Ecological Engineering 38 (2012) 11–19

Contents lists available at SciVerse ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Growth of the dominant macrophyte *Carex aquatilis* is inhibited in oil sands affected wetlands in Northern Alberta, Canada

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ARTICLE INFO

Article history:
Received 8 March 2011
Received in revised form 3 August 2011
Accepted 10 September 2011
Available online 4 November 2011

Keywords:
Biological indicators
Chlorophyll *a* fluorescence transients
Land reclamation
Mining
Water sedge
Salinity

ABSTRACT

Carex aquatilis could be a suitable species for wetland reclamation in mined boreal landscapes as those of the oil sands industry (Northern Alberta). We compared the performance of *C. aquatilis* plants established in oil sands industrial wetlands (directly affected by processed materials), on-site indirectly affected wetlands, and off-site natural wetlands. We studied leaf chemistry, fluorescence, gas exchange rates (net photosynthesis and transpiration rates), and morphological features of plants. Despite higher photochemistry efficiency in oil sands populations, plants did not channelize surplus energy into increased carbon assimilation rates. Oil sands populations registered lower culm heights and leaf lengths than natural populations. Plants growing in industrial wetlands were shorter and accumulated more sodium in leaves than plants from indirectly affected wetlands. Evidence indicated that *C. aquatilis* was a promising species for reclamation as it was tolerant to pollution. Though it survived, *C. aquatilis*, showed a restricted growth in the oil sands wetlands thereby possibly limiting carbon assimilation at the stand level. Oil sands wetlands amended with freshwater and established over non-industrial materials provided better growing conditions for *C. aquatilis* and demonstrated management tools for local reclamation efforts.

1. Introduction

Bitumen mining in the oil sands region of north-eastern Alberta (Canada) requires the deep removal of all vegetation, soil, and subsoil; consequently, the structure and function of pre-existing wetlands is entirely lost in the mined area. Petroleum companies in the oil sands region are attempting to develop peat-accumulating wetlands in the disturbed landscape as required by their specific mine closure policies (Price et al., 2010; Rooney and Bayley, 2011). While reports have demonstrated that peatland restoration is possible in both organic and mineral soils (Lucchese et al., 2010; Rochefort et al., 2003; Vitt et al., 2011), peatland reclamation success in the oil sands landscapes is doubtful (Purdy et al., 2005). In this regard, one of the main concerns is the self-sustainability of peat-forming wetlands as the industrial landscape is characterized by chemical conditions derived from processed waters and tailings that exceed the tolerance limits of many peat-forming plant species indigenous to the oil sands region (Harris, 2007; Trites and Bayley, 2009a, 2009b).

Information about the effects of some recalcitrant organic pollutants produced during mining (e.g. naphthenic acids, polycyclic aromatic hydrocarbons, and other residual hydrocarbons) indicates that they can negatively affect plant functions (Alkio et al., 2005; Apostol et al., 2004; Kamaluddin and Zwiazek, 2002; Liu et al., 2009); however, there is some broad consensus developing among environmental scientists that the most problematic pollution outcomes for peat-forming vegetation are the high levels of salinity and alkalinity left after mine operation (Renault et al., 1998, 1999; Trites and Bayley, 2009a, 2009b). In fact, on-site waters have salinity and alkalinity values that exceed thresholds stated to be detrimental to peatlands mosses and levels fall within the range that can affect other peat-forming macrophytes, hence, they would be the most important regulators of community composition (Harris, 2007; Trites and Bayley, 2009a, 2009b). The negative effects of sodium and other pollutants on plant performance could be alleviated by the augmented nitrogen available in oil sands effluents due to their high concentrations of ammonia (Bendell-Young et al., 2000). The identification and propagation of peat-forming native plant species capable of thriving in the chemical environment of the

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doi:10.1016/j.ecoleng.2011.09.002

oil sands wetlands is essential for developing self-sustaining peatlands; one of the oil sands companies' main reclamation goals.

The wetlands of closure landscapes have high levels of salinity and alkalinity for three overriding reasons: First, shale overburden and bitumen-impregnated sediments are of marine origin and contain residual oceanic sodium chloride (Hein and Cotterill, 2006). Second, as part to the mandatory zero discharge policy, oil sands companies must recycle the process-affected waters creating oil sands processed water (OSPW), further concentrating sodium, chloride and sulfate ions and other pollutants in stored wastewaters (Allen, 2008; Giesy et al., 2010). Third, tailings are additionally enriched with salts during bitumen extraction by the addition of gypsum to separate oil from sand and clay particles (Allen, 2008). Suspended sediments in tailings have to settle and consolidate before being used as reclamation material so tailings technologists created several different byproducts: sandy and bitumen-rich mature fine tailings (MFT) and gypsum-impregnated consolidated tailings (CT) (Kotylar et al., 1996). Substrates to be reclaimed must be capped with low salinity overburden, subsoil, or peat-mineral substrates before attempting vegetation establishment in reclaimed areas (Rowland et al., 2009).

Three major categories of wetlands currently occur in the reclaimed landscape: barrensaline flats, marshes, and shallow ponds. Industrial wetlands are directly affected by salinity and pollution as a result of their exposure, alone or in combination, to the OSPW, MFT, or CT used as reclamation material; whereas chemical conditions are expected to be less stressful to plants in indirectly affected wetlands as they are filled with freshwater. Indirectly affected wetlands are also less exposed to pollution as salts and other pollutants ultimately reach these wetlands through tailings ponds' dyke seepage, upward advective and diffusive transport from underlying shale overburden or tailings seepage from adjacent reclaimed uplands, and aerial deposition (Harris, 2007). Natural off-site wetlands in the area can only be exposed to oil sands pollution by airborne deposition or groundwater influx.

Carbon accumulation and water storage are among the most important wetland functions that petroleum mining companies attempt to recreate in the reclaimed landscape (Harris, 2007). Peat-forming wetlands are essential to maximize both of those processes; however, since peat-forming systems are not yet present inside the closure landscapes, initial peat accumulation relies on marshes and their associated vegetation. *Carex aquatilis* Wahlenb. (Water sedge) is a widespread peat-forming plant species found in both peatlands and marshes in the Boreal Plains of North America (Bayley and Mewhort, 2004; Trites and Bayley, 2009a; Vitt and Chee, 1990). Water sedge has also colonized oil sands-affected marshes and ponds (Trites and Bayley, 2009a) but with lower cover than in natural wetlands (MC Roy, in preparation). Consequently, plant performance evaluations of *C. aquatilis* populations established in oil sands wetlands and subsequent comparison with populations growing in natural conditions will help explain differences in vegetation cover, productivity, competition, succession and other essential ecological contrasts. As plants convert sunlight energy into biomass, plant performance can largely determine biomass accumulation rates at the stand level as well as plant competitive abilities; hence, plant community assemblages (Bazzaz, 1996; Lambers et al., 2008). In that way, plant physiological performance can provide insights into the success of reclamation attempts.

