The unseen iceberg: plant roots in arctic tundra

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Supporting information Table S1 A list of the papers containing information on tundra rooting distribution and dynamics used in this review. Each row is a paper, book chapter, or thesis, and the topics covered are indicated by abbreviations: SC is standing crop, P is production, T is turnover, D is depth distribution, O is morphology, A is aerenchyma, M is mycorrhizas, N is nutrient cycling, C is carbon cycling, and E is environmental forcing.

#	Paper / Book Chapter / Thesis or Dissertation	SC	P	T	D	O	A	M	N	C	E
	1950–1970										
1	Aleksandrova, 1958 (*Botanicheskii Zhurnal* 43: 1748-1762)	SC									
2	Vikhireva-Vasilkova et al.,1964 (*Problemy Severa* 8: 130-147)	SC									
3	Aleksandrova, 1969 (*Problemy Botaniki* 11)	SC									
4	Khodachek, 1969 (*Botanicheskii Zhurnal* 54: 1059-1075)	SC			D						
5	Pavlova, 1969 (*Vestnik of the Moscom University*, Biology Series 5: 62-67)	SC									
6	Dennis & Johnson, 1970 (*Arctic and Alpine Research* 2: 253-266)	SC	P		D						
7	Shamurin, 1970 (*Book A*, pp. 25-29)	SC									
	1971–1980										
8	Rakhmanina, 1971 (*Book B*, pp. 37-42)	SC									
9	Gorchakovsky & Andreyashkina, 1972 (*Book C*, pp. 113-116)	SC	P								
10	Ignatenko *et al*., 1972 (*Book C*, pp. 140-149)	SC			D						
11	Wielogolaski, 1972 (*Arctic and Alpine Research* 4: 289-306)	SC									
12	Billings *et al*., 1973 (*Book D*, pp. 57-63)		P							C	
13	Chapin, 1974 (*Ecology* 55: 1180-1198)	SC	P		D	O			N		E
14	Wein & Bliss, 1974 (*Arctic and Alpine Research* 6: 261-274)	SC									
15	Allessio & Tieszen, 1975 (*American Journal of Botany* 62: 797-807)		P							C	
16	Bliss, 1975 (*Book E*, pp. 17-60)	SC	P	T							
17	Kallio, 1975 (*Book E*, pp. 193-223)	SC	P								
18	Kjelvik & Kärenlampi, 1975 (*Book F*, pp. 111-120)	SC									

19	Østbye *et al*., 1975 (*Book E*, pp. 225-264)			T		O					E
20	Rosswall *et al*., 1975a (*Book E*, pp. 265-294)			T		O					E
21	Rosswall *et al*., 1975b (*Book F*, pp. 268-278)			T							E
22	Shaver & Billings, 1975 (*Ecology* 56: 401-409)		P	T	D	O				C	
23	Wielgolaski, 1975 (*Book F*, pp. 121-128)	SC	P	T	D						
24	Billings *et al*., 1976 (*Arctic and Alpine Research* 8: 247-250)	SC			D						
25	Chapin & Bloom, 1976 (*Oikos* 26: 111-121)				D	O			N		E
26	Shaver & Billings, 1976 (*Flora* 165: 247-267)					O				C	
27	Billings *et al*., 1977 (*Arctic and Alpine Research* 9: 129-137)		P							C	
28	Dennis, 1977 (*Arctic and Alpine Research* 9: 113-127)	SC	P	T	D	O					E
29	Muc, 1977 (*Book G*, pp. 157-184)	SC	P		D				N		
30	Shaver & Billings, 1977 (*Oecologia* 28: 57-65)		P		D						E
31	Svoboda, 1977 (*Book G*, pp. 185-216)	SC							N		
32	Vitt & Pakarinen, 1977 (*Book G*, pp. 225-244)	SC			D						
33	Webber, 1977 (*Arctic and Alpine Research* 9: 105-111)	SC									
34	Bell & Bliss, 1978 (*Canadian Journal of Botany* 56: 2470-2490)	SC	P	T	D	O			N		E
35	Billings *et al*., 1978 (*Book H*, pp. 415-434)		P	T	D	O				C	E
36	Chapin, 1978 (*Book H*, pp. 483-508)					O			N		E
37	Chapin *et al*., 1978 (*Oikos* 31: 189-199)								N		
38	Dennis *et al*., 1978 (*Book H*, pp. 113-140)	SC	P	T	D						E
39	Miller & Laursen, 1978 (*Book H*, pp. 229-238)					O		M			
40	Webber, 1978 (*Book H*, pp. 37-112)	SC	P								
41	Chapin & Slack, 1979 (*Oecologia* 42: 67-79)	SC				O			N	C	E
42	Shaver & Cutler, 1979 (*Arctic and Alpine Research* 11: 335-342)	SC			D						
43	Shaver *et al*., 1979 (*Journal of Ecology* 67: 1025-1046)	SC			D						
44	Chapin *et al*., 1980a (*Book I*, pp. 140-185)	SC	P	T	D	O	A		N	C	
45	Chapin *et al*., 1980b (*Journal of Ecology* 68: 189-209)	SC							N	C	
46	Flower-Ellis, 1980 (*Book J*, pp. 163-179)	SC			D					C	
47	Kummerow & Russell, 1980 (*Oecologia* 47: 196-199)		P		D						
48	Kummerow *et al*., 1980 (*Arctic and Alpine Research* 12: 335-342)	SC							N		E
49	Miller *et al*., 1980 (*Book I*, pp. 66-101)			T		O					E
	1981–1990										

