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Net Assimilation and
Photosynthate Allocation of
Populus Clones
Grown Under
Short-Rotation Intensive
Culture:

Physiological and
Genetic Responses
Regulating Yield

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Net Assimilation and Photosynthate Allocation of *Populus* Clones Grown under Short-Rotation Intensive Culture: Physiological and Genetic Responses Regulating Yield

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Prepared September 1994

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I. INTRODUCTION

The overall objective of this project was to determine the differential responses of poplar clones from sections Tacamahaca and Aigeiros of the genus *Populus* to varying levels of applied water and nitrogen. Above- and below-ground phenology and morphology, photosynthate allocation, and physiological processes were examined. By manipulating the availability of soil resources, we have been able to separate inherent clonal differences from plastic responses, and to determine genotype-environment interactions. We also have been able to make some contrasts between trees grown from hardwood cuttings and coppice sprouts. Our overall hypothesis was that carbon allocation during growth is greatly influenced by interactions among moisture, nitrogen, and genotype, and that these interactions greatly influence yield in short-rotation plantations.

As is true of any project, some of our original expectations were not realized, whereas other initially unforeseen results were obtained. The reduced funding from the Biofuels Feedstock Development Program (BFDP) during the last few years of the project slowed us down to some extent, so progress was not been as rapid as we might have hoped. The major problem associated with this funding shortfall was the inability to employ skilled and unskilled student labor. Nonetheless, we were able to accomplish most of our original goals. All of the principal investigators on this project feel that we have made progress in advancing the scientific underpinning of short-rotation woody biomass production.

Poplar Ecophysiology Research at Michigan State University:

At the outset of this report we would like to emphasize the scope of the poplar ecophysiology program at Michigan State University during the term of our BFDP project. This program represented one of the centers of basic and applied research on short-rotation poplar in the United States, or the World, for that matter. It was interdisciplinary, interdepartmental within the university, interconnected with other BFDP projects and poplar researchers, and supported by a range of funding sources. The BFDP-funded project was the core of this program, with other research thrusts spinning out from it. The great value of such a program is that overall forward momentum can be maintained, even if one component of the program is cut back or eliminated. Nonetheless, the termination of our BFDP funding has been a major setback to poplar research at Michigan State University.

Table I-1 shows the integrated and multifarious nature of the Michigan State poplar program. Whereas poplar research has long been associated with Michigan State University, the granting of the DOE/BFDP contract to D.I. Dickmann and K.S. Pregitzer was seed money that fostered the expansion and diversification of the program. With continued support from the BFDP the program would have continued to grow and diversify. Now lacking this support, the program's future is less certain. Of course, the departure of K.S. Pregitzer from Michigan State has created a void at the PI level. The results to date of the projects related to

the main BFDP project are reported under Section III of this report, Abstracts of Related Research.

Table I-1. Projects comprising the poplar ecophysiology program at Michigan State University during the period 1987 to 1993.

Project Title	Principal Investigators	Source of Funding
Net assimilation and photosyn- thate allocation of <i>Populus</i> clones grown under short-rotation, intensive culture.	D.I. Dickmann, K.S. Pregitzer, and P.V. Nguyen	U.S. DOE, Biofuels Feedstock Develop- Crops Program
Plant biological diversity in a short-rotation <i>Populus</i> landscape	K.S. Pregitzer, K.L. Gross, and L.E. Huberty	U.S. DOE, Biofuels Feedstock Develop- ment Program
The interaction of various levels of water and nitrogen on the physiology of poplar clones	D.I. Dickmann and Z. Liu	U.S.D.A., C.S.R.S. McIntire-Stennis Program
Modeling the effect of ideotype traits on first-year growth of poplar	D.I. Dickmann	International Energy Agency, Task V Tree Ideotype Activity
Selection and testing of poplar clones for southern Michigan	D.I. Dickmann	Michigan Agricultural Experiment Station
Organisms in an agricultural landscape: perennial biomass cultivation using hybrid poplar	K.S. Pregitzer et al.	National Science Foundation, Long Term Ecological Research Program
Video analysis of root systems: understanding terrestrial carbon budgets	K.S. Pregitzer	Michigan Energy and Resource Research Assoc.
Fine root and soil organic matter turnover in C, N, and P cycling of <i>Populus</i> plantations	E.A. Paul and K.S. Pregitzer	National Science Foundation

Project Personnel:

In addition to the authors of this report, several graduate students and staff members at Michigan State University made major contributions to the BFDP and related projects.

Ronald L. Hendrick, Graduate Research Assistant in Forestry

William R. Horwath, Graduate Research Assistant in Crop and Soil Science

Randy Kelvickas, Department of Forestry Technician

Zhijun Liu, Graduate Research Assistant in Forestry

Kathleen G. Maas, Graduate Research Assistant in Forestry

Cooperators in the overall poplar ecophysiology program included:

William R. Enslin, Center for Remote Sensing, Michigan State University

James A. Flore, Department of Horticulture, Michigan State University

Kay L. Gross, Kellogg Biological Station, Michigan State University

George E. Host, Natural Resources Research Institute, University of Minnesota-Duluth

Jud G. Isebrands, U.S. Forest Service, North Central Forest Experiment Station

Eldor A. Paul, Department of Crop and Soil Sciences, Michigan State University

G. Philip Robertson, Kellogg Biological Station, Michigan State University

Louis Zsuffa, Faculty of Forestry, University of Toronto

Project Goals and Objectives:

The goals and objectives of this project are embodied in the tasks and hypotheses set down in the original proposal. The work done throughout the course of this project was keyed into them.

Major Task No. 1.

Quantify the differences in net assimilation and photosynthate allocation among *Populus* clones and determine why differences in assimilation and carbon allocation occur.

Major Task No. 2.

Determine if differences in assimilation and carbon allocation among *Populus* clones before coppicing remain unchanged following coppicing.