Our specific goals were to compare the physiological performance (leaf fluorescence and gas exchange rates) and morphological features of *C. aquatilis* plants growing in industrial, indirectly affected, and natural wetlands. Our working hypotheses were based on the chemical differences among wetlands and their degree of exposure to pollution: (1) *C. aquatilis* plants growing in oil sand wetlands have lower physiologic and morphologic performance than plants growing in natural wetlands, (2) *C. aquatilis* plants growing in oil sands industrial wetlands have lower physiologic and morphologic performance compared to plants growing in indirectly affected wetlands and (3) performance parameters tightly related to the carbon assimilation potential of plants are negatively affected by the salinity and nitrogen availability in individual wetlands.

2. Materials and methods

2.1. Study area and plant description

This study was conducted in the Fort McMurray region of northeastern Alberta on Syncrude Canada Ltd. and Suncor Energy Inc. leases as well as natural undisturbed wetlands in the proximity. Vegetation in the area has been classified as Mid Boreal Mixedwood Ecoregion (Strong and Leggat, 1992). The climate is sub-humid, characterized by long cold winters and short cool summers. Mean summer and winter daily temperatures of the region are 13.5 and −13.2 °C, respectively (Strong and Leggat, 1992). Mean annual precipitation in the area is around 450 mm and potential evapotranspiration is 519 mm (Devito and Mendoza, 2007).

Carex aquatilis is a perennial obligate wetland sedge that can thrive in both organic and mineral sediments and can be found as a co-dominant component of the vegetation in the wetlands where it occurs (Cooper et al., 2007). *C. aquatilis* is an early but slow colonizer of disturbed areas. Studies indicate that it can perform well in short- and long-term revegetation endeavors after crude-oil spills (Kershaw and Kershaw, 1986) and can also be reintroduced in mined and disturbed fens (Cooper and MacDonald, 2000; Vitt et al., 2011).

2.2. Wetlands selection and chemical analysis

We incorporated the variability of wetlands found in the oil sands leases and pristine natural areas in the region. A total of 18 wetlands were selected among which six were natural (off-site) and 12 were on-site wetlands situated inside the oil sands mining leases. On-site wetlands were classified as industrial (*i.e.* directly affected by OSPW, CT or MFT) or indirectly affected (*i.e.* wetlands which do not receive any direct input effluents) (Table 1). Selected natural wetlands showed no evident signs of being impacted by oil sands pollution. The number of wetlands of each type selected for the physiological measurements was five while those selected for morphological measurements was six (Table 1).

The high levels of salinity, alkalinity, mineral concentration, and pollutants in the oil sands wetlands have already been addressed by other authors who studied the same as well as other wetlands inside the leases (Bendell-Young et al., 2000; Crowe et al., 2001; Purdy et al., 2005; Trites and Bayley, 2009a). In this work we included water chemistry data of samples taken during the same season and in the same wetlands in which measurements were made (Table 2). Electrical conductivity, salinity and dissolved oxygen (DO) measurements were taken using a handheld YSI Model 85 (YSI Inc., Yellow Springs, OH, USA); pH and oxidative reductive potentials (ORP) were measured with a portable Hanna HI98121 (Hanna Instruments, Mauritius). Water samples were collected, frozen and immediately submitted to analysis for sodium, chloride, potassium and total nitrogen. Mature leaves blades of two plants per wetland were analyzed for sodium, chloride, potassium, total phosphorus (TP) and total Kjeldahl nitrogen (TKN). After harvesting, leaf samples were quickly rinsed, blotted and frozen at −20 °C.

Table 1
Characteristics, analysis done, and coordinates of the industrial, indirectly affected (IA), and natural wetlands studied in the oil sands region.

Name	Type	Sediment	Water	Analysis	Latitude (N)	Longitude (W)
4m-CT	Industrial	CT/peat	OSPW	P, M	56°59′31.76″	111°32′05.37″
MFT-South	Industrial	MFT	OSPW	P, M	56°59′31.76″	111°32′05.37″
Test Pond 5	Industrial	CT	OSPW	P, M	57°05′03.99″	111°41′39.12″
Test Pond 8	Industrial	CT	OSPW	P, M	57°05′01.53″	111°41′33.73″
Test Pond 10	Industrial	MFT	OSPW	P, M	57°05′01.06″	111°41′29.02″
Mike's Pond	Industrial	MFT/Clay	OSPW	M	57°06′39.55″	111°40′50.11″
Natural S	IA	Mineral/peat	Freshwater	P, M	56°58′50.30″	111°30′37.67″
Duck	IA	Mineral/peat	Freshwater	P, M	56°59′15.70″	111°32′21.74″
Species	IA	Mineral	Freshwater	P, M	56°59′37.39″	111°32′08.42″
Test Pond 1	IA	Mineral	Freshwater	P, M	57°05′06.69″	111°41′35.15″
Fireweed	IA	Mineral/peat	Freshwater	P, M	57°04′57.36″	111°41′36.25″
North Beaver	IA	Mineral/peat	Freshwater	M	57°06′44.62″	111°41′24.60″
N-20	Natural	Mineral/peat	Freshwater	P, M	56°44′41.48″	111°29′55.16″
Dam	Natural	Mineral/peat	Freshwater	P, M	56°56′36.89″	111°38′49.55″
Beaver lodge	Natural	Mineral/peat	Freshwater	P, M	56°30′53.40″	111°16′15.84″
Mosquito	Natural	Mineral/peat	Freshwater	P, M	56°36′41.99″	111°20′00.71″
Jumping dog	Natural	Mineral/peat	Freshwater	P, M	56°56′19.08″	111°39′41.85″
Broken wing	Natural	Mineral/peat	Freshwater	M	56°58′10.14″	111°41′13.26″

CT: consolidated tailings; MFT: mature fine tailings; OSPW: oil sands processed water; P: physiological measurements; M: morphological measurements.

Chemical analysis of water and leaf samples was done in the Natural Resources Analytical Laboratory of the University of Alberta.

