

1 **Title**

2 **Deeper snow alters soil nutrient availability and leaf nutrient**
3 **status in high Arctic tundra**

4

5 **Authors**

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19 **Abstract:**

20 Nitrogen (N) mineralization, nutrient availability, and plant growth in the Arctic are often restricted by low
21 temperatures. Predicted increases of cold-season temperatures may be important for plant nutrient availability and
22 growth, given that N mineralization is also taking place during the cold season. Changing nutrient availability
23 may be reflected in plant N and chlorophyll content and lead to increased photosynthetic capacity, plant growth,
24 and ultimately carbon (C) assimilation by plants. In this study, we increased snow depth and thereby cold-season
25 soil temperatures in high Arctic Svalbard in two vegetation types spanning 3 moisture regimes. We measured
26 growing-season availability of ammonium (NH_4^+), nitrate (NO_3^-), total dissolved organic carbon (DOC) and
27 nitrogen (TON) in soil; C, N, $\delta^{15}\text{N}$ and chlorophyll content in *Salix polaris* leaves; and leaf sizes of *Salix*, *Bistorta*
28 *vivipara*, and *Luzula arcuata* at peak season. Nutrient availability was significantly higher with increased snow
29 depth in the two mesic meadow vegetation types, but not in the drier heath vegetation. Nitrogen concentrations
30 and $\delta^{15}\text{N}$ values of *Salix* leaves were significantly higher in all vegetation types, but the leaf sizes were
31 unchanged. Leaves of *Bistorta* and *Luzula* were significantly larger but only significantly so in one moist
32 vegetation type. Increased N and chlorophyll concentrations in leaves indicate a potential for increased growth (C
33 uptake), supported by large leaf sizes for some species. Responses to cold-season soil warming are vegetation
34 type- and species-specific, with potentially stronger responses in moister vegetation types. This study therefore
35 highlights the contrasting effect of snow in a tundra landscape and has important implications for projections of
36 whole tundra responses to climate change.

37

38 **Keywords:** winter processes; mineralization; Arctic; Svalbard; plant growth

39

40 **Introduction**

41 Cold temperatures and long cold-seasons in the Arctic keep nutrient availabilities and thereby primary production
42 low (Shaver & Chapin III, 1980; Nadelhoffer *et al.*, 1992). Accelerated mineralization of the large stocks of soil
43 organic matter (SOM) stored in the active layer under a warming climate could increase nutrient availability in
44 Arctic soils (Nadelhoffer *et al.*, 1992; Weintraub & Schimel, 2003; Schimel *et al.*, 2004), causing plants to grow
45 faster and increase assimilation of CO₂ from the atmosphere (Shaver & Chapin III, 1980; Wookey *et al.*, 1994,
46 1995; Sturm *et al.*, 2005), and increasing N content of plant tissues (Welker *et al.*, 2005). Indeed, previous
47 decades' warming in the Arctic may already be increasing its carbon (C) sink capacity through increased plant
48 growth (Epstein *et al.*, 2013).

49 Arctic ecosystem future C budgets, however, are unknown due to a poor understanding of complex interactions of
50 ecosystem processes and climate variables. For instance, warming of soils during the cold season has been shown
51 to increase decomposition and whole year C effluxes in the Arctic (Morgner *et al.*, 2010; Björkman *et al.*, 2010).
52 Together with growth induced increases of litter availability, this could (a) match C uptake by plant growth and
53 keep the net C exchange unchanged, (b) may be insufficient to match C uptake (Sistla *et al.*, 2013), or (c) exceed
54 plant C uptake and storage and lead to ecosystems serving as net C sources (Mack *et al.*, 2004; Cornelissen *et al.*,
55 2007). The relative strength of each flux, i.e. from atmosphere to ecosystem through plant assimilation and the
56 reverse through ecosystem respiration, will determine the net C budget change of active layer soils in the Arctic.
57 Besides litter quantity and temperature constraints, litter quality might be equally important for mineralization
58 rates, hence adding to the complexity of C budget models. Berg (2000) showed that high concentrations of small
59 molecular nitrogen (N) compounds increase mineralization rates during early stages of decomposition. In later
60 stages, however, N seems to chemically react with lignin to form humic acids and other recalcitrant compounds
61 which are relatively stable. Thus, litter with initially high N content (low C:N ratio) could decrease C
62 mineralization rates during later stages of decomposition when litter turns into SOM and chemically stabilize soil
63 C. From that perspective, raised nutrient concentrations in soil leading to increased litter N content could initially
64 increase net ecosystem respiration (R_{eco}). However, in the long run this could decrease R_{eco} and retain C in the
65 ecosystem (Weintraub & Schimel 2003).

66 Net nitrogen mineralization in Arctic soils might be mainly a cold-season process (Hobbie & Chapin III, 1996;
67 Schimel *et al.*, 2004), driven by restricted access to soil C for microbes in frozen soils, while N limitation during
68 thawed periods caused by simultaneous microbial and plant uptake leading to competition (Schimel & Bennett,
69 2004) promotes microbial immobilization of mineral N (Schimel *et al.*, 2004). Most Arctic ecosystems are N
70 limited and nutrient addition leads to increased plant growth (Shaver & Chapin III, 1986; Parsons *et al.*, 1994;
71 Wookey *et al.*, 1994, 1995). Mineralization rates for both C and N are temperature-dependent (Weintraub &
72 Schimel, 2003; Schimel *et al.*, 2004; Grogan & Jonasson, 2006). Thus, given the long duration of the cold-season
73 in Arctic ecosystems, SOM accumulates in the organic soil horizon (Post *et al.*, 1982; Gorham, 1991). The
74 dependency of microbial activity on temperature in frozen soils is larger than that of thawed soils (Morgner *et al.*,
75 2010). Therefore, even a small increase of cold-season soil temperatures could stimulate mineralization of Arctic
76 tundra soils, leading to increased CO₂ emissions during the cold-season (Nobrega & Grogan, 2007; Morgner *et al.*
77 *al.*, 2010; Björkman *et al.*, 2010), release of N bound in SOM (Jonasson *et al.*, 1999; Schimel *et al.*, 2004) and
78 increased N availability during the growing-season, with all the above mentioned implications on plant growth
79 and decomposition (Schimel *et al.*, 2004; Sturm *et al.*, 2005; Welker *et al.*, 2005). Indeed, cold-season
80 temperatures are already rising, and a further increase is suggested by general circulation models (ACIA, 2005;
81 Solomon *et al.*, 2007; Førland *et al.*, 2011).

82 Despite the importance of nitrogen to Arctic carbon budgets, and the role of winter conditions in controlling N
83 availability, only few studies have investigated how winter temperatures affect winter N dynamics and how that
84 may influence the following growing season N-plant growth dynamics. However, a series of studies from Toolik
85 Lake, Alaska have shown that higher winter temperatures can increase plant available N in the soil (Schimel *et al.*
86 *al.*, 2004) and that litter N may increase accordingly (Welker *et al.*, 2005).

87 In this study we test the hypothesis that plant growth and leaf N content responds positively to warmer cold-
88 season soil conditions caused by deepened snow. Therefore, we measured the availability of ammonium (NH₄⁺),
89 nitrate (NO₃⁻), and total dissolved organic nitrogen (TON) in active layer soil and the corresponding plant
90 performance measured as C, N, and chlorophyll contents of plant leaves.