Major Task No. 3.

Develop breeding strategies and modify silvicultural prescriptions for increasing biomass productivity of short-rotation *Populus* plantations.

Summary of Original Hypotheses:

A. Certain clones allocate more carbon to the production of fine roots, these roots turn over more rapidly than other clones, and these differences are inherent in the genome.

B. Patterns of below-ground allocation do not vary among clones as moisture and nitrogen availability are altered, although individual genets will exhibit plasticity in response to changing environments.

C. Clones that exhibit the greatest above-ground (or conversely below-ground) growth at high levels of moisture and nitrogen will perform similarly at low levels of resource availability.

D. The above-ground / below-ground distribution of carbon is under strong genetic control, and it is largely regulated by the setting of buds on the major shoot axes.

E. Poplar clones will vary in vigor of coppicing and in the length of time that root reserves fuel shoot regrowth, and, therefore, in the time needed for the new shoots to become self-sufficient.

F. Very little fine root growth will occur, and fine root necrosis will be high, until the shoots of coppiced plants become an exporter of photosynthate.

G. After the first growing season, the above- and below-ground physiology of coppiced plants will be indistinguishable from their progenitors.

H. The above-ground / below-ground distribution of carbon is under strong genetic control, and it is largely regulated by the setting of buds on the major shoot axes.

I. Poplar clones will vary in vigor of coppicing and in the length of time that root reserves fuel shoot regrowth, and, therefore, in the time needed for the new shoots to become self-sufficient.

J. Very little fine root growth will occur, and fine root necrosis will be high, until the shoots of coppiced plants become an exporter of photosynthate.

K. After the first growing season, the above- and below-ground physiology of coppiced plants will be indistinguishable from their progenitors.

L. The above-ground / below-ground distribution of carbon is under strong genetic control, and it is largely regulated by the setting of buds on the major shoot axes.

M. Poplar clones will vary in vigor of coppicing and in the length of time that root reserves fuel shoot regrowth, and, therefore, in the time needed for the new shoots to become self-sufficient.

N. Very little fine root growth will occur, and fine root necrosis will be high, until the shoots of coppiced plants become an exporter of photosynthate.

O. After the first growing season, the above- and below-ground physiology of coppiced plants will be indistinguishable from their progenitors.

P. The above-ground / below-ground distribution of carbon is under strong genetic control, and it is largely regulated by the setting of buds on the major shoot axes.

Q. Poplar clones will vary in vigor of coppicing and in the length of time that root reserves fuel shoot regrowth, and, therefore, in the time needed for the new shoots to become self-sufficient.

R. Very little fine root growth will occur, and fine root necrosis will be high, until the shoots of coppiced plants become an exporter of photosynthate.

S. After the first growing season, the above- and below-ground physiology of coppiced plants will be indistinguishable from their progenitors.

T. The above-ground / below-ground distribution of carbon is under strong genetic control, and it is largely regulated by the setting of buds on the major shoot axes.

U. Poplar clones will vary in vigor of coppicing and in the length of time that root reserves fuel shoot regrowth, and, therefore, in the time needed for the new shoots to become self-sufficient.

V. Very little fine root growth will occur, and fine root necrosis will be high, until the shoots of coppiced plants become an exporter of photosynthate.

W. After the first growing season, the above- and below-ground physiology of coppiced plants will be indistinguishable from their progenitors.

X. The above-ground / below-ground distribution of carbon is under strong genetic control, and it is largely regulated by the setting of buds on the major shoot axes.

Y. Poplar clones will vary in vigor of coppicing and in the length of time that root reserves fuel shoot regrowth, and, therefore, in the time needed for the new shoots to become self-sufficient.

Z. Very little fine root growth will occur, and fine root necrosis will be high, until the shoots of coppiced plants become an exporter of photosynthate.

Section II:

Reports of Research Based on the Original Proposal

D.I. Dickmann, P.V. Nguyen, and K.S. Pregitzer, "Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones," *Forest Ecology and Management* (submitted).

K.S. Pregitzer, D.I. Dickmann, R. Hendrick, and P.V. Nguyen, "Whole-tree carbon and nitrogen partitioning in young hybrid poplars," *Tree Physiology* 7:79-93 (1990).

P.V. Nguyen, D.I. Dickmann, K.S. Pregitzer, and R. Hendrick, "Late-season changes in allocation of starch and sugar to shoots, coarse roots, and fine roots in two hybrid poplar clones," *Tree Physiology* 7:95-105 (1990).

D.I. Dickmann, P.V. Nguyen, and K.S. Pregitzer, "Irrigation and nitrogen fertilization affect whole-tree biomass and nitrogen distribution in two hybrid poplar cultivars during their second year of growth," *Tree Physiology* (submitted).

D.I. Dickmann, Z. Liu, P.V. Nguyen, and K.S. Pregitzer, "Photosynthesis, water relations, and growth of two hybrid *Populus* genotypes during a severe drought," *Canadian Journal of Forestry Research* 22:1094-1106 (1992).

III. ABSTRACTS OF RESEARCH RELATED TO THE ORIGINAL PROPOSAL

The following section consists of abstracts of reports, theses, manuscripts, and published papers of research done under projects related to our major BFDP project (see Table I-1 on page 2 of this report). Complete copies of these documents are available from the authors of this report.

Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. I. Morphology and growth

ZHIJUN LIU AND DONALD I. DICKMANN

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Received March 24, 1992

LIU, Z., and DICKMANN, D. I. 1992. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. I. Morphology and growth. *Can. J. Bot.* 70: 2265–2270.