2.3. Performance indicators and sampling procedures

Physiological measurements of *C. aquatilis* plants were carried out during the first fortnight of June, 2010 near noon on clear days. During all the sampling period gas exchange parameters were measured when photosynthetic photon flux density (PPFD) was above 1800 μmol m^{-2} s^{-1} to ensure photosynthesis light saturation. Leaf fluorescence was measured simultaneously with gas exchange parameters. Morphological measurements were carried out during the first week of August, 2010. All the measurements were made in the emergent vegetation zone or in the boundaries between the wet meadow zone and open water in ponds where the emergent zone was not present. In some of smallest industrial wetlands we found less than seven *C. aquatilis* stands. Then, taking into account that *C. aquatilis* plants have a vigorous vegetative growth through long rhizomes, we studied well-spaced plants (>1 m between plants) to increase the likelihood of choosing different individuals.

Chlorophyll *a* fluorescence transients were studied in dark-adapted leaves of ten *C. aquatilis* plants per population with a Hansatech Pocket PEA (Hansatech Instruments Ltd., King's Lynn, Norfolk, UK). Measured leaves were dark-adapted with leaf clips for 20 min. The transients were induced by a light pulse of 3500 μmol m^{-2} s^{-1} with a peak wavelength of 627 nm provided by a high intensity LED. The fast polyphasic fluorescence rise (OJIP rise) until F_M was recorded from 10 μs to 1 s. The fluorescence intensity at 50 μs was considered as F_0 (Strasser and Strasser, 1995).

The photosynthetic capacity of different plant samples can be related to the first steps of the sunlight energy transduction and the associated fluorescence OJIP rise (Strasser et al., 2000). In this way, a suite of key leaf fluorescence parameters were selected to cover all the main basic experimental signals, fluxes, quantum yields and vitality indices related to the structure and function of photosystem 2 (PSII) (Bussotti et al., 2007; Christen et al., 2007). The studied parameters embraced the main energy fluxes addressed by the theory of bio-membranes, *i.e.* photons absorbed by the antenna (ABS), trapped excitons (TR_0), electron transport beyond Q_A (ET_0), and dissipated energy (DI_0) (Strasser et al., 2000). Table 3 summarizes the definitions and derivations of the fluorescence transient parameters (for further details see Strasser et al., 2000).

Gas exchange rates (net CO_2 exchange and transpiration) and stomatal conductance were measured in young fully expanded and well-exposed leaf blades in a similar position on each *C. aquatilis* plant (seven replications per population) using a infrared gas analyzer provided with a narrow leaf chamber (LCi, ADC Bioscientific Ltd., Herts, UK).

Seven plants per population were chosen for culm height measurement, *i.e.* the height of plants taken from the rooted sediment level to the apex of the inflorescence. Blade, sheath, leaf lengths, and blade widths were measured in fully expanded leaves on the same plants.

Table 2
Water quality parameters, and results of the orthogonal contrasts for the industrial, indirectly affected, and natural (off-site) wetlands in the oil sands region.

	Industrial	Indirectly affected	Natural	*P*-values *a priori* contrasts	
				OS vs. natural	Industrial vs. affected
Salinity (ppt)	1.66 ± 0.42	0.31 ± 0.09	0.11 ± 0.03	0.0009	0.0011
EC (μs cm^{-1})	3435 ± 782	607 ± 166	204 ± 65	0.0011	0.0007
pH	8.8 ± 0.2	7.9 ± 0.2	7.6 ± 0.3	0.0254	0.0388
DO (mg L^{-1})	5.4 ± 0.7	5.4 ± 0.6	4.1 ± 0.6	0.1614	0.9669
ORP (mV)	60 ± 12	100 ± 14	129 ± 8	0.0079	0.0542
Na (mg L^{-1})	271 ± 141	100 ± 65	15.7 ± 6.6	0.026	0.138
Cl (mg L^{-1})	111 ± 53	10.0 ± 4.4	11.7 ± 5.6	0.034	0.007
K (mg L^{-1})	5.1 ± 2.2	5.4 ± 3.0	0.9 ± 0.3	0.172	0.956
K/Na	0.091 ± 0.073	0.069 ± 0.005	0.080 ± 0.019	0.625	0.546
TDN (ppm)	1.4 ± 0.3	1.9 ± 0.9	2.7 ± 1.3	0.668	0.914

Values are means ± S.E. from 6 of each wetland types. OS: oil sands wetlands; EC: electrical conductivity; DO: dissolved oxygen; ORP: oxidative reductive potentials; TDN: total dissolved nitrogen.

Table 3
Derivation of the JIP-test parameters directly obtained from the recorded fluorescence transients.

Parameter	Derivation
F_0 (fluorescence at 50 µs; assumed to be initial)	F_0
F_M (maximal fluorescence intensity)	F_M
F_v (variable fluorescence)	$F_v = F_M - F_0$
M_0 (slope at the origin of normalized fluorescence rise)	$dV/dt_0 = (F_{300\,\mu s} - F_0/(F_M - F_0)$
ABS/RC (calculated absorption per reaction centre)	$(M_0/V_j)/(1 - F_0/F_M)$
F_V/F_M (maximum quantum yield of primary photochemistry)	$1 - F_0/F_M$
DI_0/ABS (maximum quantum yield of non photochemical deexcitation)	F_0/F_M
ET_0/TR_0 (probability that a trapped exciton moves an electron further than Q_A)	$1 - V_j$
ET_0/ABS (probability that a absorbed photon moves an electron further than Q_A)	$(1 - F_0/F_M)(1 - V_j)$
Performance Index	$(V_j/M_0)(F_v/F_M)(F_v/F_0)(ET_0/(dQ_A^-/dt_0))$

After Christen et al. (2007) and Strasser et al. (2000). $V_j = (F_{2\,ms} - F_0)/(F_M - F_0)$.

2.4. Statistical analysis

All variables were analyzed through one-way ANOVA. Plant performance data were analyzed using orthogonal *a priori* contrasts to compare: (1) the performance of *C. aquatilis* plants growing in oil sands wetlands with that of plants growing in natural populations and (2) the performance of *C. aquatilis* plants growing in industrial wetlands with that of plants growing in indirectly affected wetlands. Differences in water quality parameters between wetlands were examined by using orthogonal contrasts with the purpose of relating plant performance with wetland conditions. The relationships between plant performance, sodium and nitrogen availabilities in leaf blades, and water salinity in each of the wetlands were determined through regression analysis. Parameters tightly related to the carbon assimilation potential of plants (Performance Index, net photosynthetic rates and blade lengths) were also analyzed. In the regression analysis, data of industrial and indirectly affected wetlands were pooled to obtain a single linear regression for the oil sands environments. All datasets were checked to ensure the normality and homogeneity of variances. Datasets for Performance Index, salinity, sodium, chloride, potassium and total dissolved nitrogen (TDN) were natural logarithm transformed and those of conductivity, water and leaf K/Na ratios were square root transformed prior ANOVAs (Sokal and Rohlf, 2003). All results are presented as non-transformed means ± S.E.

