team research with scientists from other agencies, universities, and international institutions;
7. employ diverse university and high school students (including international fellows) to give them experience with forest science methods;
8. publish in multiple reputable international peer-reviewed journals; and
9. conduct conferences and workshops in the field on practical forest science applications.

The Lab currently has multiple laboratories for genetics, physiology, phytotechnologies, and landscape ecology research, as well as growth chambers and greenhouses located on-site. In addition, the Hugo Sauer Nursery and Rhinelander Experimental Forest offer opportunities for manipulative studies, long-term monitoring, and education in support of multiscale ecosystem research and management. The current mission of the Lab is to develop and deliver scientific knowledge and tools relating ecological changes across scales and disturbance gradients to better integrate science with sustainable forestry, landscape-scale restoration, and contemporary conservation challenges. A primary component of this is to advance the use of poplars and other SRWCs for ecosystem services and to develop phytotechnologies using these selected trees for ecosystem recovery, remediation, and restoration along the urban to rural continuum.

Overall, there have been an amazing number of poplar scientific accomplishments at the Rhinelander Lab since its beginnings in a single rented office space at a local bank and since the first page of the first volume of the *Canadian Journal of Forest Research* was published in 1971. As previously noted, national research priorities have changed. Personnel have changed. And science budgets have oscillated to reflect research priority changes. In addition to the legacy of this work on mentoring and developing generations of researchers, as well as in the technology and applications that resulted from this research, documentation and dissemination of decades-long accomplishments live on among the shelves of scientific libraries and online bibliographies. The reader of this historical record of Rhinelander's poplar science and the key scientists behind this research will clearly be aware of how important the *Canadian Journal of Forest Research* has been in archiving those findings.

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References

Berrang, P., Karnosky, D.F., Mickler, R.A., and Bennett, J.P. 1986. Natural selection for ozone tolerance in *Populus tremuloides*. Can. J. For. Res. **16**(6): 1214–1216. doi:10.1139/x86-216.

Borlaug, N.E. 2007. Sixty-two years of fighting hunger: personal recollections. Euphytica, **157**(3): 287–297. doi:10.1007/s10681-007-9480-9.

Ceulemans, R., and Isebrands, J.G. 1996. Carbon acquisition and allocation. *In* Biology of Populus and its implications for management and conservation. *Edited by* R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, Ont. pp. 355–399.

Ceulemans, R., Scarascia-Mugnozza, G., Wiard, B.M., Braatne, J.H., Hinckley, T.M., Stettler, R.F., et al. 1992. Production physiology and morphology of *Populus* species and their hybrids grown under short rotation. I. Clonal comparisons of 4-year growth and phenology. Can. J. For. Res. **22**(12): 1937–1948. doi:10.1139/x92-253.

Chappelka, A., Karnosky, D., and Percy, K. 2001. Pollution on forest ecosystems. Environ. Pollut. **115**(3): 317–481.

Chun, Y.W., and Hall, R.B. 1984. Survival and early growth of *Populus alba* × *P. grandidentata* in vitro culture plantlets in soil. J. Korean For. Soc. **66**: 1–7.

Coleman, M.D., Isebrands, J.G., Dickson, R.E., and Karnosky, D.F. 1995*a*. Photosynthetic productivity of aspen clones varying in sensitivity to tropospheric ozone. Tree Physiol. **15**(9): 585–592. doi:10.1093/treephys/15.9.585. PMID:14965916.

Coleman, M.D., Dickson, R.E., Isebrands, J.G., and Karnosky, D.F. 1995*b*. Carbon allocation and partitioning in aspen clones varying in sensitivity to tropospheric ozone. Tree Physiol. **15**(9): 593–604. doi:10.1093/treephys/15.9.593. PMID:14965917.

Coleman, M.D., Dickson, R.E., Isebrands, J.G., and Karnosky, D.F. 1996. Root growth and physiology of potted and field grown trembling aspen exposed to tropospheric ozone. Tree Physiol. **16**(1–2): 145–152. doi:10.1093/treephys/16.1-2.145. PMID:14871758.

Crist, J.B. 1983. Synopsis of utilization research on SRIC raw materials. *In* Intensive plantation culture: 12 years research. USDA For. Serv. Gen. Tech. Rep. NC-91. *Edited by* E.A. Hansen. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. pp. 115–118.

Davis, T.D., and Haissig, B.E. 1994. Biology of adventitious root formation. Springer, New York. doi:10.1007/978-1-4757-9492-2.

Davis, T.D., Haissig, B.E., and Sankhla, N. 1988. Adventitious root formation in cuttings. Dioscorides Press, Portland, Ore.

Dickmann, D.I. 1971*a*. Photosynthesis and respiration by developing leaves of cottonwood. Bot. Gaz. **132**(4): 253–259. doi:10.1086/336588.

Dickmann, D.I. 1971*b*. Chlorophyll, ribulose-1 diphosphate carboxylase, and Hill reaction activity in developing leaves of *Populus deltoides*. Plant Physiol. **48**(2): 143–145. doi:10.1104/pp.48.2.143. PMID:16657751.