Repeated progressive drought and flooding stress were imposed on hybrid poplar clones *Populus × euramericana* 'Eugenei', and *Populus tristis* × *Populus balsamifera* 'Tristis' grown in pots in a greenhouse under two nitrogen levels. In both clones the rate of leaf initiation was promoted only in high-N plants subjected to minimum water stress. Water stress alone did not retard the rate of leaf initiation, but it significantly reduced leaf expansion of 'Eugenei', whereas only flooding led to smaller leaves in 'Tristis'. The addition of N stimulated leaf expansion, leaf chlorophyll and N concentrations, and leaf and stem biomass production across soil moisture levels, but the greatest effect of N was associated with minimum water stress. High N altered carbon allocation towards the aboveground portions, leading to lower root to shoot ratios. High N also appeared to stimulate initiation of fine roots. Soil moisture determined the amount of biomass that accumulated in roots, with highest root production in well-watered pots and lowest in flooded pots, with the droughted treatment in between. Leaves became thinner as soil moisture decreased from flooding. Stem biomass of 'Tristis' declined more under flooding than under drought, whereas 'Eugenei' displayed a greater reduction of stem biomass in droughty than in flooded soil.

Absciscic acid accumulation in leaves of two contrasting hybrid poplar clones affected by nitrogen fertilization plus cyclic flooding and soil drying

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¹ *Department of Forestry, Michigan State University, East Lansing, MI 48824-1222, USA*

Received November 18, 1991

Summary

Cuttings of hybrid *Populus* clones Tristis and Eugenei growing in pots in a greenhouse were treated with nitrogen fertilizer at two rates and subjected to repeated soil flooding or drying. Periodically, gas exchange measurements and radioimmunoassays, to determine absciscic acid (ABA) concentrations, were made on recently mature leaves.

In both clones, photosynthesis and stomatal conductance were depressed five days after flooding, but leaf ABA concentrations remained relatively constant. In contrast, an initial, 9-day period of soil drying resulted in substantial ABA accumulation in leaves, which closely correlated with declines in photosynthesis and conductance. A second soil drying cycle of up to 9 days was less effective in modifying gas exchange and leaf ABA concentrations. High-N supply stimulated leaf ABA production as the soil dried. On the resumption of watering, gas exchange in Tristis recovered fully and rapidly and leaf ABA concentrations quickly returned to control values, whereas gas exchange in Eugenei recovered slowly and leaf ABA concentrations remained high for longer.

Gas exchange in Eugenei was unaffected by soil drying until leaf ABA concentrations exceeded 100 ng g_{dw}⁻¹, whereas Tristis showed a reduction in stomatal conductance and photosynthesis at leaf ABA concentrations of only 10 ng g_{dw}⁻¹. A rise in internal CO₂ concentrations was associated with increased leaf ABA concentrations in Tristis, but not in Eugenei. Clonal differences in the relationship between gas exchange and leaf ABA concentration suggest contrasting physiological strategies for survival under prolonged drying conditions.

Maas, Kathleen, G. 1992. The effects of planting density and weed control on the partitioning of nitrogen and carbon in a hybrid poplar plantation. M.S. Thesis, Michigan State University, 154 pp.

A plantation of *Populus x euramericana* cv. Eugenei was established in 1989 to determine the effects weed control and planting density have on community-level carbon and nitrogen (N). A split-plot design with random blocking was used. Three planting densities were split on the presence or absence of weeds. Above-ground biomass and N content of trees and weeds were determined by destructive sampling. Equations were developed to estimate tree-stand biomass. At the end of the third growing season, cumulative above-ground biomass was equivalent in those communities that were fully occupying the site. Nitrogen content on the community level was not influenced by weed control. By the end of the third growing season weed competition did not significantly influence individual tree growth at the high planting density, but the presence of weeds had a significant negative impact on tree growth at the lower planting densities.

INJECTION OF NITROGEN-15 INTO TREES TO STUDY NITROGEN CYCLING IN SOIL

WILLIAM R. HORWATH, ELDOR A. PAUL,
AND KURT S. PREGITZER

Abstract

Most ^{15}N dilution techniques disturb either the soil or N-pool size. The objective of this study was to develop a method of labeling the roots of *Populus* trees with ^{15}N without physically disturbing the soil. Such a method would enable the direct measurement of the flux of ^{15}N from dead roots into the soil organic matter. Leaf and root biomass were labeled by injection of ^{15}N directly into the vessel elements of hybrid *Populus* trees during their second growing season. The ^{15}N was uniformly distributed throughout the canopy and root system. The rate and amount of ^{15}N turnover from plant tissue can be determined by pool transfer or through differences in plant ^{15}N concentrations. The ^{15}N was detected in the dead-root pool 8 wk after injection, indicating root turnover. Results demonstrate the ability to measure the contribution of fine-root litter to N-cycling processes without disturbing the soil environment.

**THE DYNAMICS OF CARBON, NITROGEN AND SOIL ORGANIC
MATTER IN *POPULUS* PLANTATIONS**

By

William Richard Horwath

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Departments of Crop and Soil Science
and
Forestry

1993

ABSTRACT

THE DYNAMICS OF CARBON, NITROGEN AND SOIL ORGANIC MATTER IN *POPULUS* PLANTATIONS

By

William Richard Horwath

Short-rotation intensive-culture forestry is similar to agricultural systems requiring increased nutrient input and management. The expense and environmental concerns associated with fertilizers have raised questions about the sustainability of these ecosystems. Sustainability of production oriented ecosystems can be aided by understanding the mineralization-immobilization potential of the soil microbial biomass. The soil microbial biomass is central to a complex system of soil organic fractions that control soil fertility, production and environmental contamination.

The lack of root turnover studies has led to a inadequate understanding of the role of root turnover as substrate soil microbial biomass and organic matter formation. The current study was designed to determine: (i) the role of below-ground production and turnover in nutrient cycling processes; (ii) the contribution of leaf and root litter as substrate for the maintenance of soil organic matter; and (iii) relate soil microbial biomass and organic matter dynamics to plant carbon and nitrogen allocation patterns.