91

92 **Materials and methods**

93

94 Study site

95 The study site in Adventdalen is about 12 km East of Longyearbyen, Western Spitsbergen (78°17'N, 16°07'E).

96 Situated on the SW Advent river bank, an area of approximately 2 km² is dominated by the two evergreen dwarf
97 shrubs *Dryas octopetala* and *Cassiope tetragona*, and the deciduous dwarf shrub *Salix polaris*. See Morgner *et al.*

98 (2010) and Cooper *et al.* (2011) for details. Soil development at the site is poor and based on a parent material

99 dominated by aeolian and fluvial deposits (Tolgensbakk *et al.*, 2000) and continuous permafrost at 80-100 cm

100 depth. A typical soil profile (Strebel *et al.*, 2010) consists of an upper O-horizon ranging from 0.2 to 6 cm with

101 slightly decomposed organic matter and many plant roots. Below that, a dark brown A-horizon of 1 to 5 cm

102 overlay a B/C-horizon consisting of grey silt. Living plant roots are found to a depth of about 45 cm. The soil

103 texture varies from the soil fraction finer than 63 µm representing 20-40% by mass. The mean grain size is about

104 200 µm. Soil in situ pH values range from 5.0 to 6.5 down the profiles and assigned to moderately acidic soils.

105 The content of SOC and total N are highest in the top-soil and decreased with depths. At the mesic site, SOC is

106 27% in the O-horizon, 15-25% in the A-horizon, 3-8% in the top of B/C and below 3% in the deeper B/C-

107 horizons. At the wetter sites, SOC is 28% in the H-horizon, 6% in the A-horizon, 3.5-5.5% in the top B/C-horizon

108 and 2.5-3.0% in the deeper B/C-horizons. The C/N ratio generally decreases with depth and is about 15-25 in the

109 upper 25 cm of the soil profile.

110 Mean July temperatures (1975-2012) of 6.4°C were recorded at the closest meteorological station at Svalbard

111 Airport, Longyearbyen (WMO station 99849), located approximately 15 km from the research site. The coldest

112 month is March with an average temperature of -13.7°C. Annual precipitation sums are low (c. 190 mm), most of

113 which falls as snow during the November-May period (c. 120 mm). The background snow conditions at the study

114 site were similar to those observed at the airport (Morgner *et al.*, 2010).

115

116 Experimental setup and design

117 The influence of snow depth on soil and leaf nutrition status and plant growth was tested within an experimental
118 setup of snow fences (6m long and 1.5m high) which were erected before first snowfall in 2006 perpendicular to
119 the prevailing winter wind direction along the valley from south-east. The fences reduce wind speed and deposit
120 wind transported snow on their lee side, thereby creating a snow patch of approximately 1.5m depth at the deepest
121 point approximately 3 to 12m distance from the fences. This kind of snow addition has several environmental
122 implications including warmer ground temperatures during winter, delayed snow melt and therefore start of the
123 growing season as well as colder and wetter soils in early growing season. The experimental setup is described in
124 more detail elsewhere (Morgner *et al.*, 2010). Data used for this study was collected during the snow-free season
125 2012.

126 Two snow depth regimes were investigated, *Normal* (natural unmanipulated snow cover 10-35 cm deep,
127 representative of most of the study area) and *Deep* (experimentally increased snow cover approx. 150 cm deep, 3-
128 12m behind fences), in eight replicates. The fences each had a buffer zone of approximately 50x50m and were
129 arranged in 3 blocks (with 2 and 3 plots each) to compare the snow regimes in the three different vegetation types.

130 One of the three blocks was in *Cassiope* heath, dominated by *Cassiope tetragona* and *Dryas octopetala*,
131 interspersed with a few graminoids. The soil here was shallow, rocky and dry with a soil solution pH of around
132 6.1. The other two blocks were in mesic Meadow, dominated by graminoids such as *Alopecurus magellanicus* and
133 *Luzula arcuata* ssp. *confusa*, with *Dryas* and *Cassiope* present but the graminoid dominance was stronger than the
134 evergreen dwarf shrub component. Both Meadow blocks had a soil solution pH of around 5.7. The generalist
135 deciduous dwarf shrub *Salix polaris* was equally present across the whole study area.

136

137 Sampling procedures, equipment and protocols

138 Sampling of soil and leaves started 20 July 2012, approximately 45 and 31 days after snow melt in *Normal* and
139 *Deep*, respectively (Semenchuk *et al.*, 2013), and well into the growing season, i.e. approx. 22 and 1 day after the
140 majority of *Salix* leaves emerged in *Normal* and *Deep* (Cooper *et al.* 2011; own observations). Sampling was
141 conducted weekly until 20 September, i.e. approximately 3-4 weeks after the majority of *Salix* leaves were
142 senesced and the leaves of all other observed species had partly or fully senesced (Cooper *et al.* 2011; own
143 observations).

144 Soil from the top 5 cm was collected approximately weekly from 20 July to 20 September 2012 (see Fig. 1).
145 Within each plot and snow regime, one sub-plot (0.5x0.5m) was designated for soil collection, and one 5cm deep
146 soil core was collected at each sampling date with a 5cm wide steel cylinder. Each core was cleaned of above
147 ground plant material (alive and litter) and divided into 0-2cm and 2-5cm depth sections. Within 24h after
148 collection, three grams of each sample were suspended in 30ml distilled water and the extraction water filtered
149 through a 0.45µm syringe filter. Values of pH of the extraction water were measured directly after filtering with a
150 WTW Multiparameter (WTW, Weilheim, Germany). The filtered extraction water were then frozen at -18 °C
151 until analyzed for NO₃⁻ (water) and NH₄⁺ (water) with a flow injection analyzer (5000 FIASTAR, Höganäs,
152 Sweden), for total dissolved organic N (TON) with a 0.5M K₂SO₄ extraction of the same soil samples in the same
153 flow injection analyser, and for total dissolved organic C (TOC) in the water extraction using the non-purgeable
154 organic carbon (NPOC) method with a Shimadzu TOC-5000A.

155 Each time a soil core was collected, water content of the surrounding soil was measured three times with a Theta
156 Probe ML2x (Delta-T Devices, Cambridge, UK), which measured volumetric soil water content integrated over
157 the 6cm surface layer. The probe was inserted into soil without vegetation cover to ensure full contact of the
158 electrodes. These water content measurements were used to transpose the other soil variables into units per g dry
159 soil. Leaves of *Salix polaris* were collected approximately weekly from 20 July to 14 September 2012 (see Fig.
160 3). At each sampling date, 10 leaves were randomly chosen within each plot and snow regime based on specific
161 distances to the snow fences and that leaves representing all parts of individual plants. Before collection, the
162 combined chlorophyll *a+b* content of each leaf was measured five times with a non-destructive method using a

163 hand-held Dualex Scientific instrument (optical transmittance of two near-infrared wavelengths; Force-A, Orsay
164 Cedex, France). Leaves of other species were not used as they were too small to fill the instrument chamber. The
165 *Salix* leaves were then collected, oven-dried at 55 °C for 36h, all ten leaves per sampling date and snow regime
166 pooled, and pulverized in a ball mill. Finally, 3-4mg of the homogenized leaf samples were then put in tin
167 capsules and analyzed in a Eurovector EA coupled to an Isoprime isotope ratio mass spectrometer for N and C
168 concentrations and $\delta^{15}\text{N}$.

169 Peak growing season sizes of *Salix polaris* and *Luzula arcuata* ssp. *confusa* individuals were measured as the
170 summed lengths of all green leaves per individual (excluding petiole or ligule). For the peak sizes of *Bistorta*
171 *vivipara* (syn. *Polygonum viviparum*) individuals, leaf lengths and widths were measured and leaf areas were
172 calculated as ellipses. Four individuals in six permanently installed sub-plots per plot and snow regime were
173 measured with calipers once during the growing season. Measuring date, i.e. the time at which peak size was
174 assumed, was obtained from weekly growth measurements in the same experiment during the preceding year
175 (Rumpf *et al.*, 2014) and determined by assessing the number of snow free days needed to reach peak size per
176 sub-plot and species. The number of days needed post- snow melt to reach peak size in *Normal* and *Deep* were 56
177 and 69 respectively for *Bistorta*, 44 and 55 for *Luzula*, and 53 and 54 days for *Salix*..