Dickmann, D.I. 2006. Silviculture and biology of short-rotation woody crops in temperate regions: then and now. Biomass Bioenergy, **30**(8–9): 696–705. doi:10.1016/j.biombioe.2005.02.008.

Dickmann, D.I., and Kuzovkina, J. 2014. Poplars and willows of the world, with emphasis on silviculturally important species. *In* Poplars and willows: trees for society and the environment. Food and Agriculture Organization (FAO) of the United Nations and CABI, Wallingford, Oxfordshire, UK. pp. 8–91. doi:10.1079/9781780641089.0008.

Dickmann, D.I., and Stuart, K.W. 1983. The culture of poplars in eastern North America. Michigan State University Press, East Lansing, Mich.

Dickmann, D.I., Isebrands, J.G., Eckenwalder, J.E., and Richardson, J. 2001. Poplar culture in North America. NRC Research Press, National Research Council of Canada, Ottawa, Ont.

Dickson, R.E. 1987. Diurnal changes in leaf chemical constituents and ^{14}C partitioning in cottonwood. Tree Physiol. **3**(2): 157–171. doi:10.1093/treephys/3.2.157. PMID:14975828.

Dickson, R.E., and Isebrands, J.G. 1991. Leaves as regulators of stress response. *In* Response of plants to multiple stresses. *Edited by* H.A. Mooney, W.E. Winner, and E.J. Pell. Academic Press, San Diego. pp. 3–34. doi:10.1016/C2009-0-02664-6.

Dickson, R.E., and Larson, P.R. 1975. Incorporation of ^{14}C-photosynthate into protein during leaf development in young *Populus* plants. Plant Physiol. **56**(2): 23–27. doi:10.1104/pp.56.1.23.

Dickson, R.E., Coleman, M.D., Riemenschneider, D.E., Isebrands, J.G., Hogan, G.D., and Karnosky, D.F. 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated CO_2 and O_3. Can J. For. Res. **28**(11): 1706–1716. doi:10.1139/x98-150.

Dickson, R.E., Lewin, K.F., Isebrands, J.G., Coleman, M.D., Heilman, W.E., Riemenschneider, D.E., et al. 2000. Forest atmosphere carbon transfer and storage (FACTS II): the aspen free air CO_2 and O_3 enrichment (FACE) project: an overview. USDA For. Serv. Gen. Tech. Rep. NC-214. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-GTR-214.

Dickson, R.E., Coleman, M.D., Pechter, P., and Karnosky, D.F. 2001. Growth and crown architecture of two aspen genotypes exposed to interacting ozone and carbon dioxide. Environ. Pollut. **115**(3): 319–334. doi:10.1016/S0269-7491(01)00225-1. PMID:11789916.

Donahue, R.A., Davis, T.D., Michler, C.A., Riemenschneider, D.E., Carter, D.R., Marquardt, P.E., et al. 1994. Growth, photosynthesis, and herbicide tolerance of genetically modified hybrid poplar. Can. J. For. Res. **24**(12): 2377–2383. doi:10.1139/x94-306.

Erickson, R.O., and Michelini, F.J. 1957. The plastochron index. Am. J. Bot. **44**(4): 297–305. doi:10.1002/j.1537-2197.1957.tb10544.x.

Fillatti, J.J., Sellmer, J., McCown, B., Haissig, B.A., and Comai, L. 1987. *Agrobacterium* mediated transformation and regeneration of *Populus*. Mol. Gen. Genet. **206**(2): 192–199. doi:10.1007/BF00333574.

Friend, A.L., Scarascia-Mugnozza, G.E., Isebrands, J.G., and Heilman, P.E. 1991. Quantification of two-year-old hybrid poplar root systems: morphology, biomass, and ^{14}C distribution. Tree Physiol. **8**(2): 109–119. doi:10.1093/treephys/8.2.109.

Gardiner, E.S., Ghezehei, S.B., Headlee, W.L., Richardson, J., Soolanayakanahally, R.Y., Stanton, B.J., and Zalesny, R.S., Jr. 2018. The 2018 Woody Crops International Conference, Rhinelander, Wisconsin, USA, 22–27 July 2018. Forests, **9**(11): 693–727. doi:10.3390/f9110693.

Gordon, J.C. 1975. The productive potential of woody plants. Iowa State J. Res. **49**(3): 267–274.

Gordon, J.C. 2001. Poplars: trees of the people, trees of the future. For. Chron. **77**(2): 217–219. doi:10.5558/tfc77217-2.

Gordon, J.C., and Larson, P.R. 1968. Seasonal course of photosynthesis, respiration, and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. Plant Physiol. **43**(10): 1617–1624. doi:10.1104/pp.43.10.1617. PMID:16656946.

Gustafson, E.J., Kubiske, M.E., Sturtevant, B.R., and Miranda, B.R. 2013. Scaling Aspen-FACE experimental results to century and landscape scales. Landscape Ecol. **28**(9): 1785–1800. doi:10.1007/s10980-013-9921-x.

