

**NUTRIENT UPTAKE BY HYBRID POPLAR IN COMPETITION
WITH WEED SPECIES UNDER GROWTH CHAMBER AND FIELD
CONDITIONS USING THE SOIL SUPPLY AND NUTRIENT
DEMAND (SSAND) MODEL**

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By
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ABSTRACT

Success of hybrid poplar plantations will rely on the efficient management of nutrients and weeds. Relatively little is known about the root uptake characteristics of hybrid poplar and weeds, their belowground interactions and particularly, the quantitative understanding of nutrient uptake using mechanistic models under weed-competing conditions. Therefore, the objectives of this study were to investigate the effects of dandelion and quackgrass on the growth of hybrid poplar, to establish their root uptake characteristics and to quantify their nutrient uptake using the soil supply and nutrient demand (SSAND) model. In a pot study, hybrid poplar stem height, root collar diameter, shoot and root biomass, root length, and N, P and K uptake significantly decreased in the presence of dandelion and quackgrass weeds. Similar weed competition effects on growth of hybrid poplar were also observed in the field at the Pasture and Alfalfa sites where hybrid poplar was grown with and without weeds for 50, 79 and 100 days. In a hydroponic experiment, I_{\max} values for $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, P and K varied significantly among hybrid poplar seedlings and dandelion and quackgrass weed species and was greatest for dandelion followed by hybrid poplar and then quackgrass. The K_m values were lowest for quackgrass compared to the other plant species for all of the nutrients. Simulation results from the SSAND model for the pot study showed that N uptake was underpredicted in hybrid poplar by 58 to 73%, depending upon soil type and weed treatment. Incorporation of N mineralization as a model input improve the hybrid poplar N uptake predictions by 24 and 67% in the Pasture and Alfalfa soil, respectively, when grown without weeds. SSAND model underestimated P uptake by 84-89% and overestimated K uptake by 28 to 59% for hybrid poplar depending upon the soil type and weed treatment. In the field, N uptake by hybrid poplar was in close agreement to measured N uptake in the control treatment. N uptake was greatly underestimated for both hybrid poplar and weeds in the weed treatment. Including changing water content greatly improves the N uptake by hybrid poplar and weeds in weed treatments. Results from this study suggest weed control is an essential practice to establish successful hybrid poplar plantations. Also, SSAND model can be an effective tool for predicting the nutrient uptake under two plant species competing environment if all the processes of nutrient supply are adequately described in the model.

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TABLE OF CONTENTS

PERMISSION TO USE	i
ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	viii
1 INTRODUCTION	1
1.1 References	4
2 LITERATURE REVIEW	5
2.1 Plant Competition	5
2.1.1 Aboveground and belowground competition	5
2.1.2 Competition in managed ecosystems	8
2.1.3 Weed competition in hybrid poplar plantations	8
2.2 Root Uptake Characteristics	11
2.2.1 Measurement of nutrient uptake kinetics	11
2.2.2 Factor affecting nutrient uptake kinetics	12
2.2.3 Estimated values of N, P and K uptake kinetics for tree species and weeds	14
2.3 Nutrient Uptake Modeling	14
2.4 Verification of Simulation Models in Tree Species	21
2.5 References	23
3 GROWTH OF HYBRID POPLAR AS AFFECTED BY DANDELION AND QUACKGRASS COMPETITION	32
3.1 Introduction	32
3.2 Materials and Methods	33
3.2.1 Soils and soil preparation	33
3.2.2 Treatments and experimental design	35
3.2.3 Planting and maintenance of pots	35
3.2.4 Sample collection and analyses	36
3.2.5 Statistical analyses	37
3.3 Results	37
3.3.1 Aboveground growth parameters of hybrid poplar and weeds	37
3.3.2 Belowground growth parameters of hybrid poplar seedling and weed species	43
3.3.3 Nutrient uptake by hybrid poplar and weed species	47
3.3.4 Soil solution chemistry	50
3.4 Discussion	50
3.5 References	56
4 NUTRIENT UPTAKE KINETICS FOR HYBRID POPLAR AND TWO COMPETITIVE WEED SPECIES	60
4.1 Introduction	60
4.2 Methods and Materials	61

4.2.1	Plant material and growth conditions.....	61
4.2.2	Depletion experiment and uptake kinetics	62
4.2.3	Processing of plant material.....	63
4.2.4	Statistical analyses	63
4.3	Results	64
4.3.1	Plant root and shoot parameters	64
4.3.2	Nutrient uptake kinetics	64
4.3.3	Plant tissue nutrient concentrations.....	68
4.4	Discussion	68
4.4.1	Kinetics of NH ₄ -N and NO ₃ -N Uptake	68
4.4.2	Kinetics of P and K uptake	73
4.4.3	Implications for belowground competition.....	73
4.5	REFERENCES	76
5	NUTRIENT UPTAKE OF HYBRID POPLAR IN COMPETITION WITH WEEDS USING THE SOIL SUPPLY AND NUTRIENT DEMAND (SSAND) MODEL	80
5.1	Introduction	80
5.2	Materials and Methods	81
5.2.1	Estimation of model input parameters	81
5.2.2	Nutrient uptake modeling.....	84
5.3	Results	86
5.4	Discussion	91
5.5	References	102
6	MODELLING NUTRIENT UPTAKE FOR HYBRID POPLAR AS AFFECTED BY WEED COMPETITION IN THE FIELD	106
6.1	Introduction	106
6.2	Materials and Methods	107
6.2.1	Site description and experimental design.....	107
6.2.2	Measurements and samplings	108
6.2.2.1	Hybrid poplar	108
6.2.2.2	Weeds.....	109
6.2.3	N uptake modeling	109
6.2.3.1	Soil parameters.....	110
6.2.3.2	Plant parameters.....	112
6.2.4	Statistical analysis	112
6.3	Results	112
6.3.1	Soil moisture	112
6.3.2	Effects of weeds on hybrid poplar growth	114
6.3.3	N uptake modeling	117
6.3.4	Sensitivity analysis.....	120
6.4	Discussion	124
6.4.1	Hybrid poplar- weeds competition.....	124
6.4.2	N uptake predictions for hybrid poplar in control treatment.....	124
6.4.3	N uptake predictions under weed competition conditions	126
6.5	References	128
7	GENERAL DISCUSSION AND SUMMARY	130
	APPENDIX A.....	133

LIST OF TABLES

Table 2.1. Hybrid poplar height, diameter at breast height (DBH), and wood volume on September 30 each year in response to five groundcovers, Malheur Experiment Station, Oregon State University, Ontario, OR (adapted from Shock et al., 2002).	10
Table 2.2. I_{\max} and K_m values for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in various tree species and weeds. Note the difference in units for reported I_{\max} values (a and b represent $\mu\text{mol cm}^{-2} \text{s}^{-1}$ and $\mu\text{mol g}^{-1} \text{h}^{-1}$, respectively).	15
Table 2.3. I_{\max} and K_m values for P and K in various tree species and weeds.	16
Table 2.4. Nutrient uptake models and their characteristics.	19
Table 3.1. Physical and chemical characteristics of the Pasture and Alfalfa soils.	34
Table 3.2. Effect of weed competition on seedling survival (%) of hybrid poplar grown with different densities of dandelion and quackgrass weeds in Alfalfa and Pasture soils at harvest-I (47 and 49 DAP for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 DAP for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion plants per pot.	38
Table 3.3. Probability levels from the three-way analysis of variance for hybrid poplar growth and nutrient uptake parameters. Hybrid poplar seedlings were grown for 47 and 97 days in the Pasture soil and 49 and 105 days in the Alfalfa soil with different densities of dandelion and quackgrass weeds. Effect of source of variation on hybrid growth and nutrient uptake parameters is considered significant at $p < 0.05$	40
Table 3.4. Mean half-distance (cm) between all roots in the treatments grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 DAP for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 DAP for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion plants per pot.	46
Table 3.5. Mean shoot concentration and uptake for hybrid poplar grown with different densities of dandelion and quackgrass weeds in the Alfalfa and Pasture soils at harvest-II (97 and 105 DAP for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion plants per pot.	48

Table 4.1. Selected root and shoot parameters for plant species grown in the hydroponic solution experiment.....	65
Table 4.2. Mean N, P and K tissue concentrations for hybrid poplar, dandelion and quackgrass at the end of depletion experiment.	71
Table 5.1. Range of soil and plant input parameters used in SSAND model.	85
Table 5.2: Linear regression of predicted (y) vs observed (x) nutrient uptake for weeds. 89	
Table 6.1. Range of plant and soil input parameters used for N uptake modeling in field study.....	111
Table 6.2. Shoot and root growth parameters of hybrid poplar in control and weed treatment for the Pasture and Alfalfa site after 50, 79 and 100 days after planting (DAP).	114
Table 6.3. Growth and N uptake by weeds in the weedy treatment at each harvest for the Pasture and Alfalfa site.	116
Table 6.4. Linear regression of predicted (y) vs. observed (x) N uptake by hybrid poplar in control and weedy treatments.	118
Table 6.5. Linear regression of predicted (y) vs. observed (x) N uptake by weeds in weed treatment.	119

LIST OF FIGURES

Figure 2.1. Schematic description of nutrients supply in soil to the root surface.....	18
Figure 3.1. Effect of weed competition on (a) stem height and (b) root collar diameter of hybrid poplar grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for the Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for the Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$	41
Figure 3.2. Dry shoot biomass of (a) hybrid poplar seedlings and (b) weed species grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$	42
Figure 3.3. Fresh root biomass of (a) hybrid poplar seedlings and (b) weed species grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$	44
Figure 3.4. Root length of (a) hybrid poplar seedlings and (b) weed species grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$	45

Figure 3.5. Total N, P and K (root + shoot) uptakes for hybrid poplar seedling (a, c and e) and weed species (b, d and f) grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$ 49

Figure 3.6. Changes in soil solution nitrogen and potassium concentration in (a) Pasture and (b) Alfalfa soil at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively) under various densities of hybrid poplar seedling and weed species. Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$ 51

Figure 4.1. I_{max} and K_m values for nitrate and ammonium uptake by hybrid poplar, quackgrass and dandelion grown in hydroponic nutrient solution. Error bars represent one standard deviation. Bars with the same letter within each nutrient are not significantly different ($p \geq 0.05$). Data with “*” indicates a significant difference ($p < 0.05$) between nitrate-N and ammonium-N within each plant species. 66

Figure 4.2. I_{max} and K_m values for phosphorus and potassium uptake by hybrid poplar, quackgrass and dandelion grown in hydroponic nutrient solution. Error bars represent one standard deviation. Bars with the same letter within each nutrient are not significantly different ($p > 0.05$). 67

Figure 4.3. Michaelis-Menten curves for (a) nitrate and (b) ammonium uptake for hybrid poplar, quackgrass and dandelion. 69

Figure 4.4. Michaelis-Menten curves for (a) phosphorus and (b) potassium uptake for hybrid poplar, quackgrass and dandelion. 70

Figure 5.1. SSAND model predicted and observed nitrogen uptake by hybrid poplar grown without weed competition, without (▲) and with (■) nitrogen mineralization incorporation in the model, for (a) Pasture and (b) Alfalfa soil. 87

Figure 5.2. SSAND model predicted and observed nitrogen uptake by hybrid poplar grown with weed competition, without (▲) and with (■) nitrogen mineralization incorporation in the model, for (a) Pasture and (b) Alfalfa soil. 88

Figure 5.3. SSAND model predicted and observed phosphorus uptake by hybrid poplar grown (a) without and (b) with weed competition for the Pasture (▲) and Alfalfa (■) soil. 90

Figure 5.4. SSAND model predicted and observed potassium uptake by hybrid poplar grown (a) without and (b) with weed competition for the Pasture (▲) and Alfalfa (■) soil. 92

Figure 5.5. Sensitivity analysis for ammonium uptake by hybrid poplar grown without weed competition in Pasture (a and c) and Alfalfa (b and d) soil. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to ammonium uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{li} = initial soil solution concentration, K_d = Solid-liquid partition coefficient. 93

Figure 5.6. Sensitivity analysis for nitrate uptake by hybrid poplar grown without weed competition in the Pasture (a and c) and Alfalfa (b and d) soil. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to nitrate uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{li} = initial soil solution concentration. 94

Figure 5.7. Sensitivity analysis for phosphorus uptake by hybrid poplar grown without weed competition in the Pasture (a) and Alfalfa (b) soil. Results were similar for harvest-I and harvest-II simulations. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to phosphorus uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{li} = initial soil solution concentration, K_d = Solid-liquid partition coefficient. 95

Figure 5.8. Sensitivity analysis for potassium uptake by hybrid poplar grown without weed competition in the Pasture (a and c) and Alfalfa (b and d) soil. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to potassium uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{li} = initial soil solution concentration, K_d = Solid-liquid partition coefficient. 96

Figure 6.1. Change in volumetric water content at the Pasture and Alfalfa site during the study period. 113

Figure 6.2. Sensitivity analysis of predicted (a) ammonium and (b) nitrate uptake for hybrid poplar grown in control treatment at Pasture site. Results are expressed relative to nutrient uptake under the initial conditions. Each parameter was varied individually while all other parameters were held constant. Parameters used for sensitivity analysis are L_v

(root length density), C_{li} (initial soil solution concentration), r_o (root radius), V_o (water influx rate), I_{max} (maximum nutrient influx rate), K_m (Michaelis-Menten constant) and K_d (solid-liquid partition coefficient)..... 121

Figure 6.3. Sensitivity analysis of predicted (a) ammonium and (b) nitrate uptake for hybrid poplar grown in control treatment at Alfalfa site. Results are expressed relative to nutrient uptake under the initial conditions. Each parameter was varied individually while all other parameters were held constant. Parameters used for sensitivity analysis are L_v (root length density), C_{li} (initial soil solution concentration), r_o (root radius), V_o (water influx rate), I_{max} (maximum nutrient influx rate), K_m (Michaelis-Menten constant) and K_d (solid-liquid partition coefficient)..... 122

Figure 6.4. Sensitivity analysis of predicted (a) ammonium and (b) nitrate uptake for hybrid poplar grown in weed treatment (trends for similar for the Pasture and Alfalfa site). Results are expressed relative to nutrient uptake under the initial conditions. Each parameter was varied individually while all other parameters were held constant. Parameters used for sensitivity analysis are L_v (root length density), C_{li} (initial soil solution concentration), r_o (root radius), V_o (water influx rate), I_{max} (maximum nutrient influx rate), K_m (Michaelis-Menten constant) and K_d (solid-liquid partition coefficient).
..... 123

1 INTRODUCTION

The concept of growing trees on farmland is not entirely new and farmers have practiced agroforestry for thousands of years. This practice has been adopted on a very limited scale to meet some of the domestic demands for fuelwood and timber supply, fruit production, animal fodder, medicinal value and landscape and aesthetic values (King, 1987). During the past few years, however, there has been a growing interest towards the cultivation of fast-growing tree species, particularly hybrid poplar, on a large scale due to the increasing demand for pulp, paper and other wood products, to relieve the harvesting pressure on native forests, to combat the increasing greenhouse gas emission threat (Liberloo et al., 2006), and to diversify farm income (Yemshanov et al., 2005).

Several management practices are required to successfully establish tree plantations and, among them, nutrient management is very important (Balandier et al., 2006; Thompson and Pitt, 2003; Wagner et al., 2006). Nutrient management can be affected by various soil and climatic factors and, furthermore, its advantage to the trees will depend upon how effectively weeds are controlled in the plantations (Balandier et al., 2006). Weed species competition for nutrients and moisture in plantations occurs particularly during the initial establishing years when tree species do not have large and deep root systems to access resources from deep soil layers (Nambiar and Sands, 1993). Therefore, it is very important to understand the mechanisms which affect nutrient uptake under a weed-competing environment in order to make weed and nutrient management more viable economically.

Nutrient uptake at the root surface occurs from the soil solution. Several soil processes such as buffering power, mineral weathering and organic matter mineralization-immobilization determine the concentration of nutrients in the soil solution (Barber, 1995). Transport of nutrients in the soil to the root surface is controlled by mass flow and diffusion while uptake at root surfaces is considered to

follow Michaelis-Menten kinetics (Barber, 1995). These factors can be integrated into mathematical models in order to quantify nutrient uptake and this approach has been used successfully in a simplified system of one plant species (Barber, 1995; Rengel, 1993; Silberbush, 2002). However, under plant competition environment, soil and plant factors interact in a more complex way depending upon the root size and uptake characteristics of competing plant species. Smethurst and Comerford (1993) using the COMP8 model predicted the phosphorus (P) and potassium (K) uptake for slash pine (*Pinus elliottii* Engelm. var. *elliottii*) and grass (*Panicum aciculare*) which were grown in competition to each other. They found that some of the predictions were not accurate, probably because some of the processes responsible for supplying P and K in the soil and uptake at root surface were not adequately described in the model (Smethurst and Comerford, 1993). Here in this study, attempts are being made to predict nutrient uptake by hybrid poplar in competition with weed species using the Soil Supply and Nutrient Demand (SSAND) model which can incorporate soil mineralization input and changing soil water content.

For this study, therefore, it was hypothesized that growth of hybrid poplar would decrease in the presence of weeds due to the competition for nutrients. The second hypothesis is that including N mineralization and changing soil water content as input variables in the SSAND model will improve predictions of N uptake. These hypotheses would be tested through series of experiments with the following objectives:

- 1) To investigate the effects of weeds on the growth of hybrid poplar under both growth chamber and field conditions by examining the below- and aboveground characteristics of hybrid poplar and weeds.
- 2) To quantitatively describe the N, P and K uptake characteristics of hybrid poplar seedlings, and dandelion and quackgrass weed species.
- 3) To predict nutrient uptake by hybrid poplar in competition with selected weeds by incorporating N mineralization and changing soil moisture content in the SSAND model under growth chamber and field conditions.

This thesis is comprised of six chapters, which provide the details of various experiments conducted to meet the overall objectives and to test the proposed hypotheses.

Chapter 2 is a literature review which includes various aspects and mechanisms of plant competition: specifically, belowground competition, root nutrient uptake characteristics and nutrient uptake modeling.

Chapter 3 examines the competition effects of dandelion and quackgrass weed species on aboveground and belowground growth of the hybrid poplar as well as nutrient dynamics in soil solution.

Chapter 4 is a solution culture study that establishes the values for N, P and K uptake characteristics (I_{\max} and K_m) of hybrid poplar, dandelion and quackgrass roots using Michaelis-Menten kinetics.

Chapter 5 attempts to predict N, P and K uptake by hybrid poplar grown without and with weeds using the SSAND model after incorporating the data obtained from Chapters 3 and 4, and from some independent measurements.

Chapter 6 deals with the competition effects of weeds on the growth of hybrid poplar under field conditions and subsequently predicts N uptake using the SSAND model.

Chapter 7, finally, summarizes the salient results from Chapters 3 to 6 to conclude this study in terms of meeting the objectives and testing the hypotheses and implications for future research.

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2 LITERATURE REVIEW

2.1 Plant Competition

Competition is an important ecological process in both natural and agricultural plant communities. Competition can be aboveground and/or belowground (Grace and Tilman, 1990; Wilson, 1988). Aboveground competition is mainly described as shoot competition where shoots of competing species compete for light, while belowground competition involves roots of different species growing in the same volume of soil competing for nutrients and water (Casper and Jackson, 1997; Grace and Tilman, 1990; Wilson, 1988).

2.1.1 Aboveground and belowground competition

Several plant and soil factors can affect competition among plant species. Aboveground competition is affected by plant morphological and physiological traits such as leaf area, plant height and shoot biomass, photosynthetic and dark respiration rates, and leaf nitrogen (N) content (Balandier et al., 2006; Gaudet and Keddy, 1988), which directly or indirectly control a plant's ability to capture the aboveground light resource. Aboveground competition is relatively more important when soil resources are in sufficient supply and roots are less competing (Wilson, 1988). Gerry and Wilson (1995) reported that the competitive responses of six plant species were not influenced by the initial size of the plants. They concluded initial plant size may not confer a competitive advantage for light if plants are limited by soil resources. Wilson (1988) reviewed 23 studies on plant competition that involved both below- and aboveground competition and concluded that belowground competition was more intense than shoot competition. Therefore, it can be concluded that in most ecosystems where the supply of soil nutrients and water is limiting, belowground competition can be more important than aboveground competition. The importance of belowground competition also has been reviewed comprehensively in the literature for plants in general (Caldwell and Richards, 1986; Casper and Jackson, 1997; de Kroon et al., 2003) and more specifically

for forests and woodlands (Coomes and Grubb, 1998; Nambiar and Sands, 1993) and agroforestry systems (Schroth, 1998). All of these reviews maintain that plants in a given ecosystem compete for a broad range of soil resources, including water and all essential nutrients. Factors influencing belowground competition may vary depending upon the soil physical environment, and the physiology and genetics of plants involved in competition. Various belowground plant traits can influence the ability of plants for belowground competition such as root growth rate, root biomass, root radius, root length density, surface area, and rooting depth (Casper and Jackson, 1997; Schenk and Jackson, 2002). Such factors help the plants in occupying a greater volume of soil and greater access to soil nutrients and soil moisture. The importance of root attributes in plant competition also increased under conditions where availability of soil resources to the plant roots is limited by ion mobility, and the soil processes which govern their mobility. Movement of nutrients to the roots is mainly controlled by three processes i.e. root interception, mass flow and diffusion (Barber, 1995). Root interception, generally, is considered to be less important (Barber, 1995), but its significance cannot be ignored under conditions of high root density because of the greater physical access of roots to the soil resources. Mass flow of water, driven by plant transpiration, carries dissolved nutrients to the roots and the availability of nutrients at the root surface depends upon the rate of water movement to the roots and the concentration of dissolved nutrients. This process is considered more important for the supply of nitrate to plant roots. Whereas the movement of less mobile nutrients bound to the soil surface, for example potassium and phosphate ions, is controlled by the diffusion process by creating a local concentration gradient. Therefore, the supply of nutrients to plant roots depends upon diffusion and mass flow, which occur simultaneously. In a competition scenario, plants with large and extensive root systems have the advantage to exploit greater soil resources because of greater root surface area available for uptake and reduced distance to be traveled by less mobile nutrients to the root surface.

Once nutrients have reached the root surface, nutrient uptake by roots can also play a role in the competitive ability of plants through its uptake kinetics. Plant species with greater values of I_{\max} (maximal influx at high concentration) and lower K_m

(concentration where influx rate is half of the I_{\max}) certainly will have the competitive advantage over the other competing plant species, when the supply of nutrients from the soil is non-limiting (Aerts, 1999; Jungk and Claassen, 1997). Also, the advantage of superior kinetic parameters for a plant will also depend upon the amount of roots present for that species in a competing environment because these parameters often are expressed on a per unit root surface area, root length or root weight basis (Jungk and Claassen, 1997). Therefore, a competitive advantage of superior kinetic parameters for a given plant species may be masked in the presence of other plant species which have a relatively larger root system.

Allelopathy is another indirect mechanism of belowground plant competition in which the growth of one plant species is inhibited by another plant species through the release of toxic chemicals from the roots (Grace and Tilman, 1990; Norby and Kozlowski, 1980; Obaid and Qasem, 2005; Wardle et al., 1998). Several weed species are known to release toxic allelopathic chemicals (Qasem and Foy, 2001). The ability of quackgrass (*Elymus repens*) to produce allelopathic chemicals (Hagin, 1989; Korhammer and Haslinger, 1994; Schulz et al., 1994) and adversely affect the growth of other plant species growth has been reported (Kommedahl et al., 1957; Schulz et al., 1994). Likewise, allelopathic effects of certain annual species on tree growth have also been reported by Smith et al. (2001). They reported that tall fescue (*Festuca arundinacea*), bermudagrass (*Cynodon dactylon*) and cutleaf evening primrose (*Oenothera laciniata*) leachate decreased pecan trunk weight by 22%, root weight by 17%, and total tree dry weight by 19%, compared to the control treatment.

Mycorrhizae can also affect plant competition, although the role that mycorrhizae play in plant competition is complicated and needs to be understood more clearly (Allen and Allen, 1990; Kernaghan, 2005; Newman, 1988; Watkinson and Freckleton, 1997). Mycorrhizae have been shown to increase plant competition between plant species (West, 1996). In a growth chamber study, Marler et al. (1999) reported that the growth of *Festuca idahoensis* while competing with *Centaurea maculosa* significantly decreased in the presence of arbuscular mycorrhizal fungi and the growth of *F. idahoensis* was 171% greater when arbuscular mycorrhizal fungi were not present.

In contrast, mycorrhizae have also been shown to help in the nutrient sharing between the competing plant species thereby indirectly decreasing plant competition (Newman, 1988). Mycorrhizae may potentially increase the pool of belowground resources by capturing the quantities of inaccessible nutrients that would otherwise be unavailable to competing plant species (Allen and Allen, 1990).

2.1.2 Competition in managed ecosystems

In natural ecosystems, the composition of plant communities is mainly decided by the competing ability of plants for the existing resources in that system (Grace and Tilman, 1990). However, in agricultural or managed plant systems, competition can be altered in favour of the desired plant species of economic importance by eliminating unwanted plant species (weeds) from the system by various methods. The presence of weeds in agricultural systems can cause economic losses through direct reductions in crop yields, cost of control and reduced crop quality (Zimdahl, 2004). Similar adverse effects of weeds have also been identified in forests and intensively managed tree plantation systems (Balandier et al., 2006; Thompson and Pitt, 2003; Wagner et al., 2006). Therefore, in managed ecosystems, competition is often described as weed competition because of their negative effects on the growth of the desired plant species. Weeds are a major impediment to the development of agricultural crops and tree species which affect their growth through various mechanism of below- and aboveground competition as described above.

2.1.3 Weed competition in hybrid poplar plantations

Roots of 1-yr-old poplar trees can spread horizontally up to 2.7 m (Friend et al., 1991) and more than 60% of the total root mass of 4-yr-old hybrid poplar clones occurred in the upper 0.36 m of the soil (Heilman et al., 1994), which demonstrates the shallow rooting nature of young poplar trees. Because of their shallow rooting, hybrid poplar encounters severe competition from weeds for soil resources, such as nutrients and moisture, which ultimately affects the aboveground tree biomass production. Poplar growth is sensitive to the amount of weed-free area around the tree, and controlling competing vegetation is a key to successful poplar establishment and production (Buhler et al., 1998; Heilman et al., 1995). Nitrogen is a nutrient that often limits the

growth of young poplar trees (Hansen et al., 1988) and weeds substantially decrease the growth of poplar trees primarily through competition for N present in soil solution or available from fertilizers (McLaughlin et al., 1987). Failure to control weed competition will result in high tree mortality and a growth reduction of >50% for surviving trees (Hansen and Netzer, 1985). Buhler et al. (1998) observed an increase in the height and diameter of stem, and number of leaves from 1 August to 6 September by 73, 104 and 67%, respectively, where there was continuous weed control. In comparison, trees with poor weed control grew less during the same period (37, 45 and 34% for the same growth traits). In another study in southwestern Michigan, USA, Marino et al. (1998) reported that in the presence of weeds, poplars were significantly shorter, had a smaller basal diameter, initiated fewer shorter branches, and had fewer living branches that spread outward compared to the weed controlled trees. In a nursery study at three different sites, Sixto et al. (2001) observed that poplar tree height decreased 19 to 56% for non-weeded plots compared to the weeded plots during the first growing season, depending upon the sites and method of weed control used.

In some agroforestry systems, intercropping or use of ground cover crops is considered to be an effective means for controlling weeds during establishment of some woody crop plantations including hybrid poplar plantations (Williams and Gordon, 1992). Intercropping can also generate a short-term return from an herbaceous agricultural crop during the early and unprofitable years in tree plantations (Burgess et al., 1996; Williams and Gordon, 1992). Furthermore, agroforestry has become increasingly popular in areas previously dominated by agricultural crops (Williams and Gordon, 1992). However, studies with woody crop plantations (Nambiar and Sands, 1993) and orchards (Hogue and Neilsen, 1987) have shown the negative effects of cover crops on tree growth, especially in the first few years after establishment. In a three-year study with hybrid poplar, Shock et al. (2002) reported that intercropping or use of ground cover crops significantly reduced the tree height, diameter at breast height and wood volume (Table 2.1). They concluded that the first two years of poplar plantation growth are very critical and that plantations must be free from the weeds or groundcover in order to ensure a healthy stand. They observed that the wood volume for

Table 2.1. Hybrid poplar height, diameter at breast height (DBH), and wood volume on September 30 each year in response to five groundcovers, Malheur Experiment Station, Oregon State University, Ontario, OR (adapted from Shock et al., 2002).

Groundcover	Tree Height (m)			DBH (cm)			Volume (m ³ ha ⁻¹)		
	1997	1998	1999	1997	1998	1999	1997	1998	1999
Bare soil	2.94a†	5.97a	8.61a	1.9a	7.3a	11.1a	0.18a	4.72a	15.6a
Mowed weeds	2.28b	5.16bc	8.82a	1.1c	5.1c	9.2b	0.05c	2.08c	11.6b
Alfalfa	2.05b	4.47c	6.96b	1.0c	4.3c	7.0c	0.04c	1.41c	6.0c
Wheat‡	2.31b	5.10bc	8.10a	1.2c	5.3c	9.1b	0.06c	2.21c	10.5b
Squash§	2.71a	5.58ab	8.85a	1.5b	6.1b	10.4a	0.10b	3.18b	14.6a

† Within columns, means followed by the same letter are not significantly different according to Duncan's Multiple Range test.

‡ Wheat was not planted in 1999, and the plots were treated as a mowed weeds treatment.

§ Squash was not planted in 1999, and the plots were treated as a bare-soil treatment.

the bare-soil plots was 34% greater than mowed weed plots, 88% greater than wheat plots, and 260% greater than the alfalfa plots by the end of the second year.

2.2 Root Uptake Characteristics

Mobility of nutrient ions in the soil to the root surface is controlled mainly via mass flow and diffusion processes. The absorption of nutrients from soil solution by roots, once they reach the root surface, is affected by root parameters such as radius, density and surface area (Jungk, 2002) and most importantly, by the physiological uptake characteristics of the root which regulate the entry of nutrient ions at the root surface (BassiriRad et al., 2000; Clarkson, 1985).

2.2.1 Measurement of nutrient uptake kinetics

Nutrient uptake kinetics are measured at different external ion concentrations to determine ion influx at the root surface. Usually, ion influx increases with increasing ionic concentration in the external solution until saturation kinetics are reached and ion influx rate becomes independent of external solution ion concentration. This relationship of ion influx as a function of external solution ion concentrations can be described by Michaelis-Menten kinetics by the following equation (Nielsen and Barber, 1978):

$$I_n = \frac{I_{\max} (C - C_{\min})}{K_m + (C - C_{\min})} \quad [2.1]$$

where I_n ($\mu\text{mol cm}^{-2} \text{s}^{-1}$) is the nutrient ion influx, I_{\max} ($\mu\text{mol cm}^{-2} \text{s}^{-1}$) is the maximal nutrient influx rate at high concentrations C , K_m (μM) is the Michaelis–Menten constant and is the nutrient concentration where influx is $0.5 * I_{\max}$, and C_{\min} (μM) is the nutrient concentration below which influx ceases (i.e., influx = efflux).

There are a number of methods which allow for the determination of the Michaelis-Menten kinetic parameters for nutrient uptake. These methods involve using either excised or intact roots for nutrient uptake under a range of external nutrient solution concentrations. For the excised root methods, root segments are placed into bathing solutions supplied with radioactive tracers and uptake is estimated from the accumulation of the tracer in the root tissues (Epstein, 1972; Shock and Williams, 1984). Use of this technique can be appealing due to the easy handling of samples and greater

repetition of experiments within a short time period, but leakage of solute from the cut root end (Bryce and Ap Rees, 1985) may cause the uptake kinetic analysis to be less accurate. This limitation can be overcome by measuring the nutrient uptake kinetics by growing intact root systems in hydroponic solutions using the depletion method (Claassen and Barber, 1974) or growing intact root systems in solutions where nutrient concentrations are kept constant during the growing period (Mullins and Edwards, 1988; Wild et al., 1979). The latter approach can be criticized because the concentration of nutrients in the soil solution under field conditions does not remain constant. Therefore, the depletion method may provide a more realistic description of nutrient uptake kinetics in the field. In the depletion method, intact roots are allowed to deplete the nutrient from a solution of known concentration over a period of time for measuring the uptake kinetics (Claassen and Barber, 1974). Kinetic parameters measured by the depletion procedure have been used successfully to predict nutrient uptake by plants growing in the soil (Barber, 1995).