50	Chapin, 1981 (*Arctic and Alpine Research* 13: 83-94)					O			N	C	E
51	Jones & Gore, 1981 (*Book K*, pp. 239-256)	SC	P								
52	Tikhomirov *et al*., 1981 (*Book K*, pp. 227-238)	SC									
53	Wielgolaski *et al*., 1981 (*Book K*, pp. 187-225)	SC	P	T							
54	Chapin & Tryon, 1982 (*Holarctic Ecology* 5: 164-171)					O			N	C	E
55	Ellis & Kummerow, 1982 (*Oecologia* 54: 136-137)		P								E
56	Kummerow & Krause, 1982 (*Holarctic Ecology* 5: 187-193)								N		E
57	Limbach *et al*., 1982 (*Holarctic Ecology* 5: 150-157)									C	E
58	Miller, 1982 (*Holarctic Ecology* 5: 125-134)					O		M			
59	Miller *et al*., 1982 (*Holarctic Ecology* 5: 117-124)	SC			D	O					
60	Stoner *et al*., 1982 (*Holarctic Ecology* 5: 172-179)	SC			D				N		
61	Chapin, 1983 (*Polar Biology* 2: 47-52)		P						N	C	E
62	Kummerow *et al*., 1983 (*American Journal of Botany* 70: 1509-1515)	SC	P			O		M			
63	Maessen et al., 1983 (*Canadian Journal of Botany* 61: 1680-1691)	SC							N		
64	Bliss *et al*., 1984 (*Holarctic Ecology* 7: 305-324)	SC									
65	Bliss & Svoboda, 1984 (*Holarctic Ecology* 7: 325-344)	SC	P								
66	Miller *et al*., 1984 (*Ecological Monographs* 54: 361-405)	SC	P	T	D	O			N	C	E
67	Chapin *et al*., 1986 (*Journal of Ecology* 74: 167-195)								N	C	E
68	Malmer & Wallén, 1986 (*Oikos* 46: 200-206)								N		
69	Shaver *et al*., 1986 (*Journal of Ecology* 74: 257-278)	SC	P			O			N		E
70	Wallén, 1986 (*Oikos* 46: 51-56)	SC			D					C	
71	Marion *et al*., 1987 (*Holarctic Ecology* 10: 230-234)				D				N		
72	Nams & Freedman, 1987 (*Holarctic Ecology* 10: 128-136)	SC							N		
73	Chapin *et al*., 1988 (*Ecology* 69: 693-702)	SC			D			M	N		
74	McGraw & Chapin, 1989 (*Ecology* 70: 736-749)	SC							N		E
75	Henry *et al*., 1990 (*Canadian Journal of Botany* 68: 2660-2667)	SC		T						C	E
76	Kohn & Stasovski, 1990 (*Mycologia* 82: 23-35)							M			
77	Marion & Kummerow, 1990 (*Holarctic Ecology* 13: 50-55)								N		E
	1991–2000										
78	Koch *et al*., 1991 (*Oecologia* 88: 570-573)	SC				O	A		N		
79	Shaver & Chapin, 1991 (*Ecological Monographs* 61: 1-31)	SC	P	T					N		
80	Jonasson & Callaghan, 1992 (*New Phytologist* 122: 179-186)				D	O					