Gustafson, E.J., Kubiske, M.E., Miranda, B.R., Hoshika, Y., and Paoletti, E. 2018. Extrapolating plot-scale CO_2 and ozone enrichment experimental results to novel conditions and scales using mechanistic modeling. Ecol. Proc. **7**: 31. doi:10.1186/s13717-018-0142-8.

Gustafson, E.J., Miranda, B.R., and Sturtevant, B.R. 2020. How do forest landscapes respond to elevated CO_2 and ozone? Scaling Aspen FACE plot-scale experimental results. Ecosphere, **11**(6): e03162. doi:10.1002/ecs2.3162.

Haissig, B.E., and Riemenschneider, D.E. 1993. Strategic planning for applying biotechnology to woody plant genetics and breeding. *In* Micropropagation of woody plants. *Edited by* M.R. Ahuja. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 485–500. doi:10.1007/978-94-015-8116-5.

Hall, R.B., and Hanna, R.D. 1995. Exchange, evaluation, and joint testing of genetic stock. Biomass Bioenergy, **9**(1–5): 81–87. doi:10.1016/0961-9534(95)00081-X.

Hansen, E.A. 1981. Root length in young hybrid *Populus* plantations: its implications for border width of research plots. For. Sci. **27**(4): 808–814. doi:10.1093/forestscience/27.4.808.

Hansen, E.A. 1991. Poplar woody biomass yields: a look to the future. Biomass Bioenergy, **1**(1): 1–7. doi:10.1016/0961-9534(91)90046-F.

Hansen, E.A. 1992. Mid-rotation yields of biomass plantations in the north central United States. USDA For. Serv. Res. Pap. NC-309. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-RP-309.

Hansen, E.A. 1994. A guide for determining when to fertilize hybrid poplar plantations. USDA For. Serv. Res. Pap. NC-319. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-RP-319.

Hansen, E.A., and Netzer, D.A. 1985. Weed control using herbicides in short rotation intensively cultured poplar plantations. USDA For. Serv. Res. Pap. NC-260. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.

Hansen, E.A., Netzer, D.A., and Tolsted, D.N. 1993. Guidelines for establishing poplar plantations in the north-central U.S. USDA For. Serv. Res. Note NC-363. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-RN-363.

Hansen, E.A., Ostry, M.E., Johnson, W.D., Tolsted, D.N., Netzer, D.A., Berguson, W.E., and Hall, R.B. 1994. Field performance of *Populus* in short-rotation intensive culture plantations in the north-central U.S. USDA For. Serv. Res. Pap. NC-320. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-RP-320.

Heilman, P.E., Peabody, D.V., Jr., DeBell, D.S., and Strand, R.F. 1972. A test of close-spaced, short-rotation culture of black cottonwood. Can. J. For. Res. **2**(4): 456–459. doi:10.1139/x72-069.

Hendrey, G.R., and Kimball, B.A. 1994. The FACE program. Agric. For. Meterol. **70**(1–4): 3–14. doi:10.1016/0168-1923(94)90044-2.

Hinckley, T.M., Ceulemans, R., Dunlap, J.M., Figliola, A., Heilman, P.E., Isebrands, J.G., et al. 1989. Physiological, morphological, and anatomical components of hybrid vigor in *Populus*. *In* Structural and functional responses to environmental stresses. *Edited by* K.H. Kreeb, H. Richter, and T.M. Hinckley. SPB Academic Publishing, The Hague, Netherlands. pp. 199–217.

Holton, M.K., Lindroth, R.L., and Nordheim, E.V. 2003. Foliar quality influences tree–herbivore–parasitoid interactions: effects of elevated CO_2, O_3, and plant genotype. Oecologia, **137**(2): 233–244. doi:10.1007/s00442-003-1351-z. PMID:12898383.

Host, G.E., and Isebrands, J.G. 1994. An interregional validation of ECOPHYS, a growth process model of juvenile poplar clones. Tree Physiol. **14**(7-8-9): 933–945. doi:10.1093/treephys/14.7-8-9.933. PMID:14967660.

Host, G.E., Rauscher, H.M., Isebrands, J.G., and Michael, D.A. 1990. Validation of photosynthate production in ECOPHYS, an ecophysiological growth process model of *Populus*. Tree Physiol. **7**(1-2-3-4): 283–296. doi:10.1093/treephys/7.1-2-3-4.283. PMID:14972924.

Houghton, J. 1989. Our changing planet: the FY 1990 Research Plan. US Global Change Research Program. 118. Washington, D.C.

Isebrands, J.G., and Dickson, R.E. 1991. Measuring carbohydrate production and distribution: radiotracer techniques and applications. *In* Techniques and approaches to forest tree ecophysiology. *Edited by* J.P. Lassoie and T.M. Hinckley. CRC Press, Boca Raton, Fla. pp. 358-392.

Isebrands, J.G., and Larson, P.R. 1980. Ontogeny of the major veins in the lamina of *Populus deltoides* Bartr. Am. J. Bot. **67**(1): 23–33. doi:10.1002/j.1537-2197.1980.tb07621.x.

Isebrands, J.G., and Nelson, N.D. 1982. Crown architecture of short-rotation intensively cultured *Populus*. II. Branch morphology and distribution of leaves within the crown of *Populus* 'Tristis' as related to biomass production. Can. J. For. Res. **12**(4): 853–864. doi:10.1139/x82-127.