178 Statistical analyses

179 All data were analyzed with linear mixed effects models (LMEs) or generalized LMEs of the lme4 package in R
180 v. 2.15.2 (R Development Core Team, 2012; Bates *et al.*, 2013) to examine the effect of snow regime and
181 vegetation type (i.e. block) and their interaction on each parameter. Due to the nature of the data (pooled or
182 individual measurements, time series or single measurement), different mixed effects and covariates including
183 interactions were used for different response variables. Prior to analysis, the distributions of all response variables
184 were examined visually and data transformations or generalized LMEs applied accordingly. We present back-
185 transformed estimates of all data which required transformation. Although we base our conclusions mainly on full
186 model estimates, model simplification with AIC was performed for each model and is referred to when trends

187 from the full models were on the border of being significant. We chose this approach to be able to show and
188 interpret the full range of variables in the model including the non-significant ones, since model selection would
189 remove the non-significant terms.

190 Soil chemistry data (i.e. NO_3^- , NH_4^+ , TON and TOC) were collected weekly and measured in two depths (0-2cm
191 and 2-5cm), and sampling date and depth and their interaction with snow regime were included as covariates,
192 respectively. Only one sample was taken per plot, so the random effects were plot within block. All data is
193 Gamma distributed, however, NO_3^- and NH_4^+ data include zeroes which represent values below the detection limit
194 of the instrument and could therefore not be discarded. For that reason, log-transformation over the whole dataset
195 was not possible (log of zero is not defined). Instead, we divided the analysis in two parts. (1) Occurrences below
196 the detection limit (i.e. zero) were modeled as presence-absence data with a generalized LME on a binomial
197 distribution. (2) Values above the detection limit were modeled independently excluding zeroes. In that case, log-
198 transformation was used to normalize the Gamma distributed data. Nitrate and NH_4^+ data required only step 2.

199 Leaf chemistry data (i.e. N concentration, C concentration, C:N ratio, $\delta^{15}\text{N}$, and chlorophyll) were collected
200 weekly and sampling date and its interaction with snow regime were included as covariate. Due to the pooling of
201 leaf material, random effects in the leaf chemistry models were defined as plot within block, whereas availability
202 of chlorophyll data of each individual leaf and replicate measurement required the random effects of replicate
203 within leaf within plot within block. C:N ratio was Gamma distributed, and we log-transformed the data to
204 normalize it. The other variables were Gaussian distributed and did not require transformation.

205 Plant size measurements were collected only once, i.e. at growing season peak, so the sampling date was not
206 included as a covariate. Since leaf size data was collected sub-plot wise, the random effect structure was sub-plot
207 within plot within block. Leaf size was Gamma distributed, and we log-transformed the data to normalize it.

208

209 **Results**

210 Soil temperature and moisture, and melt out

211 Soil temperatures during the cold-season 2011-12 were more stable and 0 -12 °C warmer in *Deep* than in *Normal*,
212 due to the insulation effect of the deepened snow pack; this was typical for all cold-seasons since the fences were
213 erected in 2006 (Morgner *et al* 2010, Semenchuk *et al.* 2013). Post snow-melt soil temperatures did not differ
214 significantly between snow regimes, but were ca. 1 degC warmer in *Deep* than in *Normal* when averaged over the
215 whole growing season (see Semenchuk *et al.* (2013) for details). In 2011 the increased snowpack delayed
216 snowmelt by up to 16 days (average snowmelt at day of year 166 and 155 in *Deep* and *Normal*, respectively,
217 linear mixed model estimates) and *Salix* leaf emergence was delayed by 2 days (day of year 184 in *Normal* and
218 186in *Deep*, linear mixed model estimates, data not shown), while *Salix* leaf senescence occurred 12 days later in
219 *Deep* (day of year 231 in *Normal* and 243in *Deep*, linear mixed models estimates, data not shown).

220 Volumetric soil moisture fluctuated during the sampling period due to rainy and dry periods, but was significantly
221 higher in *Deep* than in *Normal* during the first weeks, i.e. mid-growing season, but was not significantly different
222 during the end of the season (Fig. 1). However, increased soil moisture reported in *Deep* was due to the strong
223 effect in the Heath site, but not in the other sites. Under *Normal* conditions, the Heath site was drier than the
224 Meadow sites, but was elevated to Meadow moisture levels in *Deep*. Meadow 2 was the moistest site under *Deep*
225 conditions, but it was not significantly moister than Meadow 1 under *Normal* conditions.

226 Soil solution

227 Soil solution pH was not altered by snow regime and did not vary with soil depth. However, the soil solution from
228 the Heath site was significantly less acidic than soil from Meadow sites (Fig. 1).

229 Nitrate (NO₃⁻) concentrations in the soil solution were around 0.06 µg g⁻¹ dry soil in *Deep* and below the detection
230 limit in *Normal* (median) throughout the entire sampling period. The higher concentrations in *Deep* were only
231 significant in the 2-5cm soil horizon (Fig. 2e) and the Meadow 2 site, not in Heath (Fig. 2i). No significant
232 temporal trends can be seen during the sampling period, i.e. summer and autumn (Fig. 2a). The probability of

233 measuring values above the detection limit was around 0.83 for *Normal* and 0.99 for *Deep* throughout the entire
234 sampling period (data not shown).

235 Ammonium (NH_4^+) concentrations in the soil solution were around 0.28 and 0.1 $\mu\text{g g}^{-1}$ dry soil in *Deep* and
236 *Normal*, respectively (median), throughout the entire measurement period. This increase was significant in both
237 soil horizons, but much stronger in 2-5cm depth (Fig. 2f). The interactions between snow regime and vegetation
238 types as well as the additive effect of vegetation type were removed during model selection with AIC, so there
239 were no significant differences between vegetation types (Fig. 1j). A temporal trend was only seen during the first
240 two sampling dates in *Deep* (i.e. after green up and before senescence), after which the NH_4^+ concentrations
241 decreased to a constant level for the rest of the sampling period (Fig. 2b). The probability of measuring values
242 above the detection limit was close to 1 in both snow regimes (data not shown).

243 Soil solution TON and TOC concentrations were not different between snow regimes or vegetation types (Fig. 2k,
244 l). Some fluctuations could be seen throughout the sampling period, with no clear trends (Fig. 2c, d).

245 *Salix polaris* leaf chemistry

246 The N concentrations in *Salix* leaves decreased in the course of the sampling period from ca. 4 and 3% during
247 mid-growing season to around 1.5 and 1% at the end of senescence in *Deep* and *Normal*, respectively (Fig. 3a).
248 This trend was most pronounced from onset of senescence to leaf shedding. There was a trend of higher N
249 concentrations in leaves in the two Meadow sites than in Heath but this was not significant (Fig. 3f). *Salix* leaf C
250 concentrations were not different between snow depth regimes, but decreased slightly from around 44 to 42% in
251 the course of the sampling period (Fig. 3b). This trend remained also after model simplification with AIC.
252 Interestingly, the C concentrations in leaves were similar in Heath and Meadow 2, but significantly lower in
253 Meadow 1 (Fig. 3g).