81	Vare *et al*., 1992 (*Mycorrhiza* 1: 93-104)								M			
82	Atkin *et al*., 1993 (*Oecologia* 96: 239-245)									N		
83	Chapin *et al*., 1993 (*Nature* 361: 150-153)	SC				O				N		
84	Atkin & Cummins, 1994 (*Plant and Soil* 159: 187-197)									N		
85	Kielland, 1994 (*Ecology* 75: 2373-2383)				D					N		
86	Kielland & Chapin, 1994 (*Oikos* 70: 443-448)									N		
87	Stewart & Freedman, 1994 (*Book L*, pp. 123-136)	SC								N		E
88	Atkin, 1996 (*Plant, Cell, and Environment* 19: 695-704)				D					N		E
89	BassiriRad *et al*., 1996 (*New Phytologist* 133: 423-430)	SC								N	C	E
90	Chapin *et al*., 1996 (*Journal of Vegetation Science* 7: 347-358)				D		A	M		N	C	E
91	Gebauer *et al*., 1996 (*Plant and Soil* 178: 37-48)	SC			D	O	A			N		
92	Hobbie, 1996 (*Ecological Monographs* 66: 503-522)		P	T		O				N	C	E
93	Michelsen *et al*., 1996 (*Oecologia* 105: 53-63)				D			M		N		
94	Nadelhoffer *et al*., 1996 (*Oecologia* 107: 386-394)									N		
95	Schimel & Chapin, 1996 (*Ecology* 77: 2142-2147)									N		
96	Shaver *et al*., 1996 (*Arctic and Alpine Research* 28: 363-379)											E
97	Vare *et al*., 1997 (*Arctic and Alpine Research* 29: 93-104)							M		N	C	
98	Hobbie & Chapin, 1998 (*Ecology* 79: 1526-1544)	SC								N	C	E
99	Michelsen *et al*., 1998 (*Oecologia* 115: 406-418)							M		N		
100	Ping *et al*., 1998 (*Journal of Geophysical Research* 103: 28917-28928)				D							
101	Shaver *et al*., 1998 (*Ecological Monographs* 68: 75-97)									N		E
102	Bilbrough *et al*., 2000 (*Arctic, Antarctic, and Alpine Research* 32: 404-411)									N		
103	Gill & Jackson, 2000 (*New Phytologist* 147: 13-31)			T		O						E
104	Visser *et al*., 2000 (*New Phytologist* 148: 93-103)	SC				O	A					E
	2001–2010											
105	Joabsson & Christensen, 2001 (*Global Change Biology* 7: 919-932)	SC			D						C	
106	van der Wal *et al*., 2001 (*Polar Biology* 24: 29-32)	SC										
107	Loya *et al*., 2002 (*Global Biogeochemical Cycles* 16: 48)			T							C	
108	McKane *et al*., 2002 (*Nature* 415: 68-71)									N		
109	Nadelhoffer *et al*. 2002 (*Plant and Soil* 242: 107-113)		P							N		E
110	Ruotsalainen *et al*., 2002 (*Mycorrhiza* 12: 29-36)							M		N		
111	Grogan & Jonasson, 2003 (*Ecology* 84: 202-218)	SC								N		