Isebrands, J.G., and Richardson, J. 2000. 21st Session of the International Poplar Commission (IPC-2000): poplar and willow culture: meeting the needs of society and the environment. Vancouver, Wash. USDA For. Serv. Gen. Tech. Rep. NC-215. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-GTR-215.

Isebrands, J.G., and Richardson, J. 2001. Poplar and willow culture: meeting the needs of society and the environment: Poplar Council of the United States, Poplar Council of Canada. For. Chron. **77**(2): 215. doi:10.5558/tfc77215-2.

Isebrands, J.G. and Richardson, J. 2014. Poplars and willows: trees for society and the environment. Food and Agriculture Organization (FAO) of the United Nations and CABI, Wallingford, Oxfordshire, UK.

Isebrands, J.G., Sturos, J.A., and Crist, J.B. 1979. Integrated utilization of biomass: a case study of short rotation intensively cultured *Populus* raw material. TAPPI, **62**(7): 67–70.

Isebrands, J.G., Nelson, N.D., Dickmann, D.I., and Michael, D.A. 1983. Yield physiology of short rotation intensively cultured poplars. *In* Intensive plantation culture: 12 years research. USDA For. Serv. Gen. Tech. Rep. NC-91. *Edited by* E.A. Hansen. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. pp. 77–93.

Isebrands, J.G., Ceulemans, R., and Wiard, B. 1988. Genetic variation in photosynthetic traits among *Populus* clones in relation to yield. Plant Physiol. Biochem. **26**(4): 427–437.

Isebrands, J.G., Dickson, R.E., and Ceulemans, R. 1990. Dynamics of ecophysiological processes in tree crowns and forest canopies. Tree Physiol. **7**(1–4): 1–367.

Isebrands, J.G., McDonald, E.P., Kruger, E., Hendrey, G., Percy, K., Pregitzer, K., et al. 2001. Growth responses of *Populus tremuloides* clones to interacting elevated carbon dioxide and tropospheric ozone. Environ. Pollut. **115**(3): 359–371. doi:10.1016/S0269-7491(01)00227-5. PMID:11789918.

Karnosky, D.F. 1981. Potential for forest tree improvement via tissue culture. BioScience, **31**(2): 114–120. doi:10.2307/1308253.

Karnosky, D.F., Gagnon, Z.E., Reed, D.D., and Witter, J.A. 1992. Effects of genotype on the response of *Populus tremuloides* Michx. to ozone and nitrogen deposition. Water Air Soil Pollut. **62**(3–4): 189–199. doi:10.1007/BF00480254.

Karnosky, D.F., Gagnon, Z.E., Dickson, R.E., Coleman, M.D., Lee, E.H., and Isebrands, J.G. 1996. Changes in growth, leaf abscission, and biomass associated with seasonal tropospheric ozone exposures of *Populus tremuloides* clones and seedlings. Can. J. For. Res. **26**(1): 23–37. doi:10.1139/x26-003.

Karnosky, D.F., Percy, K.E., Chappekka, A.H., Simpson, C., and Pikkarainen, J. 2003*a*. Air pollution, global change, and forests in the new millennium. Elsevier, Amsterdam. Available from https://www.elsevier.com/books/air-pollution-global-change-and-forests-in-the-new-millennium/karnosky/978-0-08-044317-1.

Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., et al. 2003*b*. Tropospheric O_3 moderates responses to temperate hardwood forests to elevated CO_2: a synthesis of molecular to ecosystem results from the Aspen FACE project. Funct Ecol. **17**(3): 289–304. doi:10.1046/j.1365-2435.2003.00733.x.

Kramer, P.J. 1956. The role of physiology in forestry. For. Chron. **32**(3): 297–308. doi:10.5558/tfc32297-3.

Kubiske, M.E., Quinn, V.S., Marquardt, P.E., and Karnosky, D.F. 2007. Effects of elevated atmospheric CO_2 and/or O_3 on intra- and interspecific competitive ability in aspen. Plant Biol. (Stuttg.), **9**(2): 342–355. doi:10.1055/s-2006-924760. PMID:17236101.

Kubiske, M.E., Foss, A.R., Burton, A.J., Jones, W.S., Lewin, K.F., Nagy, J., et al. 2015. Supporting 13 years of global change research: the history, technology, and methods of the Aspen FACE experiment. USDA For. Serv. Gen. Tech. Rep. NRS-153. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pa. doi:10.2737/NRS-GTR-153.

Landsberg, J.J. 1986. Physiological ecology of forest productivity. Academic Press, London.

Larson, P.R. 1962. Auxin gradients and regulation of cambial activity. *In* Tree growth. *Edited by* T.T. Kozlowski. Ronald Press, New York. pp. 97–117.

Larson, P.R. 1963. Stem form development of forest trees. For. Sci. **9**(Suppl. 2): 1–42. doi:10.1093/forestscience/9.s2.a0001.