Two-year-old *Populus euramericana* cv. Eugenei trees were labeled with ^{14}C and ^{15}N in the field. The ^{15}N was injected into the stem to label leaves and roots without labeling the soil. The ^{14}C labeling was done in a Plexiglas chamber under ambient conditions. The tree-soil system was

sampled for one year. Labeled leaf litter was placed onto unlabeled tree plots to differentiate the contribution of leaf and root derived carbon and nitrogen to soil over a two year period.

The ^{14}C required two weeks to stabilize in the root system and averaged 20% of soil respiration. One year later, 32% of applied ^{14}C and 33% of the injected ^{15}N was recovered. Reserves in the root system were sufficient to replace fine roots one and one half times. This represented significantly less C than leaf litter, yet similar amounts of ^{14}C were found in soil from both litters. Leaf litter appeared to dominate N cycling since ^{15}N was not detected in root labeled soil. Kinetic analysis of incubated soil showed a greater contribution of C and N to soil organic fractions from leaf litter. The turnover of labile soil ^{14}C in both leaf and root litter labeled soil was 14-64 days. The ^{14}C in pools of intermediate resistance had a turnover time of 2-16 years and increased with soil depth.

Effects of leaf display on light interception and apparent photosynthesis in two contrasting *Populus* cultivars during their second growing season

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Summary

Effects of the contrasting leaf display of poplar cultivars Eugenei (*Populus × euramericana*) and Tristis (*P. tristis* × *P. balsamifera*) on light interception and photosynthesis were studied in the second year of growth in an irrigated plantation near Rhinelander, Wisconsin, USA (lat. 45° N). Leaves on the current terminal (CT) and on proleptic branches were measured between 0900 and 1500 h on five clear days from June to September 1980.

Leaf orientation-based differences between these cultivars were evident as the second growing season progressed and the crowns of the trees in the plantation grew together. Leaves of Eugenei are erectophile or tilted from the horizontal. In this cultivar light penetrated throughout the crown; many leaves on the lowest branches were illuminated as fully as those on the upper CT and had higher photosynthetic rates than equivalent leaves in Tristis. However, by early September many of the lower branches on Eugenei trees had abscised. In the planophile Tristis, adaxial photon flux densities (PPFD) of leaves on the lower portion of the CT and on branches were only a fraction of those measured on the upper CT. This pattern became more extreme as the season progressed. Few of the lower branches of Tristis abscised during the growing season. Photosynthesis rates, especially on a whole-leaf basis, were closely related to incident PPFDs in both cultivars. The ecological significance of these results are discussed, as well as the hypothesized effect of leaf inclination on crop productivity.

**PLANT BIOLOGICAL DIVERSITY
IN A
SHORT-ROTATION *POPULUS* LANDSCAPE**

Final report: December 15, 1992

**Dr. Kurt S. Pregitzer, Principal investigator
Department of Forestry, Michigan State University
East Lansing, Michigan 48824-1222**

**Dr. Katherine L. Gross and Lisa E. Huberty, Co-Investigators
Kellogg Biological Station
Hickory Corners, Michigan 49060**

ABSTRACT

One concern about culturing poplar plantations for biomass production is their potential detrimental effect on plant and animal diversity in the agricultural landscape. In 1989, six agronomic treatments and one native succession treatment were established in the Long Term Ecological Research project in agriculture at Kellogg Biological Station. These treatments allowed us to 1) quantify the impact of increasing poplar stand density on plant species richness, diversity, and evenness, 2) compare plant diversity in a poplar plantation with other agronomic systems, and 3) compare plant diversity in a poplar plantation with a successional community.

The data from the first year (1989) suggest that poplar plantations do not reduce plant diversity; they may even enhance it by changing the dominance hierarchy in the understory. Annual dicots and monocots dominated all of the treatments in 1989, while perennial monocots and dicots were minor components. As poplar stand density increased, the understory plant biomass decreased, species richness increased (from 11 to 17), and diversity increased (from 1.57 to 1.79). Species richness, diversity, and evenness were greater in the medium density poplar understory than in the fertilized native succession community and the medium corn density

conventional till treatment, though species composition was similar. The species richness, diversity, and evenness were similar in the poplar understory and the no-till treatment, though the no-till community included more biennial and perennial species.

In the second year of this study (1990), species composition in the poplar understory, no-till treatment, and successional treatment shifted from dominance by annuals to dominance by biennials, perennial dicots, and nitrogen-fixing perennials. Understory species richness increased (from 21 to 26), and the diversity index increased (from 1.07 to 1.68) as poplar stand density increased. Species richness and the diversity index were lower in the native succession plant community than in the poplar understory, though the species composition was similar. The conventional till treatment was dominated by annual dicots and monocots, and the species richness was half that of the poplar understory. Species richness was lower in the no-till treatment than in the poplar treatment, though the diversity indices and species composition were similar. Thus, in the second year of this study, poplar plantations did not reduce plant diversity relative to the native succession and agronomic treatments.

In 1991, species richness, diversity, and evenness increased from low to medium poplar density, but was similar at the medium and high poplar density. Although species richness was similar in the native succession and poplar understory, the diversity index was greater in the native succession, probably due to greater biomass evenness across species in the native succession. A similar pattern of more equitable biomass distribution was observed in the annually disturbed conventional till treatment, and accounted for higher diversity indices in the conventional till than in the poplar understory. Species richness, diversity indices, and evenness were greater in the no-till

corn treatment than in the poplar treatment. Thus, in 1991, poplar plantations did not reduce species richness relative to the native succession and conventional till treatments, but they did reduce richness and diversity relative to the no-till treatment.

Poplar plantations (at least in the first three years of growth) do not appear to have a negative effect on plant diversity relative to native succession and annual crops, such as soybean and corn. A perennial woody crop can compete better than these annual crops with biennial and perennial species. Thus, there is a potential to balance poplar production with plant diversity. However, the impact of the poplar plantation on plant diversity must be followed as the plantation matures and after coppicing to confirm this conclusion.