112	Henry & Jefferies, 2003 (*Journal of Ecology* 91: 627-636)								N		
113	van Wijk *et al*., 2003 (*Journal of Ecology* 91: 664-676)	SC							N		E
114	Grogan *et al*., 2004 (*Soil Biology & Biochemistry* 36: 641-654)	SC							N	C	E
115	Kutzbach *et al*. 2004 (*Biogeochemistry* 69: 341-362)				D	O	A			C	
116	Olsrud & Christensen, 2004 (*Soil Biology & Biochemistry* 36: 245-253)	SC								C	
117	Read *et al*., 2004 (*Canadian Journal of Botany* 82: 1243-1263)							M			
118	Ruotsalainen *et al*., 2004 (*Arctic, Antarctic, and Alpine Research* 36: 239-243)							M			
119	Ping *et al*., 2005 (*Soil Science Society of America Journal* 69: 1761-1772)				D						
120	Sullivan & Welker, 2005 (*Oecologia* 142: 616-626)	SC	P			O					E
121	Tye *et al*., 2005 (*Global Change Biology* 11: 1640-1654)								N		
122	Clemmensen & Michelsen, 2006 (*Canadian Journal of Botany* 84: 831-843)	SC				O		M			E
123	Clemmensen *et al*., 2006 (*New Phytologist* 171: 391-404)	SC						M	N		E
124	Hobbie & Hobbie, 2006 (*Ecology* 87: 816-822)							M	N		
125	Wang & Qui, 2006 (*Mycorrhiza* 16: 299-363)							M			
126	Bardgett *et al*., 2007 (*Soil Biology & Biochemistry* 39: 2129-2137)	SC							N		
127	Bjork *et al*., 2007 (*New Phytologist* 176: 862-873)	SC			D	O			N		E
128	Parton *et al*., 2007 (*Science* 315: 361-364)			T						C	
129	Sullivan *et al*., 2007 (*Oecologia* 153: 643-652)	SC	P	T	D	O				C	E
130	Clemmensen *et al*., 2008 (*Oecologia* 155: 771-783)							M	N		
131	Nowinski *et al*., 2008 (*Ecosystems* 11: 16-25)			T	D					C	E
132	Sorensen *et al*., 2008 (*Arctic, Antarctic, and Alpine Research* 40: 171-180)								N		
133	Sullivan *et al*., 2008 (*Ecosystems* 11: 61-76)	SC	P						N	C	E
134	Campioli *et al*., 2009 (*Ecosystems* 12: 760-776)	SC	P		D	O			N	C	
135	Borden *et al*., 2010 (*Soil Science Society of America Journal* 74: 580-592)				D						
136	Edwards & Jefferies, 2010 (*Journal of Ecology* 98: 737-744)								N		
137	Freschet *et al*., 2010a (*Journal of Ecology* 98: 362-373)								N		
138	Freschet *et al*., 2010b (*New Phytologist* 186: 879-889)								N		
	2010–2013										
139	Deslippe & Simard, 2011 (*New Phytologist* 192: 689–698)							M		C	E
140	Hill & Henry, 2011 (*Global Change Biology* 17: 276–287)	SC		T						C	E
141	Sloan, 2011 (Dissertation, University of Sheffield, England)	SC	P	T				M	N		E
142	Freschet *et al*., 2012a (*Functional Ecology* 26: 56-65)			T					N	C	

143	Freschet *et al*., 2012b (*Journal of Ecology* 100: 619-630)			T				N	C	
144	Keuper, 2012 (Dissertation, VU University, The Netherlands)	SC			D			N		E
145	Strom *et al*., 2012 (*Soil Biology & Biochemistry* 45: 61–70)					A			C	
146	Hicks Pries *et al*., 2013 (*Global Change Biology* 19: 649–661)								C	
147	McConnell *et al*., 2013 (*Environmental Research Letters* 8: 045029)	SC							C	
148	Segal, 2013 (Thesis, University of Alaska, Anchorage)	SC	P	T				N	C	E
149	Sloan *et al.* 2013 (*Global Change Biology* 19: 3668–3676)	SC	P	T						E

Books:

A. *Biological foundations of utilisation of nature of the Far North*. **1970.** Syktyvkar: Komi Publishing House (cited in Tikhomirov *et al*., 1981).