Larson, P.R. 1979. Establishment of the vascular system in seedlings of *Populus deltoides* Bartr. Am. J. Bot. **66**(4): 452–462. doi:10.1002/j.1537-2197.1979.tb06245.x.

Larson, P.R. 1985. Rachis vascularization and leaflet venation in developing leaves of *Fraxinus pennsylvanica*. Can. J. Bot. **63**(12): 2383–2392. doi:10.1139/b85-341.

Larson, P.R. 1994. The vascular cambium. Springer-Verlag, Berlin, Germany.

Larson, P.R., and Gordon, J.C. 1969*a*. Leaf development, photosynthesis, and ^{14}C distribution in *Populus deltoides* seedlings. Am. J. Bot. **56**(9): 1058–1066. doi:10.1002/j.1537-2197.1969.tb09760.x.

Larson, P.R., and Gordon, J.C. 1969*b*. Photosynthesis and wood yield. Agric. Sci. Rev. **7**(1): 7–14.

Larson, P.R., and Isebrands, J.G. 1971. The plastochron index as applied to developmental studies of cottonwood. Can. J. For. Res. **1**(1): 1–11. doi:10.1139/x71-001.

Larson, P.R., and Isebrands, J.G. 1972. The relation between leaf production and wood weight in first year-root sprouts of two *Populus* clones. Can. J. For. Res. **2**(2): 98–104. doi:10.1139/x72-020.

Larson, P.R., and Isebrands, J.G. 1974. Anatomy of the primary–secondary transition zone in stems of *Populus deltoides*. Wood Sci. Tech. **8**(1): 11–26. doi:10.1007/BF00350638.

Licht, L.A., and Isebrands, J.G. 2005. Linking phytoremediated pollutant removal to biomass economic opportunities. Biomass Bioenergy, **28**(2): 203–218. doi:10.1016/j.biombioe.2004.08.015.

Loya, W.M., Pregitzer, K.S., Karberg, N.J., King, J.S., and Giardina, C.P. 2003. Reduction of soil formation by tropospheric ozone under increased carbon dioxide levels. Nature, **425**(6959): 705–707. doi:10.1038/nature02047. PMID:14562100.

Mahama, A.A., Hall, R.B., and Zalesny, R.S., Jr. 2011. Differential interspecific incompatibility among *Populus* hybrids in sections *Aigeiros* Duby and *Tacamahaca* Spach. For. Chron. **87**(6): 790–796. doi:10.5558/tfc2011-096.

McAlpine, R.G., Brown, C.L., Herrick, A.M., and Ruark, H.E. 1966. Silage sycamore. For. Farmer, **26**(1): 16–17.

McComb, A.L., and Hansen, N.J. 1954. A natural occurring aspen–poplar hybrid. J. For. **52**(7): 528–529. doi:10.1093/jof/52.7.526.

McDonald, E.P., Kruger, E.L., Riemenschneider, D.E., and Isebrands, J.G. 2002. Competitive status influences tree growth responses to elevated CO_2 and O_3 in aggrading aspen stands. Funct Ecol. **16**(6): 792–801. doi:10.1046/j.1365-2435.2002.00683.x.

Michler, C.A. 1988. Herbicide-tolerant forest trees via in vitro selection. Agricell Rep. **10**(4): 27.

Mickler, R.A., Birdsey, R.A., and Hom, J. 2000. Responses of northern US forests to environmental change. Springer-Verlag, New York. doi:10.1007/978-1-4612-1256-0.

Milthorpe, F.T. 1956. The growth of leaves. Butterworths Scientific Publications, London.

Moran, E.V., and Kubiske, M.E. 2013. Can elevated CO_2 and ozone shift the genetic composition of aspen (*Populus tremuloides*) stands? New Phytol. **198**(2): 466–475. doi:10.1111/nph.12153. PMID:23356555.

Nelson, N.D., and Ehlers, P.E. 1984. Comparative carbon dioxide exchange for two *Populus* clones grown in growth room, greenhouse, and field environments. Can. J. For. Res. **14**(6): 924–932. doi:10.1139/x84-164.

Nelson, N.D., and Haissig, B.E. 1984. Biotechnology in the Forest Service's North Central Forest Experiment Station. *In* Proceedings of the International Symposium of Recent Advances in Forest Biotechnology. Michigan Biotechnology Institute, Traverse City, Mich. pp. 139–154.

Nelson, N.D., and Isebrands, J.G. 1983. Late season photosynthesis and photosynthate distribution in an intensively cultured *Populus nigra* × *laurifolia* clone. Photosynthetica, **17**(4): 537–549.

Nelson, N.D., Burk, T.E., and Isebrands, J.G. 1981. Crown architecture of short-rotation, intensively cultured *Populus*. I. Effects of clone and spacing on first-order branch characteristics. Can. J. For. Res. **11**(1): 73–81. doi:10.1139/x81-010.

Nelson, N.D., Berguson, W.E., McMahon, B.G., Meilan, R., Smart, L.B., Gouker, F.E., et al. 2019*a*. Discovery of geographically robust hybrid poplar clones. Silvae Genet. **68**(1): 101–110. doi:10.2478/sg-2019-0018.