2.2.2 Factor affecting nutrient uptake kinetics

Several plant and environmental factors can affect nutrient uptake kinetics. Plant factors include crop variety or crop cultivar, age of roots or plant and the nutritional status of the plant. Environmental factors include the composition of the nutrient solution, rooting temperature and the duration of uptake experiment (Clarkson, 1985; Le Bot et al., 1998).

Variations in uptake kinetics parameters among different crop cultivars have been observed for $\text{NO}_3\text{-N}$ in red maple (*Acer rubrum*) tree seedlings (Kelly et al., 2000), wheat (*Triticum aestivum*) (Rodgers and Barneix, 1988) and potato (*Solanum tuberosum*) (Sharifi and Zebarth, 2006), and for P in wheat (Egle et al., 1999), corn (*Zea mays*) (Nielsen and Barber, 1978) and spring barley (*Hordeum vulgare*) (Romer and Schenk, 1998). Kelly et al. (2000) determined the $\text{NO}_3\text{-N}$ uptake parameters for red maple in a hydroponic system using two cultivars that differed in root production and water use efficiency. Estimates of I_{\max} varied between experiments with means ranging from 1.5×10^{-5} to $5.9 \times 10^{-5} \mu\text{mol cm}^{-2} \text{s}^{-1}$. Means for K_m ranged from 2.04×10^{-5} to $5.23 \times 10^{-5} \mu\text{mol cm}^{-3}$, while C_{\min} values were consistent at $0.001 \mu\text{mol cm}^{-3}$ (the limit of analytical detection) across all experiments.

Plant age also affects the nutrient uptake kinetic parameters of plant species. Nutrient influx was observed to decrease with increased plant or root age (Bhat et al., 1979; Sharifi and Zebarth, 2006; Wild and Breeze, 1981). The reduction in calculated I_{\max} as the plants matured may be attributed to a reduced uptake rate by older roots (Bar-Yosef and Kafkafi, 1971) and/or to a reduced proportion of the root system active in uptake (Robinson et al., 1991) and also to decreased demand per unit root length due to increased root length with plant age (Kuhlmann and Barraclough, 1987).

Uptake kinetics of root can vary in plants which are grown with different nutrition or in plants of different nutritional status (Drew et al., 1984; Glass, 1977; Jungk et al., 1990; White, 1973). In a study on soybean and maize grown with different P nutrition to obtain plants with different P status, Jungk et al. (1990) found that I_{\max} declined drastically with increasing % P in the plant tissues, while K_m did not change much. Similarly, inverse relationships between the nutrient concentration in the root and I_{\max} values were found by Siddiqi et al. (1990) for $\text{NO}_3\text{-N}$ and Glass (1977) for K.

Adam et al. (2003) investigated the influence of root-zone temperature on the kinetics of net $\text{NO}_3\text{-N}$ uptake by using solution-grown "Autumn Flame" and "Franksred" (Red Sunset) ramets as representatives of red maple (*Acer rubrum*). Averaged over both cultivars in all experiments, I_{\max} estimates were 120, 150, and 170 $\text{nmol m}^{-2} \text{s}^{-1}$ for the root-zone treatments that had temperatures of 14, 24, and 34°C, respectively. Values of K_m increased with root-zone temperature and averaged 88, 140, and 190 μM whereas C_{\min} decreased and averaged 66, 38, and 18 μM for the 14, 24, and 34°C treatments, respectively. They concluded that it was necessary to account for root-zone temperature when estimating $\text{NO}_3\text{-N}$ uptake.

Kinetic parameter values are also affected by the depletion curve obtained from the hydroponics depletion method (Claassen and Barber, 1974). Use of partial depletion curves could lead to the erroneous kinetic parameters and subsequently erroneous uptake predictions for the nutrient of interest (Van Rees, 1994). Therefore, it is always important to deplete the nutrient from the soil solution to a sufficiently low concentration in order to obtain the correct kinetic parameter values. Decreasing the concentration in solution to some low extent is also useful for calculating the C_{\min} where the net nutrient influx is zero (Bhat, 1981).

2.2.3 Estimated values of N, P and K uptake kinetics for tree species and weeds

Various studies have been conducted to measure the uptake kinetics for forest and agroforestry plantation tree species and some parallel information is also available for the weed species which coexist in tree plantation environments (Table 2.2 and Table 2.3). Large variations are observed in uptake kinetic values for $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, P and K among the tree species due to one or several reasons as explained above in Section 2.2.2. Comparison of kinetic parameters between plant species is sometimes difficult because the units for the uptake kinetic parameters vary from study to study. Based upon the literature, values for root uptake characteristics for some tree and weed species are reported in Table 2.2 for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ and in Table 2.3 for P and K.

2.3 Nutrient Uptake Modeling

Availability of nutrients in the soil and their acquisition by plants is a function of complex biotic and abiotic processes associated with the soil and plant characteristics, past management practices and current nutrient addition (Barber, 1995). Soil and plant associated factors may interact in various ways in order to supply the nutrients to the plant. In such a complex interacting environment, therefore, it is difficult to assess experimentally the role of individual factors in plant nutrition. In order to understand the complexity of these systems and to evaluate the role of individual soil and plant factors in plant nutrition, mechanistic nutrient uptake models are needed. The underlying processes which govern the supply of nutrients in the soil to the root surface and subsequent uptake have been integrated into mechanistic nutrient uptake models (Rengel, 1993).

To date, various mechanistic nutrient uptake models have been developed and tested (Barber and Cushman, 1981; Reginato et al., 2000; Smethurst and Comerford, 1993a; Tinker and Nye, 2000; Yanai, 1994). This approach has been used very successfully in a variety of conditions and for variety of plant species (Barber, 1995; Tinker and Nye, 2000). The supply of soil nutrients to the root surface using solute-transport theory and the use of Michaelis-Menten kinetics to describe the uptake at root surface are common processes described in all uptake models (Rengel, 1993; Silberbush, 2002). Mass flow and diffusion are the two major soil processes which are included in the

Table 2.2. I_{\max} and K_m values for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in various tree species and weeds. Note the difference in units for reported I_{\max} values (a and b represent $\mu\text{mol cm}^{-2} \text{s}^{-1}$ and $\mu\text{mol g}^{-1} \text{h}^{-1}$, respectively).

Plant species	$\text{NH}_4\text{-N}$		$\text{NO}_3\text{-N}$		References
	I_{\max} (a= $\mu\text{mol cm}^{-2} \text{s}^{-1}$) (b= $\mu\text{mol g}^{-1} \text{h}^{-1}$)	K_m (μM)	I_{\max} (a= $\mu\text{mol cm}^{-2} \text{s}^{-1}$) (b= $\mu\text{mol g}^{-1} \text{h}^{-1}$)	K_m (μM)	
Tree species					
Aspen	1.3×10^{-5} a	217	0.58×10^{-5} a	337	(Hangs et al., 2003)
	5.53-9.88 b	45-60	0.30-3.0 b	3.4-11.7	(Min et al., 2000)
White spruce	2.0×10^{-5} a	206	0.45×10^{-5} a	345	(Hangs et al., 2003)
Jack pine	1.1×10^{-5} a	270	0.21×10^{-5} a	351	(Hangs et al., 2003)
Eucalypt	5.3×10^{-6} a	16	3.7×10^{-6} a	18	(Garnett et al., 2003)
Spruce	1.86-2.44 b	19.8-41.0	0.11-0.13 b	13.6-21	(Kronzucker et al., 1995; 1996)
Pine	2.07-2.22 b	32-45	0.04-0.35 b	6-153	(Min et al., 2000)
Red maple	-	-	1.5×10^{-5} - 5.9×10^{-5} a	204 - 523	(Kelly et al., 2000)
Hybrid poplar	-	-	2.85×10^{-5} a	712	(Kelly and Ericsson, 2003)
Weeds					
Calamatogrostis	8.5×10^{-5}	126	1.8×10^{-5} a	230	(Hangs et al., 2003)
Fireweed	5.8×10^{-5}	164	1.3×10^{-5} a	275	(Hangs et al., 2003)

Table 2.3. I_{\max} and K_m values for P and K in various tree species and weeds.

Plant species	P		K		References
	I_{\max} ($\mu\text{mol cm}^{-2} \text{s}^{-1}$)	K_m (μM)	I_{\max} ($\mu\text{mol cm}^{-2} \text{s}^{-1}$)	K_m (μM)	
Tree species					
Red maple	5.49×10^{-6}	15	3.80×10^{-6}	10	(Kelly and Kelly, 2001)
Loblolly Pine	2.68×10^{-7}	16	1.4×10^{-6}	30	(Kelly et al., 1992)
Slash Pine	-	-	3.61×10^{-6}	29	(Van Rees et al., 1990)
Hybrid poplar	1.51×10^{-6}	0.87	1.76×10^{-5}	27	(Kelly and Ericsson, 2003)
Weeds					
Dandelion	3.25×10^{-6}	-	-	-	(Levang-Brilz and Biondini, 2003)
<i>Agropyron cristatum</i>	3.73×10^{-6}	-	-	-	(Levang-Brilz and Biondini, 2003)
<i>Elymus canadensis</i>	1.19×10^{-6}	-	-	-	(Levang-Brilz and Biondini, 2003)

models to determine the nutrient supply to the root surface (Figure 2.1). Both these processes act simultaneously. Supply of nutrients by mass flow is a function of the transpiration rate of the plants and the concentration of the nutrient in the soil solution. When the demand for nutrients by plants exceeds the demand met by mass flow, then nutrients move towards the root surface by diffusion due to the concentration gradient (Barber, 1962). Movement of nutrients in soil is dependent upon the effective diffusion coefficient of the ion of interest, volumetric water content (VWC), impedance factor, and the buffer power of the soil (Jungk and Claassen, 1997). Nutrient uptake at the root surface in the models is described by Michaelis-Menten type kinetics (Nielsen and Barber, 1978) (Figure 2.1). Michaelis-Menten kinetics assumes that nutrient uptake at the root surface increases with increasing nutrient concentration in the soil solution until saturation kinetics are reached. Equations describing all these processes are integrated mathematically to predict the total nutrient uptake by the plant and compared with experimentally measured uptake the plant tissue (Barber, 1995).

Initially, nutrient uptake was based on a theoretical consideration of the processes involved in ion flux to a single root growing in soil, ignoring root competition (Nye, 1966; Passioura, 1963). Later approaches incorporated root growth to adequately reflect absorption by actively growing plant roots in soil (Claassen and Barber, 1976). Several modifications were made in order to improve the uptake prediction from time to time, which included rhizosphere acidification (Nye, 1981), root hairs (Itoh and Barber, 1983), root exudates (Nye, 1984) and root competition (Claassen et al., 1986). Some of the mechanistic models and their important characteristics are listed in Table 2.4.

To use these mechanistic models, information on soil nutrient supply, root morphological characteristics, and root uptake kinetics are required for the soil and plant species of interest. All these models were developed based upon assumptions to simplify the equations used in the model in order to predict the nutrient uptake from the soil (Barber, 1995; Tinker and Nye, 2000). A few assumptions are specific to particular models, but most of the following assumptions are common to all nutrient uptake models. For example, the mechanistic-based models assume that nutrient uptake occurs evenly along roots that are uniformly distributed in homogeneous and isotropic soil; nutrients

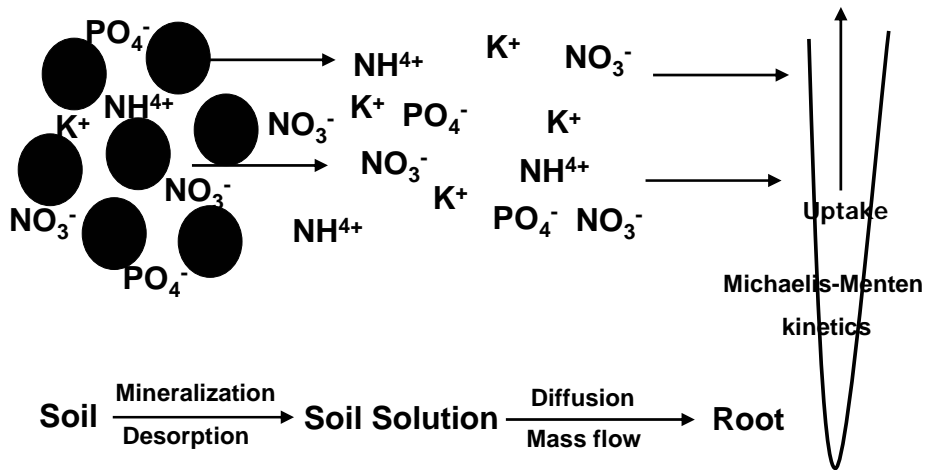


Figure 2.1. Schematic description of nutrients supply in soil to the root surface

Table 2.4. Nutrient uptake models and their characteristics.

Model	Characteristics	Reference
Nye-Marriott (NM)	Mass flow and diffusion, uptake by single root from infinite medium, Michaelis-Menten Kinetic	Nye and Marriott (1969)
Baldwin-Nye-Tinker (BNT)	Mass flow and diffusion, steady-state depletion profile near the root	Baldwin et al. (1973)
Bhat-Nye-Baldwin (BNB)	BNT + uptake by root hair	Bhat et al. (1976)
Claassen-Barber (CB)	NM + root growth	Claassen and Barber (1976)
Barber-Cushman (BC)	CB + root competition	Barber and Cushman (1981)
Itoh-Barber	BC + Root hairs	Itoh and Barber (1983)
Hoffland et al.	Mass flow and diffusion, inter-root competition, finite soil volume, inter-root distance (r_1) decrease with increasing root density	Hoffland et al. (1990)
COMP8	BNT approach, competition between plant species, inter-root distance (r_1) variable	Smethurst and Comerford (1993a)
Yanai	Steady state concentration profile, root competition	Yanai (1994)
Soil Supply and Nutrient Demand (SSAND)	COMP8 + variable root growth, variable soil water content, incorporation of mycorrhizae and mineralization inputs	Comerford et al. (2006)

move to the roots by a combination of mass flow and diffusion, and absorption of nutrients occurs only at the root surface, following the Michaelis-Menten kinetics; influx

characteristics are not affected by plant or root age and are independent of the rate of water absorption; and the availability of nutrients to the plant roots can be approximated by determining the equilibrium solution concentration and ability of the soil solid phase to buffer or sustain the solution phase concentration of that nutrient over time (Barber, 1995; Rengel, 1993; Silberbush, 2002).

Equations that describe both root growth and nutrient availability/movement are combined in the model and provide a means to mechanistically describe the influence of changes in root growth, root competition, and soil nutrient supply on nutrient uptake. Most of the models simulate nutrient uptake for roots of only one species in one homogeneous volume of soil. However, in some models, attempts have been made to simulate the nutrient uptake by roots of two plant species, where analytical solutions were used for calculating the volume of soil allocated to each root and the concentration at the root surface (Tinker and Nye, 2000). Using this approach, Smethurst and Comerford (1993a) proposed a COMP8 model, which simulated nutrient uptake under competing and contrasting root systems and helped in quantitatively understanding the processes involved in nutrient uptake with plant competition. They applied the concept of the depletion zone in the model, where depletion zones increased with time until it reached the no-transfer boundary which is function of the competition ability of different plants (Baldwin and Nye, 1974).

The solute transport theory of mass flow and diffusion to simulate nutrient uptake by plants has been tested successfully under a variety of soil-plant conditions (Section 2.4), but under some conditions the simulation models have been shown to be inadequate in predicting uptake. These underpredictions in uptakes may be a result of some components of the soil-root system not being adequately incorporated such as root length development with time, changing soil water content over a period of time and nutrient inputs from the mineralization process (Smethurst and Comerford, 1993b). To address some of above mentioned problems, Comerford et al. (2006) presented the Soil Supply and Nutrient Demand (SSAND) model which is a revision of the previously published

COMP8 model (Smethurst and Comerford, 1993a) that can incorporate variables that change with time such as root growth, soil water content and nutrient mineralization.

2.4 Verification of Simulation Models in Tree Species

The Barber-Cushman nutrient uptake model, as described by Barber and Cushman (1981), has been used successfully to describe nutrient uptake for a variety of woody species (Gillespie and Pope, 1990; Kelly and Kelly, 2001; Kelly and Ericsson, 2003; Kelly et al., 1992; Kelly et al., 1994; Smethurst and Comerford, 1993b; Van Rees et al., 1990). Van Rees et al. (1990) compared predicted nutrient uptake using the Barber-Cushman and Baldwin-Nye-Tinker models with observed uptake in slash pine seedlings grown in low potassium supplying soil. Potassium uptake was overpredicted by 31 to 50% in greenhouse studies, which was attributed to the non-uniform distribution of roots along the pot wall. In field studies, underpredictions of K uptake by 0.48 and 0.83 times were attributed to the presence of abundant ectomycorrhizal hyphae, a contribution of which was not incorporated in the simulations. However, the predictions were excellent for seedlings grown at a tree nursery when fertilizer amendments were included. Using the same model, Kelly and Ericsson (2003) simulated N, P and K uptake in hybrid poplar (*Populus nigra* × *maximowiczii* (NM-6)) for a 105-day period in response to the addition of a slow release 17–6–12 fertilizer at rates equivalent to 0, 75, or 150 kg ha⁻¹ of N. Model predictions of uptake improved with increases in the amount of fertilizer added. Uptake estimates at the 150 level were 96, 120, and 98% of observed uptake for N, P, and K, respectively. The model predicted that the supply of N was not adequate to support sustained plant uptake throughout the study period. Plant uptake and soil supply observations confirmed that N uptake occurred primarily in the first half of the growth period and then soil N supply was quickly depleted.

The COMP8 model developed by Smethurst and Comerford (1993a) for competing and contrasting root systems was tested under both greenhouse and field conditions. In the greenhouse study, the model was tested on slash pine (*Pinus elliottii* Engelm. Var. *elliottii*) and grass (*Panicum aciculare*) grown in soils with low and high initial soil solution P and K concentrations under different tree:weed ratios (Smethurst and Comerford, 1993b). For high initial P and K soil solution concentrations, the model quantitatively predicted K uptake in both pine and grass and P uptake in pine for most of

the cases of the different tree:grass ratios; however, predictions for P uptake in grass were not accurate. For the low initial soil solution P and K concentrations, uptake simulations by the model were erroneous for P and K in both pine and grass. They concluded that an inadequate description of the processes like mineralization and mycorrhizae, in the model might be the possible reasons for the inaccurate prediction for low initial soil solution P and K concentrations. Under field conditions, predicted versus observed uptake of either K or P by pine were not significantly different from a 1:1 line (Smethurst et al., 1993). Hence, the model quantitatively predicted the effect of weeds on uptake of these nutrients by pine. However, uptake of both nutrients by weeds was over-predicted by 300-400%.

Overall, in conclusions, this literature review reveals that weeds severely compete with forest tree species for water and nutrients, which result in serious loss to tree and plant vigour. This effect of weed competition in poplar plantations is also well documented. N uptake kinetic parameters are reported for some forest tree species and under-story plants but no information is available on dandelion and quackgrass weeds and, furthermore, information on N uptake kinetic parameters for poplar tree species is not adequate. Most of the modeling work in the forest species is restricted to pine using the Barber-Cushman model (Barber and Cushman, 1981); however, some reporting on other tree species are also available. Furthermore, simulations are only restricted to the nutrient uptake by one plant species. Although, very few studies are available on the quantitative understanding of the nutrient uptake by competing and contrasting plant species (Smethurst and Comerford, 1993b; Smethurst et al., 1993), understanding of the processes affecting the nutrient uptake under such condition is still inadequate. The SSAND model has been presented which deals with the soil and plant processes more elaborately with the provision of using variable root growth, changing soil water content with time and can incorporate inputs from mycorrhizae and mineralization (Comerford et al., 2006). Verification and utilization of this model for quantitative understanding of nutrient uptake under competing environment still has to be done. This literature review also reveals that most modeling work has focused on P and K in forest trees, but very little work has been done for N uptake, particularly under weed competition scenarios.

2.5 References

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3 GROWTH OF HYBRID POPLAR AS AFFECTED BY DANDELION AND QUACKGRASS COMPETITION

3.1 Introduction

Increasing farm input costs and lower returns, along with persistent inclement weather for growing agricultural crops have led Saskatchewan farmers to explore alternate sources of farm income. Considerable interest has emerged from the farming community for planting fast-growing tree species on agricultural lands to diversify farm income. Similar interest in fast-growing tree species has been recognized in the forest sector, as provincial and federal agencies observe increasing pressure on native forests for forest harvesting due to the increased demand for paper and wood products.

Establishment of hybrid poplar plantations may be a viable alternative to generate additional farm income (Yemshanov et al., 2005) and also to meet the fibre demand for the forest industry because of poplar's relatively fast growth rate (Bergez et al., 1989; Heilman et al., 1994) and ability to produce large amounts of woody biomass (Hansen, 1991). Rotation periods for hybrid poplar plantations generally vary from 15 to 20 years, significantly shorter than the 60 to 80 years required for native trembling aspen and pine tree species to reach maturity (Yemshanov et al., 2005). Furthermore, wood quality for hybrid poplar is suitable for the manufacture of timber products and quality paper (Francis et al., 2005; Heilman et al., 1995). Under the Kyoto protocol, Canada is committed to offset atmospheric greenhouse gases emissions. One mechanism to help meet this commitment is the growing of hybrid poplar plantations because of their potential to sequester large amounts of atmospheric carbon in the woody biomass (Liberloo et al., 2006). Apart from this, the suitability of hybrid poplar already has been demonstrated for shelterbelts in the prairies (Zsuffa et al., 1996).

Weed management is the most critical cultural practice for successful tree plantations (Balandier et al., 2006; Thompson and Pitt, 2003; Wagner et al., 2006). Weeds compete with tree species for moisture and nutrients because of their greater root surface area and more efficient mechanisms for nutrient uptake (Casper and Jackson,

1997; Nambiar and Sands, 1993). Therefore, understory competition can result in severe loss of tree vigor and wood quality, and ultimately limit the profitability of tree plantations (Watt et al., 2005). Although various studies have looked at the influence of weeds on aboveground characteristics of hybrid poplar (Buhler et al., 1998; Shock et al., 2002; Sixto et al., 2001), very few attempts have been made to study the effect of weeds on belowground characteristics of hybrid poplar (Casselman et al., 2006). Those studies lacked parallel information on the performance of weed species grown along with hybrid poplar and the resultant effect of weed competition on soil nutrient dynamics. Weed species differ in above- and belowground growth characteristics and their strategy for acquiring soil resources can vary depending upon soil fertility (Blackshaw et al., 2003). Two weed species, dandelion (*Taraxacum officinale*) and quackgrass (*Elymus repens*) were selected for this study based upon their different growth characteristics, and also their dominance in agricultural fields in Saskatchewan where the potential exists for large-scale hybrid poplar plantations (Leeson et al., 2003). Therefore, the objective of this study was to examine hybrid poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) growth in competition with dandelion and quackgrass, as well as to evaluate their effect on soil nutrient dynamics in a controlled growth chamber.

3.2 Materials and Methods

3.2.1 Soils and soil preparation

Two surface layer (0-15cm) bulk soil samples were collected in September 2003 from the hybrid poplar research trial sites located near Meadow Lake, Saskatchewan, Canada (54° 7' N and 109° 30' W). Before establishing the field research trials in 2002, one site had been managed as mixed-grass pasture dominated by brome grass (*Bromus carinatus*) and the other as an alfalfa (*Medicago sativa*) field. The soil at the Alfalfa site was classified as an Orthic Gray Luvisol and at the Pasture site was classified as Brunisolic Gray Luvisol. Soil texture was a loamy sand for the Pasture soil and a sandy loam for the Alfalfa soil. Soil characteristics for both soils are provided in Table 3.1.

Soils were air-dried, and passed through a 5 mm sieve to remove large roots and stones. Each bulk soil sample was thoroughly mixed and homogenized before transferring to 6 L pots (3.8 kg for the Pasture and 4 kg for the Alfalfa soil) and brought

Table 3.1. Physical and chemical characteristics of the Pasture and Alfalfa soils.

Soil	Texture	Bulk density (g cm ⁻³)	pH	EC (μS cm ⁻¹)	Organic C (%)	Inorganic N† (μg g ⁻¹)
Pasture	Loamy sand	1.10	5.4	170	3.56	28.2
Alfalfa	Sandy loam	1.22	4.7	175	2.18	37.3

† KCl extractable-N (NO₃-N + NH₄-N).

to 15% volumetric water content (VWC). The soil surface area for each pot was approximately 155 cm².

3.2.2 Treatments and experimental design

Five treatments were established and included a control with a single hybrid poplar in a pot with no weeds (SHP), and treatments with one hybrid poplar seedling with four levels of weed competition: four dandelion (D) plants (SHP + 4D), eight dandelion plants (SHP + 8D), one quackgrass (QG) plant (SHP + 1QG), and three quackgrass plants (SHP + 3QG). These treatments were selected based upon their respective range of plant densities found in different geographical regions of Saskatchewan (Schroeder 2005; personal communication). Each treatment was replicated four times in a completely randomized design (two soil types, two harvest times and five weed treatments). All treatment pots were placed in a Conviron® controlled environment chamber (Controlled Environments Inc., Pembina, ND) under an 18 h day:6 h night photoperiod, with an air temperature of 22:18°C (day:night). Lighting was provided with racks of Cool White VHO fluorescent and incandescent lights (Sylvania, Drummondville, ON). Photon flux density was approximately 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

3.2.3 Planting and maintenance of pots

One hybrid poplar cutting (7.5 cm long), soaked overnight in water, was planted in each pot. One week after planting the cuttings, weed species seeds were sown in pots at four times the desired weed density at a 1 cm depth. After complete weed emergence, extra weed plants were removed by hand to achieve the required weed density. Pots were maintained at approximately 20% VWC throughout the study period by watering the pots every other day to compensate for water loss due to evapotranspiration. Water loss was determined by weighing the pots. Every other week until the first harvest and then every week from the first harvest to the second harvest, VWC in the pots was measured directly using a portable water content sensor (HydrosenseTM, Campbell Scientific, Australia). This enabled us to correct for the amount of water required to maintain the pots at 20% VWC taking into account the increasing plant biomass during the growing period. Pots were watered with distilled water to avoid any nutrient input from the water. White plastic beads were placed on the soil surface to reduce evaporation.

3.2.4 Sample collection and analyses

The first harvest (harvest-I) was made at 47 and 49 days after planting (DAP) the hybrid poplar cuttings and the second harvest (harvest-II) at 95 and 105 DAP for the Pasture and the Alfalfa soils, respectively. Hybrid poplar seedlings were measured for stem height and root collar diameter at each harvest. Aboveground shoots of both hybrid poplar and weed species were harvested just above the root collar. Immediately after harvest, the shoots of the hybrid poplar seedlings and weed species were oven-dried at 65°C for 72 h and individual dry weight determined. Roots of all species were harvested and carefully separated by wet washing through a 1 mm mesh. Fresh root biomass of each species was measured and stored at -25°C until further analysis. Dry root biomass was determined by oven-drying roots at 65°C for 72 h after root length measurements were complete.

The oven-dried root and shoot tissue samples were ground to pass through a 1-mm screen using a Thomas-Wiley Mill (Thomas Scientific, Swedesboro, NJ). Ground samples were wet digested in sulphuric acid and hydrogen peroxide and measured for total N, P and K concentrations (Kalra, 1998). Nutrient uptake was determined by multiplying the tissue nutrient concentration with dry tissue biomass. Total nutrient uptake was calculated by adding the root and shoot uptake, without accounting for the nutrient present in the cuttings.

Total root length for each species was determined by adding the root lengths calculated separately for three root diameter classes, i.e. <1, 1-2 and >2 mm. Root length for <1mm diameter class roots was determined on sub-samples of fresh roots which were scanned using Root Length+ software (Berntson, 1992). These sub-samples were then oven-dried at 65°C and weighed. A linear relationship was developed between root length and dry weight for the root subsamples ($r^2 \geq 0.90$) to calculate the total root length based upon total dry biomass for <1 mm roots. Since very few roots were found in other diameter classes the root length was determined manually using a metric scale ruler.

A measure of root competition was estimated by determining the mean half-distance between roots (r_1), which was calculated as follows:

$$r_1 = (\pi L_V)^{-1/2} \quad [3.1]$$

where L_V is the root length density, defined as root length per unit volume of soil (cm cm^{-3}) (Van Rees et al., 1994). The mean half-distance between roots for the weed treatments was calculated by combining root length density of the hybrid poplar seedling and weed species.

Prior to the removal of the roots by wet washing, representative soil samples were collected from each pot at each harvest for measurement of nutrient concentrations in soil solution. Soil samples were incubated for 24 h at field capacity, and soil solution extracted by centrifugation (Elkhatib et al., 1987). Nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), and P (PO_4^-) concentrations in both soil solution and tissue samples were determined using a Technicon II autoanalyzer (Technicon Instruments Corp., NY). Potassium was analyzed on the Varian Spectra AA 220 atomic absorption spectrophotometer (Varian Inc., Palo Alto, CA).

3.2.5 Statistical analyses

The main objective of this study was to investigate the effect of different weed treatments on hybrid poplar growth parameters in different soils at different harvest times. Therefore, a three-way analysis of variance (ANOVA) was performed only on the different growth parameters of hybrid poplar seedlings using a completely randomized design. No such analysis was carried for weed species growth parameters. Data for hybrid poplar exhibited unequal group size because of mortality of hybrid poplar seedling in some replicates during the course of experiment. A Games-Howell post-hoc test was used to compare the group means which accounts for unequal group size as well as unequal group variance. Within each group, hybrid poplar and weed data were analyzed for homogeneity of variance. However, for weeds all replicates were included for statistical analysis. Statistical analyses were performed at the 0.05 probability level using SPSS version 13.0 (SPSS Inc. Chicago, IL).

3.3 Results

3.3.1 Aboveground growth parameters of hybrid poplar and weeds

Survival of hybrid poplar seedlings was affected by the presence of weeds (Table 3.2). No seedling mortality was observed in the pots where hybrid poplar seedlings were grown without any weeds (SHP treatment); however, in weed treatment pots, seedling

Table 3.2. Effect of weed competition on seedling survival (%) of hybrid poplar grown with different densities of dandelion and quackgrass weeds in Alfalfa and Pasture soils at harvest-I (47 and 49 DAP for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 DAP for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion plants per pot.

Treatment	Harvest-I		Harvest-II	
	Pasture	Alfalfa	Pasture	Alfalfa
	----- % -----			
SHP	100	100	100	100
SHP + 1QG	100	100	100	75
SHP + 3QG	75	75	100	50
SHP + 4D	50	50	50	75
SHP + 8D	50	75	50	50

survival varied from 50 to 100% depending upon the weed treatment (Table 3.2). In general, aboveground growth of the hybrid poplar seedlings was affected by the soil type, time of harvest and weed treatment (Table 3.3). Significant interactions of weed competition with both soil type and harvest timings were found to affect the growth of hybrid poplar as revealed by generally significant S x W and H x W interactions (Table 3.3). Stem height was more affected by weed treatments in the Pasture soil than the Alfalfa soil (Figure 3.1a). In the Pasture soil at harvest-I, all of the weed treatments except the hybrid poplar grown with one quackgrass plant, reduced the stem height compared to poplar grown without any weeds. In contrast, none of the weed treatments affected stem height in the Alfalfa soil at harvest-I. At harvest-II, however, a negative effect of weeds on stem height was observed in all weed treatments in both the soils. Between harvests-I and harvest-II, stem height in the SHP treatment increased 2.3 and 5.7 times in the Pasture and Alfalfa soil, respectively (Figure 3.1a). However, seedlings grown with weeds did not show much increment in stem height between harvest-I and harvest-II (Figure 3.1a).