Liu, Z. and Dickmann, D.I. 1993. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. II. Gas exchange and water relations. Can. J. Bot. (in press)

Repeated progressive drought and flooding stress were imposed on two hybrid poplar clones (*Populus x euramericana* 'Eugenei' and *P. tristis x P. balsamifera* 'Tristis') grown under two levels of nitrogen (N). Diurnal responses of gas exchange variables were measured periodically. Over a period of 18 days of flooding, plants displayed no reduction in photosynthesis during the initial days, followed by a midday depression, and finally whole-day declines as flooding was prolonged. Supplemental N enabled plants to resist the negative effects of flooding on photosynthesis and conductance. Under well-watered conditions, additions of N enhanced photosynthesis; when soil water was restricted, however, photosynthesis of high-N plants drastically decreased. The experience of one cycle of progressive drought substantially improved the capacity of plants to maintain a stable rate of photosynthesis during another drought cycle, whereas a 10-day period of stress interruption appeared to increase the physiological vulnerability of high-N plants to another drought cycle. Drought-stressed plants gained full and quick recovery of photosynthesis upon relief from stress. In contrast, flooded plants did not recover until nine days after removal of stress. Flooding did not invoke midday leaf water deficits, nor did two cycles of progressive soil drying of up to 10 days. After a period of water-stress interruption followed by another drought cycle, stomata of Eugenei tended to lose their sensitivity to declining soil moisture, resulting in moderate leaf water deficits. Tristis, on the other hand, appeared better able to maintain the adaptation produced by drought, even after stress was interrupted.

Section IV: Synthesis Papers

During the course of this project several papers were written by us with the objective of reviewing and synthesizing the knowledge that exists in certain areas of the biology and culture of short-rotation woody plants. While not included in our original objectives, these papers have served to coalesce our thinking on topics directly embodied in this project.

D.I. Dickmann and K.S. Pregitzer, "The structure and dynamics of woody plant root systems," pp. 95-123 in *Ecophysiology of Short Rotation Forest Crops*, ed. C.P. Mitchell, J.B. Ford-Robertson, T.M. Hinckley, and L. Sennerby-Forsse, Elsevier Science Publishers Ltd., New York (1992).

D.I. Dickmann and R.L. Hendrick, "Modeling adventitious root system development in trees: clonal poplars," in *Proceedings of First International Symposium on the Biology of Adventitious Root Formation*, ed. T.D. Davis and B.E. Haissig, Plenum Press, New York (1994).

D.I. Dickmann, "Role of physiology in forest tree improvement," *Silva Fennica* 25(4):248-256 (1992).

D.I. Dickmann, M.A. Gold, and J.A. Flore, "The ideotype concept and the genetic improvement of tree crops," in *Plant Breeding Reviews* Vol. 12, ed. J. Janick, John Wiley & Sons, New York (1994).

V. CONCLUSIONS

Summary of Major Accomplishments:

In the original project proposal, a number of specific questions were set forth in our discussion of the major tasks to be undertaken. In addition, additional questions can now be proposed that relate directly to these tasks. Our summary of accomplishments for Major Tasks Nos. 1 and 2 will take the form of answers to these questions. The answers relate directly to the two *Populus* cultivars we investigated -- *Tristis* and *Eugenei* --, although wider intra- and inter generic applicability may be appropriate.

Major Task No. 1

Q. How does water availability interact with genotype to regulate carbon fixation and growth?

A. There is a fairly strong genotype-environment interaction in poplar with respect to growth, photosynthesis, and stomatal physiology across the range of water availability, from flooding to optimal water to drought. *Tristis* is the most sensitive of the two clones we examined to flooding, whereas *Eugenei* is more sensitive to drought. *Tristis* has a higher rate of net carbon fixation than *Eugenei*, and it can maintain photosynthesis at higher levels of water stress. *Tristis* also shows stronger stomatal control of water loss than does *Eugenei*, and *Tristis* has a higher water-use efficiency under water stress. However, photosynthetic physiology, leaf expansion, and growth are reduced by flooding more in *Tristis* than *Eugenei*.

Q. How does nitrogen (N) availability interact with genotype to regulate carbon fixation and growth?

A. Both *Tristis* and *Eugenei* responded similarly to N availability. High levels of N increased shoot:root ratios, photosynthesis rates, and rates of biomass accumulation under well-watered conditions. High levels of N also enabled plants to resist the negative effects of flooding. But when plants were water stressed, high N levels drastically decreased photosynthesis rates, leaf expansion, and growth when compared to well-watered plants.

Q. What is the relationship of photosynthetic rate, stomatal physiology, and plant water status to growth?

A. In general, we found that looking at just a few physiological parameters can give a very misleading impression of growth potential. For example, *Tristis* always shows higher photosynthesis rates, higher leaf conductances, less negative leaf water potentials, and higher water use efficiencies than *Eugenei* under drought. Yet regardless of environmental conditions, *Eugenei* always grows much faster than *Tristis*. Therefore, a more complete picture of physiological, morphological, and

phenological characteristics is necessary before a prediction of relative growth rates among *Populus* cultivars can be made.

Q. Is assimilate allocation a rigidly deterministic process under strong genetic control, or is it a "plastic" response governed by environment?

A. Individual clones partition carbon in different ways, and the degree to which they are plastic appears to be genetically controlled. But individual clones are plastic in different ways. *Tristis*, a strongly root-oriented clone, is more plastic in terms of carbon allocation to roots than *Eugenei*, but *Tristis* exhibits little plasticity in above-ground partitioning, except during flooding. *Eugenei*, in contrast, responds to a changing environment mainly by adjusting leaf area and shoot growth.