254 The C:N ratio of *Salix* leaves was always significantly higher in *Normal* than in *Deep* and that difference
255 increased toward the end of the measurement period (Fig. 3c). In both regimes, C:N increased towards the end of

256 the measurement period. No difference was found between vegetation types, and this was supported by model
257 simplification (Fig. 3h).

258 Except for the first two sampling dates, the chlorophyll *a+b* contents of *Salix* leaves were significantly higher in
259 *Deep* than in *Normal*. In both regimes, chlorophyll content was constant (*Normal*) or increased slightly (*Deep*) in
260 late July/ early August, but decreased in parallel towards the end of the growing season (Fig. 3d) as senescence
261 progressed in both snow regimes. Chlorophyll content was higher at deeper snow depth from Heath < Meadow 2
262 < Meadow 1, and that effect was strongest in *Deep* (Fig. 3i).

263 The $\delta^{15}\text{N}$ content of *Salix polaris* leaves were significantly higher in *Deep* than in *Normal*, both across the
264 growing season (Fig. 3e) and across vegetation types (Fig. 3j). The $\delta^{15}\text{N}$ followed the trend in N concentration and
265 showed an effect of vegetation type, with slightly elevated values in *Deep*, with no interaction between vegetation
266 type and treatment.

267

268 Plant sizes

269 *Bistorta vivipara* plants in *Normal* were largest in heath and smallest in Meadow 1, while in *Deep* no vegetation
270 type difference was observed. Treatment effects were therefore only significant (according to model
271 simplification) in Meadow 1 where deeper snow gave rise to plants with a larger leaf area (Fig. 4a).

272 *Luzula arcuata* plants in *Normal* had longer leaves in Meadow 2 than in Heath or Meadow 1 (Fig. 4b). In *Deep*,
273 *Luzula* leaves were longer in Meadow 1 than in the other two vegetation types. Treatment effects were thus seen
274 for both Meadow 1 and 2 so that plants in *Deep* were larger than in *Normal* in Meadow 1, but smaller than in
275 *Normal* in Meadow 2. This trend retained in the model after model simplification and was significant.

276 *Salix polaris* in *Normal* had approximately the same leaf length across all vegetation types and both snow regimes
277 (Fig. 4c). In Meadow 2, *Salix* leaf lengths in *Deep* were shorter than in *Normal*; this was not significant following
278 model simplification.

279

280 **Discussion**

281 Soil nutrient concentrations (especially NH_4^+), measured 6 years after continuous snow depth enhancement with
282 resulting soil temperature increase, were elevated during the growing-season, especially in the meadow sites. An
283 increase of soil NH_4^+ and NO_3^- concentrations as a result of thicker snow cover and therefore warmed cold-
284 seasons has also been reported at Toolik Lake, Alaska (Schimel *et al.*, 2004). These soils were isolated from plant
285 roots, while in our study plant roots were intact and successfully competed with microbial immobilization and
286 assimilated some of the extra N available prior to the first sampling date, i.e., during 30 to 45 days after snow
287 melt. This corresponds to recent findings of high plant N uptake during the cold season or early spring (Larsen *et*
288 *al.*, 2012), potentially soon after soil thaw. The concentrations of NO_3^- and NH_4^+ may have been higher at the end
289 of the cold-season and prior to microbial and vegetative competition of nutrients, i.e., before we started sampling.
290 The decreasing values of NH_4^+ in *Deep* after the first two sampling dates, i.e., 4 and 5 weeks after snow melt,
291 could thus be interpreted as the remaining peak of N after snow melt. These observations, however, have to be
292 interpreted with caution, since they might be confounded by the combination of simultaneous microbial
293 mineralization and immobilization by both microbes and plants (Hobbie & Gough, 2002). In the Alaskan study by
294 Schimel *et al.* (2004), the effects were more pronounced in moist tussock tundra than in dry heath tundra.
295 Similarly, in our study we find smaller or no effects in the drier, coarse grained Heath soil, while effects were
296 consistent across both Meadow sites. Welker *et al.* (2005) found similar differences in foliar N content between
297 vegetation types in the same study site in Alaska following winter warming. This suggests a generally greater
298 stability of drier as opposed to moister vegetation types, which may be attributable to the dominating species or
299 functional groups in the respective vegetation types.

300 *Salix polaris* leaves from deepened snow plots had higher N content, which corresponds to the findings of Welker
301 *et al.* (2005) from the aforementioned Toolik lake study. In addition, we show that *Salix* chlorophyll content and
302 $\delta^{15}\text{N}$ were also increased. All these three plant-related variables are signs of enhanced growing-season soil N

303 availability and demonstrate successful competition for N by plants in their interaction with microorganisms. It
304 has previously been shown that high plant $\delta^{15}\text{N}$ may reflect high N availability, both on a regional scale in the
305 Arctic (Michelsen *et al.*, 1998) and at the global scale (Craine *et al.*, 2009) This is firstly because when N
306 availability is high, N lost from the ecosystem is more likely to be depleted in ^{15}N , which increases the $\delta^{15}\text{N}$ of
307 leaves. Gaseous N loss during nitrification and the leaching of ^{15}N -depleted nitrate can cause the remaining N
308 pool (and subsequently plants) to be enriched in ^{15}N . Secondly, plants experiencing high N availability are less
309 dependent on mycorrhizal fungi for N acquisition than at low N availability, and less exposed to ^{15}N depletion
310 during transfer of N from mycorrhizal fungi to host plants (Craine *et al.*, 2009). Furthermore ammonium-N has a
311 higher $\delta^{15}\text{N}$ than organic N, of which a high content in the latter characterizes many nutrient poor arctic soils
312 (Yano *et al.*, 2009), and slow decomposition of plant materials that are often depleted in ^{15}N (i.e., ericoid and
313 ectomycorrhizal plants) is the likely reason for the large pool size and ^{15}N depletion of the organic N pool (Yano
314 *et al.*, 2009). Altogether, this suggests that the inorganic N supply was ample in *Deep* but more limited in *Normal*
315 snow depth in all vegetation types.

316 *Salix* leaves from deepened snow, however, were neither longer nor more numerous than leaves in unmanipulated
317 plots. In fact, in Meadow 2, the *Salix* leaves were shorter in *Deep* than *Normal*. No difference or a slight
318 reduction in growth of *Salix* in the deep snow regime in the same experiment the previous year was also reported
319 by Rumpf *et al.* (2014). For this species the increase in N may not offset the shorter growing season following
320 delayed snowmelt, or K and P availability may limit the plants' growth response to increased N. Increased soil
321 nutrient availability was reflected in larger leaf sizes of *Bistorta vivipara* and *Luzula arcuata* ssp. *confusa* in one
322 of the two meadow sites. Both meadow sites had increased soil N in the deeper snow regime, but the soil K
323 concentration and pH of Meadow 2 were lower than the other sites, which may have been limiting factors in the
324 utilization of increased N for plant growth. However, as we could not destructively sample a large area because
325 the plots needed to be protected for longer term sampling, we cannot exclude that C is also allocated to other
326 organs than leaves, for instance woody stems, below ground runners, overwintering corms, roots, or reproductive

327 structures (Parsons *et al.*, 1994; Wookey *et al.*, 1994; Sullivan & Welker, 2005), which calls for cautious
328 interpretation of the data presented here and in Rumpf *et al.* (2014).