Seedling root collar diameter was affected by the harvest time and weed treatment (Table 3.3). Significant H x W interaction indicated that weed treatment effects on root collar diameter were different at each harvest time (Table 3.3). Seedling root collar diameter was not affected by the weed treatment by harvest-I in both soils. At harvest-II, however, seedling root collar diameter in the SHP treatment was greater than that for seedlings grown with weeds in both soils ($p < 0.05$) (Figure 3.1b).

Weed treatment effect on dry shoot biomass of hybrid poplar was different in each soil and each harvest as shown by significant S x W and H x W interactions (Table 3.3). Dry shoot biomass for hybrid poplar seedlings at harvest-I was not affected by the weeds in both the soils except the SHP+8D treatment in the Pasture soil. At harvest-II, however, seedling shoot biomass in the SHP treatment was greater compared to seedling shoot biomass in the weed treatments in both the soils. Hybrid poplar seedlings produced less dry shoot biomass in the Alfalfa soil compared to the Pasture soil at both harvest dates in treatments where seedlings were grown without weeds (SHP treatment) (Figure 3.2a).

Table 3.3. Probability levels from the three-way analysis of variance for hybrid poplar growth and nutrient uptake parameters. Hybrid poplar seedlings were grown for 47 and 97 days in the Pasture soil and 49 and 105 days in the Alfalfa soil with different densities of dandelion and quackgrass weeds. Effect of source of variation on hybrid growth and nutrient uptake parameters is considered significant at $p < 0.05$.

Source of variation	Stem height	Root collar diameter	Dry shoot biomass	Fresh root biomass	Root length	Half distance between roots	Total N uptake	Total P uptake	Total K uptake
Soil (S)	<0.0001	0.075	0.0009	0.0008	0.0029	<0.0001	0.2637	0.0006	0.0004
Harvest (H)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Weed (W)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
S x H	0.9126	0.075	0.5815	0.0052	0.0189	<0.0001	0.0082	0.5704	0.6528
S x W	<0.0001	0.081	0.0007	<0.0001	0.0002	<0.0001	0.7186	0.0007	0.0014
H x W	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
S x H x W	0.7046	0.081	0.9440	<0.0001	0.0032	<0.0001	<0.0001	0.9922	0.7842

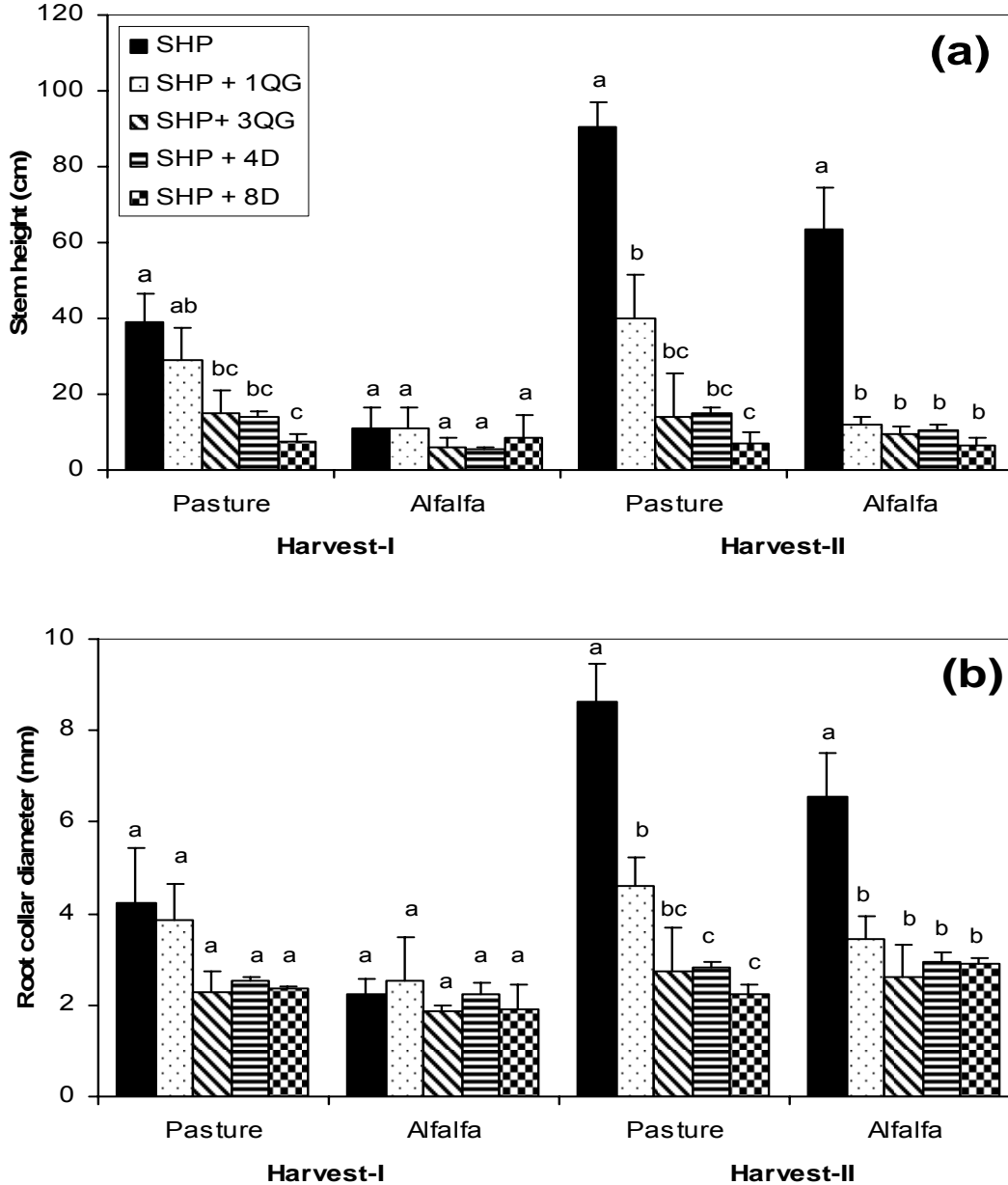


Figure 3.1. Effect of weed competition on (a) stem height and (b) root collar diameter of hybrid poplar grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for the Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for the Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$.

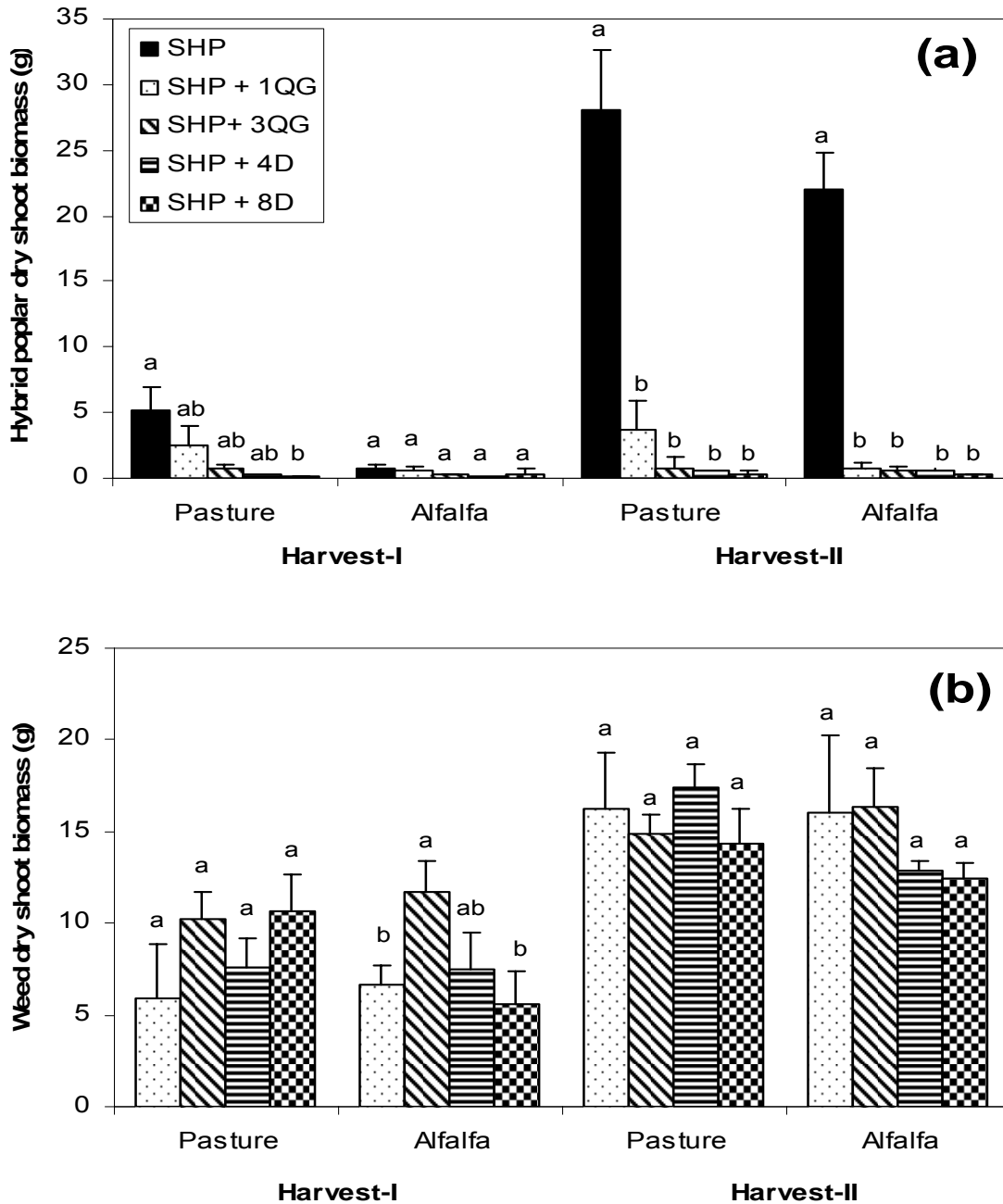


Figure 3.2. Dry shoot biomass of (a) hybrid poplar seedlings and (b) weed species grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$.

Dry shoot biomass for weeds was greater compared to hybrid poplar seedling shoot biomass where both were grown together (Figure 3.2). Overall, the weeds produced similar shoot biomass in all treatments regardless of density, except at harvest-I in the Alfalfa soil where weed biomass for SHP+ 3QG was greater than the SHP+1QG and SHP+8D weed treatments (Figure 3.2b).

3.3.2 Belowground growth parameters of hybrid poplar seedling and weed species

Similar to aboveground growth parameters, belowground parameters were also affected by soil type, harvest date and weed treatment (Table 3.3). At harvest-I, there was no difference in fresh root biomass for hybrid poplar seedlings among all the treatments; however, root biomass at harvest-II was larger for the SHP seedlings compared to seedlings in all of the weed treatments (Figure 3.3a). Fresh root biomass of hybrid poplar grown without weeds was lower in the Alfalfa soil than the Pasture soil at harvest-II (Figure 3.3a). Fresh root biomass of the weeds was several-fold higher than fresh root biomass of the hybrid poplar seedlings (Figure 3.3). Root biomass production by quackgrass tended to increase with increasing weed density in both soils (Figure 3.3b). Dandelion root biomass showed the opposite trend, and tended to decrease as weed density increased.

Total root length of the hybrid poplar seedlings ranged from 0.10 to 280.1 m (Figure 3.4a). These root lengths were considerably smaller than those for the weed species which ranged from 130.0 to 5850.0 m (Figure 3.4b). Root length, generally, varied between the weed species and was greater for dandelion at each harvest in both the soils. However, no root length differences were observed between the weed density of respective weed species except in the quackgrass weed treatment for the Alfalfa soil at harvest-I. The mean half-distance (r_1) between roots was highest in the SHP treatment compared to weed treatment pots (Table 3.4). The mean half-distance between roots decreased from harvest-I to harvest-II in all treatments. Within weed treatments, r_1 tended to be smaller in the dandelion treatments compared to the quackgrass treatments, although were only statistically significant ($p = 0.05$) in the Pasture soil at harvest-II. Generally, r_1 decreased with increasing density of weeds (Table 3.4).

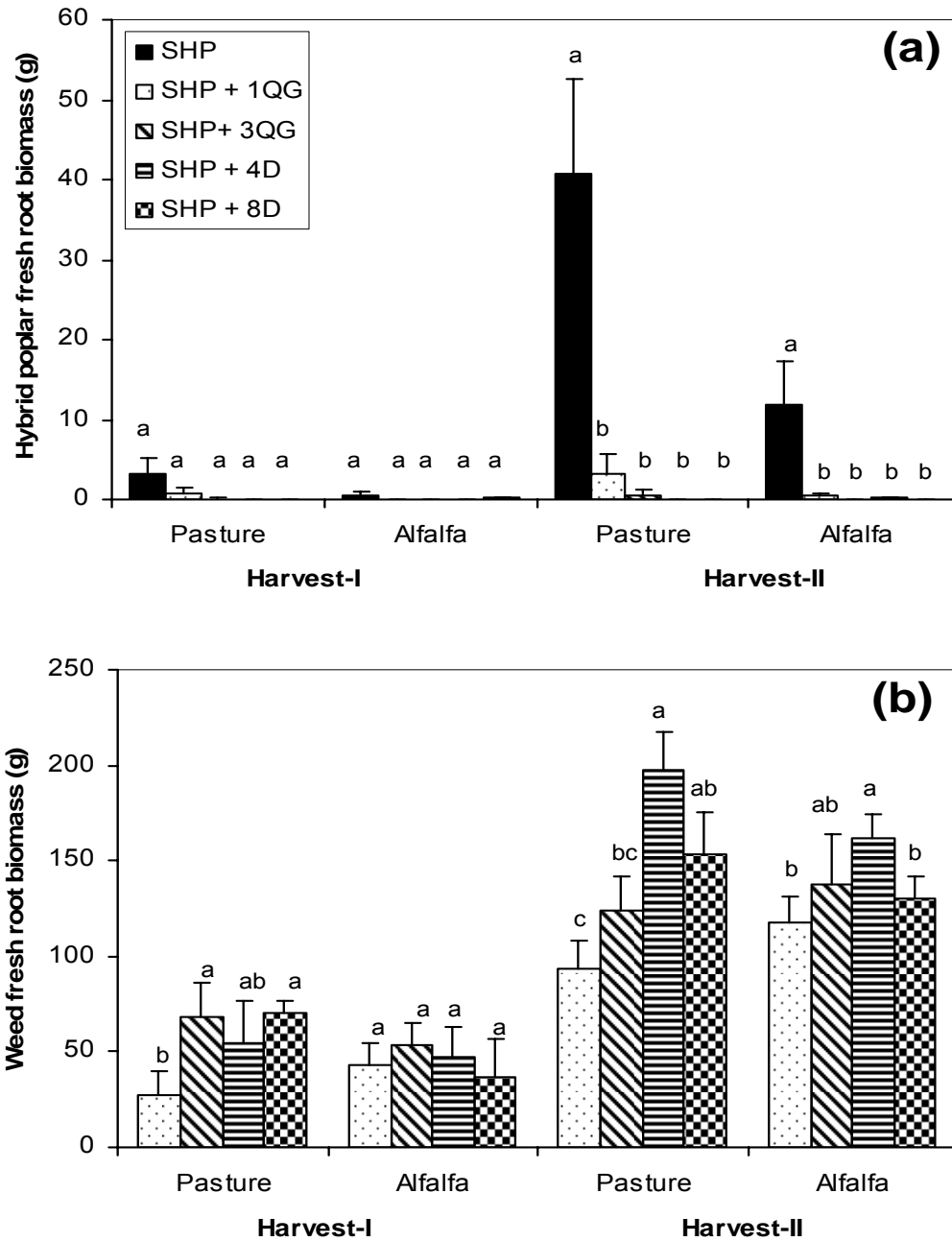


Figure 3.3. Fresh root biomass of (a) hybrid poplar seedlings and (b) weed species grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$.

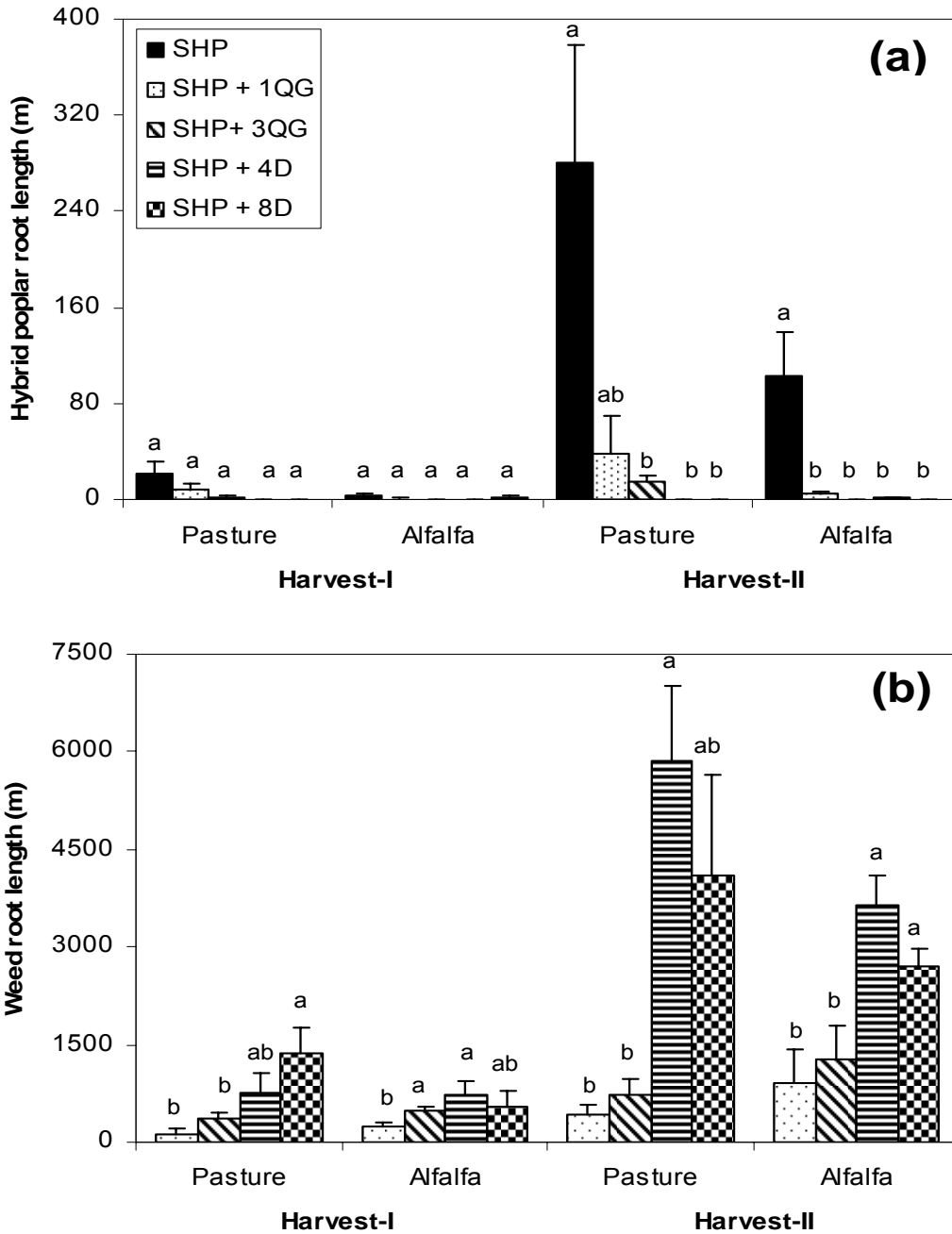


Figure 3.4. Root length of (a) hybrid poplar seedlings and (b) weed species grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$.

Table 3.4. Mean half-distance (cm) between all roots in the treatments grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 DAP for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 DAP for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion plants per pot.

Treatment	Harvest-I		Harvest-II	
	Pasture	Alfalfa	Pasture	Alfalfa
	----- cm -----			
SHP	0.78 (0.24) †a‡	1.79 (0.43)a	0.21 (0.04)a	0.33 (0.07)a
SHP + 1QG	0.33 (0.09)b	0.20 (0.02)b	0.16 (0.03)ab	0.12 (0.04)b
SHP + 3QG	0.19 (0.03)b	0.15 (0.01)b	0.13 (0.02)b	0.10 (0.03)b
SHP + 4D	0.14 (0.05)b	0.12 (0.02)b	0.04 (0.00)c	0.05 (0.00)b
SHP + 8D	0.09 (0.03)b	0.15 (0.03)b	0.05 (0.01)c	0.06 (0.00)b

† Value in parentheses represents the standard deviation.

‡ Within each soil class and harvest, means followed by the same letter are not significantly different according to Games-Howell post-hoc test ($p \geq 0.05$).

3.3.3 Nutrient uptake by hybrid poplar and weed species

Overall, nutrient uptake in hybrid poplar seedlings was affected by soil type, time of harvest and weed treatment (Table 3.3). The one exception was the effect of soil type on N uptake (Table 3.3). Significant S x W and H x W interactions indicated that nutrient uptake was affected differently by the weed treatments in each soil and at each harvest (Table 3.3). By the end of the experiment, hybrid poplar shoot N and P concentrations between the SHP and weed treatments in most cases did not vary significantly; however, shoot K concentration for the SHP treatment was higher than the other treatments, except for SHP + 1QG treatment in the Pasture soil (Table 3.5). Shoot N, P and K concentrations ranged from 6.6-17.7, 0.9-2.0 and 4.2-16.8 mg g⁻¹, respectively, depending upon the soil type and treatment. Hybrid poplar shoot nutrient concentrations in the SHP treatment of the Alfalfa soil were greater than that of the Pasture soil, especially for N where the difference was almost two-fold (Table 3.5). In both soil types, hybrid poplar shoot N uptake was substantially higher in the SHP treatment compared to the weed treatments (Table 3.5). Shoot N uptake for the SHP treatment was higher for the Alfalfa soil; however, P and K uptake was similar for both soil types. Among the weed treatments, in general, hybrid poplar did not show significant differences for N, P and K uptake (Table 3.5).

Similar to shoot nutrient uptake, hybrid poplar seedlings showed consistently higher total (root + shoot) nutrient uptake in the SHP treatment compared to the hybrid poplar seedlings grown with weed species (Figure 3.5). Nutrient uptake by shoots represented 60 to 99% of the total nutrient uptake by the hybrid poplar depending upon the nutrient and treatment.

In general, total N and P uptake by hybrid poplar was greater in the SHP treatment compared to all other treatments in both soils at both harvests. The exceptions were the SHP+1QG treatment at harvest-I (Figure 3.5a and Figure 3.5c). Total K uptake by hybrid poplar for the SHP treatment was greater than that for all other treatments for both harvests in both the soils (Figure 3.5e).

Table 3.5. Mean shoot concentration and uptake for hybrid poplar grown with different densities of dandelion and quackgrass weeds in the Alfalfa and Pasture soils at harvest-II (97 and 105 DAP for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion plants per pot.

Treatment	N		P		K	
	Pasture	Alfalfa	Pasture	Alfalfa	Pasture	Alfalfa
----- Shoot concentration (mg g ⁻¹) -----						
SHP	9.3 (0.6)†a‡	17.7 (0.6)a	1.2 (0.0)a	1.5 (0.1)a	13.0 (1.1)a	16.5 (1.5)a
SHP + 1QG	6.6 (0.7)b	10.4 (1.0)b	1.5 (0.3)a	0.9 (0.2)a	13.1 (0.8)a	10.8 (2.5)ab
SHP + 3QG	9.9 (4.6)a	10.8 (2.6)ab	2.0 (0.7)a	1.1 (0.3)a	6.8 (0.2)b	7.3 (0.2)b
SHP + 4D	9.0 (0.7)a	11.3 (3.6)ab	1.0 (0.1)a	1.1 (0.4)a	5.5 (0.7)bc	8.9 (2.5)b
SHP + 8D	12.9 (2.5)a	15.2 (2.4)ab	1.4 (0.4)a	1.4 (0.2)a	4.2 (0.3)c	6.3 (1.3)b
----- Shoot uptake (mg pot ⁻¹) -----						
SHP	262 (41)a	390 (41)a	35 (5)a	34 (5)a	362 (37)a	362 (51)a
SHP + 1QG	24 (14)b	8 (4)b	5 (3)b	1 (0)b	47 (26)b	9 (7)b
SHP + 3QG	16 (1)b	5 (2)b	3 (2)b	1 (0)b	24 (4)b	4 (2)b
SHP + 4D	5 (0)bc	6 (2)b	1 (0)b	1 (0)b	3 (0)b	5 (2)b
SHP + 8D	4 (2)c	4 (1)b	0 (0)b	0 (0)b	1 (0)b	2 (1)b

† Value in parentheses represents the standard deviation.

‡ Within each soil class, means with the same letter are not significantly different ($p \geq 0.05$).

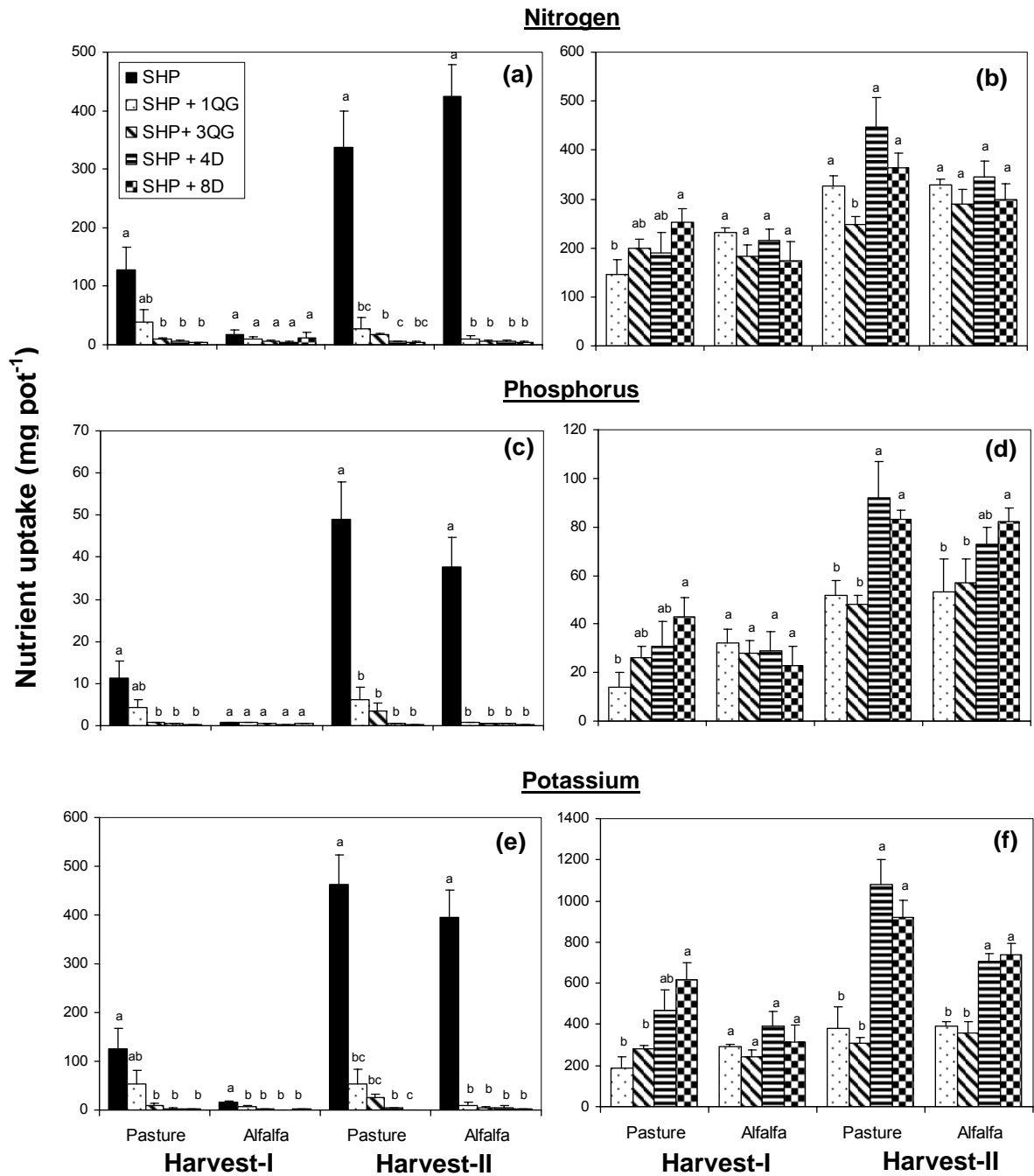


Figure 3.5. Total N, P and K (root + shoot) uptakes for hybrid poplar seedling (a, c and e) and weed species (b, d and f) grown in the Pasture and Alfalfa soils at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively). Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$.

Total N uptake varied between dandelion and quackgrass among the different weed treatments in the Pasture soil at both harvests; however, no differences were found in the Alfalfa soil at either harvest (Figure 3.5b). Dandelion and quackgrass showed significant differences in total P uptake at both harvests in the Pasture soil and at harvest-II in the Alfalfa soil (Figure 3.5d). Total K uptake followed similar trends to total P uptake (Figure 3.5f).

3.3.4 Soil solution chemistry

The Alfalfa soil had higher N ($\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$) and K concentrations compared to the Pasture soil at the start of the experiment (Figure 3.6). Initial concentrations of P were extremely low (0.5 mg L^{-1}) in both soils (data not shown). Concentrations of N and K in soil solution decreased for all treatments at both harvests in both the soils (Figure 3.6). The magnitude of N and K depletion from soil solution, however, was several times greater in the weed treatments compared to the SHP treatment (Figure 3.6). Nitrogen and K were almost exhausted from soil solution at harvest-I, particularly in the Alfalfa soil (Figure 3.6). Soil solution P concentrations did not show any clear trends during the growing period and no significant change was observed from the initial concentration at each harvest in both soils (data not shown).

3.4 Discussion

The presence of dandelion and quackgrass severely affected hybrid poplar growth and nutrient uptake through various competition processes. Although reduced hybrid poplar growth in the presence of weeds was reported in other studies, no information is available for individual weed species effects. Hansen and Netzer (1985) reported that failure to control weed competition resulted in high poplar tree mortality and a 50% or greater reduction in growth of surviving trees. In another study, Buhler et al. (1998) observed a 73 and 104% increase in height and caliper diameter of hybrid poplars, respectively, when the weeds were controlled intensively. In comparison, trees with less intensive weed control experienced only a 37 and 45% increase for the respective traits during the same period. In a nursery study at three different sites, poplar stem height decreased 19 to 56% compared to weed-free plots during the first growing season depending upon the sites and method of weed control (Sixto et al., 2001).