3. Results

3.1. Water chemistry

During the experimental period in which measurements on *C. aquatilis* plants were carried out, large and statistically significant water chemistry differences between oil sands and natural wetlands were detected (Table 2). Oil sands wetlands had higher salinity, electrical conductivity, pH, sodium, and chloride than natural wetlands ($P < 0.05$ in all cases; Table 2). Oil sands wetlands also showed significantly lower oxidative reductive potentials (ORP) than natural wetlands ($P < 0.05$) (Table 2).

Significant differences in water chemistry were also found between industrial and indirectly affected wetlands (Table 2). Industrial wetlands had higher salinity, electrical conductivity, and pH but lower chloride concentrations than indirectly affected wetlands ($P < 0.05$; Table 2).

3.2. Leaves nutritional and ionic status

There were no significant differences found in nutritional status of *C. aquatilis* leaf blades with respect to total nitrogen and phosphorus contents between plant populations exposed to oil sands pollution and those established in natural wetlands ($P > 0.05$; Table 4). Potassium concentrations in leaf blades were slightly, and significantly higher in the oil sands wetlands compared to values of plants growing in natural populations ($P < 0.05$; Table 4). In spite of the elevated sodium accumulated in leaf blades of plants established in industrial wetlands (Table 4), the highly variable results only permitted the detection of marginal differences in sodium contents ($0.05 < P < 0.010$; Table 4), but significant differences in chloride concentrations between plants established in oil sands and natural wetlands ($P < 0.05$; Table 4). Leaf chemistry analysis of *C. aquatilis* leaf blades indicated deep differences between industrial and indirectly affected wetlands in sodium and potassium contents (Table 4). Sodium concentrations were one order of magnitude higher in the industrial wetlands compared to indirectly affected wetlands ($P < 0.05$; Table 4). Potassium and K/Na ratios were significantly lower in blades of plants from the industrial wetlands compared to plants from the indirectly affected wetlands ($P < 0.05$; Table 4).

3.3. Physiological results

There were no significant differences among *C. aquatilis* plants growing in the different types of wetlands in some of the basic fluorescence signals measured (Table 5; Fig. 1). Initial

Table 4
Carex aquatilis blade leaves nutrient and ion contents and results of the ANOVAs and orthogonal contrasts for the industrial, indirectly affected, and natural (off-site) wetlands in the oil sands region.

	Industrial	Indirectly affected	Natural	*F*-value	*P*-value	*P*-values *a priori* contrasts	
						OS vs. natural	Industrial vs. affected
TKN (ppm)	15.8 ± 1.7	14.7 ± 0.9	14.9 ± 0.6	0.24	0.789	0.833	0.520
TP (ppm)	1.28 ± 0.14	1.47 ± 0.15	1.35 ± 0.9	0.54	0.577	0.890	0.306
K^+ (wt %)	1.29 ± 0.11	1.60 ± 0.05	1.21 ± 0.05	8.94	0.003	0.014	0.006
Na^+ (µmol g^{-1} DW)	148.8 ± 86.7	13.7 ± 5.1	20.6 ± 10.7	7.02	0.007	0.091	0.005
Cl^- (µmol g^{-1} DW)	200.4 ± 32.5	137.2 ± 23.3	88.4 ± 20.1	4.72	0.025	0.022	0.104
K^+/Na^+	11.3 ± 4.1	58.1 ± 15.0	58.1 ± 11.7	6.56	0.009	0.201	0.004

Values are means ± S.E. from 6 of each wetland types. $df = 2$, $df_{error} = 15$. OS: oil sands wetlands, TKN: total Kjeldahl nitrogen, TP: total phosphorous.

Table 5
Results of one-way ANOVA for the analyzed physiological and morphological variables of *Carex aquatilis* plants growing in industrial, indirectly affected, and natural wetlands in the oil sands region.

	MS error	*F*-value	*P*-value
F_0	1.9×10^5	0.80	0.4715
F_M	6.5×10^6	1.28	0.3146
F_v	1.0×10^7	1.95	0.1844
M_0	1.5×10^{-4}	4.55	0.0339^{*}
ABS/RC	0.01	0.73	0.5005
F_v/F_m	6.1×10^{-4}	4.17	0.0422^{*}
DI_0/ABS	6.6×10^{-4}	3.30	0.0720
ET_0/TR_0	2.5×10^{-3}	5.69	0.0183^{*}
ET_0/ABS	2.2×10^{-3}	6.69	0.0112^{*}
Performance Index	0.12	8.29	0.0055^{**}
Net photosynthesis rate	1.26	0.14	0.8476
Transpiration rate	1.00	0.11	0.8892
Stomatal conductance	4.6×10^{-3}	0.33	0.7250
Culm height	128.69	13.91	0.0004^{***}
Leaf sheath length	33.61	4.67	0.0266^{*}
Leaf blade length	107.82	6.31	0.0103^{*}
Leaf length	236.61	6.18	0.0110^{*}

$df = 2$, $df_{error} = 15$ (morphological measurements) and 12 (physiological measurements).
Significance levels are presented.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

fluorescence (F_0), maximal fluorescence (F_M) and variable fluorescence (F_V) were, on average, statistically similar among wetlands types ($P > 0.05$; Table 5; Fig. 1a–c). Significant differences were found in M_0 (which represents the relative rate of Q_A reduction) between *C. aquatilis* plants growing in oil sands and in natural wetlands ($P < 0.05$; Fig. 1d).