329 Increased leaf N levels could have several possible effects on decomposition processes in this system, with
330 implications on long-term carbon balance and feedbacks on plant growth. Assuming that the litter of the most
331 productive deciduous species reacted similarly and had higher N concentrations in winter warmed plots to those
332 shown in Welker *et al.* (2005), soil C could be stabilized through humification processes by chemical reaction of
333 lignin degradation products with NO_3^- and NH_4^+ after an initial increase of mineralization rates during early
334 phases of decomposition of undecomposed litter (Berg, 2000; Weintraub & Schimel, 2003). Increased leaf litter N
335 could lead to a possible feedback mechanism between N and C mineralization, with two hypothetical pathways
336 influencing the C balance during the Arctic growing season: (1) increased N could stabilize soil C through
337 formation of humic acids during later stages of composition of heavily decomposed material, which deprives
338 microbes of easily accessible C during the growing-season and thereby reduces respiration, as found by our group
339 in the same study site (Semenchuk *et al.*, in prep). A reported loss of C after 20 years of nutrient addition reported
340 by Mack *et al.* (2004) supports this hypothesis by attributing fertilization mediated C losses to stimulation of
341 decomposition of organic material in decomposed stages prior to stabilization processes (Weintraub & Schimel,
342 2003). It is possible that initial losses of labile C were large compared to C inputs and might have ceased at any
343 point during the 20 years of fertilizer addition, which is impossible to track by single pool size measurements as
344 done there (Mack *et al.*, 2004). (2) The excess mineral N increases plant growth and C uptake from the
345 atmosphere and thereby adds more C to the ecosystem's stocks without adding C available for mineralization and
346 recycling to the atmosphere. However, no clear conclusion on the fate of this C can be deduced from the
347 literature yet, and more experiments have to be done to quantify relative C flux changes and to verify or falsify
348 these two hypothetical pathways or to identify new potential mechanisms which link N and C cycles.

349 Litter quality of a given habitat, and thereby SOM quality and mineralization rates, is largely plant species-
350 specific and therefore a product of the habitat's species composition. Different species inherently produce litter
351 with varying C:N ratios, lignin and secondary compound contents (Hobbie, 1996; Cornelissen *et al.*, 2007; Aerts

352 *et al.*, 2012) that influence decomposition and mineralization processes. However, the conditions under which
353 plants grow also provoke changes of litter quality (Shaver & Chapin III, 1980; Körner, 1989; Kudo *et al.*, 1999;
354 Aerts *et al.*, 2012) and thereby influence litter and SOM qualities. As a result, effects of environmental
355 perturbations such as soil temperature increase on N and C dynamics can vary across vegetation types (Weintraub
356 & Schimel, 2003; Schimel *et al.*, 2004; Welker *et al.*, 2005) and can additionally be expected upon vegetation
357 composition changes (Sturm *et al.*, 2005). This study does not have the capacity to show species specific changes
358 in leaf chemistry after cold-season warming – the aperture of the Chlorophyll instrument was too small for other
359 species, and only *Salix* leaves were analyzed. This does therefore not allow conclusions on overall litter quality of
360 the whole system. However, we did show that *Salix* reacted consistently across vegetation types with increased N
361 content after warmed cold-seasons. Since this species is present in both vegetation types in similar frequencies
362 (own observations), and is a major contributor to the annual litter pool, we can conclude that the total annual
363 litter-N pool is increased across the whole study area, independently of vegetation type.

364 Finally, we want to emphasize that this study focuses on the upper layers of the active layer, and not on underlying
365 permafrost layers. Permafrost is known to contain large quantities of C which is thermally stabilized, i.e.,
366 decomposition is slowed down by low temperatures and restricted access to unfrozen water. Increased soil
367 temperatures will thaw the upper layers of permafrost soil and likely release a lot of the here stored labile C (e.g.
368 Zimov *et al.*, 2006; Schuur *et al.*, 2008) in a pulse which in magnitude could potentially offset all other processes
369 treated in this article. However, we do believe that some of the hypothesized mechanisms described here could
370 also apply for long term thawing of permafrost, e.g., chemical stabilization of heavily decomposed material by
371 release of N compounds.

372 This study shows how multi-year increased snow depth has changed soil and plant N concentrations through
373 temperature-induced increases of cold-season mineralization which carried over to growing-season N availability
374 and plant N uptake. This has been shown in previous studies from Toolik lake (Schimel *et al.*, 2004; Welker *et al.*,
375 2005), strengthening the findings of these studies. By comparing with respiration data from the same study site
376 (Semenchuk *et al.*, in prep), we also hypothesize that perturbations of the N cycle could be tightly linked and

377 directly connected to the C cycle by changing both C assimilation patterns through the plant growth pathway and
378 C mineralization patterns through chemical stabilization of soil C. Future studies are needed to test that hypothesis
379 and to produce reliable sink and source strengths to be able to forecast future trends of the recent Arctic C cycle.

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384

385 **References**

386 ACIA (2005) *Arctic climate impact assessment*. New York, Cambridge University Press.

387 Aerts R, Callaghan T V, Dorrepaal E, van Logtestijn RSP, Cornelissen JHC (2012) Seasonal climate
388 manipulations have only minor effects on litter decomposition rates and N dynamics but strong effects on
389 litter P dynamics of sub-arctic bog species. *Oecologia*, **170**, 809–19.

390 Bates D, Maechler M, Bolker B (2013) lme4: Linear mixed-effects models using S4 classes.

391 Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and*
392 *Management*, **133**, 13–22.

393 Björkman MP, Morgner E, Cooper EJ, Elberling B, Klemetsson L, Björk RG (2010) Winter carbon dioxide
394 effluxes from Arctic ecosystems: An overview and comparison of methodologies. *Global Biogeochemical*
395 *Cycles*, **24**, 1–10.

396 Christensen TR, Jonasson S, Michelsen A, Callaghan T V, Havström M (1998) Environmental controls on soil
397 respiration in the Eurasian and Greenlandic Arctic. *Journal of Geophysical Research*, **103**, 15–21.

398 Cooper EJ, Dullinger S, Semenchuk P (2011) Late snowmelt delays plant development and results in lower
399 reproductive success in the High Arctic. *Plant science : an international journal of experimental plant*
400 *biology*, **180**, 157–67.

401 Cornelissen JHC, van Bodegom PM, Aerts R, *et al.* (2007) Global negative vegetation feedback to climate
402 warming responses of leaf litter decomposition rates in cold biomes. *Ecology letters*, **10**, 619–27.

403 Craine JM, Elmore AJ, Aidar MPM, *et al.* (2009) Global patterns of foliar nitrogen isotopes and their
404 relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New*
405 *Phytologist*, **183**, 980–992.