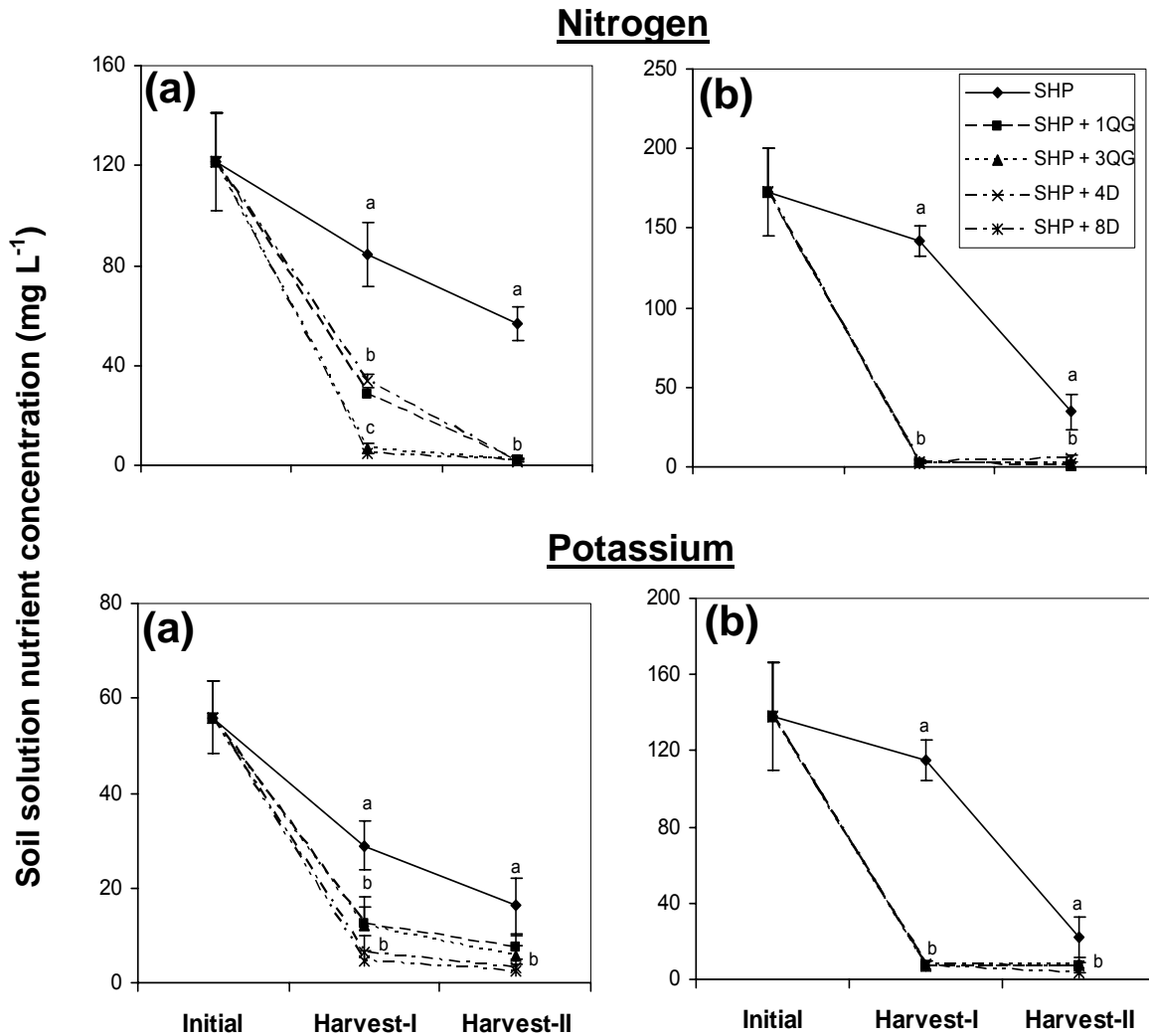


Figure 3.6. Changes in soil solution nitrogen and potassium concentration in (a) Pasture and (b) Alfalfa soil at harvest-I (47 and 49 days after planting for Pasture and Alfalfa soil, respectively) and harvest-II (97 and 105 days after planting for Pasture and Alfalfa soil, respectively) under various densities of hybrid poplar seedling and weed species. Treatments were SHP= single hybrid poplar, SHP + 1QG = single hybrid poplar + one quackgrass, SHP + 3QG = single hybrid poplar + three quackgrass, SHP + 4D = single hybrid poplar + four dandelion, SHP + 8D = single hybrid poplar + eight dandelion. Error bars represent one standard deviation. The bars with the same letter within each soil and harvest are not significantly different at $p \geq 0.05$.

Hybrid poplar shoot N concentrations, except for the SHP treatment in the Alfalfa soil, were below the critical levels (ranged from 17 to 30 mg g⁻¹) reported for N deficiency in other studies for hybrid poplar (Bungart and Huttl, 2004; Jug et al., 1999). Phosphorus and K shoot concentrations were generally in the range of the critical levels reported for these nutrients (1.0-4.4 mg g⁻¹ for P and 7-20 mg g⁻¹ for K) (Bungart and Huttl, 2004; Jug et al., 1999). It should be noted, however, that the critical values reported in the literature were based upon the leaf nutrient concentrations only, while the values from this study were based on the whole shoot biomass sample (stem and leaf). It was visually observed in the SHP treatment that a significantly higher proportion of total biomass was contributed by the woody stem suggesting that the lower shoot nutrient concentrations in this treatment may be a result of the dilution of nutrients from the woody biomass rather than reflecting nutrient deficiencies (Marschner, 1995). Zak et al. (2000) also found that N tissue concentrations were much lower in stems compared to leaf tissue for *Populus tremuloides*. Therefore, the lower nutrient concentrations for hybrid poplar in the weed free treatments reflect nutrient dilution while the low tissue concentrations for hybrid poplar in the weed treatments actually reflect the competition for nutrients from the competing weed species.

Weed competition involves competition for light, nutrients or water (Grace and Tilman, 1990). Because the pots in this study were watered regularly, the possibility of competition for water is assumed to be negligible. Therefore, light and nutrients were probably the more important factors by which dandelion and quackgrass competed with hybrid poplar seedlings during the experimental period. In this study, weed competition generally was more pronounced in the dandelion treatments, although growth reductions of almost the same magnitude were also observed in the highest quackgrass density treatment (i.e., SHP + 3QG). However, because the dandelion and quackgrass weeds were grown at different densities, it is difficult to interpret which weed species was more competitive with the hybrid poplar seedlings.

The competitive ability of weed species can be different due to differences in physical traits including plant height and mass, leaf area, root mass and root length (Blackshaw et al., 2003; Epp and Aarssen, 1989; Gaudet and Keddy, 1988). Given the broad-leaf growth nature of the dandelion coupled with its fast growth rate (Stewart-

Wade et al., 2002) compared to hybrid poplar, competition for light is expected in the dandelion treatments. Light competition, however, is expected to be less of a factor for quackgrass because of its erect stem and narrow leaves (Werner and Rioux, 1977). Density of weed plants grown along with hybrid poplar may play an important role in light competition. It is possible that the higher number of weeds in the dandelion weed treatments (4D and 8D) grown with the hybrid poplar seedlings contributed significantly to its ability to compete for light. The same may be true to some extent in the higher quackgrass density treatment (3QG). However, no parameter related to light competition was measured in our study; thus, it is difficult to quantify the amount of aboveground competition for light between hybrid poplar and weed species.

Plant competition studies have shown that much of the competition among plants takes place belowground (Casper and Jackson, 1997; Wilson, 1988), essentially for nutrients if moisture is not a limiting factor (Nambiar and Sands, 1993). Soil nutrients move to the root surface in the soil via mass flow and diffusion processes (Barber, 1995). The supply of nutrients, such as P and K, with large fractions bound to the soil matrix is often considered to be controlled by diffusion, while mobility of nitrate, the dominant form of plant available N in agricultural soils, is assumed to be controlled by mass flow. However, some studies have shown contradictory results where diffusion has been reported as the dominant process for supplying nitrate to root surfaces in some crop species (Kage, 1997; Plhak, 2003; Strebel and Duynisveld, 1989). Assuming supply of all these nutrients is controlled by diffusion, root length density of plant species can be considered another important mechanism for the belowground competition for nutrients (Nambiar and Sands, 1993). Root length density determines the size of the depletion zone around the roots. Increased rooting density decreases the size of the effective nutrient supplying zone around individual roots causing the nutrient depletion zones to overlap. It is this overlapping of depletion zones that results in nutrient competition. The average linear distance of diffusive movement for an ion in soil with time (t) can be calculated by $(\pi D_e t)^{1/2}$; where D_e is the effective diffusion coefficient in soil (Jungk and Claassen, 1997). Considering an effective-diffusion coefficient in soil of $5 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ for NO_3^- , $5 \times 10^{-9} \text{ cm}^2 \text{ s}^{-1}$ for H_2PO_4^- , and $5 \times 10^{-7} \text{ cm}^2 \text{ s}^{-1}$ for K^+ ions (Barber, 1995), the distance diffused by these nutrients in the soil for the 47-day growth period (harvest-I) in

this study would be 7.98, 0.25 and 2.52 cm, respectively. Calculated mean half-distances between roots at harvest-I varied from 0.09 to 0.15 cm for dandelion treatments and 0.15 to 0.33 cm for quackgrass treatments. Therefore, overlapping of depletion zones occurred around the roots for all the nutrients, with the exception of H_2PO_4^- in the SHP+1QG treatment in the Pasture soil. This overlapping of depletion zones caused the severe nutrient competition between the roots because of the smaller r_1 compared to the distance diffused by the respective ions. For the SHP+1QG treatment in the Pasture soil, H_2PO_4^- depletion zones would overlap between harvest-I and harvest-II because the calculated diffusion distance (0.36 cm) by harvest-II would be greater than the measured inter-root distance (0.16 cm).

These observations suggest not only interspecific competition but also intraspecific competition as 91-100% of the root length in the weed treatment pots were represented by weed species (Figure 3.4). Furthermore, the decrease in dandelion root biomass with increasing density at the second harvest also corroborates the concomitant occurrence of interspecific and intraspecific competition (Figure 3.3). This evidence further demonstrates the severity of belowground competition caused by weed species to hybrid poplar for nutrient uptake.

Allelopathy is another indirect mechanism of belowground competition (Grace and Tilman, 1990; Wardle et al., 1998), which decreases one plant species growth by another through the release of toxic chemicals from the roots (Norby and Kozlowski, 1980; Obaid and Qasem, 2005). The ability of quackgrass to produce allelopathic chemicals (Hagin, 1989; Korhammer and Haslinger, 1994; Schulz et al., 1994) and adversely affect other plant species growth has been reported (Kommedahl et al., 1957; Schulz et al., 1994). Therefore, it is also possible that substances released by quackgrass weeds could have negatively affected hybrid poplar growth in the pots.

In conclusion, this study demonstrated that the growth of hybrid poplar is greatly suppressed in the presence of dandelion and quackgrass weeds because of their superior performance in terms of root and shoot growth and absorption of soil nutrients. Some important practical implications can also be made from this study. The use of cutting plant material for hybrid poplar plantations may not be a suitable stock type if weed control is not maintained during the early establishment years. However, this conclusion

should be applied with caution because cutting size used in this study was small (7.5cm) to accommodate them in the pots. Use of larger cuttings (15-25 cm) for growing hybrid poplar may provide an extra advantage over smaller cuttings in weed competing environments because of relatively more available growing buds and deeper access to nutrients and water in the soil. Alternatively, the use of rooted cuttings may be more advantageous as a stock type against weed species because of the existing root system on the planting, which may provide a more extensive root system to overcome root competition.

3.5 References

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4 NUTRIENT UPTAKE KINETICS FOR HYBRID POPLAR AND TWO COMPETITIVE WEED SPECIES

4.1 Introduction

Agroforestry, in recent years, has been suggested as a system to meet the objectives of sustainable agriculture by diversifying farm income and reducing harvesting pressure on native forest stands for fibre requirements. Considerable research in agroforestry has been directed toward genetic improvement of plantation species as well as their suitability and adaptability for different climatic and soil conditions (Brewbaker, 1993; Buck et al., 1999; Stettler et al., 1996). Various cultural and management practices are required to establish successful agroforestry plantations, and efficient nutrient management has been suggested as a key factor for maximizing the profitability of agroforestry plantations due to the high cost of fertilizers (Mead, 2005).

Efficient fertilizer management of agroforestry plantations cannot be achieved without proper weed management (Haywood et al., 2003; Nilsson and Allen, 2003). Uncontrolled weeds decrease establishment and severely reduce the growth of plantation species through the competition for soil resources, especially nutrients (Balandier et al., 2006; Nambiar and Sands, 1993). Dandelion and quackgrass weed species are strong competitors with hybrid poplar for nutrient resources; however, the mechanisms of nutrient uptake by plants with these different root systems is unknown (Kabba et al., 2007). Therefore, an understanding of the root-uptake characteristics for the plantation species of interest and coexisting weed species is essential to enhance nutrient management for plantation systems.

Michaelis-Menten-type uptake kinetics frequently have been measured to understand the rate of nutrient influx into root systems where nutrient uptake at the root surface is described by establishing the relationship between nutrient influx into the root with the nutrient concentration in the soil solution at the root surface (Barber, 1995). This approach has been used successfully for various agricultural crops (BassiriRad et al., 2000; Bhadoria et al., 2004; Jungk et al., 1990), forest trees (Hangs et al., 2003; Kelly

and Kelly, 2001; Zerihun and BassiriRad, 2001) and weed species (Hangs et al., 2003; Pedersen et al., 1999). These uptake kinetic parameters also have been used to describe nutrient uptake at the root surface in nutrient uptake models (Barber, 1995; Tinker and Nye, 2000).

To date, very limited information is available on the nutrient-uptake kinetic parameters for hybrid poplar species (Kelly and Ericsson, 2003). Such information is also lacking for dandelion and quackgrass weed species which are common competitors in hybrid poplar plantations in Saskatchewan. Therefore, the objective of this study was to quantitatively describe the uptake of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, P and K for hybrid poplar seedlings (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) and dandelion (*Taraxacum officinale*) and quackgrass (*Elymus repens*) weed species using the Michaelis-Menten kinetics approach.

4.2 Methods and Materials

4.2.1 Plant material and growth conditions

Plant material used for the uptake kinetic studies was first grown in soil before transferring to hydroponic solutions. Hybrid poplar seedlings were grown from 7-cm long non-rooted cuttings that were soaked overnight in water before planting in 4-L pots containing Terra-Lite[®] RediEarth[®] Potting soil (W.R. Grace and Co., Ajax, Ontario, Canada). Dandelion and quackgrass were grown from seed in the pots. After growing in the pots for 50 days, the roots of all plant species were carefully separated from the soil and washed with a nutrient solution to remove adhering soil particles. Twenty-four plants from each species were transferred to 35-L aerated, nutrient solution tanks for three weeks. The nutrient solution consisted of 1.2 mM $\text{NO}_3\text{-N}$, 0.4 mM $\text{NH}_4\text{-N}$, 0.06 mM P, 0.38 mM K, 0.75 mM Ca, 0.42 mM Mg, 0.40 mM S and micronutrients of 0.1 strength Hoagland solution (Hoagland and Arnon, 1950). Solution pH was maintained between 4.8 and 5.0 using 0.05 M H_2SO_4 or NaOH and nutrient solutions were changed every three days. All species were grown in a Conviron[®] growth chamber (Controlled Environments Inc., Pembina, ND) under an 18h light:6h dark photoperiod with air temperatures of 22 and 18°C under light and dark, respectively and a relative humidity of 70%.

4.2.2 Depletion experiment and uptake kinetics

The technique outlined by Claassen and Barber (1974) was used to quantify the uptake kinetics for $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, P and K. Plant uptake kinetic parameters measured included, the maximal nutrient influx rate (I_{max}) and the Michaelis-Menten constant (K_m) which is the solution concentration at one-half of I_{max} . For uptake experiments, all plant species were transferred to fresh nutrient solution without $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, P and K for 48 h to obtain maximum uptake response during the subsequent uptake experiment. Two hybrid poplar and dandelion plants and three quackgrass plants were randomly selected and transferred to vessels containing 1 L of nutrient solution. Initial concentrations in the nutrient solution consisted of 400 μmol each for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, 100 μmol for P and 250 μmol for K. A 5 mL aliquot of solution was sampled with a syringe from the middle of each vessel immediately before root immersion, every 0.5 h for the initial 2 h and then every 1 h until the end of the depletion experiment (16 h). Solution lost through sampling and transpiration was replaced with deionized water. Samples were refrigerated (4°C) immediately and all chemical analyses were completed within the next two days.

Concentrations of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ and P in the samples collected from the hydroponic experiments were measured colorimetrically using a TechniconTM II autoanalyzer (Technicon Instruments Corp., NY). K was determined using a VarianTM atomic absorption/ flame emission spectrometer (Varian Inc. Corp., CA).

The Michaelis-Menten kinetic equation, which considers ion influx into the roots as a function of its concentration at the root surface, was used to calculate plant-uptake kinetic parameters from the depletion data (Claassen and Barber, 1974):

$$I_n = I_{\text{max}} (C_i) / [K_m + (C_i)] \quad [4.1]$$

where I_n ($\mu\text{mol cm}^{-2} \text{ s}^{-1}$) is the nutrient ion influx, I_{max} ($\mu\text{mol cm}^{-2} \text{ s}^{-1}$) is the maximal nutrient influx rate at high concentrations, C_i , and K_m (μM) is the Michaelis–Menten constant which is the nutrient concentration where influx is $0.5 I_{\text{max}}$.

To obtain Michaelis-Menten parameters, data from the depletion experiment was differentiated using 3^o polynomial equation to obtain slopes (influx rates, I_n) at individual

sampling times. To obtain the I_{\max} and K_m values, influx rates and solution concentrations were plotted linearly using the method by Hofstee (1960).

4.2.3 Processing of plant material

After completion of the depletion experiment, the roots and shoots of all plant species were separated. Shoot biomass was oven-dried at 65°C for 72 h and weighed. Fresh roots were weighed and then stored at -25°C until further analyses were done. Root length was measured by scanning root subsamples using Root Length+ software (Berntson, 1992). Linear relationships ($r^2 \geq 0.90$) were developed between root length and root dry biomass to calculate total root length for each species from the total biomass. Average root radius (r_o) was determined from the fresh weight of root biomass (F_{wr}) and total root length (L) at the time of harvesting from the equation (Barber, 1995):

$$r_o = (F_{wr} / \pi L)^{1/2} \quad [4.2]$$

where root density was assumed to be 1.00 g cm⁻³.

Dried root and shoot samples were ground separately in a Wiley Mill and digested in H₂SO₄ and H₂O₂ for total N, P and K analyses (Kalra, 1998). Concentrations of total N and P were measured colorimetrically using a TechniconTM II autoanalyzer (Technicon Instruments Corp., NY). K was determined using a Varian Spectra AA 220 atomic absorption spectrophotometer (Varian Inc., Palo Alto, CA).

4.2.4 Statistical analyses

The experiment was in a completely randomized block design with three replicates. Shoot dry mass, root fresh mass, root dry mass, total root length and root surface area are reported on a per plant basis. All measured parameters were subjected to analysis of variance (ANOVA) and means separation was conducted using Fisher's protected LSD. A similar statistical procedure was used to compare the mean I_{\max} and K_m values between the plant species for each nutrient using Fisher's protected LSD. However, mean I_{\max} and K_m values between NO₃-N and NH₄-N for each plant species were compared using Student's t-test. Data were checked for homogeneity of variance within replicates before subjecting to ANOVA. All statistical analyses were performed using SPSS 13.0 (SPSS Inc. Chicago, Illinois).

4.3 Results

4.3.1 Plant root and shoot parameters

Hybrid poplar and dandelion produced similar amounts of fresh root biomass; however, dry root biomass production differed between the species due to the presence of the tap root and some coarse roots in dandelion, which accounted for 25% of the fresh root biomass (Table 4.1). Quackgrass produced less fresh and dry root biomass than hybrid poplar and dandelion. Average root radius was largest for hybrid poplar and smallest for quackgrass (Table 4.1). Quackgrass produced a significantly longer total root system compared to hybrid poplar and dandelion, but the root surface area for quackgrass was only larger than dandelion (Table 4.1). Hybrid poplar trees accumulated more dry shoot biomass compared to the two weed species. Hybrid poplar had the highest dry shoot:dry root biomass ratio followed by quackgrass and then dandelion (Table 4.1).

4.3.2 Nutrient uptake kinetics

Depletion data for all nutrients were used to calculate the influx rates on a per unit surface area basis (Appendix A). I_{\max} values for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ ranged from $2.3 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ to $6.9 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ and $3.1 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ to $7.4 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$, respectively, among all the plant species (Figure 4.1). Dandelion had the largest I_{\max} value for $\text{NO}_3\text{-N}$ followed by hybrid poplar and quackgrass. I_{\max} values for $\text{NH}_4\text{-N}$ uptake were not different between hybrid poplar and quackgrass, but smaller than dandelion (Figure 4.1). No significant differences were observed between I_{\max} values for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ uptake for hybrid poplar and dandelion. Quackgrass had the highest I_{\max} value for $\text{NH}_4\text{-N}$ uptake as compared to $\text{NO}_3\text{-N}$ uptake. On the other hand, K_m values for $\text{NO}_3\text{-N}$ uptake varied from 59 to 95 μM but were only different between the hybrid poplar and quackgrass (Figure 4.1). Values of K_m for $\text{NH}_4\text{-N}$ uptake varied from 24 to 49 μM , although differences were not significant (Figure 4.1). Generally, K_m values for $\text{NO}_3\text{-N}$ uptake were greater than for $\text{NH}_4\text{-N}$ uptake for each plant species.

Values of I_{\max} and K_m for P and K uptake for all plant species showed trends similar to $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ uptake (Figure 4.2). Among all of the plant species, I_{\max} values for P and K uptake varied significantly and ranged from $0.61 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ to $2.03 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ and $2.1 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ to $5.71 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$, respectively. Dandelion had the largest I_{\max} values for P and K uptake followed by hybrid

Table 4.1. Selected root and shoot parameters for plant species grown in the hydroponic solution experiment.

Species	Fresh root biomass (g plant ⁻¹)	Dry root biomass (g plant ⁻¹)	Average root radius (mm)	Root surface area (cm ² plant ⁻¹)	Total root length (m plant ⁻¹)	Dry shoot biomass (g plant ⁻¹)	Dry shoot: dry root ratio (g g ⁻¹)
Hybrid poplar (n=6)	13.8a†	1.30b	0.15a	0.18a	184.0b	7.32a	5.63a
Dandelion (n=6)	13.4a	1.77a	0.13b	0.15b	188.8b	3.51b	1.98c
Quackgrass (n=9)	9.0b	1.04c	0.10c	0.19a	304.5a	4.44b	4.27b

† Means within the column followed by same letter are not significantly different by LSD ($p \geq 0.05$).

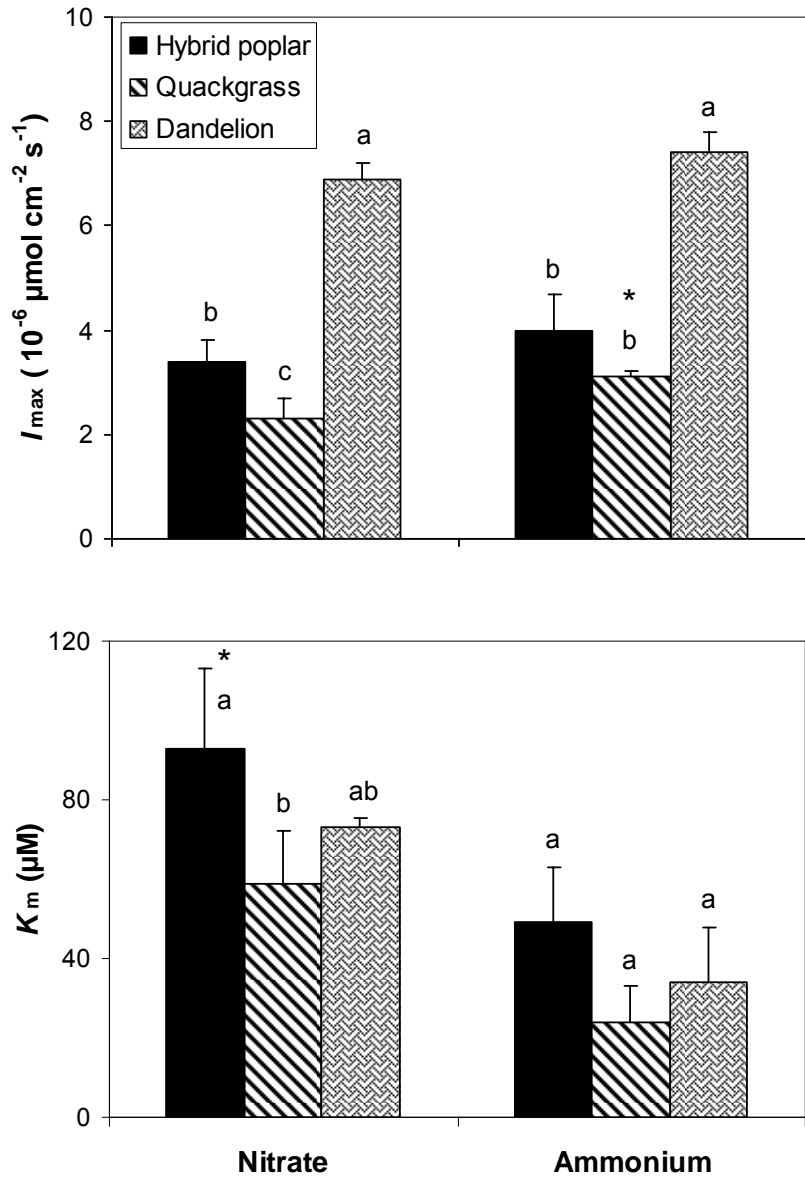


Figure 4.1. I_{\max} and K_m values for nitrate and ammonium uptake by hybrid poplar, quackgrass and dandelion grown in hydroponic nutrient solution. Error bars represent one standard deviation. Bars with the same letter within each nutrient are not significantly different ($p \geq 0.05$). Data with “*” indicates a significant difference ($p < 0.05$) between nitrate-N and ammonium-N within each plant species.

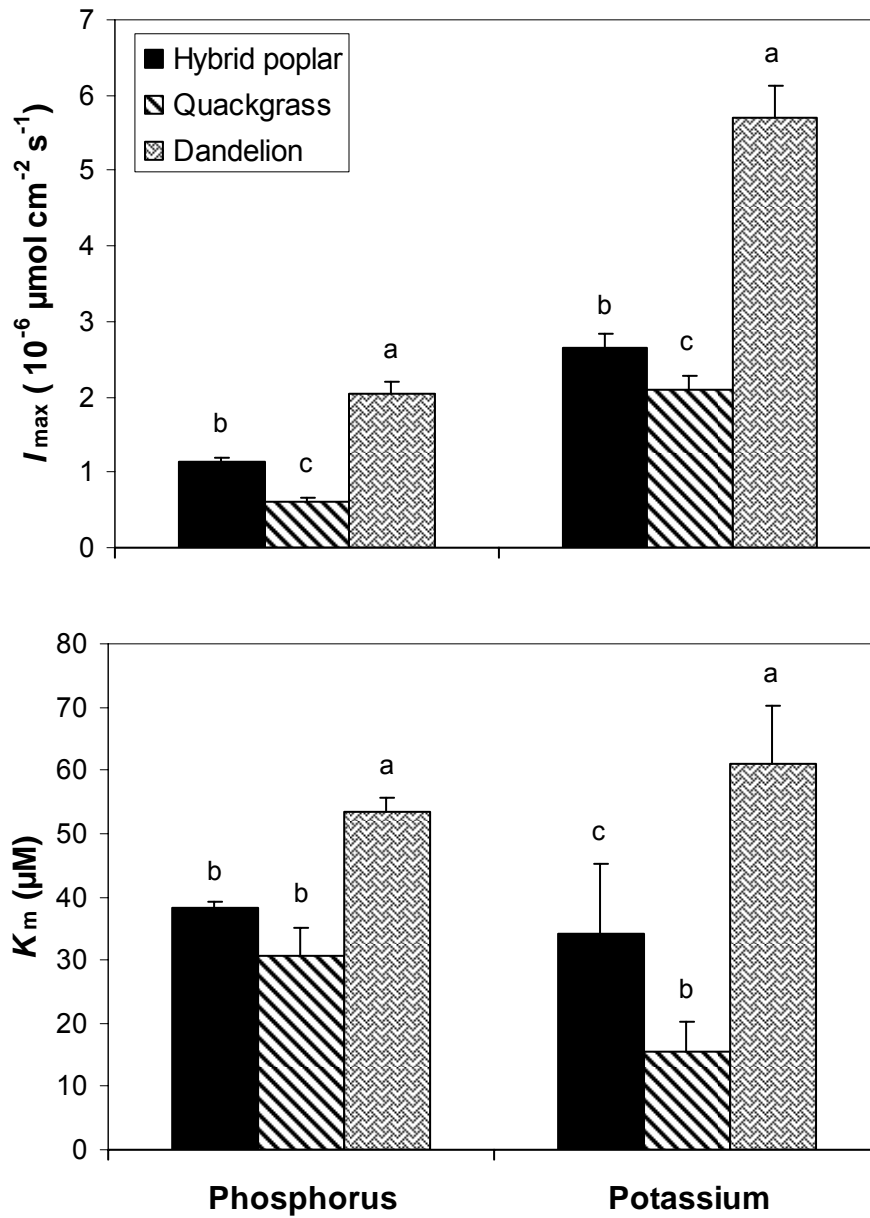


Figure 4.2. I_{\max} and K_m values for phosphorus and potassium uptake by hybrid poplar, quackgrass and dandelion grown in hydroponic nutrient solution. Error bars represent one standard deviation. Bars with the same letter within each nutrient are not significantly different ($p > 0.05$).

poplar and quackgrass. In contrast to the N uptake parameters, values of K_m followed the same trend as I_{max} . The K_m value for P uptake in dandelion was higher than hybrid poplar and quackgrass while the K_m value for hybrid poplar and quackgrass were similar. K_m values for K uptake differed among all plant species with values of 34, 16 and 61 μM for hybrid poplar, quackgrass and dandelion, respectively.

The values for I_{max} and K_m were inserted into the Michaelis-Menten equation and corresponding nutrient influx curve for each plant species was calculated within the range of corresponding nutrient concentrations used in this study (0-400 μM for NO_3 -N and NH_4 -N, 100 μM for P and 250 μM for K) (Figure 4.3 and Figure 4.4). These curves exhibited the saturable kinetics of nutrient uptake and conformed to Michaelis-Menten-type kinetics.

4.3.3 Plant tissue nutrient concentrations

Patterns of root and shoot nutrient concentrations varied among plant species (Table 4.2). Dandelion had the highest mean shoot and lowest mean root concentration for all three nutrients compared to hybrid poplar and quackgrass (Table 4.2). Mean shoot and root tissue concentration for N and P was similar between hybrid poplar and quackgrass, except for root P concentration which was higher in hybrid poplar. Mean shoot K concentration was higher in quackgrass compared to hybrid poplar, but the trends were reversed for root K concentration.