Q. To what extent can assimilate allocation be modified by environment?

A. In general, environment modifies growth more than partitioning. Water stress in *Tristis*, however, does shift carbon allocation toward fine roots. Nitrogen availability is one of the strongest modifiers of allocation; high N levels produce greater relative growth in shoots than roots.

Q. What controls biomass allocation?

A. It seems clear that allocation in *Populus* is under strong genetic control, although environmental factors, especially N, can be modifiers. This fact has important implications for tree breeding, especially in light of the record of agricultural crop breeding, where the major gains in yields to date have occurred through genotypic-based shifts in biomass allocation.

Q. What proportion of yearly assimilate production goes into fine roots in short-rotation poplars?

A. It depends on the genotype. In *Tristis*, 3 to 6 percent of total tree biomass occurs in the fine root fraction (≤ 1 mm in diameter) after two years of growth; *Eugenei* allocated about 2 percent. Though a small investment of the tree's total carbon capital, this fraction is nonetheless extremely important. Roots of all sizes account for ca. 50 percent of total dry weight in two-year-old *Tristis*, but < 40 percent in *Eugenei*.

Q. How rapid is fine root turnover in short-rotation poplars and how does this vary with clone and environment?

A. This question cannot yet be answered with any assurance. In general, fine root turnover is less than we expected; many fine roots live a long time. Turnover seems to be correlated with above-ground phenology and does seem to be affected by environment. There is probably a strong genotype correlation, also.

Major Task No. 2

Q. Is the response to coppicing highly heritable among *Populus* cultivars?

A. It would appear to be so. Both Eugenei and Tristis are strong sprouters, but their growth subsequent to cutting in relation to water availability was exactly the same as before cutting: Eugenei grew more when irrigated but Tristis showed no response to applied water.

Q. Are rates of net assimilation and patterns of carbon allocation plastic and responsive to environmental conditions subsequent to harvest?

A. Photosynthesis rates of irrigated and non irrigated sprouts did not differ during the first year after cutting; however, neither did they differ the year before the trees were cut. We have no data on carbon allocation in coppice sprouts vs. uncoppiced plants. This area is ripe for investigation. Allocation to fine roots in coppiced Tristis appears to be modified by soil water availability; stools receiving no supplemental irrigation produced more fine roots than those that were irrigated.

Q. What is the source of carbon to fuel coppice regrowth?

A. The massive loading of the coarse roots of poplars with starch and sugar during late summer and early fall surely provides the energy to fuel initial coppice regrowth. Our hypothesis is that regrowth of above- and below-ground meristems in *Populus* draws strictly on local reserve pools. Reserves located in the taproot and primary coarse roots supply expanding dormant or adventitious buds in the stumps, whereas reserves located downstream in the smaller coarse roots supply newly initiated fine roots. Further physiological studies are needed to further elucidate and quantify the dynamics of this reserve mobilization.

Q. When does current photosynthate produced by new leaves on first-year coppice sprouts become the dominant carbon source for their growth?

A. No definitive answer is possible at this time. Our hypothesis is that as soon as a few leaves on coppice shoots become fully expanded, reaching their full photosynthetic potential, the shoots become self-sufficient. Data from other species (e.g. birch) indicates that leaves on coppice sprouts have higher rates of net photosynthesis per unit leaf area, which would shorten the period of dependency on root reserves. The root systems very likely remain a major site for stored carbohydrates throughout the short-rotation period, especially during the growing season.

Q. What effect does shoot removal have on fine-root growth and turnover?

A. Even with no functioning top, we observed a flush of fine-root growth in coppiced plants during the period immediately after cutting (mid-March to mid-

May), especially in Tristis. This response was more pronounced in unirrigated plants of Tristis, whereas irrigated plants of Eugenei showed greater growth. However, the lack of uncoppiced control plants does not allow us to say any more than this. Our hypothesis is, however, that fine-root growth is not dependent upon a functioning top, provided root reserves are high.

Q. How long before a coppiced poplar plant begins to function like its progenitor?

A. Certainly by the end of the first growing season coppice sprouts are physiologically similar to uncut plants of similar size. But their shoot:root ratios, obviously, differ considerably.

Major Task No. 3

This task in our original proposal called for the development of breeding strategies and modification of silvicultural prescriptions to increase biomass productivity in short-rotation poplar plantations. This section summarizes our current thinking on these subjects.

The framework for our breeding strategy is the ideotype concept, an approach that has proven successful in agriculture but that has not been exploited by woody-plant breeders to any great extent. We suggest that it may be important in the future of tree improvement. The concept of the crop ideotype was first proposed by Donald (1968) as "a plant model which is expected to yield a greater quantity or quality of ... useful product when developed as a cultivar." Dickmann's (1985) definition of an ideotype linked it more closely to forest tree improvement: an ideotype is a model tree that will produce an economic yield that approaches maximum in a particular environment (or on a certain site), using a prescribed cultural system, and assuming a well-defined end use for the harvested products. Few tree geneticists have formulated or published ideotypes, and to our knowledge the ideotype concept is not used in the operational breeding of poplars. Dickmann et al. (1994) fully discuss the pros and cons of ideotype breeding and give examples of the application of this approach to the breeding of forest, horticultural, and multi-purpose tree crops (see p. 150-180 of this report).

A complete crop ideotype for poplars is presented in Table V-1. This ideotype outlines the many yield-related traits thought at present to contribute to high biomass productivity. Two points need to be emphasized about this poplar ideotype. First, it is not the final word on the subject; ideotypes need to be continually modified as new information becomes available. Second, this ideotype does not represent a specific breeding goal; the practical limitations of tree breeding set a limit on the number of characters included in an applied ideotype. These limitations do not negate the importance of the ideotype approach. If for no other reason, ideotypes are valuable because they stimulate thinking about plants in a holistic way. And, from a physiological point of view, an ideotype can serve as the structural framework for a research program; the ideotype both summarizes the current conception of yield-related traits of the plant, and points out where gaps in knowledge exist. Further research then allows the ideotype to be refined.