In spite of the lack of differences in some of the basic fluorescence parameters, most of the derivate parameters related to fluxes, quantum yields and vitality indices showed significant differences (Table 5 and Fig. 2). Interestingly, results showed that the overall photochemistry efficiency of *C. aquatilis* plants growing in natural populations was lower than that of plants established in the oil sands wetlands (Fig. 2). Plants established in oil sand wetlands had higher maximum quantum yield of primary photochemistry of PSII (F_V/F_M) than plants growing in natural populations ($P < 0.05$; Fig. 2b) and a higher chance that the energy absorbed by the PSII moves an electron beyond Q_A (ET_0/TR_0, ET_0/ABS; Fig. 2d and e). Accordingly, plants in the oil sands wetlands also had lower light energy dissipation (DI_0/ABS: maximum quantum yield of non-photochemical de-excitation) than plants from the natural wetlands ($P < 0.05$; Fig. 2c). Plants growing in the natural wetlands showed a visibly apparent and significantly lower Performance Index than plants growing in the oil sands wetlands ($P < 0.05$; Fig. 2f). None of the orthogonal comparisons between the industrial and indirectly affected wetlands in terms of fluorescence showed any statistical differences ($P > 0.05$; Fig. 2).

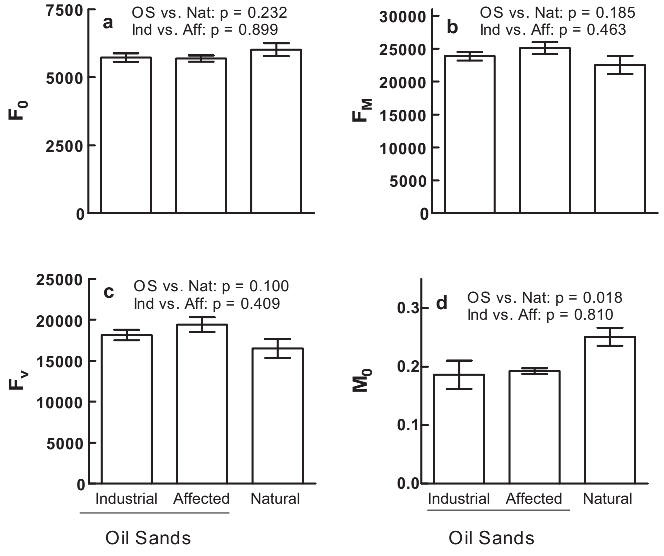

Fig. 1. Basic chlorophyll *a* fluorescence parameters measured on leaves of *Carex aquatilis* plants growing in industrial, indirectly affected wetlands in the oil sands leases, and natural off-site wetlands: (a) initial fluorescence intensity, (b) maximal fluorescence intensity, (c) variable fluorescence intensity and (d) slope at the origin of the fluorescence rise. Values are mean ± S.E. of five wetlands. Results of the *a priori* orthogonal contrasts between different types of wetlands are shown in the inset.

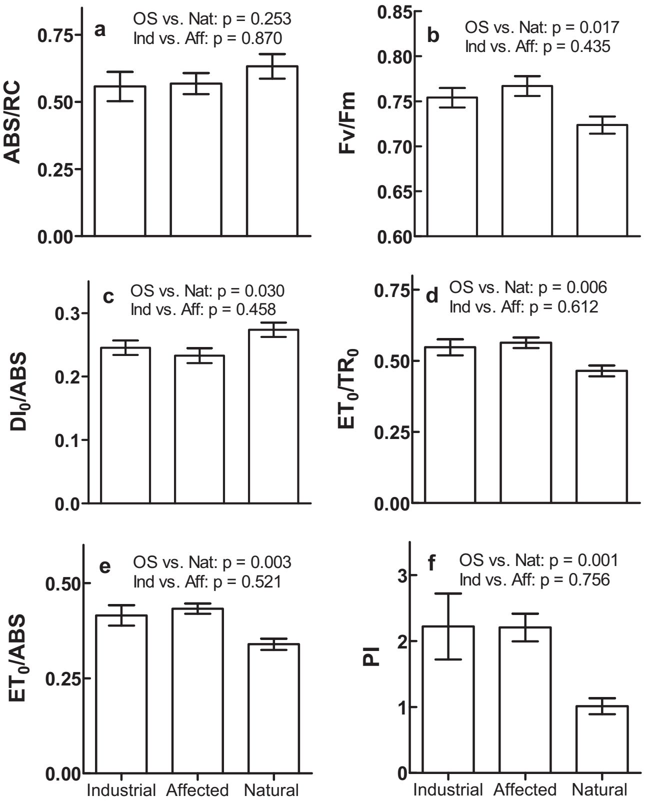

Fig. 2. Derivate chlorophyll *a* fluorescence parameters measured on leaves of *Carex aquatilis* plants growing in industrial, indirectly affected wetlands in the oil sands leases, and natural off-site wetlands: (a) light absorption per reaction centre, (b) maximum quantum yield of primary photochemistry, (c) maximum quantum yield of non-photochemical de-excitation, (d) probability that a trapped exciton moves an electron further than Q_A, (e) probability that an absorbed photon moves an electron further than Q_A and (f) Performance Index. Values are mean ± S.E. of five wetlands. Results of the *a priori* orthogonal contrasts between different types of wetlands are shown in the inset.

The photosynthetic performance of *C. aquatilis* plants was similar among wetland types ($P > 0.05$; Tables 5 and 6). Both stomatal conductance and transpiration rates of *C. aquatilis* plants were also relatively stable across different types of wetlands and did not show significant statistical differences ($P > 0.05$; Tables 5 and 6).

3.4. Morphological results

The morphological performance of *C. aquatilis* plants differed across types of wetlands (Table 5; Fig. 3). In particular, plants from the oil sands wetlands were of shorter height than plants from

Table 6
Values of the analyzed gas exchange variables and results of the orthogonal contrasts of *Carex aquatilis* plants growing at industrial, indirectly affected, and natural wetlands in the oil sands region.

	Industrial	Indirectly affected	Natural	*P*-values *a priori* contrasts	
				OS vs. natural	Industrial vs. affected
Net photosynthesis rate (μmol m^{-2} s^{-1})	3.19 ± 0.40	3.35 ± 0.58	3.56 ± 0.50	0.648	0.823
Transpiration rate (mmol m^{-2} s^{-1})	4.25 ± 0.28	4.30 ± 0.63	4.24 ± 0.33	0.760	0.738
Stomatal conductance (mol m^{-2} s^{-1})	0.18 ± 0.03	0.14 ± 0.02	0.16 ± 0.02	0.725	0.432

There were no significant differences among wetland types for these parameters (in all cases $P > 0.05$ for the one-way ANOVA tests). Values are means ± S.E. from 5 of each wetland types. OS: oil sands wetlands.

the natural populations ($P < 0.05$; Fig. 3a). Plants growing in the oil sands sites showed lower leaf sheath and blade length averages ($P < 0.05$; Table 5; Fig. 3b and c) and consequently, leaf lengths ($P < 0.05$; Table 5; Fig. 3d) as compared to their counterparts growing in the natural wetlands. Results of the orthogonal contrasts between plants growing in industrial and indirectly affected wetlands inside the oil sands showed statistical differences in culm height ($P < 0.05$; Table 5; Fig. 3a), where plants of indirectly affected wetlands have greater height than plants of industrial wetlands (Fig. 3a). Marginal statistical differences were detected for sheath ($P = 0.057$) and leaf lengths ($P = 0.090$) between plants growing in the two types of oil sands wetlands (Table 5, Fig. 3b and d) indicating plants of indirectly affected wetlands had larger leaves than plants growing in the industrial wetlands (Fig. 3d). Finally, there were no statistical differences in blade widths among habitats ($P > 0.05$; data not shown).