4.4 Discussion

4.4.1 Kinetics of NH_4 -N and NO_3 -N Uptake

All of the plant species showed a saturating Michaelis-Menten-type kinetics for NH_4 -N and NO_3 -N uptake, corresponding to a high affinity transport system (BassiriRad et al., 2000). A wide range of I_{max} and K_m values have been reported for NH_4 -N and NO_3 -N uptake for different tree species including hybrid poplar (*Populus nigra* × *maximowiczii*) (Kelly and Ericsson, 2003), aspen (*Populus tremuloides* Michx.) (Hangs et al., 2003), jack pine (*Pinus banksiana* Lamb.) (Hangs et al., 2003), lodgepole pine (*Pinus contorta* Dougl.) (Min et al., 2000), white spruce (*Picea glauca* (Monench) Voss) (Hangs et al., 2003; Kronzucker et al., 1995; Kronzucker et al., 1996), red maple (*Acer rubrum* L.) (Kelly et al., 2000) and eucalypt (*Eucalyptus nitens* (Deane and Maiden) Maiden) (Garnett et al., 2003). Values of I_{max} and K_m for NH_4 -N and NO_3 -N uptake for

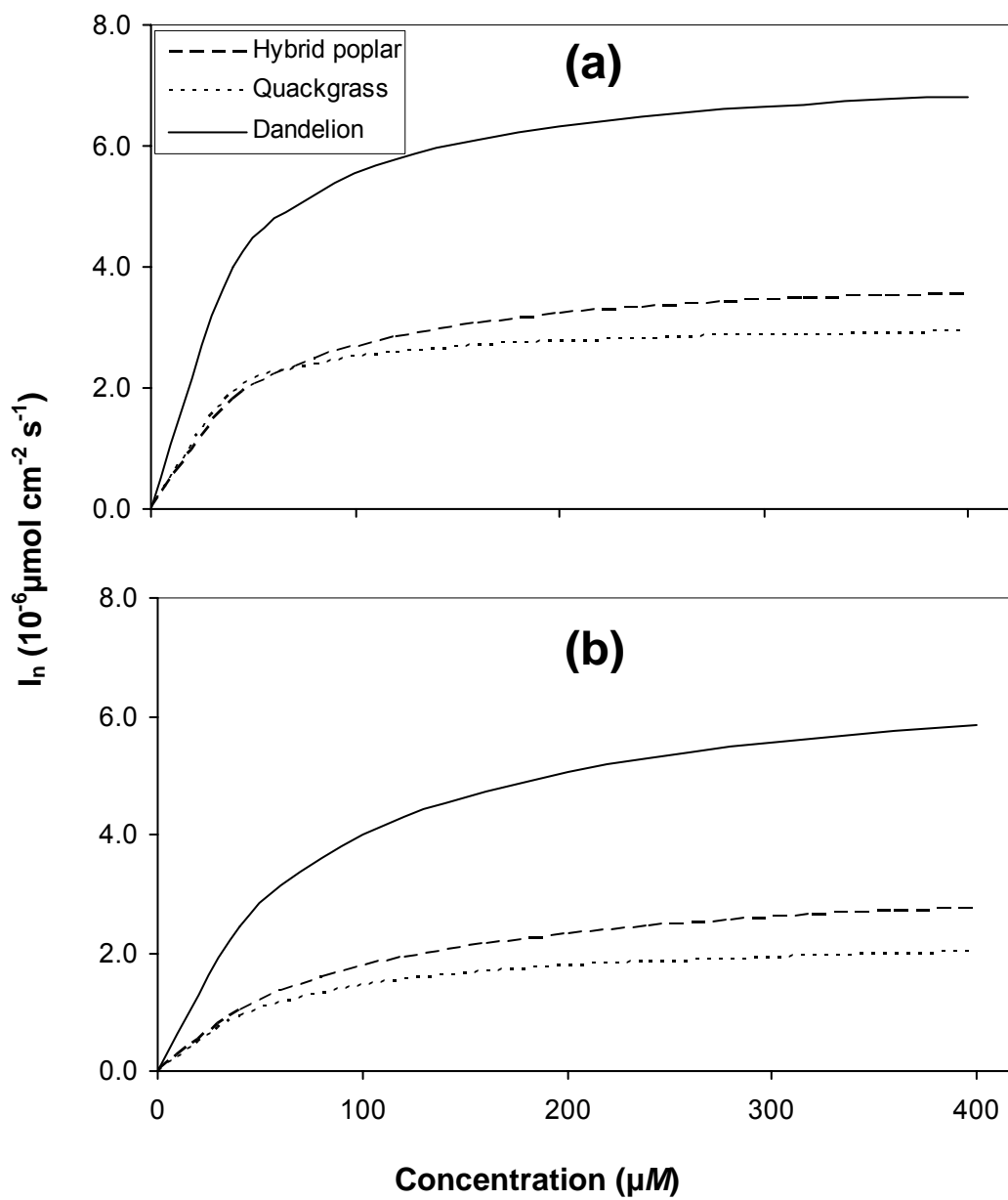


Figure 4.3. Michaelis-Menten curves for (a) nitrate and (b) ammonium uptake for hybrid poplar, quackgrass and dandelion.

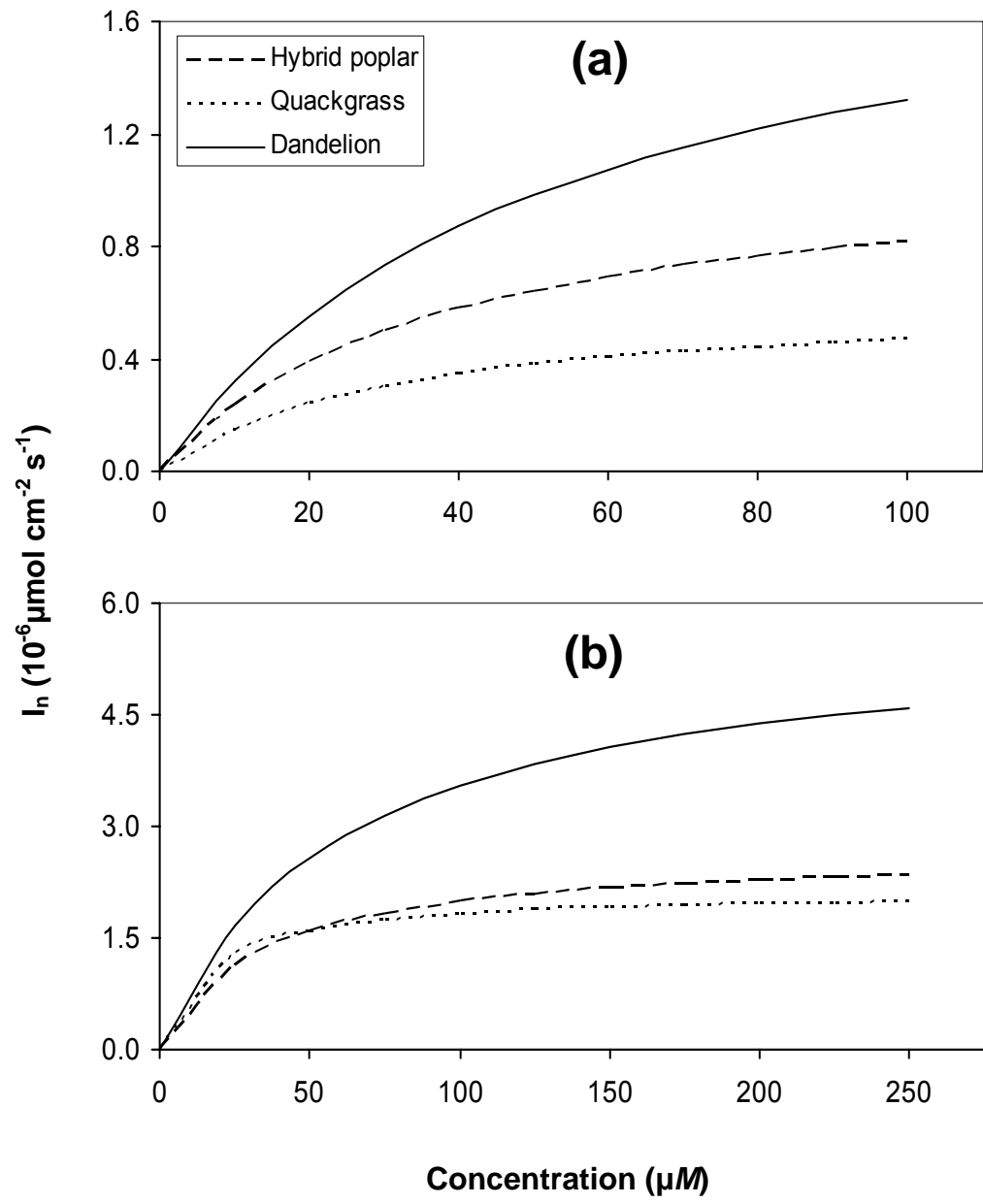


Figure 4.4. Michaelis-Menten curves for (a) phosphorus and (b) potassium uptake for hybrid poplar, quackgrass and dandelion.

Table 4.2. Mean N, P and K tissue concentrations for hybrid poplar, dandelion and quackgrass at the end of depletion experiment.

	N	P	K
	----- mg g ⁻¹ -----		
Hybrid poplar			
Shoot	20.4 (0.5)†	3.6 (0.2)	18.5 (0.2)
Root	22.4 (0.8)	5.7 (0.7)	35.7 (6.6)
Dandelion			
Shoot	29.1 (2.4)	5.0 (1.0)	33.9 (2.0)
Root	20.0 (1.6)	3.4 (0.2)	8.5 (0.3)
Quackgrass			
Shoot	19.2 (5.3)	3.7 (1.1)	25.0 (3.6)
Root	23.5 (0.7)	3.6 (0.3)	18.8 (0.6)

† Value in parentheses represents one standard deviation.

hybrid poplar found in our study are within the range of literature values reported for other tree species, with the only exception that I_{\max} value reported for $\text{NO}_3\text{-N}$ uptake ($2.85 \times 10^{-5} \mu\text{mol cm}^{-2} \text{s}^{-1}$) by Kelly and Ericsson (2003) in hybrid poplar is an order of magnitude greater than the estimated I_{\max} value in this study ($3.4 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$). Differences in I_{\max} values within the same plant species can be expected because of specific plant and experimental conditions, such as clonal differences, physiological root characteristics, nutrient status of the plant, plant age and the range of nutrient solution concentrations tested. Such parameters vary from one experiment to another depending upon the objectives of the study. In a study examining $\text{NO}_3\text{-N}$ uptake kinetics of two cultivars of red maple, Kelly et al. (2000) observed variations of two orders of magnitude in I_{\max} values within and between the cultivars.

Hybrid poplar had similar I_{\max} values for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ uptake (Figure 1). This observation is in contrast to other studies where $\text{NH}_4\text{-N}$ was the preferential source for N over $\text{NO}_3\text{-N}$ by many tree species (BassiriRad et al., 1999; Garnett et al., 2003; Hangs et al., 2003; Haynes and Goh, 1978; Marschner, 1995; Marschner et al., 1991; Min et al., 2000). This preference for N can be explained by the fact that all tree species tested in the above-mentioned studies are from cold, acidic forest soil environments, where $\text{NH}_4\text{-N}$ is often the predominant inorganic source of N. Presumably roots of forest tree species are more physiologically adapted to such environments (Cole, 1981; Kronzucker et al., 1997). Similarity of I_{\max} values between $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ uptake in hybrid poplar may occur because hybrid poplar is a genetically altered tree species with a faster growth rate coupled with higher nutrient requirements, and developed for intensively managed plantation systems. Roots of hybrid poplar may function differently in their preference for N source compared to roots of other forest tree species. Although hybrid poplar did not show a pronounced preference, in terms of I_{\max} values, for $\text{NH}_4\text{-N}$ compared to $\text{NO}_3\text{-N}$, the K_m value for $\text{NH}_4\text{-N}$ uptake was smaller compared to $\text{NO}_3\text{-N}$ uptake. This suggests that hybrid poplar may show a preference for $\text{NH}_4\text{-N}$ in environments with both $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ in low concentrations. No detailed information on the kinetic parameters describing N uptake has been reported for the weed species tested in this study. Large differences in I_{\max} values for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were observed between the dandelion and quackgrass weed species. Similarly, dandelion and quackgrass varied greatly in root

radius, root surface area, shoot biomass, shoot:root and tissue nutrient concentrations (Table 4.1 and Table 4.2). These variations may explain the differences in I_{\max} value between the weed species as noted by Clarkson (1985) in his summary of the work of several authors on factors affecting the nutrient uptake in plants. A wide range of I_{\max} values in weeds also has been reported elsewhere, and attributed to the differential growth nature of weed species (Levang-Brilz and Biondini, 2003).

4.4.2 Kinetics of P and K uptake

The mean I_{\max} value for P uptake in hybrid poplar is similar to that reported by Kelly and Ericsson (2003) and is of similar magnitude to other tree species including red maple (Kelly and Kelly, 2001) and black locust (Gillespie and Pope, 1990). The mean I_{\max} values for K uptake in hybrid poplar in our study, $2.66 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$, is lower than the value of $1.76 \times 10^{-5} \mu\text{mol cm}^{-2} \text{s}^{-1}$ reported for the same species by Kelly and Ericsson (2003), but within the range of values reported for red maple (Kelly and Kelly, 2001) and various pine species (Kelly et al., 1994; Van Rees et al., 1990).

I_{\max} values for P uptake by dandelion found in our study ($2.03 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$) is similar to values ($3.26 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$) reported by Levang-Brilz and Biondini (2003). Comparable measurements have not been reported for quackgrass. However, I_{\max} values for two *Agropyron* grass species (Levang-Brilz and Biondini, 2003) were an order of magnitude higher than our value for quackgrass ($3.73 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ and $8.30 \times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$ compared to 6.1×10^{-7} for quackgrass in this study).

Dandelion had higher I_{\max} values for both P and K uptake followed by hybrid poplar and quackgrass. The differences, however, were larger for K probably reflecting the high internal K requirements for dandelion (Tilman et al., 1999). Dandelion shoots had the highest concentrations of K compared to the other species (Table 2). Among all of the plant species I_{\max} values for K were comparatively larger than values for P, which may reflect the larger plant requirement for K owing to its importance in different cellular processes such as osmotic regulation and membrane transport (Kant et al., 2005; Marschner, 1995).

4.4.3 Implications for belowground competition

Herbaceous weeds are often considered as better competitors for nutrients than trees and commonly reported as the cause for reduced tree growth (Balandier et al., 2006;

Nambiar and Sands, 1993). Superior nutrient uptake characteristics of weed species are believed to be an important mechanism for this belowground competition (Hangs et al., 2003). Dandelion weed species had greater I_{\max} values for all of the three nutrients compared to hybrid poplar and quackgrass. The higher values of I_{\max} for all the nutrients in dandelion can be related to higher shoot demand for nutrients, as shown by the shoot nutrient status of the dandelion at the end of experiment (Table 2). Dandelion had less root surface area than hybrid poplar and quackgrass, whereas root length was similar to hybrid poplar but lower than that of quackgrass. Therefore, higher I_{\max} values for dandelion may be partly due to relatively higher nutrient demand per unit root surface area or per unit root length. I_{\max} values for quackgrass weeds, however, were lower than hybrid poplar which suggests that hybrid poplar may perform better in terms of nutrient acquisition than quackgrass when nutrient supply in soil is not limited. However, quackgrass might have a competitive edge under low nutrient supply conditions because of the lower K_m values. Therefore, the most important question is: can we predict the competitive ability of plants when grown together based upon the values of these uptake parameters? Based upon these nutrient uptake results one would predict that both hybrid poplar and quackgrass are equally as competitive, whereas dandelion has a competitive advantage because of its greater capacity for uptake. However, in a separate pot study, the growth of hybrid poplar was severely inhibited by quackgrass (Chapter 3; Kabba et al., 2007). I_{\max} values reported in various studies are frequently on a per unit root surface area basis and overall cumulative uptake of a nutrient will be a function of the size of the root system. Therefore, using these kinetic parameters as sole indicators of competitiveness for plant species under field condition may not be adequate due to the physical nature of root systems. For example, quackgrass and hybrid poplar had the same root surface area during the growing period but root length and root radius varied greatly (Table 4.1). Quackgrass had greater root length and smaller root radius than hybrid poplar (Table 4.1) which may lead to superior interception and uptake of particularly immobile nutrients such as P and K (Jungk and Claassen, 1997) and can provide a competitive advantage over the other plant species. The benefit of high I_{\max} can only be obtained if the supply of nutrients from the soil to the plant is not limited. This is not a common occurrence in field situations especially with relatively immobile nutrients.

Greater root length and smaller root radius increase the volume of soil per unit root surface area, which resulting in higher nutrient availability at the root surface because of shorter diffusion distances to be traveled by immobile nutrients to the root surface. Therefore, the competitive ability of plants can be suggested as a cumulative function of various physiological and growth parameters of the roots and shoots. Although these observations restrict generalization about the competitive ability of plants based upon just kinetic parameters, measurement of these parameters independently for each plant species is necessary for predicting nutrient uptake using models, where all of the major plant and soil parameters are accounted for in nutrient uptake predictions (Barber, 1995).

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5 NUTRIENT UPTAKE OF HYBRID POPLAR IN COMPETITION WITH WEEDS USING THE SOIL SUPPLY AND NUTRIENT DEMAND (SSAND) MODEL

5.1 Introduction

Nutrient uptake by plants growing in soil depends on the complex interaction of various soil and plant processes ranging from the nutrient supplying characteristics of the soil to the nutrient uptake characteristics of plant roots (Jungk, 2002). Movement of nutrients in the soil to the root surface is mainly through mass flow and diffusion (Barber, 1995). Both processes are controlled by a number of interacting soil and plant factors such as soil solution concentration, soil buffering power, effective diffusion coefficient and the transpirational gradient driving water flow (Jungk, 2002). Understanding these processes and their relationship to nutrient uptake and plant competition is very complex, but essential for efficiently managing nutrients in intensively managed agricultural, forestry and agroforestry systems.

Mechanistic models which mathematically describe nutrient supply in the soil and uptake at the root surface have been acknowledged as effective tools to evaluate these complex processes (Rengel, 1993). Various nutrient uptake models have been developed and validated for several crop and forest tree species under diverse experimental conditions (Barber, 1995; Barber and Cushman, 1981; Kelly et al., 1992; Rengel, 1993; Van Rees et al., 1990a). However, application of the models has generally been limited to simulating nutrient uptake by roots of only one plant species. Based upon the concept of Nye and Tinker (1977), Smethurst and Comerford (1993b) presented a model (COMP8), which simulates nutrient uptake by competing roots of contrasting plant species. This model incorporates mineralization as a nutrient input and changing water contents throughout the simulation period for calculating nutrient uptake. The COMP8 model has been recently revised and renamed as the Soil Supply and Nutrient Demand (SSAND) model (Comerford et al., 2006).

Nutrient competition is an important mechanism by which weeds affect the growth of tree species in young agroforestry plantations. Numerous studies have shown that the growth of plantation and forest tree species are affected by weeds through belowground competition for soil resources, particularly nutrients (Balandier et al., 2006; Casper and Jackson, 1997; Nambiar and Sands, 1993). However, despite the numerous literature available on weed competition effects on tree growth, a quantitative understanding of the various belowground processes occurring in plant competition and their role in nutrient uptake by competing plant species remains unclear. Only a few attempts have been made to quantify nutrient uptake by two different plant species existing in competing environments using the SSAND model (Smethurst and Comerford, 1993a). Only phosphorus (P) and potassium (K) uptake have been modeled, with no information available on nitrogen (N), the most important nutrient for plant growth. Furthermore, N mineralization is an important dynamic process that affects the availability of N to the plant throughout the growing period, but no attempt has been made to incorporate the N mineralization process in mechanistic nutrient uptake models for predicting N uptake.

The objectives of this study therefore were to: (1) check the applicability of the SSAND model to predict N, P and K uptake by hybrid poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) grown without weed competition in a controlled environment, (2) determine if incorporating N mineralization in the model would improve N uptake predictions, and (3) investigate if this model can quantitatively predict N, P and K uptake by hybrid poplar and weeds when grown together.

5.2 Materials and Methods

5.2.1 Estimation of model input parameters

Various soil and plant input parameters are required to predict nutrient uptake by hybrid poplar and weed species using the SSAND model. Details of the pot study have been reported in Chapter 3 and by Kabba et al. (2007) and are briefly reviewed here. Single seedlings of hybrid poplar were grown in pots with and without weed competition. Weed species were dandelion (*Taraxacum officinale*) and quackgrass (*Elymus repens*), both common weeds in hybrid poplar plantations in Saskatchewan. Five treatments with different weed competition density were selected based on field observations and grown with the single hybrid poplar seedling in pots: (1) no weeds (control), (2) one quackgrass

weed, (3) three quackgrass weeds, (4) four dandelion weeds, and (5) eight dandelion weeds.

Two surface soil samples were collected in bulk from two sites having Pasture and Alfalfa farm management systems near Meadow Lake, Saskatchewan, Canada. The soils are classified as Gray Luvisol according to Canadian System of Soil Classification (SCSR, 1995). Four and 3.8 kg of soil were used in each pot for growing hybrid poplar in the different treatments for the Alfalfa and Pasture soils, respectively. Pots were weighed and watered every second day in order to replace the water lost by evapotranspiration and maintained at 20% VWC throughout the study period. Hybrid poplar and weed species were harvested after 47 and 97 days for the Pasture soil and 49 and 105 days for the Alfalfa soil. At each harvest, shoot biomass of hybrid poplar and weed species were harvested separately, dried and ground for subsequent analysis. Root biomass was separated from the soil using water and mesh screens and the roots of hybrid poplar and weed species were carefully separated manually. Excessive moisture from the roots was removed using blotting paper prior to fresh root weight (F_{wr}) determination. Fresh roots were stored at -20°C until further analysis. Root length (L) was determined on scanned fresh roots using a root length computer program (Berntson, 1992). Average root radius (r_o) was calculated using the equation 4.2. Root uptake characteristics such as I_{max} , K_m and C_{min} for each plant species were determined by the depletion method as outlined by Claassen and Barber (1974) and details are reported in Chapter 4.

Nutrient concentrations in soil solution were determined by incubating the soil at field capacity for 24 h at a room temperature (22°C) and extracting the solution using the centrifugation technique (Elkhatib et al., 1987). Extracted soil solution samples were analysed for $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, P and K using the Technicon II autoanalyzer (Technicon Instruments Corp., NY) whereas K was determined on Varian Spectra AA 220 atomic absorption spectrophotometer (Varian Inc., Palo Alto, CA).

The solid-liquid partition coefficient (K_d) for $\text{NH}_4\text{-N}$, P and K was calculated by diluting the soil with 2 mM CaCl_2 (pH 4.8) solution in soil: solution ratios of 1:2, 1:10, 1:20, 1:40, 1:80 (Smethurst et al., 1999). Each treatment was replicated three times. Soil was shaken with the extracting solution for 12 h on a reciprocating rotary shaker, followed by centrifugation and filtration. Filtered samples were analysed for electrical

conductivity and pH. NH₄-N, P and K concentrations were analysed as discussed above. Determination of K_d was considered as a function of concentration in the liquid phase. Soil buffer power (b) was calculated using the equation:

$$b = \theta + \rho K_d \quad [5.1]$$

where θ is the volumetric soil water content and ρ is the soil bulk density (Van Rees et al., 1990b).

Average water influx rate (V_o) at the root surface was determined by measuring the water lost by evapotranspiration in planted pots compared to the water lost by evaporation in unplanted pots. The equation of Williams (1946) was used to calculate average V_o as follow:

$$V_o = U / [(T_2 - T_1) (L_2 - L_1) 2\pi r_o] \quad [5.2]$$

where U is the total amount of water transpired during the given growth period (T₂-T₁), L₁ and L₂ are the root length at times T₁ and T₂, respectively and r_o is the average root radius.

The effective diffusion coefficient (D_e) in soil was calculated as a function of the diffusion coefficient for that nutrient in water (D_L), volumetric soil water content (θ), impedance factor (f) and the buffer power of the soil (b) (Van Rees et al., 1990b) and was calculated as follow:

$$D_e = D_L \theta f / b \quad [5.3]$$

where f is a function of water content and is described as

$$f = 3.1\theta^{1.9} \quad [5.4]$$

N mineralization rates were obtained by incubating the soil at 22°C in three replicates under aerobic conditions (Campbell et al., 1993). One hundred grams of soil mixed with 100 g silica sand was incubated in 44.5 mm diameter columns at 20% soil

VWC (similar to the pot study) for 105 d. Solution samples were obtained at two week intervals by leaching the soil column with 0.01M CaCl₂ solution and the extract measured for NH₄-N and NO₃-N concentrations colorimetrically using the Technicon II autoanalyzer (Technicon Instruments Corp., NY). Ammonium concentration was negligible in the samples; therefore, N mineralization rates were expressed based upon the mineralized nitrate-N. N mineralization rates were expressed as $\mu\text{g cm}^{-3} \text{ s}^{-1}$ using the soil bulk density and length of the incubation period.

Root and shoot material of all plant species were dried at 65°C for 72 h and then ground in a Willey Mill to pass through a 2-mm screen. All the plant materials were digested in H₂SO₄ + H₂O₂ and measured for total N, P and K using standard techniques (Kalra, 1998). Total nutrient uptake for each pot was calculated by summing the nutrients in the root and shoot. Nutrient contents in the cuttings were not taken into account for calculating the total nutrient uptake in the hybrid poplar seedlings.

5.2.2 Nutrient uptake modeling

The SSAND model (Comerford et al., 2006) was used to simulate NO₃-N, NH₄-N, P and K uptake by hybrid poplar seedlings and weed species based upon the model input parameters provided in Table 5.1. This model was developed by incorporating the concepts and assumptions of Nye and Tinker (1977) where root competition for nutrients is defined by analytical solutions for solute transport in soil under steady state conditions. A detailed description of the model can be obtained from Comerford et al. (2006) and Smethurst and Comerford (1993b). Simulations were carried out for 47 and 97 days for the Pasture soil and 49 and 105 days for the Alfalfa soil. Model simulations were run without and with incorporating the N mineralization rates. Comparisons were made between predicted and experimentally measured nutrient uptake (observed) to determine how well the described soil and plant processes predicted nutrient uptake in this controlled experiment. Predicted vs observed nutrient uptake was compared with a 1:1 line using linear regression. For N, predicted NO₃-N and NH₄-N uptake were added together before comparing to the experimentally measured total N uptake. Nutrient uptake predictions for weeds were presented for all of the weed treatments combined.

Sensitivity analysis was carried out only for the single hybrid poplar seedlings without weeds in order to evaluate the influence of each model input parameter on

Table 5.1. Range of soil and plant input parameters used in SSAND model.

Parameters	NH ₄ -N	NO ₃ -N	P	K
Soil parameters				
Initial soil solution concentration (C_{li}), $\mu\text{g mL}^{-1}$	5-10	120-150	0.5	56-138
Soil water content (θ), cm cm^{-3}	0.20	0.20	0.20	0.20
Bulk density (ρ), g cm^{-3}	1.10-1.22	1.10-1.22	1.10-1.22	1.10-1.22
Solid-liquid partition coefficient (K_d), g L^{-1}	4.3-14.8	0	7.8-10.9	2.5-6.4
N mineralization input rate, $\times 10^{-6} \mu\text{g cm}^{-3} \text{s}^{-1}$	-	7.3-9.1	-	-
Hybrid poplar parameters				
Water influx rate (V_o), $\times 10^{-6} \text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$	1.95	1.95	1.95	1.95
Maximum nutrient influx rate (I_{max}), $10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$	4.0	3.4	1.13	2.66
Michaelis-Menten constant (K_m), $\mu\text{mol cm}^{-3}$	0.049	0.093	0.038	0.034
Minimum concentration (C_{min}), $\mu\text{mol cm}^{-3}$	0.001	0.001	0.0001	0.001
Root radius (r_o), cm	0.01-0.03	0.01-0.03	0.01-0.03	0.01-0.03
Root length density (L_v), cm cm^{-3}	0.001-11.88	0.001-11.88	0.001-11.88	0.001-11.88
Weed parameters				
Water influx rate (V_o), $\times 10^{-6} \text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$	0.15-0.23	0.15-0.23	0.15-0.23	0.15-0.23
Maximum nutrient influx rate (I_{max}), $\times 10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$	3.1-7.4	2.3-6.9	2.3-6.1	2.1-5.7
Michaelis-Menten constant (K_m), $\mu\text{mol cm}^{-3}$	0.024-0.034	0.059-0.073	0.030-0.053	0.016-0.061
Minimum concentration (C_{min}), $\mu\text{mol cm}^{-3}$	0.001	0.001	0.0001	0.001
Root radius (r_o), cm	0.01-0.03	0.01-0.03	0.01-0.03	0.01-0.03
Root length density (L_v), cm cm^{-3}	1.67-224	1.67-224	1.67-224	1.67-224

nutrient uptake considering each parameter independent of one another (Van Rees et al., 1990a). Nutrient uptake was simulated by changing each parameter ranging from 0.5 to 2 times its measured value and keeping all the other parameters constant at their initial values. Predicted uptake simulations were expressed relative to predicted nutrient uptake under the initial conditions.

5.3 Results

The SSAND model underestimated the N uptake by hybrid poplar in both soils (58 and 73% lower for the Pasture and Alfalfa soil, respectively) where hybrid poplar was grown without any weed competition (Figure 5.1). Predicted N uptake for hybrid poplar in the Pasture soil was greatly improved after the incorporation of N mineralization into the model with predictions being 7% higher than observed N uptake (Figure 5.1a). Predicted N uptake also improved for seedlings in the Alfalfa soil after N mineralization was incorporated into the model, although uptake was still underestimated by 49% (slope = 0.51) (Figure 5.1b).

Nitrogen uptake predictions for hybrid poplar seedlings were 62 and 65% less than the observed values for the Pasture and Alfalfa soil, respectively, when grown in competition with weeds (Figure 5.2). Incorporation of N mineralization as a model input, in both soils, did not improve the N uptake prediction for hybrid poplar grown with weeds (Figure 5.2).

Predicted N uptake by the competing weeds grown with hybrid poplar was overestimated for the Pasture soil by 78 and 90% without and with the incorporation of N mineralization, respectively (Table 5.2). However, predicted N uptake for weeds was greatly underestimated for the Alfalfa soil which was only 17% of the observed uptake when no N mineralization was added to the model. Incorporating N mineralization into the model greatly improved the weed N uptake predictions (slope 1.12 vs 0.17) (Table 5.2). Depending upon the soil type, $\text{NH}_4\text{-N}$ contributed 42-72% and 31-52% of the total predicted N uptake in hybrid poplar in no weed treatment when N uptake was predicted without and with incorporating N mineralization input, respectively (data not shown).

Predicted P uptake for hybrid poplar was 84 to 89% lower than that for observed P uptake depending upon the soil type and weed competition conditions (Figure 5.3). Simulated P uptake for weeds was greatly underestimated being 3.0 and 0.1% of the

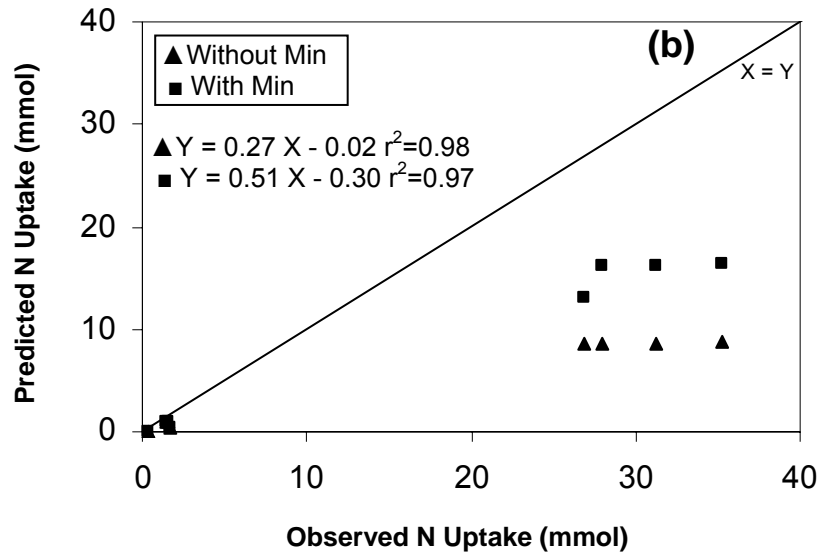
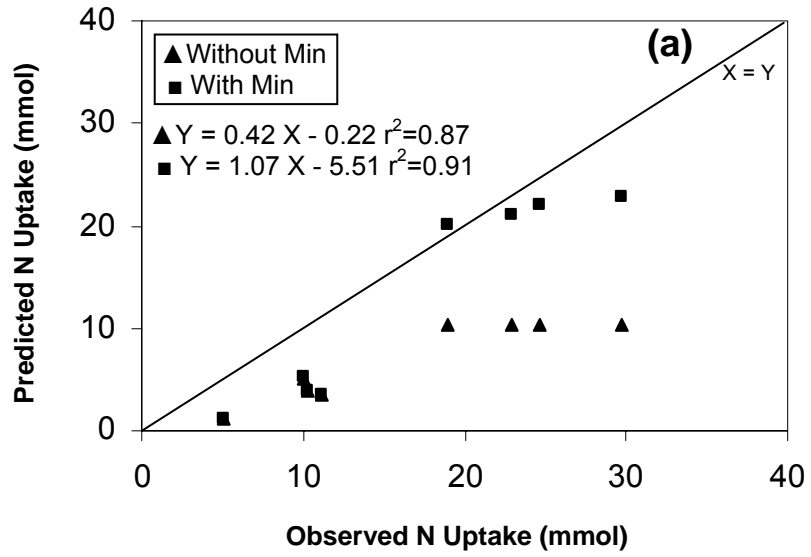


Figure 5.1. SSAND model predicted and observed nitrogen uptake by hybrid poplar grown without weed competition, without (▲) and with (■) nitrogen mineralization incorporation in the model, for (a) Pasture and (b) Alfalfa soil.