B. *Biological productivity and mineral cycling in the terrestrial plant communities*. **1971.** Leningrad: Nauka (in Russian, cited in Tikhomirov *et al*., 1981).

C. **Wielgolaski FE, Rosswall TH, eds. 1972.** *International Biological Programme, Tundra Biome: Proceedings IV. International meeting on the biological productivity of tundra. Leningrad, USSR, October, 1971*. Stockholm, Sweden: Swedish IBP Committee (cited in Wielgolaski *et al*., 1981).

D. **Bliss LC, Wielgolaski FE, eds. 1973.** *Primary production and production proccesses.* Stockholm, Sweden: IBP Tundra Biome Steering Committee.

E. **Roswall T, Heal OW, eds. 1975.** *Structure and function of tundra ecosystems*. Stockholm, Sweden: Ecology Bulletin (cited in Wielgolaski *et al*., 1981).

F. **Wielgolaski, FE, ed. 1975.** *Fennoscandian tundra ecosystems.* New York, New York, USA: Springer-Verlag.

G. **Bliss LC, ed. 1977.** *Truelove lowland, Devon Island, Canada: A high arctic ecosystem.* Edmonton, Alberta, Canada: The University of Alberta Press.

H. **Tieszen LL, ed. 1978.** *Vegetation and production ecology of an Alaskan arctic tundra.* New York, NY, USA: Springer-Verlag.

I. **Brown J, Miller PC, Tieszen LL, Bunnell FL, eds. 1980.** *An arctic ecosystem: the coastal tundra at Barrow, Alaska.* Stroudsburg, PA, USA: Dowden, Hutchinson & Ross, Inc.

J. **Sonesson M, ed. 1980.** *Ecology of a subarctic mire*. Stockholm, Sweden: Ecological Bulletins, Swedish Natural Science Research Council.

K. **Bliss LC, Heal OW, Moore JJ, eds. 1981.** *Tundra ecosystems: a comparative analysis.* New York, NY, USA: Cambridge University Press.
L. **Svoboda J, Freedman B, eds. 1994.** *Ecology of a polar oasis: Alexandra fiord, Ellesmere Island, Canada.* Toronto, Canada: Captus University Publications.

Papers, thesis, dissertation:

Aleksandrova VD. 1958. An attempt to measure the aerial and underground mass of plants in the Arctic tundra. *Botanicheskii Zhurnal* **43**:1748-1762. (In Russian.)

Aleksandrova VD. 1969. Aerial and underground mass of plants in the polar desert on Aleksandra Land Island (Franz Joseph Land). *Problemy Botaniki* **11**: 47-60. (In Russian.)

Allessio ML, Tieszen LL. 1975. Patterns of carbon allocation in an arctic tundra grass, *Dupontia fischeri* (Gramineae), at Barrow, Alaska. *American Journal of Botany* **62**: 797-807.

Atkin OK. 1996. Reassessing the nitrogen relations of Arctic plants: a mini-review. *Plant Cell and Environment* **19**: 695-704.

Atkin OK, Cummins WR. 1994. The effect of root temperature on the induction of nitrate reductase activites and nitrogen uptake rates in arctic plant species. *Plant and Soil* **159**: 187-197.

Atkin OK, Villar R, Cummins WR. 1993. The ability of several high arctic plant species to utilize nitrate-nitrogen under field conditions. *Oecologia* **96**: 239-245.

Bardgett RD, van der Wal R, Jonsdottir IS, Quirk H, Dutton S. 2007. Temporal variability in plant and soil nitrogen pools in a high-Arctic ecosystem. *Soil Biology & Biochemistry* **39**: 2129-2137.

BassiriRad H, Tissue DT, Reynolds JF, Chapin FS. 1996. Response of *Eriophorum vaginatum* to CO_2 enrichment at different soil temperatures: effects on growth, root respiration and PO_4^{3-} uptake kinetics. *New Phytologist* **133**: 423-430.

Bell KL, Bliss LC. 1978. Root growth in a polar semidesert environment. *Canadian Journal of Botany* **56**: 2470-2490.