- 406 Epstein HE, Myers-Smith I, Walker D a (2013) Recent dynamics of arctic and sub-arctic vegetation.
407 *Environmental Research Letters*, **8**, 015040.
- 408 Førland EJ, Benestad R, Hanssen-Bauer I, Haugen JE, Skaugen TE (2011) Temperature and Precipitation
409 Development at Svalbard 1900–2100. *Advances in Meteorology*, **2011**, 1–14.
- 410 Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming.
411 *Ecological applications*, **1**, 182–195.
- 412 Grogan P, Jonasson S (2006) Ecosystem CO₂ production during winter in a Swedish subarctic region: the relative
413 importance of climate and vegetation type. *Global Change Biology*, **12**, 1479–1495.
- 414 Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological*
415 *Monographs*, **66**, 503–522.
- 416 Hobbie S, Chapin III FS (1996) Winter regulation of tundra litter carbon and nitrogen dynamics.
417 *Biogeochemistry*, 327–338.
- 418 Hobbie SE, Gough L (2002) Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in
419 northern Alaska. *Oecologia*, **131**, 453–462.
- 420 Jonasson S, Michelsen A, Schmidt IK (1999) Coupling of nutrient cycling and carbon dynamics in the Arctic,
421 integration of soil microbial and plant processes. *Applied Soil Ecology*, **11**, 135–146.
- 422 Kudo G, Nordenhaell U, Molau U (1999) Effects of snowmelt timing on leaf traits, leaf production, and shoot
423 growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. *Ecoscience*, **6**, 439–
424 450.
- 425 Körner C (1989) The nutritional status of plants from high altitudes. *Oecologia*, **81**, 379–391.
- 426 Larsen KS, Michelsen A, Jonasson S, Beier C, Grogan P (2012) Nitrogen Uptake During Fall, Winter and Spring
427 Differs Among Plant Functional Groups in a Subarctic Heath Ecosystem. *Ecosystems*, **15**, 927–939.
- 428 Mack MC, Schuur E a G, Bret-Harte MS, Shaver GR, Chapin III FS (2004) Ecosystem carbon storage in arctic
429 tundra reduced by long-term nutrient fertilization. *Nature*, **431**, 440–3.
- 430 Melillo JM, Steudler P a, Aber JD, *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system.
431 *Science (New York, N.Y.)*, **298**, 2173–6.
- 432 Michelsen A, Quarmby C, Sleep D, Jonasson S (1998) Vascular plant 15 N natural abundance in heath and forest
433 tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia*,
434 **115**, 406–418.
- 435 Morgner E, Elberling B, Strebel D, Cooper EJ (2010) The importance of winter in annual ecosystem respiration in
436 the High Arctic: effects of snow depth in two vegetation types. *Polar Research*, **29**, 58–74.
- 437 Nadelhoffer K, Giblin A, Shaver G, Linkins A (1992) Microbial processes and plant nutrient availability in arctic
438 soils. In: *Arctic ecosystems in a changing Climate: an ecophysiological perspective*imate: an

- 439 *ecophysiological perspective* (eds: Chapin III FS, Jefferies R, Reynolds J, Shaver GR, Svoboda J), pp281–
440 300. San Diego, Academic.
- 441 Nobrega S, Grogan P (2007) Deeper Snow Enhances Winter Respiration from Both Plant-associated and Bulk
442 Soil Carbon Pools in Birch Hummock Tundra. *Ecosystems*, **10**, 419–431.
- 443 Parsons A, Welker J, Wookey P, Press MC, Callaghan T, Lee J (1994) Growth responses of four sub-Arctic dwarf
444 shrubs to simulated environmental change. *Journal of Ecology*, **82**, 307–318.
- 445 Post W, Emanuel W, Zinke P, Stangenberger A (1982) Soil carbon pools and world life zones. *Nature*, **298**, 156–
446 159.
- 447 R Development Core Team (2012) R: A Language and Environment for Statistical Computing.
- 448 Rumpf SB, Semenchuk PR, Dullinger S, Cooper EJ (2014) Idiosyncratic responses of high arctic plants to
449 changing snow regimes. *PloS one*, **9**, e86281.
- 450 Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology*, **85**, 591–602.
- 451 Schimel JP, Bilbrough C, Welker JM (2004) Increased snow depth affects microbial activity and nitrogen
452 mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, **36**, 217–227.
- 453 Schuur E a. G, Bockheim J, Canadell JG, *et al.* (2008) Vulnerability of Permafrost Carbon to Climate Change:
454 Implications for the Global Carbon Cycle. *BioScience*, **58**, 701.
- 455 Semenchuk PR, Elberling B, Cooper EJ (2013) Snow cover and extreme winter warming events control flower
456 abundance of some, but not all species in high arctic Svalbard. *Ecology and Evolution*,, doi:
457 10.1002/ece3.648.
- 458 Shaver G, Chapin III FS (1980) Response to fertilization by various plant growth forms in an Alaskan tundra:
459 nutrient accumulation and growth. *Ecology*, **61**, 662–675.
- 460 Sistla S a, Moore JC, Simpson RT, Gough L, Shaver GR, Schimel JP (2013) Long-term warming restructures
461 Arctic tundra without changing net soil carbon storage. *Nature*, **497**, 615–8.
- 462 Solomon S, Qin D, Manning M, *et al.* (Eds.) (2007) *Climate Change 2007 - The Physical Science Basis: Working*
463 *Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*.
464 Cambridge, Cambridge University Press.
- 465 Strebel D, Elberling B, Morgner E, Knicker H, Cooper, E.J. (2010) Cold season soil respiration in response to
466 grazing and warming in the High Arctic Svalbard. *Polar Research*, **29**, 46-57.
- 467 Sturm M, Schimel JP, Michaelson G, *et al.* (2005) Winter Biological Processes Could Help Convert Arctic
468 Tundra to Shrubland. *BioScience*, **55**, 17–27.
- 469 Sullivan PF, Welker JM (2005) Warming chambers stimulate early season growth of an arctic sedge: results of a
470 minirhizotron field study. *Oecologia*, **142**, 616–26.

- 471 Tolgensbakk J, Soerbel L, Hoegvard K (2000). Adventdalen, Geomorphological and Quaternary Geological map,
472 Svalbard 1:100 000, Spitsbergen sheet C9Q, Norsk Polarinstituttemakart nr. 32, Norsk Polarinstitut,
473 Tromsø.
- 474 Weintraub MN, Schimel JP (2003) Interactions between Carbon and Nitrogen Mineralization and Soil Organic
475 Matter Chemistry in Arctic Tundra Soils. *Ecosystems*, **6**, 129–143.
- 476 Welker JM, Fahnestock JT, Sullivan PF, Chimner RA (2005) Leaf mineral nutrition of Arctic plants in response
477 to warming and deeper snow in northern Alaska. *Oikos*, **109**, 167–177.
- 478 Wookey PA, Robinson CH, Parsons A, Welker JM, Press MC, Lee JA, Callaghan T V (1995) Environmental
479 Constraints on the Growth, Photosynthesis and Reproductive Development of *Dryas octopetala* at a High
480 Arctic Polar Semi-Desert, Svalbard. *Oecologia*, **102**, 478–489.
- 481 Wookey P, Welker JM, Parsons A, Press MC, Callaghan T V, Lee JA (1994) Differential growth , allocation and
482 photosynthetic responses of *Polygonum viviparum* to simulated environmental change at a high arctic polar
483 semi-desert. *Oikos*, **70**, 131–139.
- 484 Yano Y, Shaver GR, Giblin a. E, Rastetter EB (2009) Depleted ¹⁵N in hydrolysable-N of arctic soils and its
485 implication for mycorrhizal fungi–plant interaction. *Biogeochemistry*, **97**, 183–194.
- 486 Zimov S, Schuur E, Chapin III FS (2006) Permafrost and the global carbon budget. *Science*, **312**, 1612–1613.
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489 **Figure Legends**

490

491 **Fig. 1** Observed volumetric water content (a, d, g), pH (b, e, h), and K⁺ (c, f, i) in water extracted from 5 cm
492 deep soil cores. Results are shown for two experimental snow depth regimes as seasonal changes during the 2012
493 growing season (a-c); for two depth intervals (d-f) and for the three vegetation types (g-i). The 95% confidence
494 intervals are shown as error bars. *Normal*: unmanipulated snow depth as found representative for most of the
495 study area; *Deep*: manipulated snow depth with snow fences.