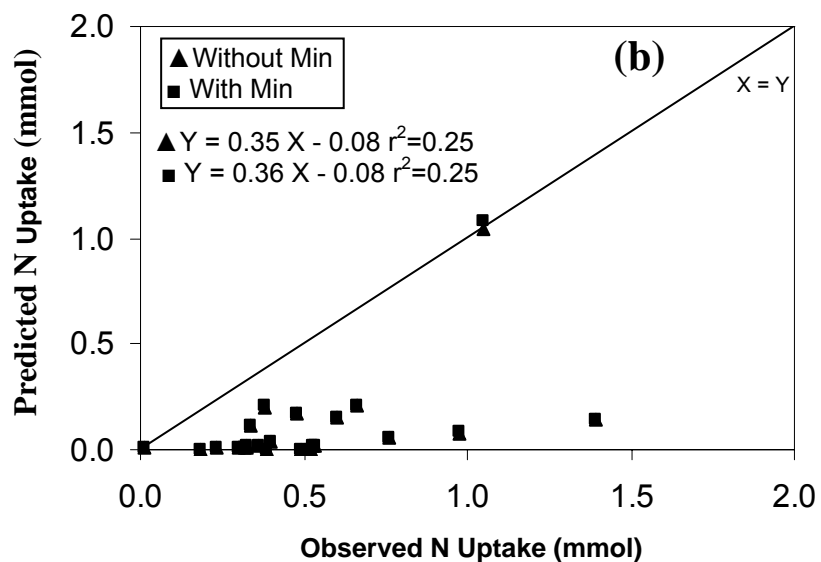
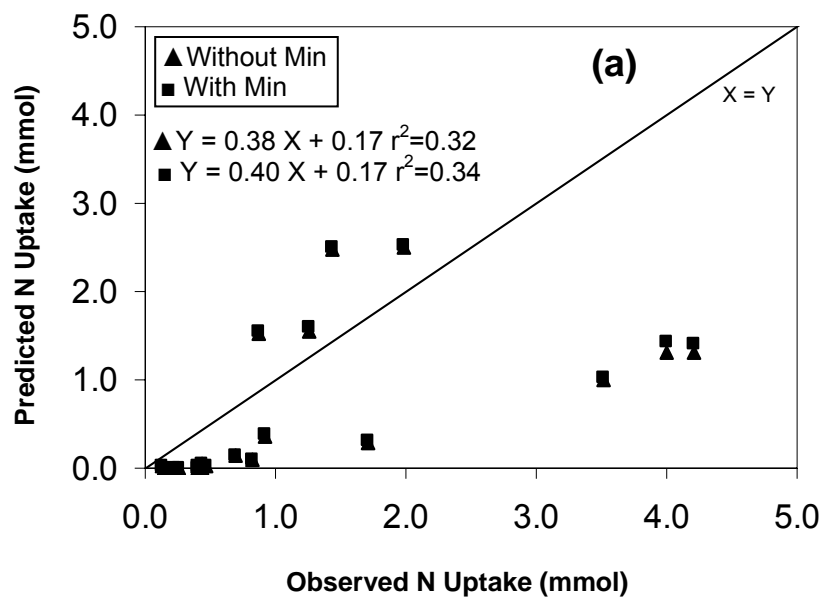


Figure 5.2. SSAND model predicted and observed nitrogen uptake by hybrid poplar grown with weed competition, without (▲) and with (■) nitrogen mineralization incorporation in the model, for (a) Pasture and (b) Alfalfa soil.

Table 5.2: Linear regression of predicted (y) vs observed (x) nutrient uptake for weeds.

Nutrient	Slope	Intercept	r^2
<u>Pasture soil</u>			
N (without min.)	1.78	-8.96	0.42
N (with min.)	1.90	-4.97	0.45
P	0.03	+0.19	0.29
K	0.19	+16.0	0.07
<u>Alfalfa soil</u>			
N (without min.)	0.17	+6.7	0.10
N (with min.)	1.12	-1.71	0.60
P	0.001	+0.17	0.24
K	0.08	+22.1	0.03

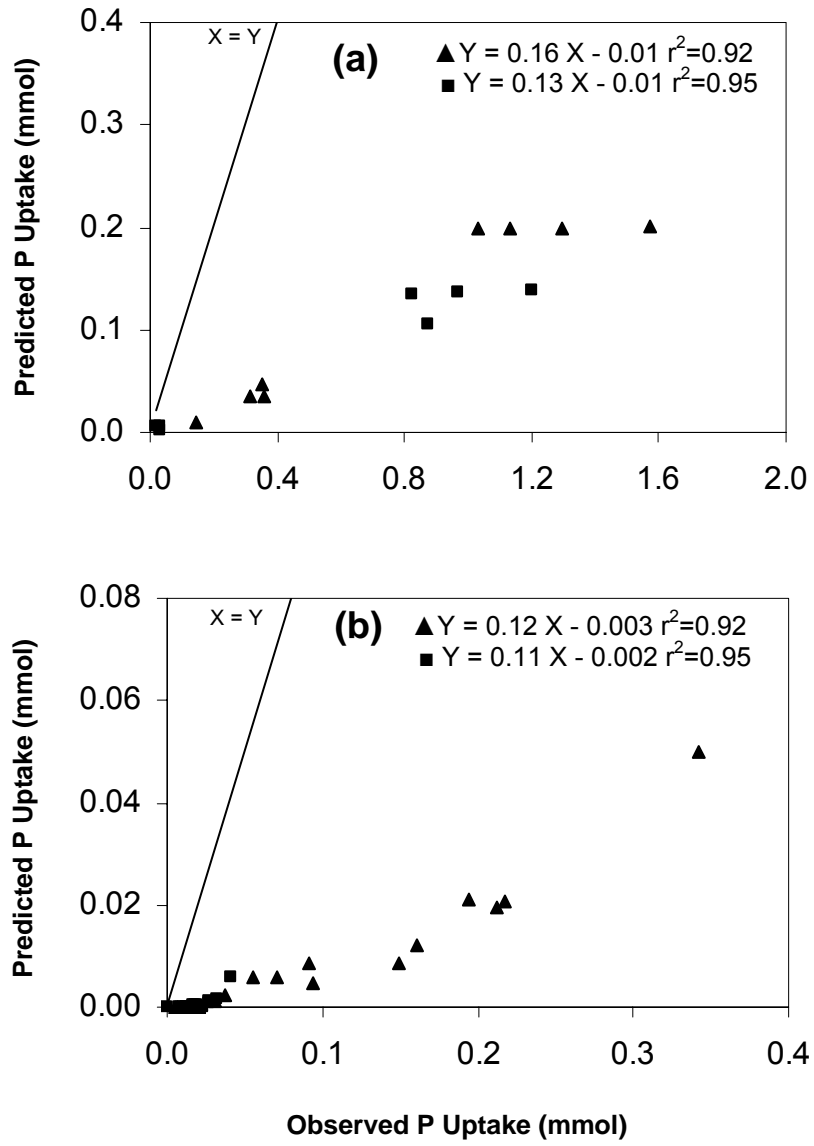


Figure 5.3. SSAND model predicted and observed phosphorus uptake by hybrid poplar grown (a) without and (b) with weed competition for the Pasture (\blacktriangle) and Alfalfa (\blacksquare) soil.

observed uptake in the Pasture and Alfalfa soils, respectively (Table 5.2).

Predicted K uptake by hybrid poplar under no weed competition was overestimated, with uptake being 43 and 59% greater than that of the observed K uptake for the Pasture and Alfalfa soils, respectively (Figure 5.4a). A similar overestimation of K uptake was observed for hybrid poplar with weed competition (Figure 5.4b). Model predictions for weed K uptake were not satisfactory both in terms of level of agreement between observed and predicted K uptake as well as the correlation coefficients (for Pasture slope = 0.19, $r^2 = 0.07$; for Alfalfa soil slope = 0.08, $r^2 = 0.03$) (Table 5.2).

Predicted $\text{NH}_4\text{-N}$ uptake in both soils was sensitive to L_v and r_o at harvest-I, while soil supplying parameters C_{li} and K_d were the only parameters affecting uptake for Harvest-II simulations (Figure 5.5). $\text{NO}_3\text{-N}$ uptake for harvest-I simulations in the Pasture soil was influenced by an increase in L_v , r_o and I_{max} values from 0.5 to 1.5 times of the original value; however, varying other parameters, in general, did not show a change in $\text{NO}_3\text{-N}$ uptake predictions (Figure 5.6). At harvest-II, $\text{NO}_3\text{-N}$ simulations in both soils were only sensitive to C_{li} (Figure 5.6). Phosphorus uptake showed similar trends in both soils where P uptake was more sensitive to changes in C_{li} for both harvests as well as L_v for harvest-I and K_d for harvest-II (Figure 5.7). Potassium uptake predictions were responsive to changes in L_v , r_o and I_{max} in both soils at harvest-I and in the Alfalfa soil at harvest-II, whereas C_{li} and K_d were the dominant parameters in the Pasture soil at harvest-II affecting the K uptake predictions (Figure 5.8).

5.4 Discussion

Nitrogen uptake in hybrid poplar was underestimated to a great extent in both soils irrespective of the weed species and density treatments (Figure 5.2 and Figure 5.3). Very few attempts have been made to predict N uptake by plants using a mechanistic modeling approach. Using the Barber-Cushman model (Barber and Cushman, 1981), Kelly et al. (2001) reported that predicted N uptake in red maple (*Acer rubrum* L.) was greatly underestimated compared to the observed N uptake; however, their study used only $\text{NO}_3\text{-N}$ for predicting total N uptake and did not account for $\text{NH}_4\text{-N}$. In our study, both $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ were used for predicting N uptake, although the predictions still largely underestimated observed N uptake. Interestingly, the amount of $\text{NH}_4\text{-N}$ present in the soil solution was only 4-6% of the total N ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) levels but contributed 40-60%

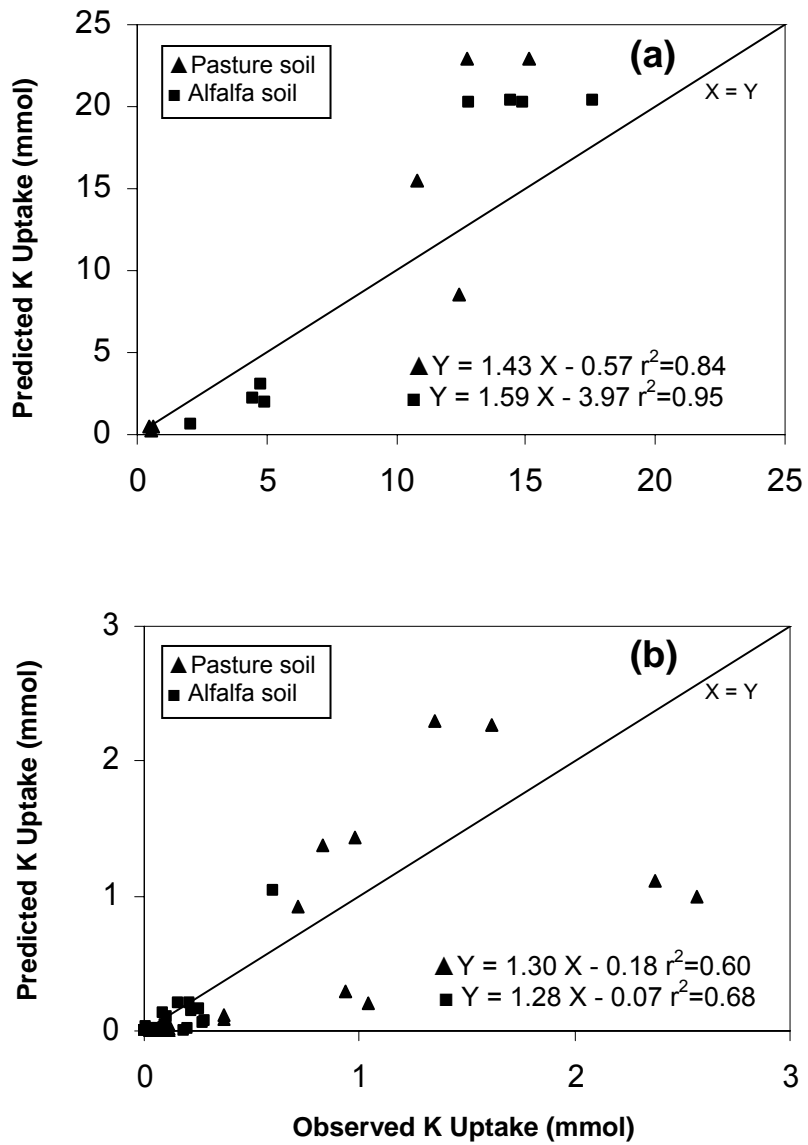


Figure 5.4. SSAND model predicted and observed potassium uptake by hybrid poplar grown (a) without and (b) with weed competition for the Pasture (▲) and Alfalfa (■) soil.

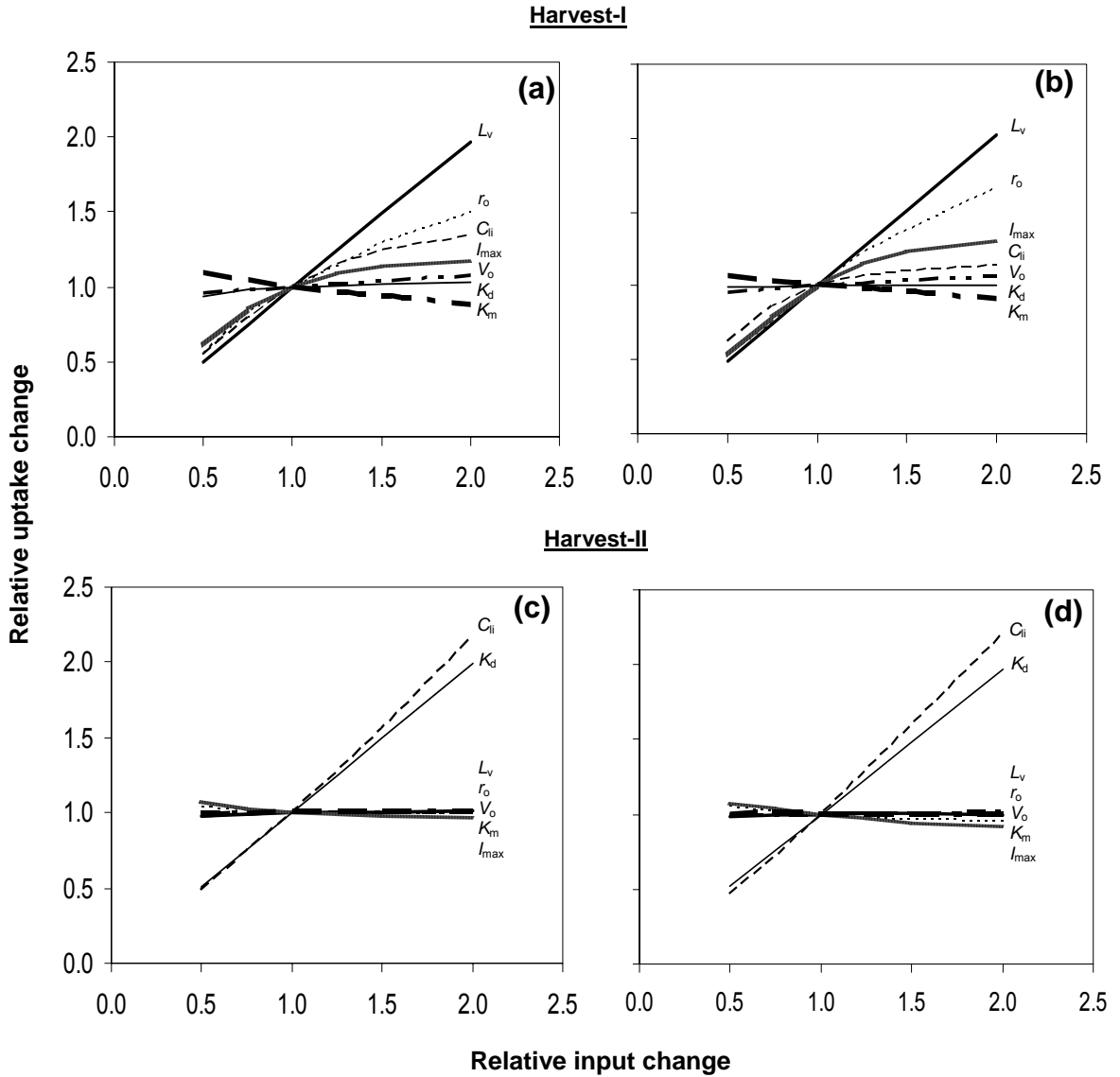
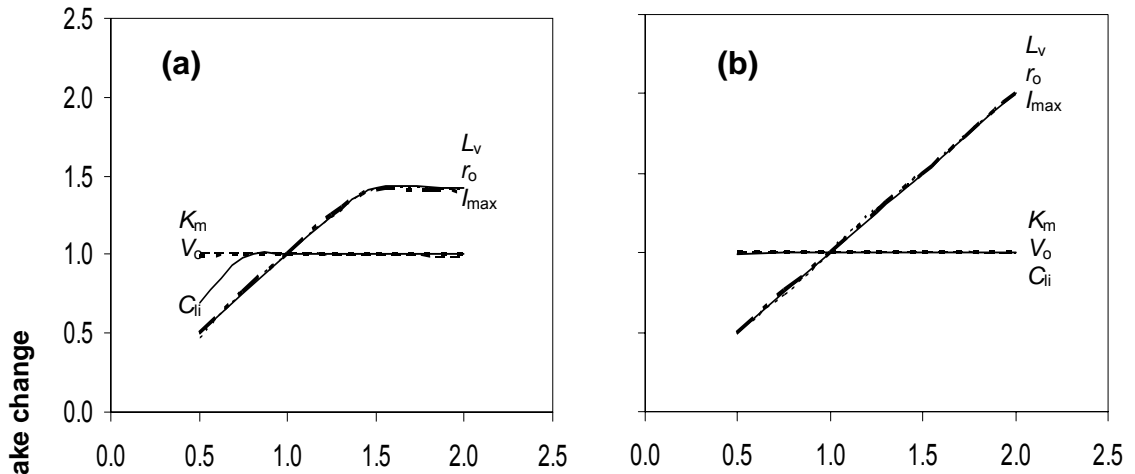


Figure 5.5. Sensitivity analysis for ammonium uptake by hybrid poplar grown without weed competition in Pasture (a and c) and Alfalfa (b and d) soil. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to ammonium uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{ii} = initial soil solution concentration, K_d = Solid-liquid partition coefficient.

Harvest-I



Harvest-II

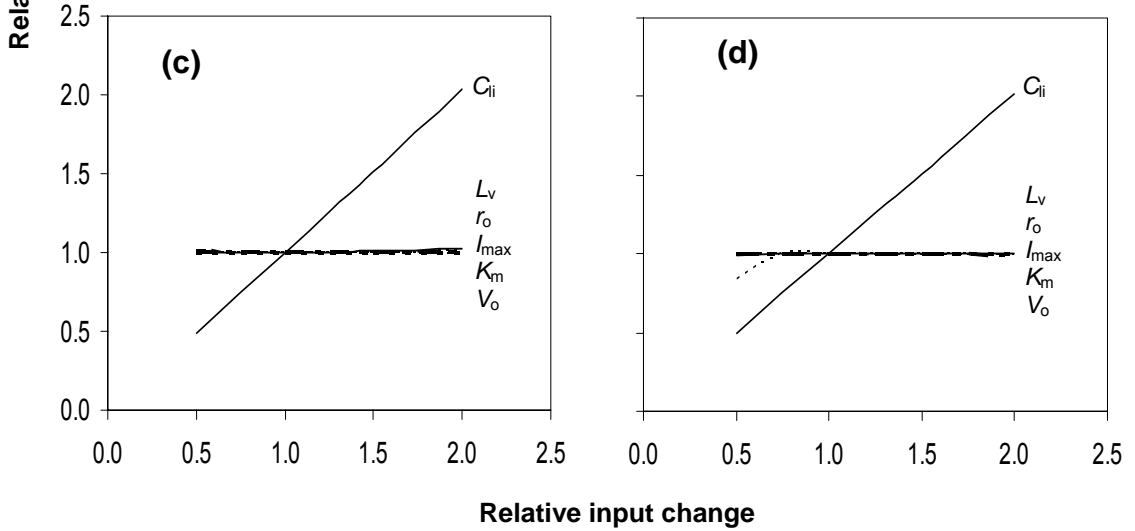


Figure 5.6. Sensitivity analysis for nitrate uptake by hybrid poplar grown without weed competition in the Pasture (a and c) and Alfalfa (b and d) soil. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to nitrate uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{ii} = initial soil solution concentration.

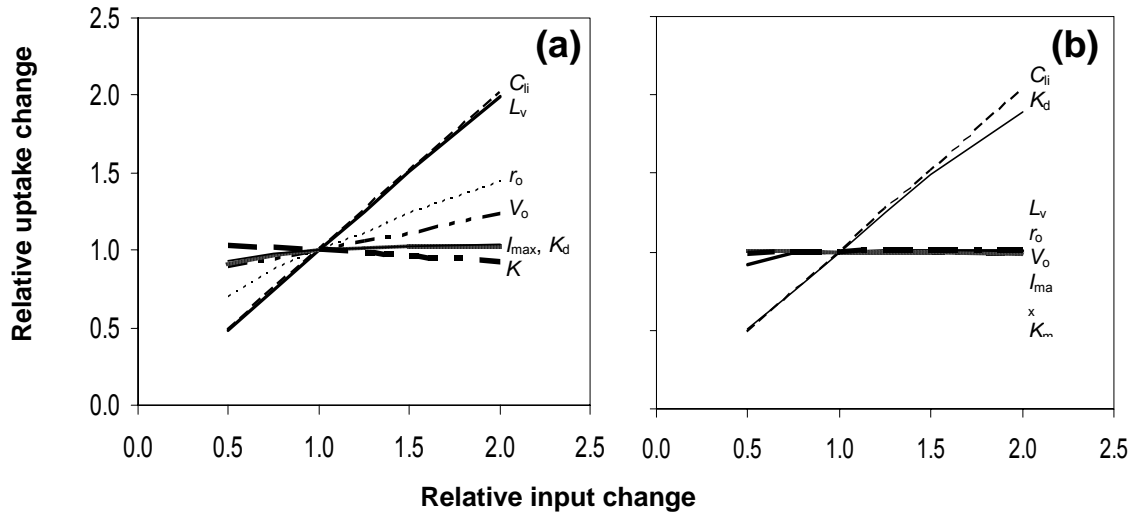


Figure 5.7. Sensitivity analysis for phosphorus uptake by hybrid poplar grown without weed competition in the Pasture (a) and Alfalfa (b) soil. Results were similar for harvest-I and harvest-II simulations. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to phosphorus uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{li} = initial soil solution concentration, K_d = Solid-liquid partition coefficient.

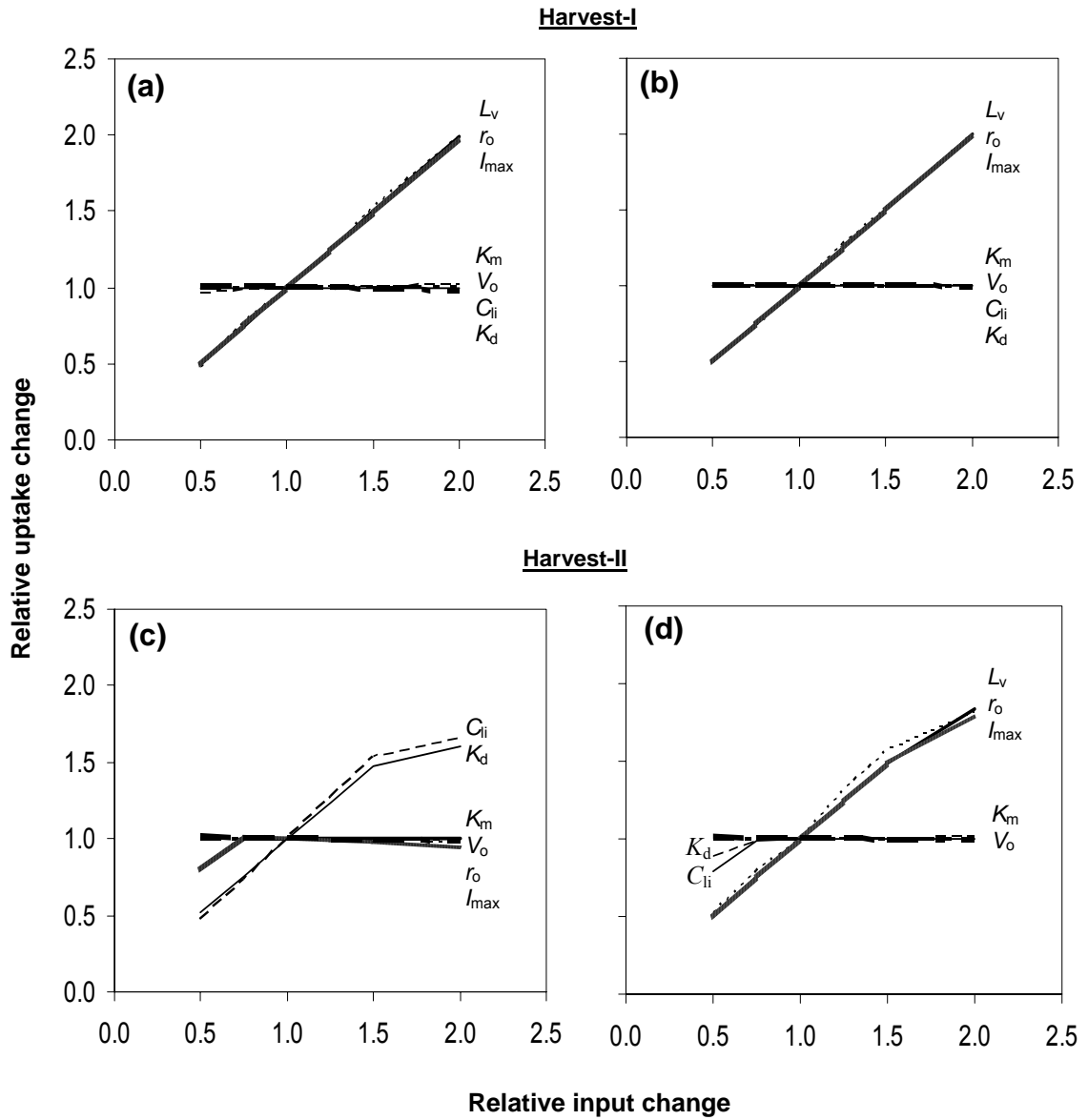


Figure 5.8. Sensitivity analysis for potassium uptake by hybrid poplar grown without weed competition in the Pasture (a and c) and Alfalfa (b and d) soil. Each parameter was changed individually while all other parameters were held constant. Results are expressed relative to potassium uptake under initial conditions. Abbreviations were L_v = root length density, r_o = root radius, I_{max} = maximum nutrient influx rate, K_m = Michaelis-Menten constant, V_o = water influx rate and C_{ii} = initial soil solution concentration, K_d = Solid-liquid partition coefficient.

of the total predicted N uptake, especially for longer simulations (i.e., Harvest-II), probably due to the buffering of $\text{NH}_4\text{-N}$ in the soil solution from the pools adsorbed on soil particles (solid phase NH_4) (Smethurst et al., 1999). Replenishment of nutrients from the solid phase plays an important role in long-term supply of nutrients to the plant. On the other hand, $\text{NO}_3\text{-N}$ is considered only present in the soil solution phase. The supply of $\text{NO}_3\text{-N}$ was exhausted during the simulation time, in particular for the second harvest period simulations, in both soils. This is contradictory to the measured soil solution values for the control treatment pots where significant amounts of $\text{NO}_3\text{-N}$ were still present in the soil solution at the end of harvest-II (Kabba et al., 2007, Chapter 3). The presence of $\text{NO}_3\text{-N}$ suggests that the availability of N to the plant is through some other pools such as N mineralization (Stevenson, 1986). It can be hypothesized that incorporation of N mineralization in the model would improve the N uptake predictions.

Incorporation of N mineralization in the model simulations in this study improved the N uptake prediction for the Pasture soil. In the Alfalfa soil, despite the improved slope between predicted vs observed N uptake, predictions were still underestimated. Sensitivity analysis for the Alfalfa soil showed that $\text{NO}_3\text{-N}$ uptake predictions were sensitive to levels of C_{li} . Therefore, it could be argued that the measurements of either C_{li} or N mineralization (which contributes to C_{li}) may not be correct where the methods used to measure these parameters yielded lower values than needed to improve the predictions. However, the same methods were used to measure these values in both soils and measured values of C_{li} and N mineralization for the Pasture soil seemed reasonably good for N uptake predictions. Another explanation for the differences in uptake may be due to the nutrition of hybrid poplar from the N present in the cuttings stock material instead of soil N, particularly at the initial growth period. The establishment and early growth of several tree species from hardwood cutting was positively related to the N reserve of the stock material (Dong et al., 2004; Eliasson, 1978; Millard, 1995). Therefore, the possibility of underestimating N uptake by the model due to N nutrition from the cutting stock material can be considered because the model only accounted for the N present in the soil. However, this explanation would lead to the overestimation of N uptake in the Pasture soil. Therefore, based upon the above multiple working hypotheses, it is difficult to deduce what factor(s) caused the N uptake underestimations in the Alfalfa soil.

Phosphorus uptake in hybrid poplar was greatly underestimated both with and without weed competition. Gross underestimation of P uptake under low P availability was reported for red maple (*Acer rubrum* L.) (Kelly and Kelly, 2001; Kelly et al., 2001) using the Barber-Cushman model (Barber and Cushman, 1981) and for slash pine (*Pinus elliottii* Engelm. var. *elliottii*) using the same model used in this study (Smethurst and Comerford, 1993a). Sensitivity analysis of P uptake revealed that predictions were more sensitive to soil supply parameters such as C_{li} and K_d and doubling the input value for either of these parameters increased P uptake by two times (Figure 5.3). Factors affecting the soil supply parameters will influence the P uptake predictions. These P uptake predictions were based upon a one time measurement of the soil solution P concentration at the start of experiment which was assumed to be the amount of P available to the plants for the growing period. The model predicted that the supply of P was exhausted midway of the simulation period. Measurement at harvest-I and harvest-II, however, showed that P was still present in the soil solution and did not change significantly from the initial soil solution P concentration (Kabba et al., 2007, Chapter 3). This suggests that during the study period significantly higher amounts of P were available in the soil solution of these low P soils through some other concomitantly occurred processes which accounts for the constant P supply to the plant and these processes are not adequately described in the existing model. Soil mineralization is a dynamic process which can be a source of P input to the soil solution throughout the growing season (Frossard et al., 2000). Although this model can incorporate the mineralization input, P mineralization estimates were not determined for this study. The model was rerun, however, assuming a P mineralization rate of $0.00000028 \mu\text{g cm}^{-3} \text{ s}^{-1}$ (Polglase et al., 1992) to determine the possible impact P mineralization on predicted P uptake. P uptake was overpredicted by 3-5 times depending upon the soil type, indicating the importance of including P mineralization estimate for P uptake modeling. Another explanation for the disagreement between predicted and observed uptake may be due to possible contributions of mycorrhizae to P uptake. It has been well established that mycorrhizae play an important role in P nutrition of plant under low P fertility conditions (Bolan, 1991; Koide, 1991). Mycorrhizae aid the plant in P uptake by: increasing the root surface area for P absorption; decreasing the distance for diffusion of phosphate ion due to greater fungal

hyphae length; and efficient transfer of P to plant roots (Bolan, 1991; Koide, 1991). Although hybrid poplar roots have mycorrhizae associations (Gunderson et al., 2007; Vozzo and Hacskeyl, 1974), in this study we did not test hybrid poplar roots for mycorrhizae infection; therefore, it was not possible to conclusively determine mycorrhizae association as a cause of P uptake underestimations. Another reason for P underestimations could be attributed to the availability of P to the plant from less labile P pools present in the soil. Plants can utilize substantial amounts of P from the less labile inorganic and organic P pools, when supply from readily available P pools is limited, especially in non-P fertilized and low-P input agricultural systems (Aulakh et al., 2003; Beck and Sanchez, 1994; Selles et al., 1999). In a long-term groundnut-based cropping system, Aulakh et al. (2003) observed that in non-P fertilized plots, after 25 years of cropping, organic-P declined by 39% of the 8-year value, while the Olsen-P decreased slightly. Mobility of P from the stock material to the plant can also be important in the uptake underestimations. Phosphorus is highly mobile in plants. P is remobilized from older tissue and transported to younger growing tissue, especially under P deficiency conditions (Bieleski, 1973; Jeschke et al., 1997).