3.5. Performance parameters vs. water and leaf chemical conditions

Performance parameters related to the carbon assimilation potential of *C. aquatilis* plants were affected by wetland salinity (Fig. 4). The Performance Index showed a significant direct relationship with salinity ($r^2 = 0.56$; $P = 0.01$; Fig. 4a), but salinity was detrimental for blade elongation ($r^2 = 0.69$; $P < 0.01$; Fig. 4c) in plants growing in the oil sands wetlands. Net photosynthesis rates were enhanced by salinity in the narrow range of salinities found in natural wetlands ($r^2 = 0.85$; $P = 0.02$; Fig. 4b), but was not related to salinity in the wider oil sands range ($r^2 = 0.04$; $P = 0.55$; Fig. 4b). Parameters were stable across the narrow sodium and total nitrogen leaf concentration ranges of plants growing in natural wetlands (Fig. 5). In *C. aquatilis* plants growing in oil sand wetlands, Performance Index values were weakly and marginally

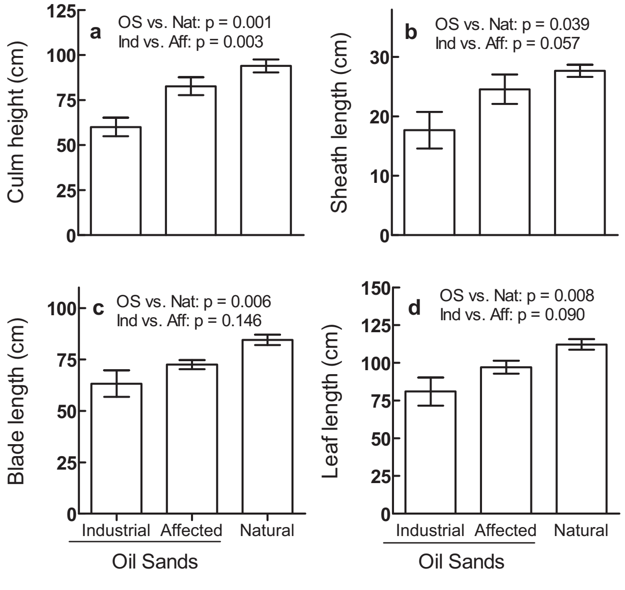

Fig. 3. Morphological parameters measured on leaves of *Carex aquatilis* plants growing in industrial, indirectly affected wetlands in the oil sands leases, and natural off-site wetlands: (a) culm height, (b) sheath length, (c) blade length and (d) leaf length. Values are mean ± S.E. of six wetlands. Results of the *a priori* orthogonal contrasts between different types of wetlands are shown in the inset.

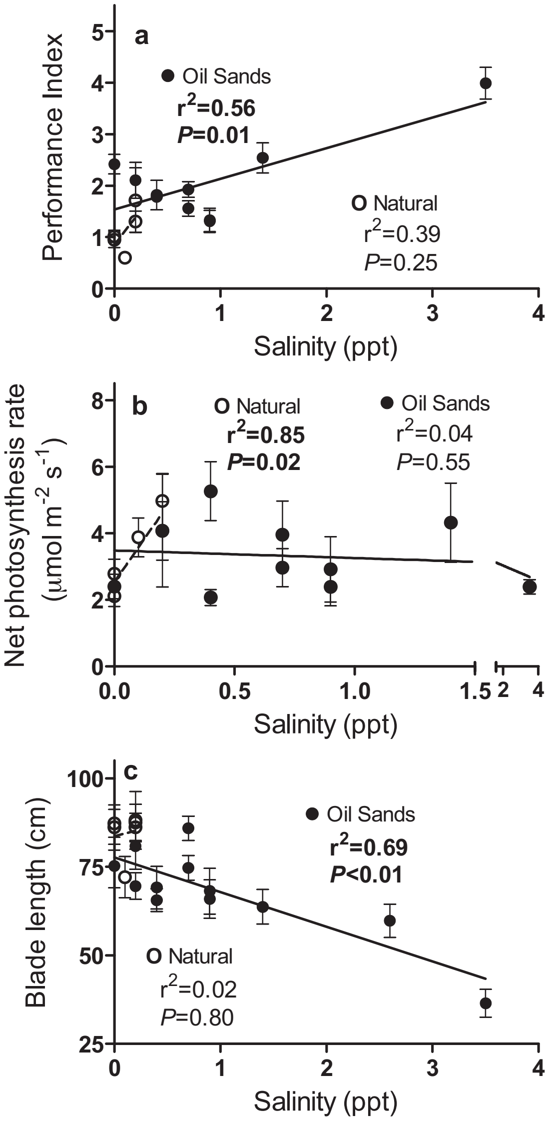

Fig. 4. Linear regressions of the main morphophysiological parameters vs. water salinity for plants growing in oil sands (closed circles) or natural (open circles) wetlands. (a) Performance Index, (b) net photosynthesis rate, and (c) blade length. Values are mean ± S.E. of ten (Performance Index) or seven (net photosynthesis rates and blade lengths) plants in each of the wetlands.