Bilbrough CJ, Welker JM, Bowman WD. 2000. Early spring nitrogen uptake by snow-covered plants: A comparison of arctic and alpine plant function under the snowpack. *Arctic Antarctic and Alpine Research* **32**: 404-411.

Billings WD, Peterson KM, Shaver GR, Trent AW. 1977. Root growth, respiration, and carbon-dioxide evolution in an arctic tundra soil. *Arctic and Alpine Research* **9**: 129-137.

Bliss LC, Svoboda J. 1984. Plant-communities and plant-production in the Western Queen Elizabeth Islands. *Holarctic Ecology* **7**: 325-344.

Bliss LC, Svoboda J, Bliss DI. 1984. Polar deserts, their plant cover and plant-production in the Canadian High Arctic. *Holarctic Ecology* **7**: 305-324.

Björk RG, Majdi H, Klemedtsson L, Lewis-Jonsson L, Molau U. 2007. Long-term warming effects on root morphology, root mass distribution, and microbial activity in two dry tundra plant communities in northern Sweden. *New Phytologist* **176**: 862-873.

Borden PW, Ping CL, McCarthy PJ, Naidu S. 2010. Clay mineralogy in Arctic Tundra Gelisols, Northern Alaska. *Soil Science Society of America Journal* **74**: 580-592.

Campioli M, Michelsen A, Demey A, Vermeulen A, Samson R, Lemeur R. 2009. Net primary production and carbon stocks for subarctic mesic-dry tundras with contrasting microtopography, altitude, and dominant Species. *Ecosystems* **12**: 760-776.

Chapin FS. 1974. Morphological and physiological mechanisms of temperature compensation in phosphate absorption along a latitudinal gradient. *Ecology* **55**: 1180-1198.

Chapin FS. 1981. Field measurements of growth and phosphate absorption in *Carex aquatilis* along a latitudinal gradient. *Arctic and Alpine Research* **13**: 83-94.

Chapin FS. 1983. Direct and indirect effects of temperature on arctic plants. *Polar Biology* **2**: 47-52.

Chapin FS, Shaver GR, Kedrowski RA. 1986. Environmental controls over carbon, nitrogen and phosphorus fractions in *Eriophorum vaginatum* in Alaskan tussock tundra. *Journal of Ecology* **74**: 167-195.

Chapin FS, Barsdate RJ, Barel D. 1978. Phosphorus cycling in Alaskan coastal tundra: Hypothesis for the regulation of nutrient

cycling. *Oikos* **31**: 189-199.

Chapin FS, BretHarte MS, Hobbie SE, Zhong HL. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* **7**: 347-358.

Chapin FS, Fetcher N, Kielland K, Everett KR, Linkins AE. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil-water. *Ecology* **69**: 693-702.

Chapin FS, Johnson DA, McKendrick JD. 1980b. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: Implications for herbivory. *Journal of Ecology* **68**: 189-209.

Chapin FS, Moilanen L, Kielland K. 1993. Preferential use of organic nitrogen for growth by a nonmycorrhial arctic sedge. *Nature* **361**: 150-153.

Chapin FS, Tryon PR. 1982. Phosphate absorption and root respiration of different plant growth forms from Northern Alaska. *Holarctic Ecology* **5**: 164-171.

Chapin FS, Slack M. 1979. Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. *Oecologia* **42**: 67-79.

Clemmensen KE & Michelsen A. 2006. Integrated long-term responses of an arctic-alpine willow and associated ectomycorrhizal fungi to an altered environment. *Canadian Journal of Botany* **84**: 831-843.

Clemmensen KE, Sorensen PL, Michelsen A, Jonasson S, Strom L. 2008. Site-dependent N uptake from N-form mixtures by arctic plants, soil microbes and ectomycorrhizal fungi. *Oecologia* **155**: 771-783.

Clemmensen KE, Michelsen A, Jonasson S, Shaver GR. 2006. Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. *New Phytologist* **171**: 391-404.