Nelson, N.D., Meilan, R., Berguson, W.E., McMahon, B.G., Cai, M., and Buchman, D. 2019*b*. Growth performance of hybrid poplar clones on two agricultural sites with and without early irrigation and fertilization. Silvae Genet. **68**(1): 58–66. doi:10.2478/sg-2019-0011.

Netzer, D.A., Tolsted, D., Ostry, M.E., Isebrands, J.G., Riemenschneider, D.E., and Ward, K.T. 2002. Growth, yield, and disease resistance of 7- to 12-year-old poplar clones in the north central United States. USDA For. Serv. Gen. Tech. Rep. NC-229. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, Minn. doi:10.2737/NC-GTR-229.

Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., et al. 2002. Altered performance of forest pests under CO_2 and O_3-enriched atmospheres. Nature. **420**(6914): 403–407. doi:10.1038/nature01028. PMID:12459738.

Percy, K.E., Nosal, M., Heilman, W., Dann, T., Sober, J., Legge, A.H., and Karnosky, D.F. 2007. New exposure-based metric approach for evaluating O_3 risk to North American aspen forests. Environ. Pollut. **147**(3): 554–566. doi:10.1016/j.envpol.2006.10.009. PMID:17140714.

Phelps, J.E. 1983. Biomass from intensively cultured plantations as an energy, chemical, and nutritional feedstock. *In* Intensive plantation culture: 12 years research. USDA For. Serv. Gen. Tech. Rep. NC-91. *Edited by* E.A. Hansen. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. pp. 131–138.

Rauscher, H.M., Isebrands, J.G., Host, G.E., Dickson, R.E., Dickmann, D.I., Crow, T.R., and Michael, D.A. 1990. ECOPHYS: an ecophysiological growth process model of poplar. Tree Physiol. **7**(1-2-3-4): 255–281. doi:10.1093/treephys/7.1-2-3-4.255. PMID:14972923.

Ribeiro, C.L., Silva, C.M., Drost, D.R., Novaes, E., Novaes, C.R.D.B., Dervinis, C., and Kirst, M. 2016. Integration of genetic, genomic and transcriptomic information identifies putative regulators of adventitious root formation in *Populus*. BMC Plant Biol. **16**: 66. doi:10.1186/s12870-016-0753-0. PMID:26983547.

Richardson, J., Cooke, J.K., Isebrands, J.G., Thomas, B.R., and Van Rees, K.J. 2007. Poplar research in Canada — a historical perspective with a view to the future. Can. J. Bot. **85**(12): 1136–1146. doi:10.1139/B07-103.