Potassium does not behave like N and P where nutrient transformations can occur in the soil (i.e. NH_4 to NO_3) as well as having additional inputs from processes such as mineralization. Thus K is a 'model' nutrient for observing nutrient uptake because it is adequately described by the basic processes described in the model and should tell us how well the basic processes describe uptake for hybrid poplar. However, in our study, K uptake by hybrid poplar in both soils, when grown under weed and control treatments, was overestimated by the SSAND model (Figure 5.5). Such overestimations were also reported in slash pine (*Pinus elliottii* Engelm. var. *elliottii*) by Van Rees et al. (1990a) and Smethurst and Comerford (1993a). Van Rees et al. (1990a) attributed these overestimations to the root growth along the pot sides which led to the violation of model assumption of uniformly distributed and parallel-grown roots. Likewise, we observed hybrid poplar root growth along the pot sides at Harvest-II in control pots. However, this explanation does not explain the overestimation of K uptake in hybrid poplar in weed treatment pots where no hybrid poplar roots were found along the pot sides. In addition, reducing K uptake due to roots growing along pot walls would have the opposite effect

for N and P uptake by reducing it even further. Another reason for the disagreement between predicted and observed K uptake can be attributed to the erroneous measurement of model inputs. Sensitivity analysis revealed that K uptake predictions were generally sensitive to changes in L_v , r_o and I_{max} . Therefore, overestimation of these parameters may result in an overprediction of K uptake; however, the same values of L_v and r_o for hybrid poplar were used for N and P uptake where the uptake predictions were either substantially underpredicted or reasonably close to the observed uptake as in case of N uptake after N mineralization was incorporated into the model for Pasture soil. On the other hand, the I_{max} value for K uptake used in the model was measured separately in a hydroponic experiment and this value is within the range, but on the lower end of the values reported in other studies for the hybrid poplar, as well as for other tree species (Kelly and Kelly, 2001; Kelly and Ericsson, 2003; Van Rees et al., 1990a). Therefore, it is not a valid argument here that the value of I_{max} for K uptake was incorrect and caused an overestimation of K uptake. Based upon this discussion, however, it is not possible to conclude which parameter caused the erroneous K uptake predictions.

Uptake predictions for the weed component were also not satisfactory except for the prediction of N uptake in the Alfalfa soil after incorporating N mineralization into the model (Table 5.2). Furthermore, correlations between predicted and observed uptake were poor, which puts into question this model's performance in predicting the nutrient uptake under a plant competition environment. Similar observation was also observed by Smethurst and Comerford (1993a) while predicting P and K by weeds grown with pine (*Pinus elliottii* Engelm. var. *elliottii*), where they invoked use of assumed Michaelis-Menten parameters of grass species for inaccurate predictions. However, we measured the Michaelis-Menten parameters independently for the weed species used in this study. Results from this study lead us to believe that nutrient uptake by two plant species under a similar competing environment is a very complex interaction of biotic and abiotic factors which may not be simply described by basic processes of nutrient supply in soil and uptake at root surface.

In conclusion, the SSAND model did not predict nutrient uptake accurately under the set of conditions provided in this study except for very a few cases. Attempts to incorporate N mineralization into the model to identify its significance for accurate N

uptake predictions were also made. Results were encouraging in the Pasture soil where incorporating estimates of N mineralization into the model sufficiently described the underestimations of N uptake by hybrid poplar when grown without weeds; however, in the Alfalfa soil, N uptake was still underpredicted after the incorporation of the N mineralization input. Phosphorus uptake by hybrid poplar grown without and with weeds was greatly underestimated by the model; while K uptake was overestimated. Nutrient uptake predictions by weeds also were not predicted accurately by the model. Results from this study suggest that nutrient uptake by plant species in competing and non-competing environments depends upon the cumulative response of the different soil and plant processes which interact in a very complex way rather than simple description of those processes provided in the nutrient uptake models.

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6 MODELLING NUTRIENT UPTAKE FOR HYBRID POPLAR AS AFFECTED BY WEED COMPETITION IN THE FIELD

6.1 Introduction

Efficient management practices during the establishment years are extremely important for tree growth in young tree plantations and weed management is among one of the most critical and expensive cultural practice (Thompson and Pitt, 2003; Wagner et al., 2006). Weeds compete with tree species for above- and belowground resources and competition for nutrients is one mechanism by which the productivity of trees in young plantations is severely reduced in the presence of weeds (Wagner et al., 2006). Therefore, control of weeds for establishing productive and economically viable young tree plantations has become imperative.

Although negative effects of weeds on the availability of nutrients to tree species has been documented by researchers (Balandier et al., 2006; Nambiar and Sands, 1993; Wagner et al., 2006), only a few attempts have been made to quantify the nutrient uptake by competing plant species using mechanistic-based nutrient uptake models (Smethurst and Comerford, 1993a; Smethurst et al., 1993). Smethurst and Comerford (1993a) reported that P and K uptake by slash pine (*Pinus elliottii* Engelm. var. *elliottii*) competing with grass (*Panicum aciculare*) could not be adequately predicted due to lack of description of some processes in the model, most importantly nutrient mineralization, which may affect nutrient uptake by plants. This hypothesis was tested in Chapter 5 where it was found that predicted N uptake by hybrid poplar was improved after the incorporation of N mineralization when grown without weed competition, however, in weed competition conditions increased predicted N uptake was only observed for weed species but not for the hybrid polar.

However, the above-mentioned studies for predicting nutrient uptake using a mechanistic nutrient uptake modeling approach under plant competing conditions were confined to controlled growth chamber conditions to minimize soil and environmental variability. Large variations in growth conditions and soil factors are observed in the field

and may influence the availability of nutrients in the soil solution for plant uptake (Burrough, 1993). For example, soil moisture always fluctuates in the field due to periodic rainfall events or irrigation practices. Changes in soil moisture content readjust the nutrient depletion zone around the roots and may influence nutrient uptake (Jungk and Claassen, 1997). Therefore accounting for this factor in nutrient uptake models is necessary to improve the understanding of nutrient uptake under field conditions. The soil supply and nutrient demand (SSAND) model has a provision of using changing soil water content over the simulation period (Comerford et al., 2006) which may enhance the nutrient uptake predictions by plant species, however, utility of this function has yet to be tested. Apart from this, it also has to be seen that how incorporation of mineralization input in the model can affect the nutrient uptake predictions under field conditions?

Among the major nutrients, competition for N is more intense between the plant species (Blackman and Templeman, 1938). Nitrogen is a nutrient that often limits the growth of young poplar trees (Hansen et al., 1988) and weeds substantially decrease the growth of poplar trees primarily because of competition for N in soil solution or fertilizer (Mclaughlin et al., 1987).

Therefore, objectives of the this study were to: (1) determine the effect of weeds on growth of hybrid poplar, (2) determine the N uptake predictions by hybrid poplar grown with and with weed competition under field conditions using the SSAND model, and (3) evaluate how predicted N uptake by hybrid poplar and weeds changes after incorporating N mineralization and changing soil water content in the model.

6.2 Materials and Methods

6.2.1 Site description and experimental design

The study was conducted in the summer of 2005 at the Alfalfa and Pasture sites located near Meadow Lake, Saskatchewan, Canada (54°7'N and 109°30'W). The Alfalfa site had been managed with a wheat (*Triticum aestivum*) -fallow cropping system from 1991 to 1995 and then with Alfalfa (*Medicago sativa*) from 1996 to 2001. The Pasture site had been managed as mixed grass pasture dominated by brome grass (*Bromus carinatus*) from 1985 to 2002. The soil at the Alfalfa site was classified as an Orthic Gray Luvisol and at the Pasture site was classified as Brunisolic Gray Luvisol (SCSR, 1995). This experiment was originally designed to investigate the effects of dandelion and

quackgrass weed species on the growth of hybrid poplar and also to predict the N uptake by hybrid poplar and the weed species. Therefore, in the summer of 2004, twelve plots (9 x 7.5 m in size) were established with three treatments: no-weeds (control), dandelion weeds and quackgrass weeds and replicated four times. In order to obtain uniform populations of dandelion and quackgrass weeds in their respective treatments, weeds in all plots were eradicated by glyphosate application (2.5 L ha^{-1}). Plots were disc plowed before planting dandelion and quackgrass weeds. Dandelion weeds were planted from seeds, whereas quackgrass weed were planted using rhizomes obtained from a nearby field. Despite efforts to establish dandelion and quackgrass weed treatments, the plots in 2005 at both sites contained a mixture of weed species such as dandelion (*Taraxacum officinale*), quackgrass (*Elymus repens*), brome grass (*Bromus carinatus*), tartary buckwheat (*Fagopyrum tataricum*), lambs quarters (*Chenopodium album*), narrow-leaved hawk's-beard (*Crepis tectorum*), barnyard grass (*Echinochloa crusgalli*) and shepard purse (*Capsella bursa-pastoris*). Therefore, both the dandelion and quackgrass weed treatments were considered as a single treatment of weed plots which resulted in eight weed treatment plots and four control plots at each site.

Hybrid poplar seedlings were grown from the 20-cm long cuttings which were soaked overnight before planting. Cuttings were planted in control and weed treatments on June 6, 2005. At the time of planting, weeds growth in weed treatment plots was at initial stage. In each treatment plot, 30 cuttings were hand-planted in five rows. Plant to plant and row to row distance was maintained at 1.5 m, respectively. During the growing season, weeds in the control plots were controlled by glyphosate application (2.5 L ha^{-1}); however, to avoid any chemical injury to hybrid poplar seedlings, weeds next to seedlings were manually removed.

6.2.2 Measurements and samplings

6.2.2.1 Hybrid poplar

Only the interior 12 hybrid poplar seedlings were measured and harvested from each plot at 50, 79 and 100 days after planting (DAP). At each harvest, two seedlings were randomly harvested from each plot for a total of eight and 16 seedlings from the control (no weeds) and weed treatments, respectively. Each seedling was measured for seedling height and root collar diameter at the time of harvest and the shoot portion was

cut at ground level and measured for dry biomass after drying at 65°C. All roots were hand excavated from the soil and roots were washed within 24 h using a 1 mm plastic mesh. Excess moisture was removed by drying the roots using blotting paper and measured for fresh root biomass. Washed roots were frozen prior to further processing. After thawing, subsamples of roots were scanned and measured for root length using root length+ software (Berntson, 1992) followed by dry weight measurement after drying at 65°C. Linear relationships ($r^2 \geq 0.90$) were developed between root length and root dry weight in order to calculate the total root length. Mean root radius (r_o) was calculated from the equation as follow (Barber, 1995):

$$r_o = (Fw / \pi L)^{1/2} \quad [6.1]$$

where, F_w is the fresh root biomass and L is the total root length. Root length density was assumed to be 1.00 g cm^{-3} .

Dried root and shoot tissue samples were ground separately in a Wiley Mill and digested in H_2SO_4 and H_2O_2 (Kalra, 1998). Total N concentration in the digested samples was determined colorimetrically using a TechniconTM II autoanalyzer (Technicon Instruments Corp., NY). Total N uptake was calculated from the total dry tissue biomass and tissue N concentration.

6.2.2.2 Weeds

All dead and live weed shoot biomass in the weed treatment was sampled from a 900 cm^2 area. Weed sampling was done 45 cm away from the sampled hybrid poplar seedlings along the seedling planting line. Within this area, two 8-cm diameter soil cores were collected from the 0-15 and 15-30 cm depths and roots were separated by wet sieving using 1 mm mesh screens. Fresh root biomass, dry shoot and root biomass, root length, root radius and total N uptake for weeds was measured as described for the hybrid poplar seedlings (Section 6.2.2.1).

6.2.3 N uptake modeling

The SSAND model was used to simulate the N uptake by hybrid poplar and weeds and details about the model can be found in Smethurst and Comerford (1993b) and Comerford et al. (2006). Simulations were done separately for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ for each species and then summed to calculate total predicted N uptake. The range of various

soil and plant parameter inputs for the N uptake simulations are given in Table 6.1, and determined as follow.

6.2.3.1 Soil parameters

The volume of soil for each hybrid poplar seedling was calculated by measuring the length of the longest lateral root and an average soil depth of 25 cm which was the extent of vertical rooting. Soil samples were collected from the 0-25 cm depth of each plot of each treatment and measured for soil solution N concentration by the centrifugation method (Elkhatib et al., 1987). Soil samples were moistened to field capacity and incubated for 24 h at room temperature before extracting the soil solution by centrifugation. Concentrations of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in soil solution were determined colorimetrically using the Technicon II autoanalyzer (Technicon Instruments Corp., NY). The solid liquid partition coefficient (K_d) for NH_4 was calculated by diluting the soil with 2 mM CaCl_2 solution in soil: solution ratios of 1:2, 1:10, 1:20, 1:40, 1:80 (Smethurst et al., 1999). Three replicated samples for each treatment were shaken for 12 h on a rotary shaker, centrifuged and filtered. Filtered samples were analysed for $\text{NH}_4\text{-N}$ concentration as discussed above. The K_d value for $\text{NO}_3\text{-N}$ was assumed to be zero. Daily soil water content was measured by Time Domain Reflectometry (TDR) probes (Campbell Scientific Inc. Edmonton, Canada) which were installed in two plots of the control and four plots of the weed treatments at a 45° angle to a 25 cm depth. Soil moisture contents were measured every hour and averaged on a daily basis.

In situ N mineralization rates were measured using the method of Adams and Attiwill (1986). Nitrogen mineralization was studied for 97 days, during which the first two samplings were done at monthly intervals and the last sampling was done after 37 days of incubation. Briefly, at each sampling, 12 PVC cores (internal diameter 5 cm) were inserted to a depth of 15 cm with minimal disturbance. Six of the cores were immediately removed for the zero day sampling and the remaining six cores left to incubate for the desired length of time. After each sampling, another 12 cores were inserted and sampled in a similar manner. The difference between the mineral-N content measured for samples incubated for the specific time interval and zero day samples was considered as the N mineralized during that time interval. Mineralized N calculated from

Table 6.1. Range of plant and soil input parameters used for N uptake modeling in field study.

Parameters	NH ₄ -N		NO ₃ -N	
	Hybrid poplar	weeds	Hybrid poplar	weeds
Soil parameters				
Initial soil solution concentration (C_{li}), $\mu\text{g mL}^{-1}$	3.7-4.9	3.7-4.9	47-90	47-51
Soil water content (θ), cm cm^{-3}	0.25-0.46	0.13-0.29	0.25-0.46	0.13-0.29
Bulk density (ρ), g cm^{-3}	1.24-1.29	1.24-1.29	1.24-1.29	1.24-1.29
Solid-liquid partition coefficient (K_d), g L^{-1}	9.6-16.3	9.6-16.3	0	0
N mineralization input rate, $\times 10^{-6} \mu\text{g cm}^{-3} \text{sec}^{-1}$	-	-	5.8-8.5	5.8-8.5
Plant parameters				
Water influx rate (V_o), $\times 10^{-6} \text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$	1.95	0.15-0.23	1.95	0.15-0.23
Maximum nutrient influx rate (I_{max}), $10^{-6} \mu\text{mol cm}^{-2} \text{s}^{-1}$	4.0	3.1-7.4	3.4	2.3-6.9
Michaelis-Menten constant (K_m), $\mu\text{mol cm}^{-3}$	0.049	0.024-0.034	0.093	0.059-0.073
Minimum concentration (C_{min}), $\mu\text{mol cm}^{-3}$	0.001	0.001	0.001	0.001
Root radius (r_o), cm	0.01-0.022	0.009-0.01	0.01-0.022	0.009-0.01
Root length density (L_v), cm cm^{-3}	0.005-0.14	0.41-11.70	0.005-0.14	0.41-11.70

all time intervals was summed to measure the total N mineralized for the entire growing period.

6.2.3.2 Plant parameters

The water influx rate (V_o) at the root surface of hybrid poplar seedlings and weed species were assumed to be the same as those measured in the pot study experiment for hybrid poplar, dandelion and quackgrass (Section 5.2.1). It was visually observed that grassy weeds were dominant at the Pasture site, while broadleaf weeds were more common at the Alfalfa site. Therefore, liquid influx rate into weed roots for the Pasture site were assumed to be the same as quackgrass, whereas at the Alfalfa site it was assumed to be similar to dandelion. A similar approach was adopted for selecting the values of the Michaelis-Menten parameters (I_{max} , K_m and C_{min}) for the weeds at the Alfalfa and Pasture sites, which were calculated for hybrid poplar, and dandelion and quackgrass weeds in a separate hydroponic experiment (Chapter 4). Root length density (L_v) for hybrid poplar and weeds was calculated from the root length and the corresponding volume of soil for each seedling. Root length and root radii were measured as described in Section 6.2.2.1.

6.2.4 Statistical analysis

Two-tailed Unpaired Student t-test was used to analyze the statistical difference between the treatments for various growth parameters for hybrid poplar separately for each site. Statistical differences of weed growth parameters and N uptake between the harvests were compared using Tukey's HSD. All statistical comparisons were performed at $p = 0.05$ using SPSS version 13.0 (SPSS Inc. Chicago, IL). Observed and predicted N uptakes were compared with a 1:1 relationship using linear regression.

6.3 Results

6.3.1 Soil moisture

During the experimental period, soil VWC at the Pasture site ranged from 0.21-0.39 $\text{cm}^3 \text{cm}^{-3}$ with an average of 0.28 $\text{cm}^3 \text{cm}^{-3}$ in the control plots, and 0.12-0.31 $\text{cm}^3 \text{cm}^{-3}$ with an average of 0.21 $\text{cm}^3 \text{cm}^{-3}$ in the weed treatment plots during the experimental period (Figure 6.1). At the Alfalfa site, VWC for the control plots ranged from 0.23- 0.39 $\text{cm}^3 \text{cm}^{-3}$ with an average of 0.30 $\text{cm}^3 \text{cm}^{-3}$ and 0.13-0.36 $\text{cm}^3 \text{cm}^{-3}$ in the Weed treatment plots with an average of 0.20 $\text{cm}^3 \text{cm}^{-3}$ (Figure 6.1).

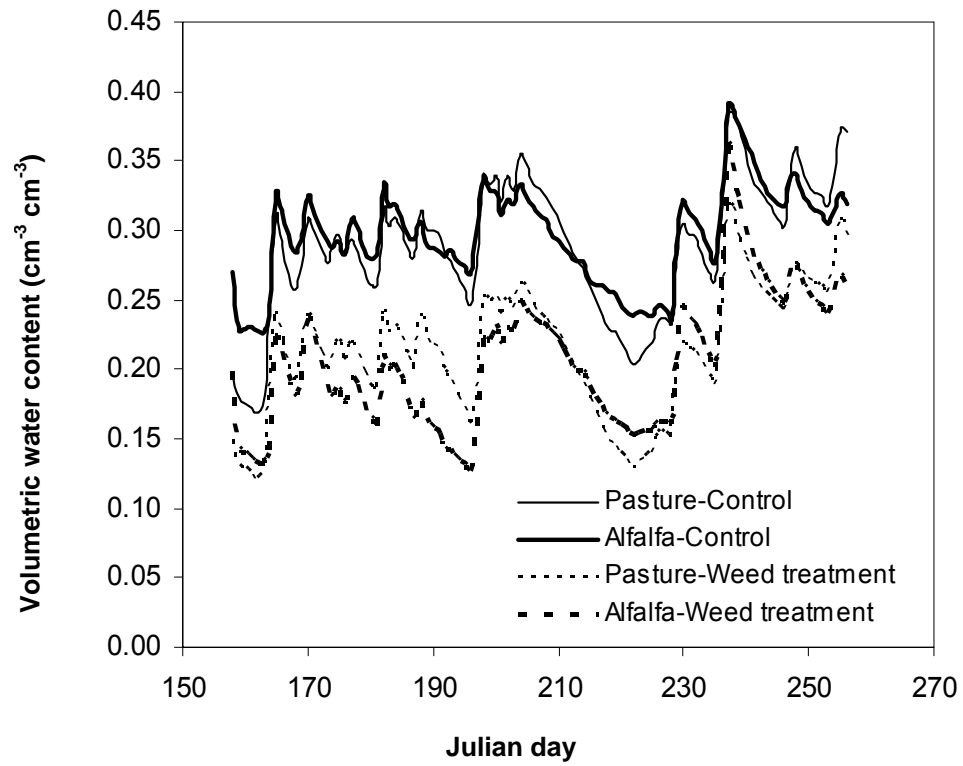


Figure 6.1. Change in volumetric water content at the Pasture and Alfalfa site during the study period.

6.3.2 Effects of weeds on hybrid poplar growth

Root collar diameter and stem height for hybrid poplar seedlings decreased significantly ($p = 0.05$) in the presence of weeds at each harvest (Table 6.2). Root collar diameter was 1.7 and 2 times greater in the control treatment compared to the weed treatment at the end of the experiment for the Pasture and Alfalfa sites, respectively. Stem height increased during the growing season in the control treatment at both sites (Table 6.2); however, stem height did not increase after 79 DAP in the weed treatments. At 100 DAP stem height was 1.75 to 2.5 times greater in the control treatment compared to the weed treatment. Similar trends were observed for dry shoot and root biomass where hybrid poplar produced more root and shoot biomass in the control treatment compared to the weed treatment (Table 6.2). Total dry biomass (root + shoot) for hybrid poplar in the control treatment at the end of the experiment was 13.6 g compared to 2.7 and 2.1 g in weed treatment for the Pasture and Alfalfa site, respectively. Root length of hybrid poplar increased throughout the experiment in the control treatment and averaged 50 and 36 m at the Pasture and Alfalfa sites, respectively (Table 6.2). Corresponding root length of hybrid poplar from the weed treatment was only 7.6 and 6.0 m for the Pasture and Alfalfa sites, respectively, at the end of experiment. Root radius of hybrid poplar generally decreased over the growth period in all treatments (Table 6.2). Root radius was different between the treatments for the first and second harvest at the Pasture site and for the second harvest at the Alfalfa site. N uptake by hybrid poplar in the control treatment was significantly higher than that in the weed treatment throughout the experiment (Table 6.2). Depending upon the site and harvest time, N uptake by hybrid poplar varied from 2.66 to 15.80 mmol plant⁻¹ in the control treatment and from 0.72 to 2.14 mmol plant⁻¹ in the weed treatment (Table 6.2).

Weed dry shoot biomass from the weed treatment increased from 120 g m⁻² on 0 DAP to 710 g m⁻² on 79 DAP at the Pasture site, whereas at the Alfalfa site this increase was evident only up to 50 DAP (from 29 g m⁻² at 0 DAP to 471 g m⁻² at 50 DAP) (Table 6.3). Dry root biomass for the Pasture site increased from 3.6 to 18.2 g during the study period but was only different at 100 DAP. No significant difference was observed for the Alfalfa site (Table 6.3). Root length density for the Pasture site significantly increased from 2.38 cm cm⁻³ at 0 DAP to 10.26 cm cm⁻³ at 100 DAP (Table 6.3). Root length

Table 6.2. Shoot and root growth parameters of hybrid poplar in control and weed treatment for the Pasture and Alfalfa site after 50, 79 and 100 days after planting (DAP).

Treatment	Pasture			Alfalfa		
	50 DAP†	79 DAP	100 DAP	50 DAP	79 DAP	100 DAP
	----- Root Collar diameter (mm plant ⁻¹) -----					
Control	5.1a‡	6.9a	7.6a	4.2a	5.3a	7.9a
Weed treatment	4.1b	4.2b	4.5b	3.4b	3.5b	3.9b
	----- Stem height (cm plant ⁻¹) -----					
Control	32.4a	54.3a	60.7a	22.8a	38.4a	66.3a
Weed treatment	29.3a	35.2b	34.7b	16.0b	24.4b	26.6b
	----- Dry shoot biomass (g plant ⁻¹) -----					
Control	2.6a	7.8a	12.5a	1.6a	3.9a	12.4a
Weed treatment	1.5b	2.4b	2.7b	0.5b	1.5b	2.1b
	----- Dry root biomass (g plant ⁻¹) -----					
Control	0.038a	0.373a	1.097a	0.009a	0.120a	0.986a
Weed treatment	0.023b	0.053b	0.157b	0.006a	0.040b	0.114b
	----- Root length (cm plant ⁻¹) -----					
Control	82a	1398a	4957a	31a	198a	3610a
Weed treatment	60a	286b	764b	15a	196a	596b
	----- Root radius (mm) -----					
Control	0.29a	0.16a	0.16a	0.22a	0.22a	0.18a
Weed treatment	0.20b	0.14b	0.14a	0.23a	0.12b	0.16a
	----- N uptake (mmol plant ⁻¹) -----					
Control	4.22a	10.76a	15.80a	2.66a	5.61a	15.65a
Weed treatment	1.27b	1.63b	1.74b	0.72b	1.67b	2.14b

† Days after planting.

‡ Means with the same letter within a site and harvest time are not significantly different at $p \geq 0.05$.

Table 6.3. Growth and N uptake by weeds in the weedy treatment at each harvest for the Pasture and Alfalfa site.

Days after planting	Dry shoot biomass		Dry root biomass		Root length density		N Uptake	
	Pasture	Alfalfa	Pasture	Alfalfa	Pasture	Alfalfa	Pasture	Alfalfa
	----- (g m ⁻²) -----		----- (g m ⁻²) -----		----- (cm cm ⁻³) -----		----- (mmol m ⁻²)-----	
0	120a†	29a	3.6a	2.8a	2.38a	1.94a	247a	65a
50	420b	471b	8.3a	3.6a	5.00ab	2.31a	570b	590b
79	710c	394b	9.1a	9.9a	5.51b	2.93a	589b	502bc
100	569bc	355b	18.2b	13.2a	10.26c	3.81a	506b	333c

† Means with the same letter within a site and harvest time are not significantly different at $p \geq 0.05$.

density for the Alfalfa site was 3.81 cm cm^{-3} by the end of experiment and it did not differ during the growing period. N uptake increased up to 50 DAP at the Pasture site. Weeds at the Alfalfa site increased N uptake up to 50 DAP and then decreased N uptake at 100 DAP (Table 6.3).

6.3.3 N uptake modeling

N uptake by hybrid poplar grown with and without weed competition was predicted using the SSAND model. Simulations were done using either an average soil water content during the entire simulation or incorporating daily soil water contents as well as N mineralization. Predicted N uptake by hybrid poplar grown in the control treatment at the Pasture site was 0.95 and 0.97 times the observed N uptake using the average and daily soil water contents, respectively (Table 6.4). Incorporating N mineralization improved N uptake predictions by 1% in both case using the average or daily water contents (Table 6.4). For the Alfalfa soil, using average and daily soil water contents N uptake predictions were 0.76 and 0.75 times the observed uptake, respectively. With the incorporation of N mineralization into the model predicted N uptake was 0.77 times the observed uptake using the average or daily soil water contents (Table 6.4).

N uptake by hybrid poplar in the weed treatment was greatly underpredicted for both the sites when an average soil water content was used (0.36 and 0.34 times for the Pasture and Alfalfa soil, respectively) (Table 6.4). N uptake was improved by 14% for the Pasture site when N mineralization was incorporated as an input; however, for the Alfalfa site corresponding improvement was only 2% (Table 6.4). N uptake predictions were enhanced to a greater extent when daily soil water content was used in the model (from 0.36 to 0.91 and 0.34 to 0.66, for the Pasture and Alfalfa sites, respectively) (Table 6.4). Incorporating N mineralization into the model further improved N uptake predictions by 4% for both sites (Table 6.4). Nitrogen uptake by the weed was underpredicted by 92 and 88% of the observed uptake at the Pasture and Alfalfa sites, respectively, when average soil water content was used for N uptake predictions, without incorporating N mineralization into the model (Table 6.5). Adding N mineralization improved N uptake predictions by 7% at the Pasture site and by 9% at the Alfalfa site.

Table 6.4. Linear regression of predicted (y) vs. observed (x) N uptake by hybrid poplar in control and weedy treatments.

Treatment	site	Soil water content	Mineralization	Slope	Intercept	r ²
Control	Pasture	Average	No-input	0.95	-3.99	0.85
			Added	0.96	-4.03	0.85
		Daily	No-input	0.97	-4.02	0.86
			Added	0.98	-4.06	0.86
	Alfalfa	Average	No-input	0.76	-2.51	0.95
			Added	0.77	-2.52	0.95
		Daily	No-input	0.75	-2.46	0.95
			Added	0.77	-2.54	0.95
Weed treatment	Pasture	Average	No-input	0.39	-0.25	0.38
			Added	0.42	-0.23	0.32
		Daily	No-input	0.91	-0.67	0.35
			Added	0.95	-0.70	0.35
	Alfalfa	Average	No-input	0.34	-0.23	0.71
			Added	0.36	-0.25	0.71
		Daily	No-input	0.66	-0.47	0.68
			Added	0.70	-0.50	0.68

Table 6.5. Linear regression of predicted (y) vs. observed (x) N uptake by weeds in weed treatment.

Site	Soil water content	Mineralization	Slope	Intercept	r^2
Pasture	Average	No-input	0.08	2.80	0.73
		Added	0.15	4.00	0.66
	Daily	No-input	0.22	7.50	0.50
		Added	0.23	8.08	0.48
Alfalfa	Average	No-input	0.12	0.75	0.69
		Added	0.21	1.20	0.68
	Daily	No-input	0.38	5.40	0.62
		Added	0.42	5.60	0.62

Using daily soil water contents in the model increased the predicted N uptake by 14 and 26% of the observed N uptake at the Pasture and Alfalfa site, respectively, compared to using an average soil water content (Table 6.5). The addition of N mineralization also slightly improved the N uptake predictions (slope 0.23 and 0.42 against 0.22 and 0.38 for Pasture and Alfalfa site, respectively).

6.3.4 Sensitivity analysis

Sensitivity analysis was carried out by changing the soil and plant input parameters to evaluate the impact of these parameters on model estimates of N uptake by hybrid poplar in the control treatment using 50 and 100 DAP harvest data for both the sites. Trends from the sensitivity analysis for both $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ were similar at both harvests for each sites; therefore, trends from the 100 DAP harvest for the Pasture site are presented in Figure 6.2 – 6.4.

At the Pasture site, $\text{NH}_4\text{-N}$ uptake by hybrid poplar in the control treatment was more sensitive to L_v followed by C_{li} . Ammonia uptake also showed some sensitivity to r_o while sensitivity to other parameter such as K_d , V_o , I_{max} and K_m was minimal (Figure 6.2a). Nitrate uptake showed a greater sensitivity to changing I_{max} , L_v and r_o inputs and predicted uptake increased linearly with increasing value of the respective parameters (Figure 6.2b). Changing the value of C_{li} , V_o and K_m had little effect on predicted $\text{NO}_3\text{-N}$ uptake by hybrid poplar (Figure 6.2). For the Alfalfa site, in the control treatment, L_v , r_o and I_{max} , showed greater sensitivity to predicted $\text{NH}_4\text{-N}$ uptake by hybrid poplar, however, results for $\text{NO}_3\text{-N}$ uptake sensitivity analysis were same as of the Pasture site (Figure 6.3). Trends of the sensitivity analysis for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ uptake by hybrid poplar in the weed treatment were similar for the both sites. In the order of decreasing, the sensitivity of different parameters with respect to $\text{NH}_4\text{-N}$ uptake were $L_v > r_o > I_{max} > C_{li}$, whereas other parameters showed very little sensitivity to predicted $\text{NH}_4\text{-N}$ uptake (Figure 6.4a). Nitrate uptake was again most sensitive to L_v , r_o and I_{max} parameters and showed no sensitivity to change in values of C_{li} , V_o and K_m (Figure 6.4b).