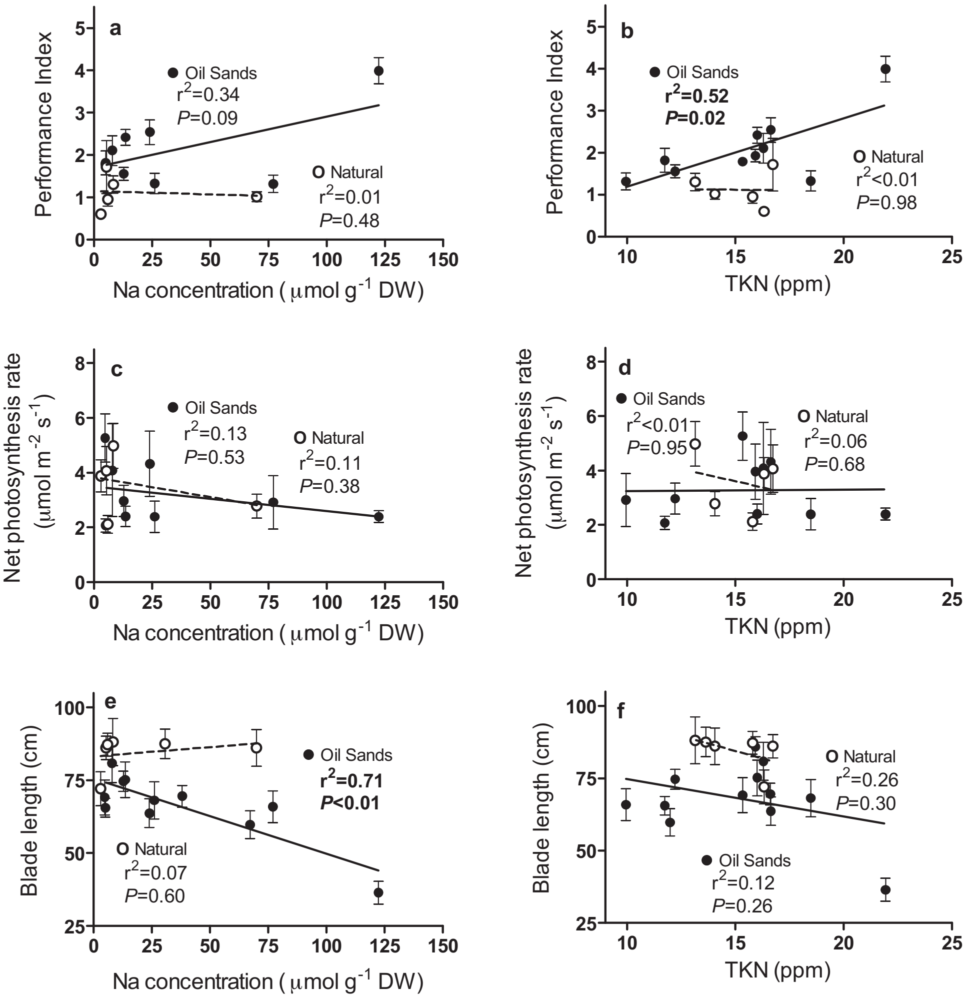

Fig. 5. Linear regressions of the main morphophysiological parameters vs. leaf blade sodium content (a, c, e) and total Kjeldahl nitrogen (b, d, f) for plants growing in oil sands (closed circles) or natural (open circles) wetlands. (a, b) Performance Index, (c, d) net photosynthesis rate, and (e, f) blade length. Values are mean ± S.E. of ten (Performance Index) or seven (net photosynthesis rates and blade length) plants in each of the wetlands.

related to sodium tissue concentrations ($r^2 = 0.34$; $P = 0.09$; Fig. 5a). Conversely, Performance Index had a direct linear relationship with total nitrogen tissue concentrations in oil sands wetlands ($r^2 = 0.52$; $P = 0.02$; Fig. 5b); wetlands with higher N availability in leaves had also more photochemically efficient plants. A strong and significant inverse relationship between blade length and sodium tissue concentrations was shown ($r^2 = 0.71$; $P < 0.01$; Fig. 5e), highlighting the negative effect of high sodium concentrations in *C. aquatilis* leaf tissues. Photosynthesis was stable across the wide range of sodium and total nitrogen tissue concentrations found in plants of the oil sands wetlands ($P > 0.01$; Fig. 5c and d).

4. Discussion

Our results indicate that *C. aquatilis* performs well in oil sands contaminated wetlands when compared to populations in unimpacted natural wetlands. Results also point out that while plants in the oil sands wetlands exhibited reduced morphological performance in terms of plant dimensions, they showed higher photochemical efficiency and similar net photosynthesis and transpiration rates as compared to plants in natural wetlands. These are outstanding results, because they highlight *C. aquatilis* as a promising species for reclamation as it is clearly able to maintain its basic physiological functions when grown in polluted oil sands wetlands.

Salinity can decrease pigment contents, photochemistry efficiencies and electron transport rates, and increase energy dissipative processes in glycophytes (Liu and Shi, 2010; Misra et al., 2001). Surprisingly, fluorescence data indicated that *C. aquatilis* plants had higher photochemical efficiency, lost less light energy in dissipation processes during the photo-absorbtion of sunlight energy, and transported the absorbed energy more efficiently when grown in the oil sands wetlands than when grown in the natural wetlands. However, *a priori* contrasts indicated a lack of differences in carbon assimilation rates among plants growing in different wetlands, suggesting that surplus photochemical energy was not allocated toward increased carbon fixation in the oil sand wetlands. Carbon assimilation is not always tightly coupled to photochemistry in stressed leaves or even in leaves of tolerant plants growing in stressful habitats (Baker et al., 2007; Maricle et al., 2007). The result here is that plants growing in the oil sands wetlands had a higher photochemical efficiency but the same net photosynthesis rates as plants in natural habitats. The implication is that electrons in the former were diverted to alternative sinks other than carbon fixation (Maxwell and Johnson, 2000). These alternative electron sinks could help to dissipate excess sunlight energy (e.g. photorespiration), to sustain nitrogen or sulfur metabolism and macromolecules biosynthesis, or even to produce oxidative stress (Baker et al., 2007; Maxwell and Johnson, 2000). Further studies aimed to identify and isolate the specific sinks to which electrons are diverted and the nature of the conservative use of sunlight energy by *C. aquatilis* during the carbon assimilation stage could reveal if such redirection of electrons represents an advantage for enduring unfavorable mineral conditions (see below) or stressful habitats.