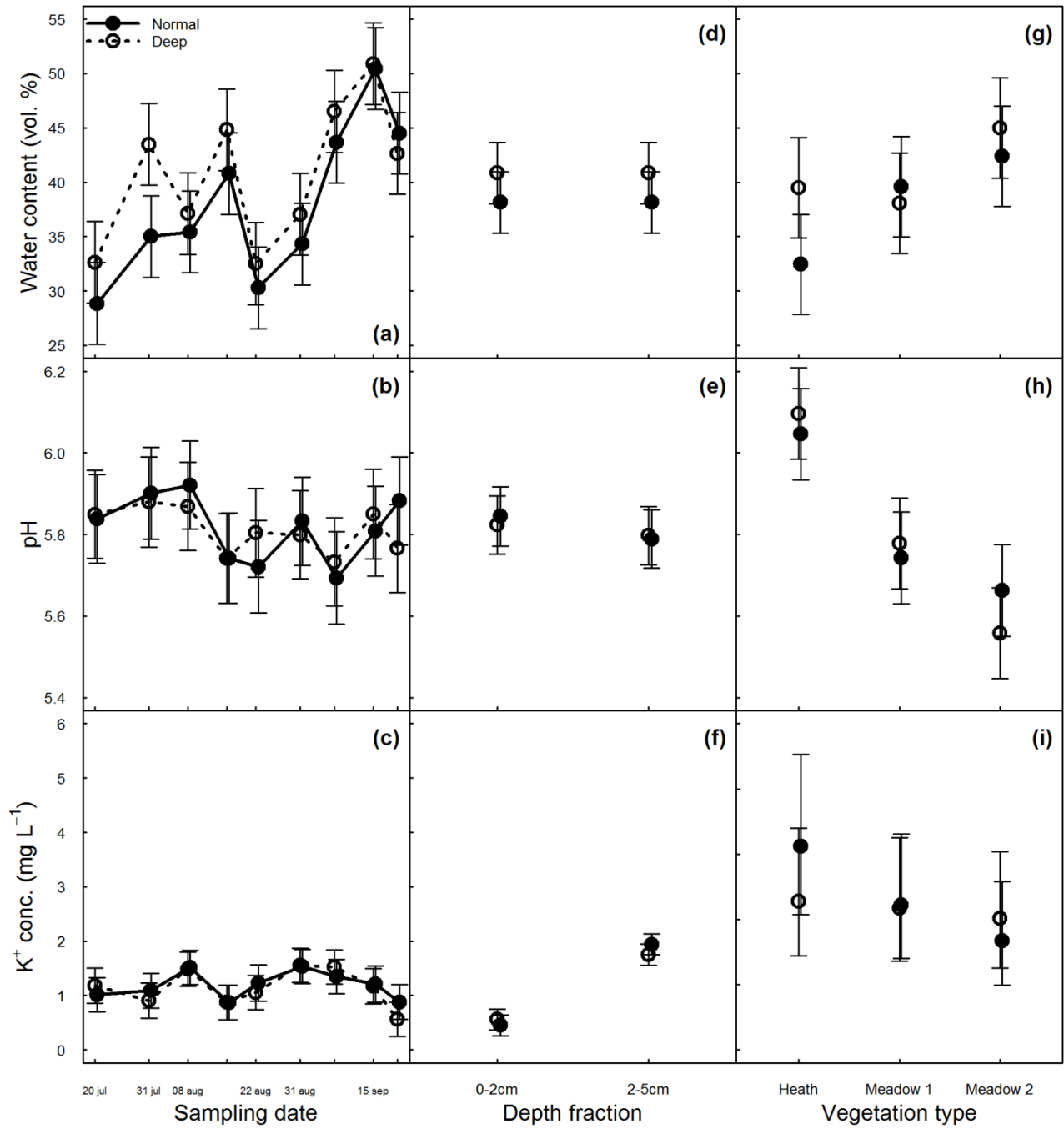
496 **Fig. 2** Observed concentrations of NO₃⁻ (a,e,i), NH₄⁺ (b,f,j), TON (c,g,k), and TOC (d,h,l) extracted from 0-5
497 cm soil cores. Results are shown for two experimental snow depth regimes as seasonal changes during the 2012
498 growing season (a-d); for two depth intervals (e-h) and for the three vegetation types (i-l).. The 95% confidence
499 intervals are shown as error bars. *Normal*: unmanipulated snow depth as found representative for most of the
500 study area; *Deep*: manipulated snow depth with snow fences.

501 **Fig.3** Observed concentrations of %N (a, f), %C (b, g), C:N ratio (c, h), chlorophyll *a+b* (d, i) and δ¹⁵N (‰) (e,
502 j) of *Salix polaris* leaves sampled in two different experimental snow depth regimes during the 2012 growing
503 season. Results are shown as seasonal changes during the 2012 growing season (a-e) and for the three vegetation
504 types (f-j). The 95% confidence intervals are shown as error bars. *Normal*: unmanipulated snow depth as found
505 representative for most of the study area; *Deep*: manipulated snow depth with snow fences.

506 **Fig. 4** Observed peak sizes of *Bistorta vivipara* (a), *Luzula arcuata* ssp. *confusa* (b) and *Salix polaris* (c)
507 individuals sampled in two experimental snow depth regimes at peak plant size during the 2012 growing season.
508 The 95% confidence intervals are shown as error bars. *Normal*: unmanipulated snow depth as found
509 representative for most of the study area; *Deep*: manipulated snow depth with snow fences.

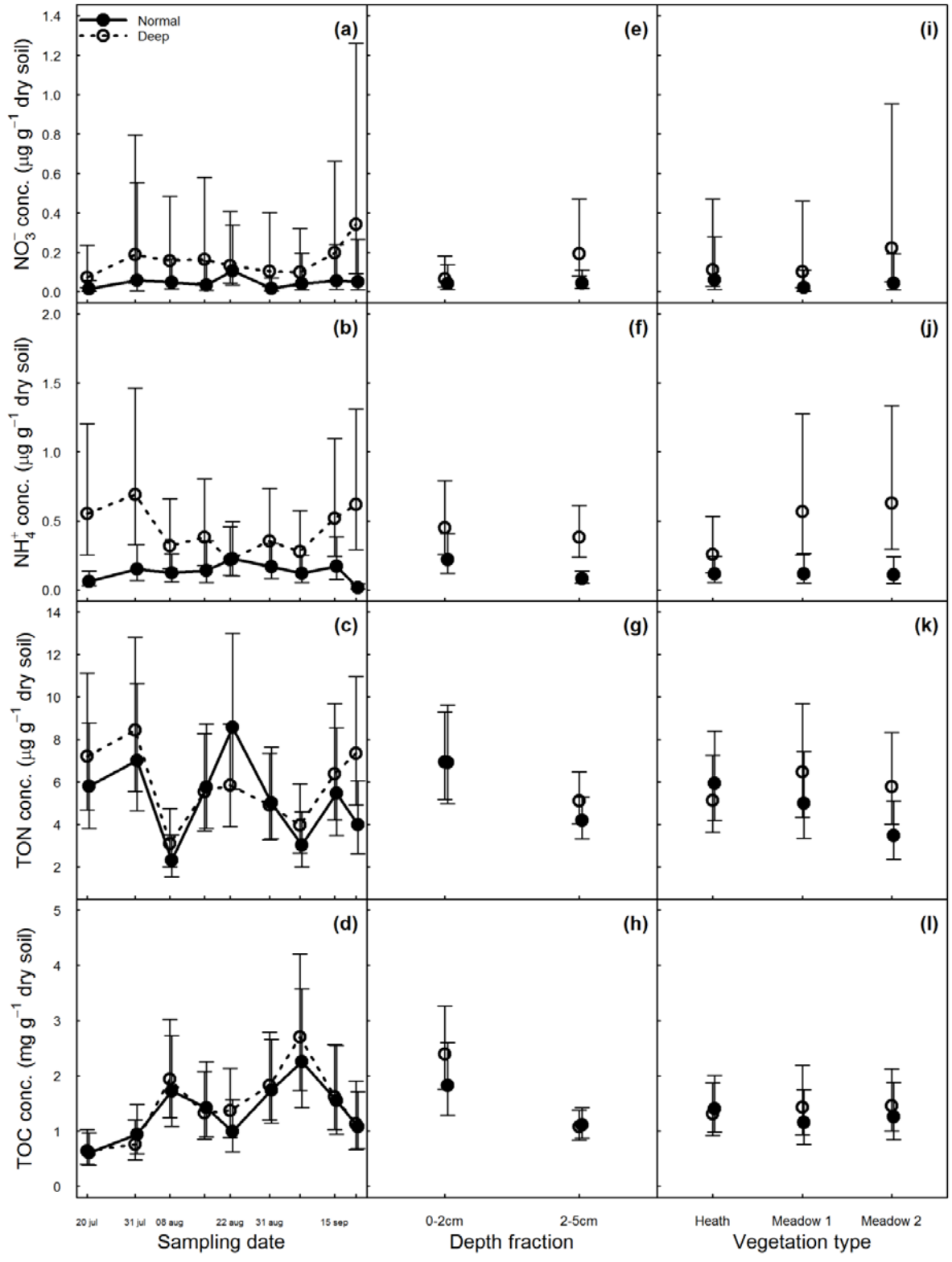
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Figure 1. Semenchuk et al. 2014