Table V-1. A complete crop ideotype for poplar trees grown for energy wood in a high-density, unirrigated, intensive silvicultural system.

Growth and physiology:

Rapid height and diameter growth

Bud flushing late enough to avoid spring frost injury

Indeterminate shoot growth with bud set just prior to first autumn frosts

Leaves with a high photosynthetic rate per unit leaf area or weight, area leaf weight, and ratio of net photosynthesis to dark respiration.

High water-use efficiency (CO_2 fixed per unit of stomatal conductance)

Stomata begin closing at moderate levels of water stress

Leaf mesophyll cells osmotically adjust to gradual dehydration

Ecological characteristics:

Weak competitor (generalized "crop" ideotype)

High nutrient-use efficiency (stemwood biomass per unit of stemwood nutrient)

Effective remobilization of nitrogen and other mobile nutrients into stems and roots prior to leaf abscission

Capable of withstanding drought through dehydration postponement; e.g. vertical (erectophile) leaf orientation or leaf abscission.

Resistant to snow, ice, and cold damage

Wind firm

Tolerant of common post- and pre-emergent herbicides

Resistant to major pathogens (especially *Septoria musiva*) and invertebrate pests

Unpalatable to mammals

(continued on next page)

Morphology:

Relatively few, small diameter, upturned branches forming a long, narrow crown

Sylleptic branching

Rapid natural pruning of dead branches

High foliage density on branches

Relatively large, vertically oriented leaves in the upper crown

Long seasonal leaf retention (except during drought)

High ratio of long (indeterminate) to short (determinate) shoots in the upper crown

Light fruiting; male

Shoot/root ratio of ca. 1.5

Stem and wood properties:

Excurrent growth habit with straight, low-taper stem

Cambium active until late in the growing season

Thin bark; small pith

High density wood ($>0.4 \text{ g cm}^{-3}$)

Wood low in gelatinous fibers; vessel content $<20\%$

Roots:

Strongly rooting hardwood cuttings

Pronounced taproot for anchorage and exploitation of deep soil nutrients and water

Many highly branched lateral and fine roots throughout the soil profile

Fine roots turn over slowly

Readily colonized by mycorrhizal fungi

Strong sink for photosynthates late in the growing season

Dickmann (1991) proposed that breeders should select from a comprehensive ideotype (e.g. Table V-1) a limited subset of characters that offer the most promise for producing the desired genetic gain, or whose economic values are greatest (see p. 141-149 of this report). The "working" ideotype thus created can be viewed as an achievable breeding goal. In fact, more than one working ideotype could be created if different breeding goals existed. Furthermore, working ideotypes can be treated as a single quantitative trait during the selection phase of a breeding program (Dickmann 1991).

The use of ideotypes in poplar breeding

Recently Pöykkö (1993) expanded the ideotype approach to tree breeding by formulating a working morphological ideotype for Scots pine (*Pinus sylvestris*) and then using it as a single quantitative selection trait. Pöykkö employed a discriminate analysis, in which a canonical variable was computed that combined normed crown variables of the working pine ideotype into a score value, K. The K value was then used as a trait in a selection index, along with stem mass, to identify superior phenotypes in a Scots pine progeny test. This work by Pöykkö is significant because it is the first real application of ideotype selection in forest tree breeding. A diagrammatic representation of the general approach used by Pöykkö is found on page 158 of this report (Dickmann et al. 1994). It becomes obvious upon study of this figure that Pöykkö's work can be a model for application of working ideotypes in poplar breeding, as well.

What follows is an outline of our conception of a poplar improvement program using the ideotype approach developed by Dickmann (1991) and Pöykkö (1993). The breeding goals are basic to any approach to short-rotation culture of woody plants. This scenario represents one cycle of breeding, from the initial controlled crossing of a limited number of rigorously selected parents to eventual identification of a few genotypes for selective release or large-scale testing. Note that a major emphasis is put on selection for disease resistance (tolerance), especially to *Septoria* canker, rooting potential of hardwood cuttings, and growth potential. Note also that the conventional selection trait -- height -- is not employed until late in the cycle. We regard this trait as irrelevant early in a breeding cycle; it has too often been over-emphasized in poplar breeding, resulting in selection and release of genotypes with high early height-growth potential but little long-term survivability. We don't need any more poplar plantations that break up at age five!

The working ideotypes proposed in this scenario are composed largely of morphological characters that are easily measurable. Whereas the complete poplar ideotype presented in Table V-1 contains several important physiological variables and root system characteristics, these characters cannot be assessed in the early stages of a breeding cycle when large numbers of genotypes must be screened. Only after the winnowing process presented below is complete, and a few genotypes are identified that will be carried forward, can these more logistically problematic characters be assessed. However, at this later stage it is important that these more detailed analyses be carried out, and clones fully characterized, before final selections are made and commercial cultivars released for wide-scale planting.

Genetic Improvement of Poplars: A Scenario Using "Working" Ideotypes

Breeding Goals: high stemwood biomass production per ha (rotations of 5-10 years);
high harvest index; stability across environments; long-term resistance to diseases

Phase 1 Selection: Seedlings started in a greenhouse in containers, containers transferred
to a lathhouse mid season -- YEAR 1

Trait #1 (Working Ideotype)

Leaf size

Leaf number

Number of days until bud set (no supplemental heat or light in greenhouse)

Phase 2 Selection: Nursery growth of planted containers -- YEAR 2

Trait #1

Septoria canker (inoculate all trees); no infection allowed

Trait # 2 (Working Ideotype)

Days between terminal bud break and bud set

Days of leaf retention beyond terminal bud set

Leaf size

Leaf number

Since Trait #1 is all or nothing, and any clone with *Septoria* infection is eliminated,
selection is based primarily on the working ideotype