Riemenschneider, D.E. 1990. Susceptibility of intra- and inter-specific hybrid poplars to *Agrobacterium tumefaciens* Strain C58. Phytopathology, **80**(10): 1099–1102. doi:10.1094/Phyto-80-1099.s.
Riemenschneider, D.E. 1994. Genomic manipulation of adventitious rooting ability. *In* Biology of adventitious root formation. *Edited by* T.D. Davis and B.E. Haissig. Springer, New York. doi:10.1007/978-1-4757-9492-2. pp. 61–76.
Riemenschneider, D.E., and Bauer, E.O. 1997. Quantitative genetic analysis of adventitious root forming ability in *Populus trichocarpa* (Torr Et. Gray). *In* Biology of root formation and development. *Edited by* A. Altman and Y. Waisel. Plenum Press, New York. pp. 193–201. doi:10.1007/978-1-4615-5403-5_36.
Riemenschneider, D.E., and McMahon, B.G. 1993. Genetic variation among Lake States balsam poplar populations is associated with geographic origin. For. Sci. **39**(1): 130–136. doi:10.1093/forestscience/39.1.130.
Riemenschneider, D.E., McMahon, B.G., and Ostry, M.E. 1992. Use of selection indices to increase tree height and to control damaging agents in 2-year-old balsam poplar. Can. J. For. Res. **22**(4): 561–567. doi:10.1139/x92-074.
Riemenschneider, D.E., McMahon, B.G., and Ostry, M.E. 1994. Population-dependent selection strategies needed for 2-year-old black cottonwood clones. Can. J. For. Res. **24**(8): 1704–1710. doi:10.1139/x94-220.
Riemenschneider, D.E., Berguson, W.E., Dickmann, D.I., Hall, R.B., Isebrands, J.G., Mohn, C.A., et al. 2001. Poplar breeding and testing strategies in the north-central U.S.: demonstration of potential yield and consideration of future research needs. For. Chron. **77**(2): 245–253. doi:10.5558/tfc77245-2.
Rockwood, D.L., Naidu, C.V., Carter, D.R., Rahmani, M., Spriggs, T.A., Lin, C., et al. 2004. Short-rotation woody crops and phytoremediation: opportunities for agroforestry? Agrofore. Sys. **61**(1-3): 51–63. doi:10.1023/B:AGFO.0000028989.72186.e6.
Rockwood, D.L., Krist, M., Isebrands, J.G., and Zhu, J.Y. 2012. Forest trees. *In* Handbook of bioenergy crop plants. *Edited by* C. Kole, C.P. Joshi, and D.R. Shonnard. CRC Press, Boca Raton, Fla. pp. 351–402.
Rudolf, P.O. 1985. History of the Lake States Forest Experiment Station. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.
Scarascia-Mugnozza, G.E., Valentini, R., Ceulemans, R., and Isebrands, J.G. 1994. Ecophysiology and genetics of trees and forests in a changing environment. Tree Physiol. **14**(7–9): 659–1095.
Scarascia-Mugnozza, G.E., Ceulemans, R., Heilman, P.E., Isebrands, J.G., Stettler, R.F., and Hinckley, T.M. 1997. Production physiology and morphology of *Populus* species and their hybrids grown under intensive culture. II. Biomass components and harvest index of hybrid and parental species clones. Can. J. For. Res. **27**(3): 285–294. doi:10.1139/x96-180.
Scarascia-Mugnozza, G.E., Hinckley, T.M., Stettler, R.F., Heilman, P.E., and Isebrands, J.G. 1999. Production physiology and morphology of *Populus* species and their hybrids grown under intensive culture. III. Seasonal carbon allocation patterns from branches. Can. J. For. Res. **29**(9): 1419–1432. doi:10.1139/x99-094.
Schreiner, E.J. 1970. Mini-rotation forestry. USDA For. Serv. Res. Pap. NE-174. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pa.
Simon, S.J., Tschaplinski, T.J., LeBoldus, J., Keefover-Ring, K., Azeem, M., Chen, J.-G., et al. 2020. Host plant genetic control of associated fungal and insect species in a *Populus* hybrid cross. Ecol. Evol. **10**(11): 5119–5134. doi:10.1002/ece3.6266. PMID:32551087.
Smith, J.H.G., and Blom, G. 1966. Decade of intensive cultivation of poplars in British Columbia shows need for long-term research to reduce risks. For. Chron. **42**(4): 359–376. doi:10.5558/tfc42359-4.
Stettler, R.F., Fenn, R.C., Heilman, P.E., and Stanton, B.J. 1988. *Populus trichocarpa* × *Populus deltoides* hybrids for short rotation culture: variation patterns and 4-year field performance. Can. J. For. Res. **18**(6): 745–753. doi:10.1139/x88-114.
Strong, T. 1989. Rotation length and repeated harvesting influence *Populus* coppice production. USDA For. Serv. Res. Note NC-350. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.
Strong, T., and Hansen, E. 1993. Hybrid poplar spacing/productivity relations in short rotation intensive culture plantations. Biomass Bioenergy, **4**(4): 255–261. doi:10.1016/0961-9534(93)90083-G.
Tolsted, D., and Hansen, E. 1992. Age of hybrid poplar stools at first cut influences third-year cutting production. USDA For. Serv. Res. Note NC-357. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. doi:10.2737/NC-RN-357.
Tuskan, G.A., Difazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U., et al. 2006. The genome of black cottonwood, *Populus trichocarpa* (Torr. & Gray). Science, **313**(5793): 1596–1604. doi:10.1126/science.1128691. PMID:16973872.
U.S. Department of Agriculture Forest Service (USDA FS). 1976. Intensive plantation culture: five years research. USDA For. Serv. Gen. Tech. Rep. NC-21. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.
Westphal, L.M., and Isebrands, J.G. 2001. Phytoremediation of Chicago's brownfields: consideration of ecological approaches and social issues. *In* Brownfields 2001 Proceedings, Chicago, Ill.