Mineral-rich oil sands waters may free *C. aquatilis* plants from the nutritional or ion deficiencies of the natural oligotrophic boreal peatlands and marshes. Accordingly, a direct relationship between Performance Index (an integrative indicator of photochemistry efficiency) and salinity was found in the oil sands wetlands indicating that salinity may be positively affecting photochemistry of *C. aquatilis* plants. Besides, regression analysis did not show a relationship between carbon assimilation rates and salinity in oil sands wetlands, yet indicated that carbon assimilation rates were strongly and positively affected in the narrow range of salinity of the natural wetlands. These results suggest a more complicated relationship of *C. aquatilis* carbon assimilation rates vs. salinity with an optimum near the lowest values of salinity found in the oil sand wetlands. While mineral-rich oil sands effluents contain high concentrations of ammonia (Allen, 2008; Bendell-Young et al., 2000), nitrogen is the main limiting nutrient in boreal peatlands and marshes (Vitt et al., 2003). Augmented nitrogen availabilities was proposed as the probable cause of the increased carbon assimilation rates of *Typha latifolia* plants exposed to oil sands effluents (Bendell-Young et al., 2000). We did not find differences in mean total N contents in *C. aquatilis* leaf blades between wetland types. We did find a significant and direct relationship between Performance Index and leaf N contents on plants established in the oil sands wetlands, suggesting that higher nitrogen availability could be the reason for an enhanced photochemical efficiency of oil sands plants with respect to plants established in natural wetlands.

Taken alone, physiological results suggested that *C. aquatilis* plants were highly tolerant to oil sands pollution. Considered in a wider context, however, morphological data complemented those of physiology and pointed out a restricted growth in the oil sands wetlands that cannot be explained by the similar carbon assimilation found among the different wetland types. Shoot growth is known to be one of the most sensitive parameters to salinity, especially sensitive to the osmotic component of that stress factor (Munns and Tester, 2008). Moreover, salinity negatively affects water relations and growth potential of wetland plants as they face difficulties in withdrawing water (Scholander et al., 1965; Pezeshki et al., 1989). Leaves of *C. aquatilis* plants established in the industrial wetlands were 38% shorter than leaves of plants growing in natural sites (Fig. 3). Although threshold electrical conductivity levels for *C. aquatilis* plants growth are unknown, conductivities in the oil sands wetlands were well above 4 dS/m (equivalent to 400 $\mu\text{s}\,\text{cm}^{-1}$; Table 2), a value stated as the threshold level that can affect growth of most plants species (Munns and Tester, 2008).

Chemical analysis of waters and *C. aquatilis* leaf blades indicated both the higher Na load in oil sands wetlands and the ability of plants to select against it. Despite the accumulation of Na in plants, leaves had higher leaf K/Na ratios than the water of wetlands in which they were grown and maintained high levels of selectivity of K against Na (Tables 2 and 4); a key determinant of plant salt tolerance (Maathuis and Amtmann, 1999). In keeping with the elevated Cl levels in the oil sands wetlands, *C. aquatilis* leaf blades showed elevated Cl contents, an ion that could be detrimental to photosynthetic efficiency at high concentrations (Misra et al., 2001). The implementation of controlled experiments to determine *C. aquatilis* tolerance levels for the accumulation of Na and Cl deserve further research as it can provide insights about limiting conditions for reclamation success with *C. aquatilis* vegetation in oil sands wetlands.

In spite of the noticeably higher sodium concentrations and lower K/Na ratios in blades of plants growing in industrial wetlands compared to those from indirectly affected sites, the hypothesized differences in *C. aquatilis* performance between both types of oil sands wetlands were not supported by physiological results. Morphological differences supported the hypothesis by one statistically significant result: greater culm height in the indirectly affected wetlands than in the industrial ones (Fig. 3). Two marginally significant results (larger sheath and leaf lengths in the indirectly affected wetlands) also suggested that plants actually responded to the chemical differences between wetlands. The meaning of these results is that *C. aquatilis* plants were subjected to milder conditions in the freshwater-filled, indirectly affected wetlands inside the oil sand leases than in the OSPW, CT or MFT affected industrial wetlands.

To summarize, the contribution of the present work is that in spite of similar or even enhanced *C. aquatilis* physiological performance in wetlands affected by oil sands pollution, morphological data indicated that these plants were subjected to chemical conditions beyond the threshold limits where growth is reduced. Plant and leaf dimensions are important features as they could affect canopy structure, leaf area index and ultimately, both carbon assimilation and productivity at the stand level (Lambers et al., 2008). In effect, variations in growth and productivity are closely related to the amount of intercepted radiation, mostly determined by the leaf area index (Ewert, 2004; Hirose et al., 1997; Monteith, 1977). One of the main goals of environmental research of the oil sands scientists is to determine if peat accumulation and carbon sequestration can be matched to pre-mine levels. Our results suggest that *C. aquatilis* stands established in oil sands wetlands might have somewhat lower abilities to assimilate and to sequester carbon than do natural populations. Encouragingly however, wetlands amended with freshwater and substrates other than the industrial ones provided less challenging conditions for the growth of *C. aquatilis* and present opportunities for reclamation in matching oil sand wetland functions to those pre-disturbance levels.

5. Conclusions

Two important results could be highlighted from the comparisons of *C. aquatilis* morphophysiological performance among wetland types.

(1) *C. aquatilis* plants had similar carbon assimilation rates but lower heights and shorter leaves in oil sands than in the natural wetlands.
(2) Plants growing in industrial wetlands were shorter than plants growing in indirectly affected wetlands inside the oil sands leases.

This study presents novel evidence that indicates that *C. aquatilis* is a promising species for oil sands wetlands reclamation as it maintains its basic physiological functions in wetlands polluted in ways typical of oil sands processing. On the other hand, plants had a restricted growth that may potentially reduce carbon assimilation at the stand level. Evidence also indicated that on-site freshwater wetlands not directly exposed to oil sands materials provided better conditions for *C. aquatilis* growth suggesting that main wetland functions (e.g.: carbon sequestration) in reclaimed oil sands wetlands could be reestablished.

Role of funding sources

Sponsors have not had any role in the study design, collection, analysis and interpretation of data or during the writing of the manuscript.

Acknowledgements

We specially thank to Dr. Jan Ciborowski for advice during the preparation of the manuscript and the kindly provision of water chemical data. We also thank Heidi Keillor for valuable field assistance and Dr. Gustavo Striker for comments on early versions of the manuscript. Josh Martin, Lory Cyprien, Chris Beierling, Carla Wytrykush, and Christine Daly provided helpful assistance in the oil sands leases. This study was supported by grants from NSERC-CND and Alberta Water Research Institute and the sponsorship of Canadian Natural Resources Limited, Imperial Oil Resources Limited, Petro-Canada Oil Sands Inc., Shell Canada Energy, Suncor Energy Inc., Syncrude Canada Ltd. and Total E and P Canada Ltd. MC Roy received a fellowship from Northern Scientific Training Program (NSTP) and the Canadian Circumpolar Institute (CCI).

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