Phase 3 Selection: Stool beds established from unrooted cutting -- YEARS 3 & 4

Trait #1

Septoria canker (none allowed; any infection eliminates a clone)

Trait #2

Rooting of cuttings (> 90% for clone to be retained)

Trait #3 (Working Ideotype)

Leaf rust

Leaf spotting

Traits #2 & #3 combined in a Selection Index or Independent Culling (YEAR 4)

Phase 4 Selection: Field plantings on several sites of unrooted cuttings from stool beds --
YEARS 5 to 10

Trait # 1

Septoria canker (none allowed; any infection eliminates a clone)

Trait #2 (Working Ideotype)

Survival (> 90% for clone to be retained)

Height

Diameter

Trait #3 (Working Ideotype)

Stem form (straight, excurrent stem)

Epicormic branches (none or few)

Sylleptic branches (desirable)

Branch diameter (small)

Branch geometry (high angle of initiation, low angle of termination)

Traits #2 & #3 combined in a **Selection Index** or **Independent Culling**
(YEAR 10)

Phase 5 Selection: Region-wide field plantings of unrooted cuttings -- YEARS 10 to 20

Trait #1 (Working Ideotype)

Survival (> 90% for clone to be retained)

Height

Diameter

Trait #2 (Working Ideotype)

Some combination of physiological and root system characteristics

∞ ∞

Silvicultural Prescriptions

In 1950 Frederick S. Baker prefaced his now-classic textbook *Principles of Silviculture* with this statement:

"A large part of this book is devoted to plant physiology of forest trees in the belief that a sufficiently wise and flexible silvicultural art can be developed on the ground only by practitioners who understand the forest as a biological entity."

Baker's quote exactly sets forth the philosophical underpinning of our original proposal, i.e. that further yield improvement in short-rotation woody crop plantations for energy will be based, in part, on basic knowledge of the physiology, ecology, and genetics of these systems. The days of the silviculturist as a strict empiricist are passing. Especially with high-input tree systems grown for maximum yield, silviculture must be based on theoretical biological knowledge of the tree and stand, and their interaction with the environment.

We believe that our project has produced some practical spin-offs, especially related to the below-ground component of short-rotation plantations. The traditional practice of silviculture is largely focused on the portion of the stand that rises above the soil surface. This is only natural, given the mysteries associated with the rhizosphere. However, as the biological knowledge base of silviculture expands to include root systems, it follows that this knowledge should evolve into new silvicultural practices that modify root structure and function in such a way that product yield is maximized and environmental damage is minimized. Management of the entire stand should be the goal of silviculturists. Our thoughts on this subject were coalesced in a review paper on roots published under the auspices of the International Energy Agency, Bioenergy Agreement Task V (Dickmann and Pregitzer 1992; see p. 95-123 of this report), but we will reiterate some of these points below.

The relative allocation of biomass to roots versus stems can be controlled in several ways to increase yield and harvest index. Maintaining soil water and nutrients at optimum levels does two things: total biomass accumulation increases (higher yields) and the proportion of that biomass partitioned to the root system declines (greater harvest index). Thus, although fertilization and, especially, irrigation are expensive, they may give a large yield return on the investment. In certain situations the management of root systems through control of soil resources could become quite sophisticated. For example, when short-rotation woody crops are grown on lands drained by ditches and dikes, the soil water table could be controlled to produce stands with an optimum root/stem biomass distribution. The depth of the water table could be varied seasonally depending on the clone(s) being grown, the age of the plantation, and natural rainfall patterns. But, as our work has shown, there can be substantial genotype x environment interactions, so the responses of commercial clones to water and nutrition must be known.

If coppice regrowth of plantations following harvest is a part of the silvicultural system, management practices in the year prior to harvest could stimulate vigorous sprouting. The goal in this case would be to manage root carbohydrate and N reserves. Mid- to late- season fertilization and irrigation would increase the buildup of dormant-season root reserves, leading to high coppice yields in the subsequent rotation. Such practices are recommended for fruit-tree management, but also may be applicable to short-rotation forests. Secondly, harvest scheduling should have some flexibility built into it, so that unirrigated sites where water stresses frequently develop can be harvested only following a relatively wet growing season. In this case roots will be at optimum vigor,

and coppiced stumps will sprout readily. To take advantage of these practices, harvests should be confined to the dormant season.

Silvicultural management of root systems also relates closely to competition management. In young plantations, competition among trees and weeds is primarily for soil resources. What are the characteristics of a tree root system that competes effectively with weeds? Are there root-based tradeoffs in yield between a situation where soil resources must be acquired in the face of competition versus one in which weed-free soil can be exploited? How do weed management practices impact root systems? There are indications, for example, that disking in older plantations can disrupt the feeder root system in the uppermost soil horizon. What characteristics of root systems lead to a minimization of intraspecific root competition when stands close? Answering these questions could provide fruitful avenues for future research.

Management of rooting in plantations also is related to the prevention of environmental degradation. Soil erosion has been identified as a problem associated with short-rotation plantation management, especially on sloping ground that has been subjected to intensive site preparation and weed control. Leaching of nitrates and other fertilizer products into ground and surface waters also warrants concern. A key to prevention of erosion and anion leaching is the rapid establishment of tree cover over the site and root occupancy of the soil. Using genotypes that rapidly exploit the available soil volume and efficiently absorb nutrients, as well as planting at high densities, are avenues to increase the rate of site occupancy. It may be necessary to thin densely planted stands when the site is occupied to produce the optimum product, but in the meantime the soil will have been conserved.

As our knowledge of root systems expands, the list of silvicultural practices aimed specifically at roots will grow. In the meantime silviculturists should be aware that virtually everything they do to manipulate a short-rotation stand will modify root structure and function. Such awareness can contribute in the future to high-yielding, environmentally benign hardwood plantations.

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