Wheeler, N.C., Steiner, K.C., Schlarbaum, S.E., and Neale, D.B. 2015. The evolution of forest genetics and tree improvement research in the United States. J. For. **113**(5): 500–510. doi:10.5849/jof.14-120.
Wullschleger, S.D., Yin, T.M., DiFazio, S.P., Tschaplinski, T.J., Gunter, L.E., Davis, M.F., and Tuskan, G.A. 2005. Phenotypic variation in growth and biomass distribution for two advanced-generation pedigrees of hybrid poplar. Can. J. For. Res. **35**(8): 1779–1789. doi:10.1139/x05-101.
Zalesny, J.A., Zalesny, R.S., Jr., Wiese, A.H., and Hall, R.B. 2007*a*. Choosing tree genotypes for phytoremediation of landfill leachate using phyto-recurrent selection. Int. J. Phytoremed. **9**(6): 513–530. doi:10.1080/15226510701709754. PMID:18246777.
Zalesny, J.A., Zalesny, R.S., Jr., Coyle, D.R., and Hall, R.B. 2007*b*. Growth and biomass of *Populus* irrigated with landfill leachate. For. Ecol. Manage. **248**(3): 143–152. doi:10.1016/j.foreco.2007.04.045.
Zalesny, R.S., Jr., and Bauer, E.O. 2007*a*. Evaluation of *Populus* and *Salix* continuously irrigated with landfill leachate I. Genotype-specific elemental phytoremediation. Int. J. Phytoremed. **9**(4): 281–306. doi:10.1080/15226510701476461. PMID:18246707.
Zalesny, R.S., Jr., and Bauer, E.O. 2007*b*. Evaluation of *Populus* and *Salix* continuously irrigated with landfill leachate II. Soils and early tree development. Intl. J. Phytoremed. **9**(4): 307–323. doi:10.1080/15226510701476594.
Zalesny, R.S., Jr., and Bauer, E.O. 2007*c*. Selecting and utilizing *Populus* and *Salix* for landfill covers: implications for leachate irrigation. Int. J. Phytoremed. **9**(6): 497–511. doi:10.1080/15226510701709689. PMID:18246776.
Zalesny, R.S., Jr., and Coyle, D.R. 2013. Short rotation *Populus*: a bibliography of North American literature, 1989–2011. USDA For. Serv. Gen. Tech. Rep. NRS-110. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pa. doi:10.2737/NRS-GTR-110.
Zalesny, R.S., Jr., and Headlee, W.L. 2015. Developing woody crops for the enhancement of ecosystem services under changing climates in the North Central United States. J. For. Exp. Sci. **31**(2): 78–90. doi:10.7747/JFES.2015.31.2.78.
Zalesny, R.S., Jr., Bauer, E.O., and Riemenschneider, D.E. 2004. Use of belowground growing degree days to predict rooting of dormant hardwood cuttings of *Populus*. Silvae Genet. **53**(1–6): 154–160. doi:10.1515/sg-2004-0028.
Zalesny, R.S., Jr., Riemenschneider, D.E., and Hall, R.B. 2005*a*. Early rooting of dormant hardwood cuttings of *Populus*: analysis of quantitative genetics and genotype × environment interactions. Can. J. For. Res. **35**(4): 918–929. doi:10.1139/x05-018.
Zalesny, R.S., Jr., Hall, R.B., Bauer, E.O., and Riemenschneider, D.E. 2005*b*. Soil temperature and precipitation affect the rooting ability of dormant hardwood cuttings of *Populus*. Silvae Genet. **54**(1–6): 47–58. doi:10.1515/sg-2005-0009.
Zalesny, R.S., Jr., Wiese, A.H., Bauer, E.O., and Riemenschneider, D.E. 2006. Sapflow of hybrid poplar (*Populus nigra* L. × *P. maximowiczii* A. Henry 'NM6') during phytoremediation of landfill leachate. Biomass Bioenergy, **30**(8–9): 784–793. doi:10.1016/j.biombioe.2005.08.006.
Zalesny, R.S., Jr., Hall, R.B., Zalesny, J.A., Berguson, W.E., McMahon, B.G., and Stanosz, G.R. 2009. Biomass and genotype × environment interactions of *Populus* energy crops in the Midwestern United States. BioEnergy Res. **2**(3): 106–122. doi:10.1007/s12155-009-9039-9.
Zalesny, R.S., Jr., Stanturf, J.A., Gardiner, E.S., Perdue, J.H., Young, T.M., Coyle, D.R., et al. 2016*a*. Ecosystem services of woody crop production systems. BioEnergy Res. **9**(2): 465–491. doi:10.1007/s12155-016-9737-z.
Zalesny, R.S., Jr., Stanturf, J.A., Gardiner, E.S., Bañuelos, G.S., Hallett, R.A., Hass, A., et al. 2016*b*. Environmental technologies of woody crop production systems. BioEnergy Res. **9**(2): 492–506. doi:10.1007/s12155-016-9738-y.
Zalesny, R.S., Jr., Headlee, W.L., Gopalakrishnan, G., Bauer, E.O., Hall, R.B., Hazel, D.W., et al. 2019*a*. Ecosystem services of poplar at long-term phytoremediation sites in the Midwest and Southeast, United States. WIREs Energy Environ. **8**(6): e349. doi:10.1002/wene.349.
Zalesny, R.S., Jr., Berndes, G., Dimitriou, I., Fritsche, U., Miller, C., Eisenbies, M., et al. 2019*b*. Positive water linkages of producing short rotation poplars and willows for bioenergy and phytotechnologies. WIREs Energy Environ. **8**(5): e345. doi:10.1002/wene.345.
Zalesny, R.S., Jr., Headlee, W.L., Soolanayakanahally, R.Y., and Richardson, J (*Editors*). 2020. Short rotation woody crop production systems for ecosystem services and phytotechnologies. MDPI Publishers, Basel, Switzerland. doi:10.3390/books978-3-03921-510-2.
Zavitkovski, J. 1981. Small plots with unplanted plot border can distort data in biomass production studies. Can. J. For. Res. **11**(1): 9–12. doi:10.1139/x81-002.
Zavitkovski, J., and Hansen, E.A. 1982. Proceedings of the North American Poplar Council Meeting, Rhinelander, Wis., 20–22 July 1982. Kansas State University, Division of Extension, Manhattan, Kans.
Zavitkovski, J., Isebrands, J.G., and Dawson, D.H. 1976. Productivity and utilization potential of short rotation *Populus* in the Lake States. *In* Proceedings of the Symposium on Eastern Cottonwood and Related Species, Greenville, Miss. 28 September – 2 October 1976. *Edited by* B.A. Thielges and S.B. Land, Jr. Louisiana State University, Baton Rouge, La. pp. 392–402.