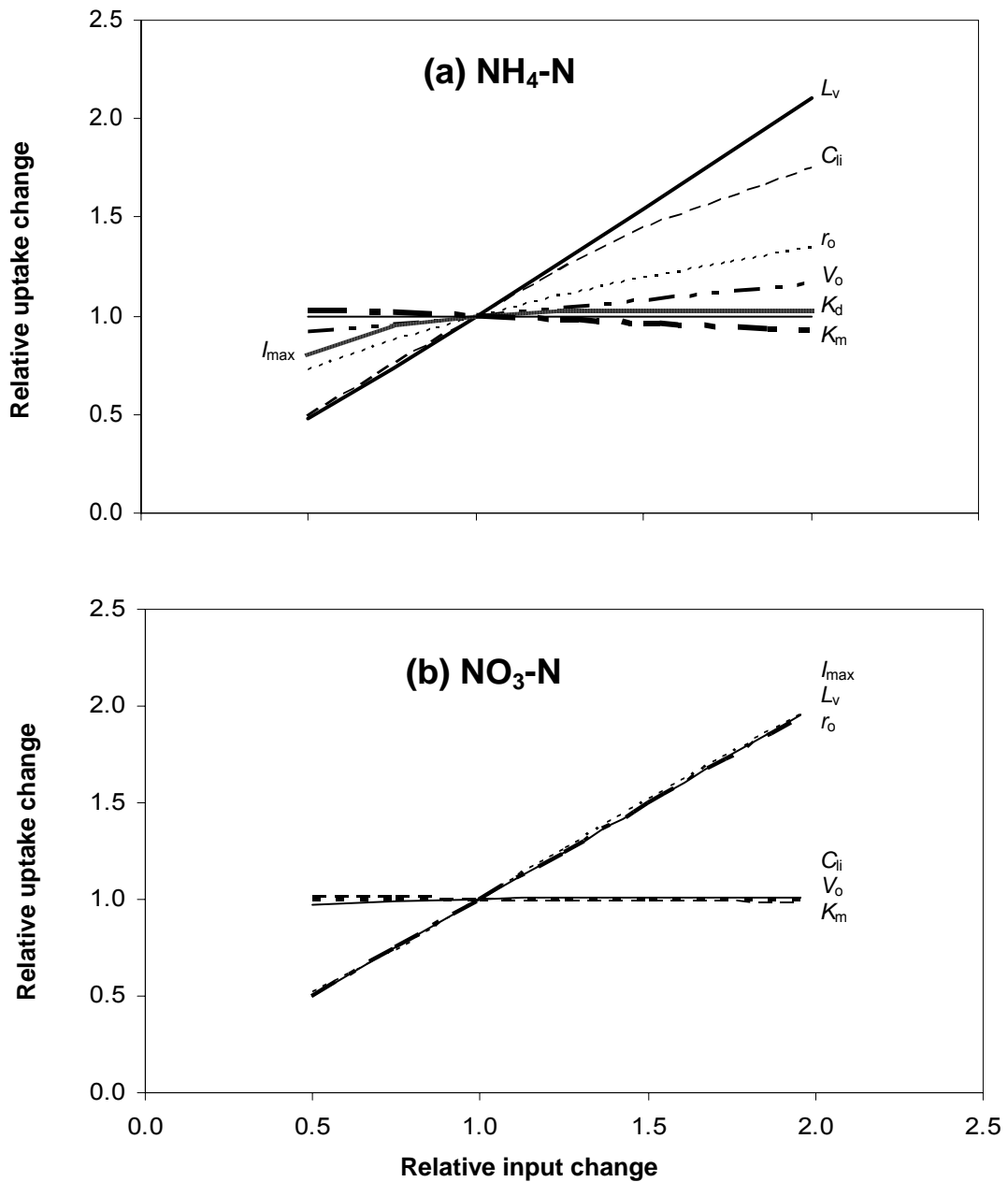


Figure 6.2. Sensitivity analysis of predicted (a) ammonium and (b) nitrate uptake for hybrid poplar grown in control treatment at Pasture site. Results are expressed relative to nutrient uptake under the initial conditions. Each parameter was varied individually while all other parameters were held constant. Parameters used for sensitivity analysis are L_v (root length density), C_{ii} (initial soil solution concentration), r_o (root radius), V_o (water influx rate), I_{max} (maximum nutrient influx rate), K_m (Michaelis-Menten constant) and K_d (solid-liquid partition coefficient).

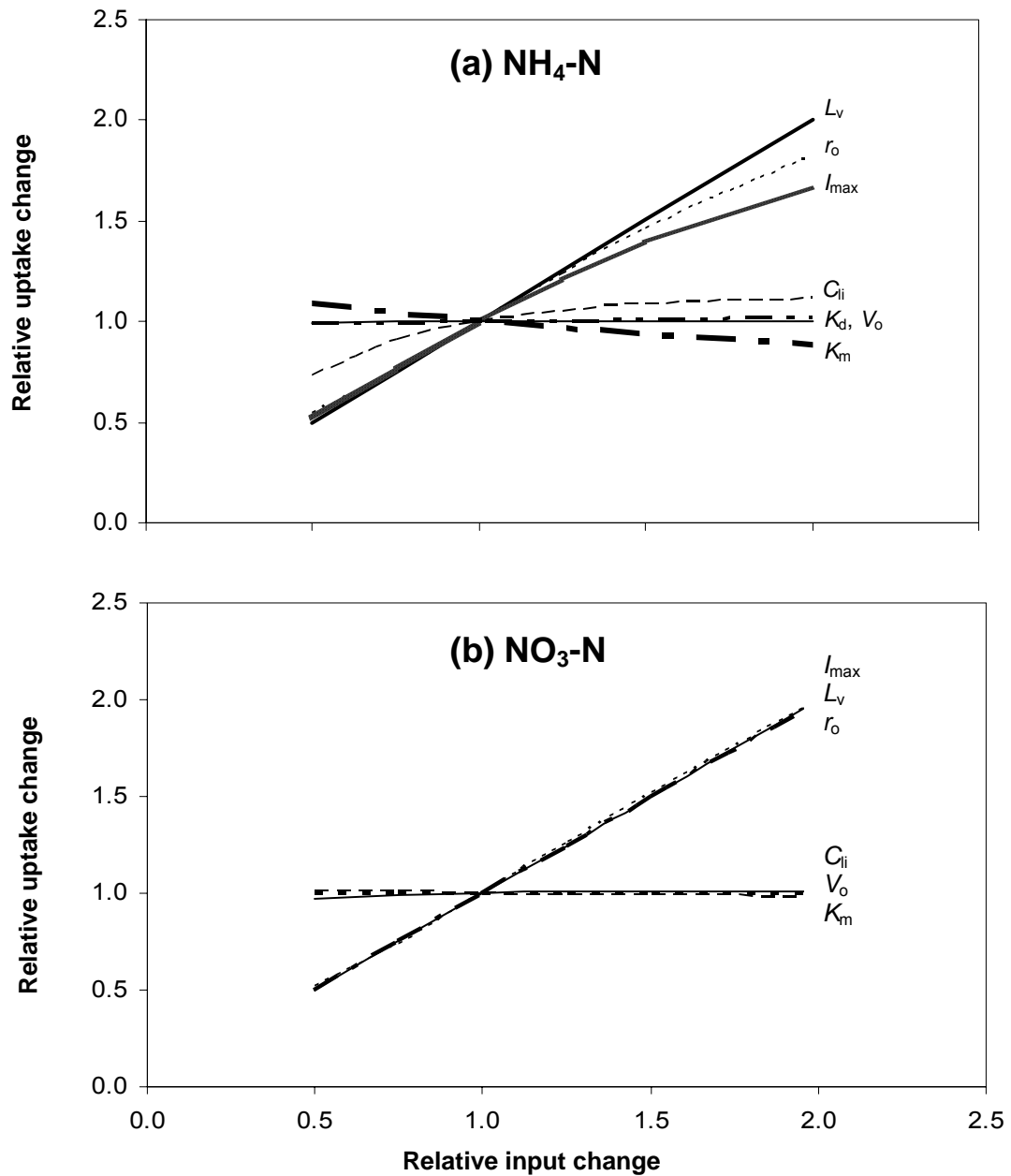


Figure 6.3. Sensitivity analysis of predicted (a) ammonium and (b) nitrate uptake for hybrid poplar grown in control treatment at Alfalfa site. Results are expressed relative to nutrient uptake under the initial conditions. Each parameter was varied individually while all other parameters were held constant. Parameters used for sensitivity analysis are L_v (root length density), C_{li} (initial soil solution concentration), r_o (root radius), V_o (water influx rate), I_{max} (maximum nutrient influx rate), K_m (Michaelis-Menten constant) and K_d (solid-liquid partition coefficient).

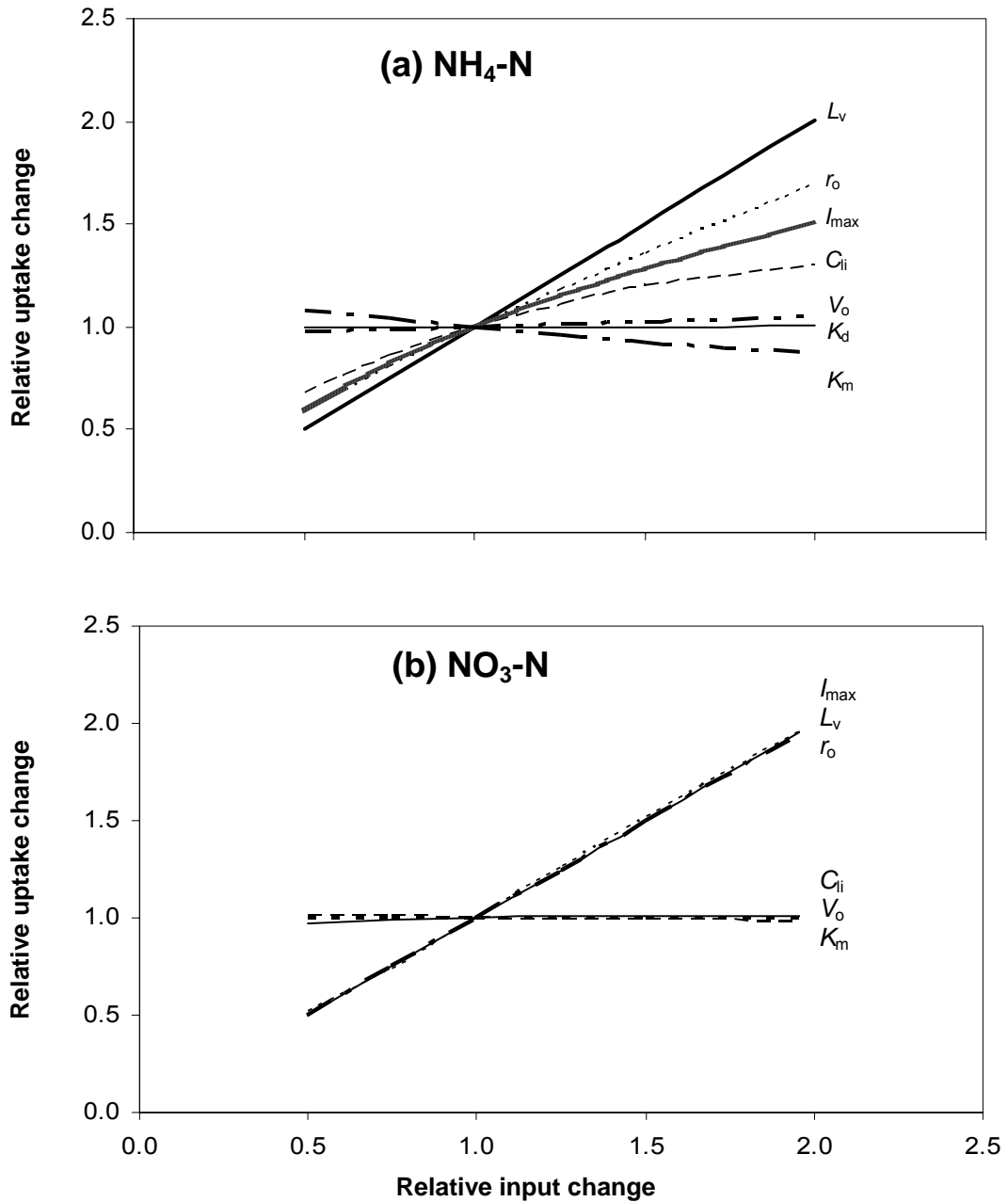


Figure 6.4. Sensitivity analysis of predicted (a) ammonium and (b) nitrate uptake for hybrid poplar grown in weed treatment (trends for similar for the Pasture and Alfalfa site). Results are expressed relative to nutrient uptake under the initial conditions. Each parameter was varied individually while all other parameters were held constant. Parameters used for sensitivity analysis are L_v (root length density), C_{li} (initial soil solution concentration), r_o (root radius), V_o (water influx rate), I_{max} (maximum nutrient influx rate), K_m (Michaelis-Menten constant) and K_d (solid-liquid partition coefficient).

6.4 Discussion

6.4.1 Hybrid poplar- weeds competition

The growth of hybrid poplar at these field sites decreased significantly in the presence of weeds. Reduction in hybrid poplar growth in the presence of weed was also observed in a two-year nursery study by Buhler et al. (1998) and in a one-year field study by Sixto et al. (2001). Weeds may compete with young hybrid poplar trees for above- and belowground resources, i. e., water, light and nutrients (Nambiar and Sands, 1993; Wagner et al., 2006). Weed treatment plots had established weeds at the start of the experiment and the concentration of N in the soil solution was lower than that in the control plots which may have caused N competition by weeds to affect the hybrid poplar seedlings. Similarly, water was another resource to which hybrid poplar seedlings may have competed with weeds as indicated by the lower soil moisture content in weed treatment plots compared to the control plots throughout the study period (Figure 6.1). Apart from the belowground competition, hybrid poplar may also have competed for aboveground resources. At the time of each harvest we visually found that hybrid poplar seedlings in the weed treatment plots were completely covered by the weed canopy suggesting that the hybrid poplar trees had light competition.

6.4.2 N uptake predictions for hybrid poplar in control treatment

The SSAND model satisfactorily predicted N uptake for hybrid poplar seedlings when grown without weed competition in the field. Predictions were excellent for the Pasture site, while for the Alfalfa site N uptake was slightly underestimated. Therefore, the theoretical concepts of solute transport to predict N uptake appears to be valid under these conditions. These results are also encouraging for using the modeling approach to predict N uptake by tree species grown in the field, because no such attempt to model N uptake by tree species has been made in the past. Most of the previous work on nutrient uptake by tree species grown under field conditions focused on P and K using the SSAND (Smethurst et al., 1993) or the Barber-Cushman model (Van Rees et al., 1990).

Although comparisons of the measured uptake values and the model predictions are excellent for the Pasture site, N uptake by hybrid poplar at the Alfalfa site was underpredicted by 24% of the observed N uptake (Table 6.4). The reason for this

underprediction of N uptake by the model is not clear. It could be speculated that the model in its present form is missing some processes which were responsible for additional supply of N to the hybrid poplar, for example, N mineralization. N mineralization is the major biological process which affects N availability to the plants over the growing period and occurs through concurrent addition and decay of organic matter in the soil (Stevenson, 1986). It was hypothesized that incorporation of N mineralization rate as an input to the model would improve N predictions. N mineralization was only incorporated for NO₃-N modeling, as 90-95% of the total N mineralized was NO₃-N. Incorporation of N mineralization rate as model input in this field study did not improve the predicted N uptake substantially (Table 4) contrary to observation in the pot study (Chapter 5). Reasons for the lack of improvement in N uptake prediction may be due to the presence of very higher concentrations of available N present in these soils and also to lower root density of hybrid poplar in the field compared to those found in the pot study. Therefore, in this study, the supply of N from the soil was not limiting for N uptake by hybrid poplar in the control treatment. The sensitivity analysis also showed that changes in C_{ii} of NO₃-N did not change the relative NO₃-N uptake for either sites at each harvest which means there were another reasons for underestimating the N uptake by hybrid poplar in the field.

Hybrid poplar seedlings were grown from cuttings and the N present in cuttings can be a source of nutrition to trigger the initial vegetative growth when roots are not sufficiently developed (Dong et al., 2004; Millard, 1995). The model only accounts for the N supplied from the soil in the simulations, but not the N which might have been transferred from the cuttings to the aboveground biomass. This may explain the underestimation of N uptake at the Alfalfa site, but would result in an overprediction for the Pasture site depending upon how much N was supplied from the cutting source. N contents were not determined for the individual cuttings at the start of the experiment, although average N concentration was measured for the cuttings in bulk. An attempt was made to estimate the N supplied from the cutting by subtracting the N content in individual cuttings at each harvest from the initial average cutting N content. With this adjustment N uptake predictions by hybrid poplar were improved for the Alfalfa site (slope 0.80-0.81 vs 0.75-0.77); however, surprisingly no difference was found for the

Pasture site. The higher observed N in the hybrid poplar at the Pasture site at all harvests made the contribution of N from the cutting to the total N uptake negligible, which resulted in no improvement of the model N uptake prediction.

The SSAND model was also tested for effect of using an average soil water content value during the simulation period or a fluctuating daily soil water content on N uptake predictions. Using the daily soil water content, the model resets the depletion zone for nutrients between the roots, i.e. no depletion zone overlapping when there is an increase in water content during rainfall events. While resetting the depletion zone, model also reset soil solution concentration at initial value which can be a cause for overestimations. However, no difference was observed between the hybrid poplar N uptake predictions using average or daily soil water content suggesting that daily change in the soil water content has little effect on the soil solution concentration and on supply through mass flow and diffusion for these soils.

6.4.3 N uptake predictions under weed competition conditions

N uptake was substantially underestimated by the SSAND model for both hybrid poplar and weed species. Reasons for underestimating N uptake by the SSAND model under a competing environment are unclear. Incorporation of N mineralization also did not improve the N uptake predictions for hybrid poplar. N uptake predictions for hybrid poplar were not sensitive to change in concentration of $\text{NO}_3\text{-N}$ that may be the reason for not improving the N uptake after incorporating N mineralization. But from this observation it can not be inferred that supply of $\text{NO}_3\text{-N}$ was not limiting factor because increased N uptake was observed for weed species after N mineralization incorporation. This suggests the importance of plant parameters in capturing the N from the soil under intense nutrient competition. Sensitivity analysis predicted N uptake by hybrid poplar increased linearly with increasing values of I_{max} , L_v and r_o . Therefore, underestimations in hybrid poplar may be due to the lower estimates of the plant parameters. The same value of I_{max} was used for predicting the N uptake by hybrid poplar in the control treatment, where prediction are reasonably good, therefore this can not be considered to measured incorrectly. It is very unlikely that measured L_v and r_o values are in lower estimate because hybrid poplar did not develop large root systems in the weed treatments and roots were excavated carefully to avoid any root loss. Therefore, it may be possible that

under intense weed competition, nutrition from the N present in the cutting may represent a relatively larger proportion of total plant N and cause the underestimation of N uptake by hybrid poplar.

Nitrogen uptake was also underestimated for weeds and incorporation of N mineralization in the model did not sufficiently improve the N uptake predictions. Root length density for the weeds in this field study was determined by the root core method. It may be possible that the root core did not represent the actual root length density in the field and may have caused the underestimation of weed root length density which led to the underestimation of weed N uptake by the model.

Using changing water soil content for N uptake predictions improved the N uptake predictions for both hybrid poplar and weeds (Table 6.4 and 6.5). The model sets the C_{ii} at initial values when there is an increase in water content, while resetting the depletion curve. This means that C_{ii} remains the same throughout the simulation period, as there were very frequent events of increasing water content and N was never limiting under the competition environment. This assumption of setting C_{ii} at the initial concentration while resetting the depletion zone in the model does not seem valid because under intense competition conditions soil nutrient concentrations would decrease over the growing period, due to increased nutrient demand for plant growth.

In conclusion, the SSAND model predictions for N uptake by hybrid poplar were in reasonable agreement with measured N uptake for hybrid poplar growing without weed competition. However, under two plant species scenario, N uptake predictions were greatly underestimated by both hybrid poplar and weed species. This suggest many interactive processes occurring at the ecosystem level affect the supply of N in the soil and then their uptake at the root surface and they are needed to be adequately described in the model for more coherent nutrient uptake predictions.

6.5 References

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7 GENERAL DISCUSSION AND SUMMARY

Adoption of hybrid poplar plantations on agricultural land has received significant attention among the farmers of western Canada as an alternate source of farm income, besides being a solution to reduce harvesting pressure on the boreal forest to meet the growing wood demand for the forest industry. Plantation success will rely on the efficient management of nutrients and weeds. Although significant research has focused on better understanding the cultural practices required for productive plantations, detailed information on the mechanisms operating belowground under weed competition conditions is imperative for enhanced nutrient and weed management practices. Further, these practices can be varied from one location to another depending upon the physical and chemical properties of the soil and climatic conditions. Certain weeds may dominant at certain locations and their varied root systems, nutrient uptake characteristics and ability to capture nutrients from the soil may influence their competing nature and therefore, extent of nutrient and weed management required for productive and economically viable hybrid poplar plantations.

In a growth chamber study, generally, dandelion and quackgrass weeds decreased the growth of hybrid poplar severely, irrespective of the weed density and also caused mortality of some hybrid poplar seedlings. Due to very high root length density, dandelion and quackgrass caused direct nutrient competition to hybrid poplar as the soil solution concentration of N, P and K was near to negligible in the weed treatment pots. Superior root uptake characteristics may be the one mechanism by which weeds compete more efficiently for nutrients with hybrid poplar. Results from the hydroponic experiment demonstrated the superiority of dandelion weeds to nutrient uptake compared to hybrid poplar by exhibiting greater I_{\max} values for N, P and K. However, for quackgrass, I_{\max} values were not very much different from hybrid poplar but the reduction in growth of hybrid poplar was again observed in the presence of one quackgrass plant. Quackgrass had lower K_m values for all the nutrients compared to hybrid poplar which suggests that under competing conditions quackgrass can capture nutrients from the soil more

efficiently when the soil solution nutrient concentration is low. Apart from the superior root uptake characteristics, the inherent capacity of weeds to produce large root biomass is another important mechanism by which weeds competed aggressively with the hybrid poplar seedlings. This mechanism can be of utmost importance when the plant species have similar root uptake characteristics. For example, in the SHP+1QG treatment, root biomass and root length density was greater for quackgrass compared to the hybrid poplar and therefore, quackgrass would have a competitive advantage over hybrid poplar despite similar root uptake characteristics.

Similar reductions in hybrid poplar growth were also observed under field conditions which pinpoint the importance of effective weed control for establishing successful hybrid poplar plantations. This study also highlights the notion that cuttings may not be the best stock type for planting hybrid poplar plantations when weed competition is going to be a problem; hence, rooted plugs can be a better alternative under such conditions because of the already established roots in the rooted material.

Mechanistic nutrient uptake models have been used extensively to describe the nutrient uptake at the root surface considering nutrient supply in the soil controlled by mass flow and diffusion. However, concentrations of the nutrients in soil solution at a given time can be a function of other active processes occurring in the soil during the growing period such as mineralization and fluctuating soil water contents. Results from the SSAND model including these important processes in the growth chamber and field studies are encouraging under single plant species nutrient uptake simulations i.e. hybrid poplar grown without weeds. Simulation results for the pot study underline the importance of incorporating the N mineralization process for predicting N uptake where N uptake predictions were substantially improved. Phosphorus uptake predictions by hybrid poplar were greatly underestimated by the model which suggests that several processes responsible for P supply to the plant are still not adequately described in the model. This perception is confirmed by the attempt to incorporate a hypothetical P mineralization value in the model which increased predicted P uptake for hybrid poplar, although overestimated it. A mycorrhizae assisted nutrient uptake mechanism is the other very important process which needs to be adequately addressed while predicting nutrient uptake using nutrient uptake models. Potassium is the nutrient which is least affected by

biological processes; however, model prediction of K uptake for hybrid poplar were overestimated. In the field, N uptake was adequately predicted by the SSAND model in the control treatment and incorporating N mineralization and changing soil water content did little to improve uptake, possibly due to the already high N concentration present in the soil solution.

Nutrient uptake predictions were more inconsistent under the two plant species system for both hybrid poplar and weeds and incorporation of N mineralization did not improve the predictions for the nutrient uptake. This emphasizes the notion that uptake under severe competition cannot be simply described by one time measurements of soil solution concentration at the start of experiment. Several processes such as mineralization, mycorrhizae, release of organic acid and root exudates, and the ability of plants to take up nutrients in organic forms, could affect the soil solution nutrient concentration and subsequently plant nutrition. These processes are not only complex but also nonlinear due to multiphasic interactions between biological, chemical and physical processes. Therefore, future research focuses on defining these mechanisms of nutrient availability under nutrient stress conditions in the model to improve our quantitative understanding of nutrient uptake in two plant species scenario.

APPENDIX A

Depletion data for calculating the I_{\max} and K_m values in a hydroponic experiment

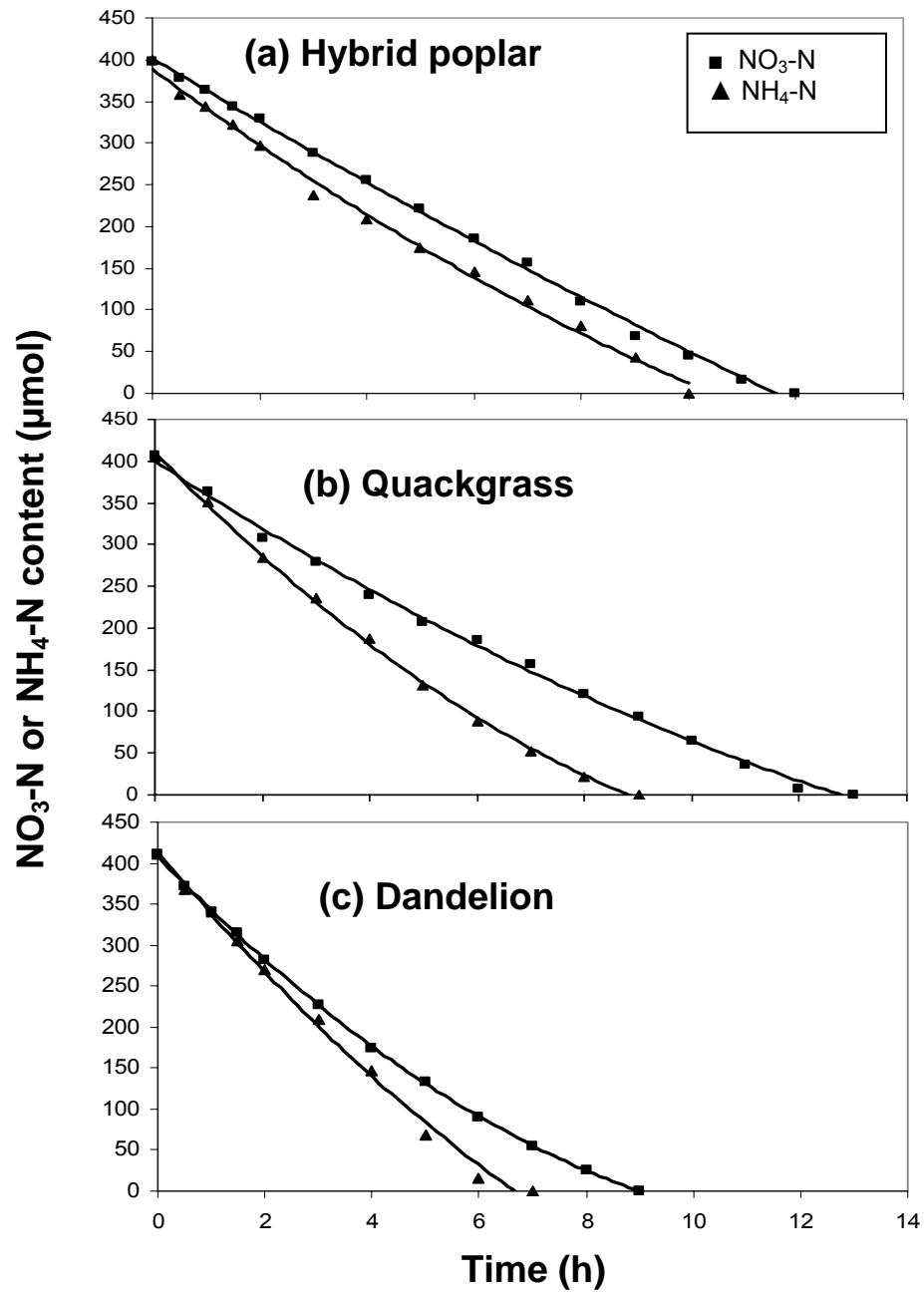


Figure A.1. Representative depletion curve for Ammonium (■) and nitrate (▲) from hydroponic nutrient solution by (a) hybrid poplar, (b) quackgrass, and (c) dandelion

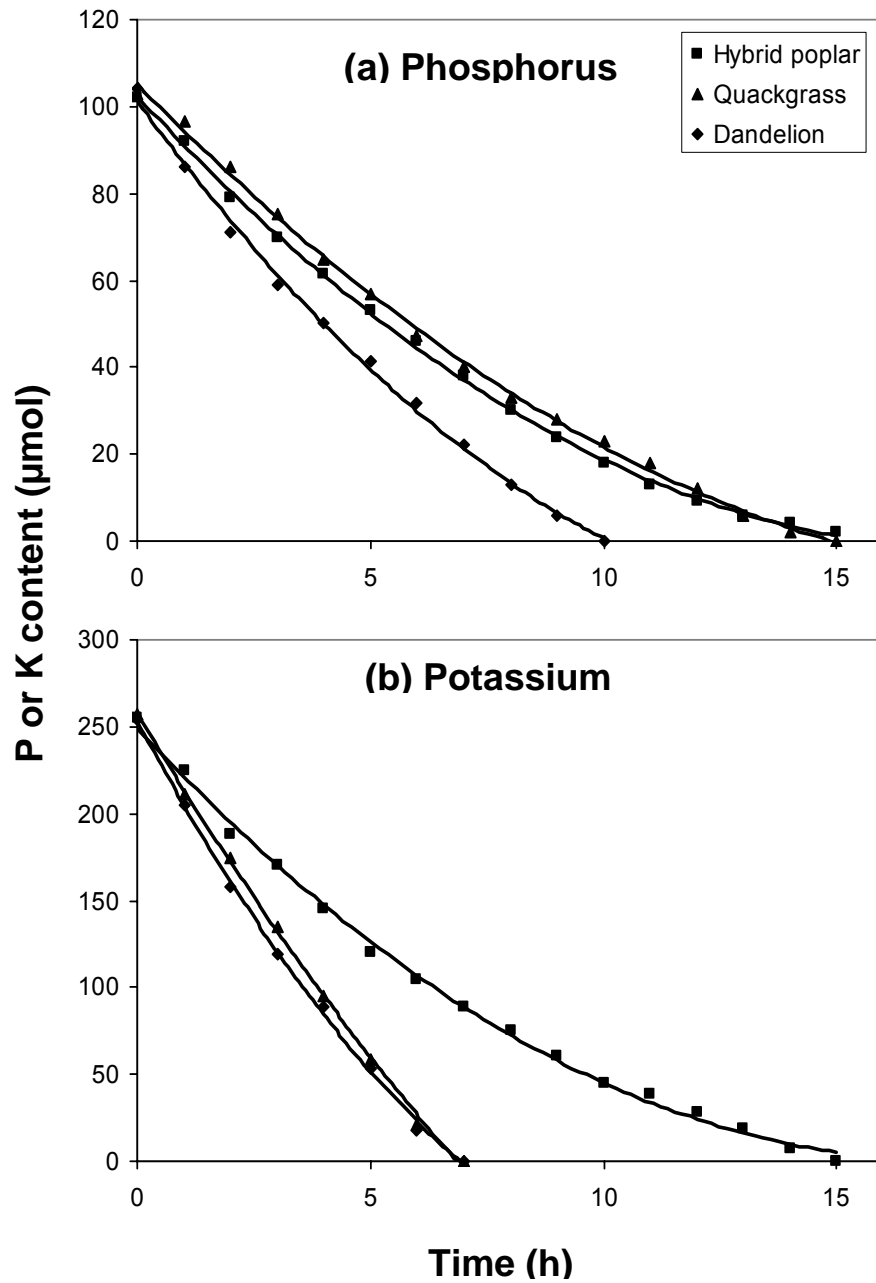


Figure.A.2. Representative depletion curve for (a) phosphorus and (b) potassium from hydroponic nutrient solution by hybrid poplar, quackgrass, and dandelion plant species.