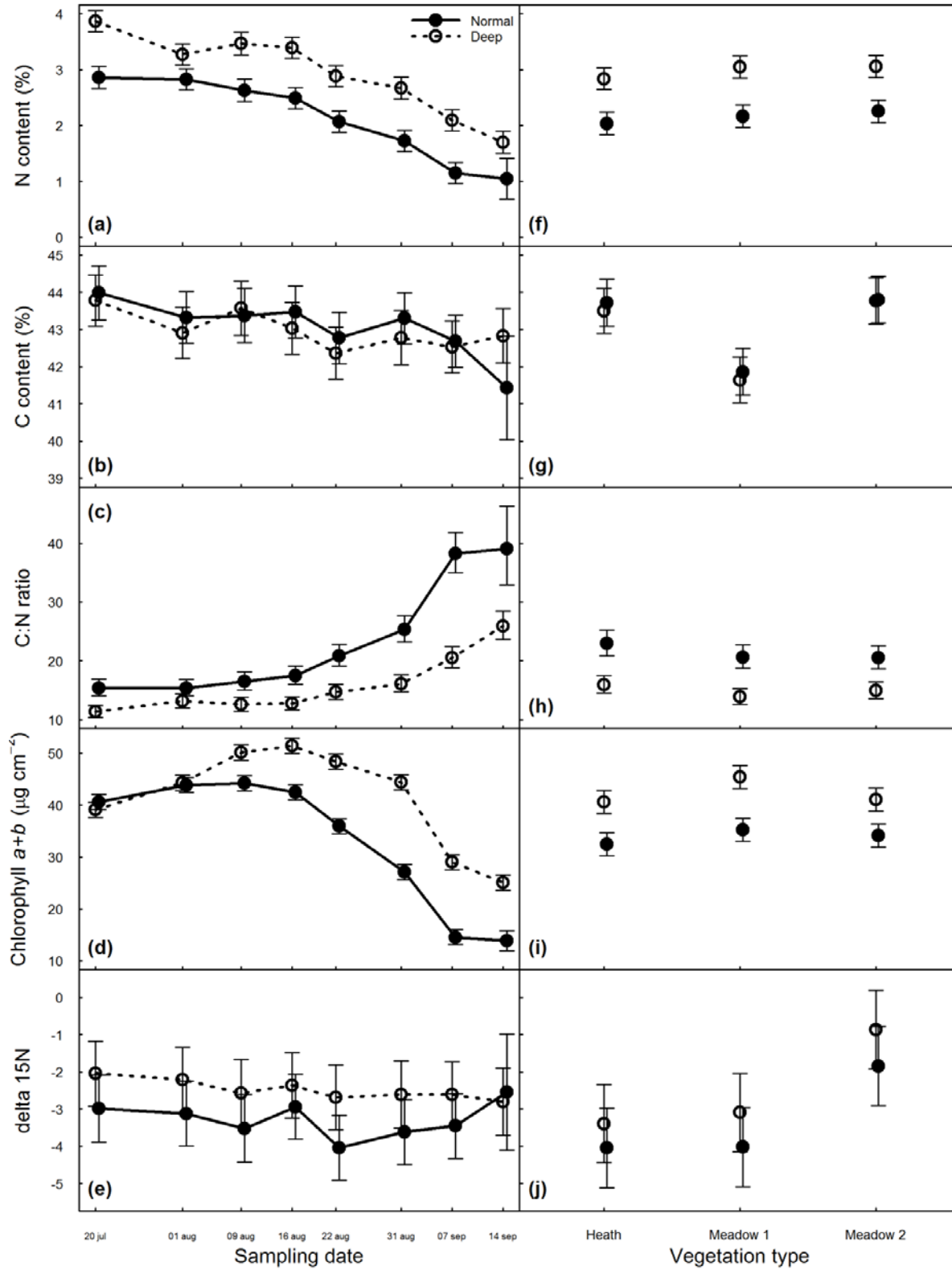


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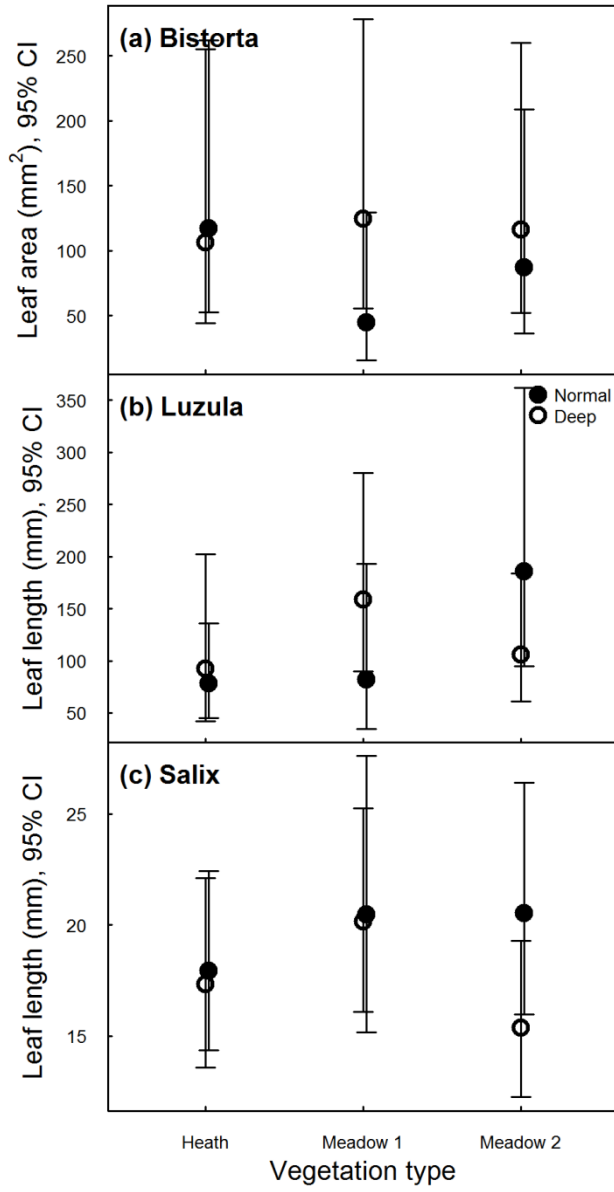
Figure 2. Semenchuk et al. 2014



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Figure 3. Semenchuk et al. 2014



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Figure 4. Semenchuk et al. 2014