Dennis JG. 1977. Distribution patterns of belowground standing crop in arctic tundra at Barrow, Alaska. *Arctic and Alpine Research* **9**: 113-127.

Deslippe JR, Simard SW. 2011. Below-ground carbon transfer among *Betula nana* may increase with warming in Arctic tundra. *New*

Phytologist **192**: 689-698

Ellis BA, Kummerow J. 1982. Temperature effect on growth rates of *Eriophorum vaginatum* roots. *Oecologia* **54**: 136-137.

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. 2010a. Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology* **98**: 362-373.

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. 2010b. Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytologist* **186**: 879-889.

Freschet GT, Aerts R, Cornelissen JHC. 2012a. A plant economics spectrum of litter decomposability. *Functional Ecology* **26**: 56-65.

Freschet GT, Aerts R, Cornelissen JHC. 2012b. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *Journal of Ecology* **100**: 619-630.

Gebauer RLE, Tenhunen JD, Reynolds JF. 1996. Soil aeration in relation to soil physical properties, nitrogen availability, and root characteristics within an arctic watershed. *Plant and Soil* **178**: 37-48.

Gill RA, Jackson RB. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**: 13-31.

Grogan P, Jonasson S. 2003. Controls on annual nitrogen cycling in the understory of a subarctic birch forest. *Ecology* **84**: 202-218.

Grogan P, Michelsen A, Ambus P, Jonasson S. 2004. Freeze–thaw regime effects on carbon and nitrogen dynamics in sub-arctic heath tundra microcosms. *Soil Biology & Biochemistry* **36**: 641-654.

Henry GHR, Svoboda J, Freedman B. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. *Canadian Journal of Botany* **68**: 2660-2667.

Henry HAL, Jefferies RL. 2003. Plant amino acid uptake, soluble N turnover and microbial N capture in soils of a grazed Arctic salt marsh. *Journal of Ecology* **91**: 627-636.

Hicks Pries CE, Schuur EAG, Crummer KG. 2013. Thawing permafrost increases old soil and autotrophic respiration in tundra: partitioning ecosystem respiration using $\delta^{13}C$ and $\delta^{14}C$. *Global Change Biology* **19**: 649-661.

Hill GB, Henry GHR. 2011. Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology* **17**: 276-287.

Hobbie JE, Hobbie EA. 2006. ^{15}N in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. *Ecology* **87**: 816-822.

Hobbie SE. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* **66**: 503-522.

Hobbie SE, Chapin FSI. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. *Ecology* **79**: 1526-1544.

Joabsson A, Christensen TR. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology* **7**: 919-932

Jonasson S, Callaghan TV. 1992. Root mechanical properties related to disturbed and stressed habitats in the Arctic. *New Phytologist* **122**: 179-186.

Keuper FK. 2012. *Direct and indirect effects of climatic changes on vegetation productivity and species composition of permafrost peatlands.* PhD thesis, VU University, Amsterdam, the Netherlands.

Kielland K. 1994. Amino-acid absorption by arctic plants: Implications for plant nutrition and nitrogen cycling. *Ecology* **75**: 2373-2383

Kielland K, Chapin FS. 1994. Phosphate uptake in arctic plants in relation to phosphate supply: the role of spatial and temporal variability. *Oikos* **70**: 443-448.

Khodachek EA. 1969. Phytomass of the tundra phytocoenoses on the west Taimyr. *Botanicheskii Zhurnal* **54**: 1059-1075. (In Russian.)

Koch GW, Bloom AJ, Chapin FS. 1991. Ammonium and nitrate as nitrogen sources in two Eriophorum species. *Oecologia* **88**: 570-573.

Kohn LM & Stasovski E. 1990. The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a High Arctic site. *Mycologia* **82**: 23-35.

Kummerow J, Ellis BA, Kummerow S, Chapin FS. 1983. Spring growth of shoots and roots in shrubs of an Alaskan muskeg. *American Journal of Botany* **70**: 1509-1515

Kummerow J, Krause D. 1982. The effects of variable nitrogen and phosphorus concentrations on *Eriophorum vaginatum* tillers grown in nutrient solutions. *Holarctic Ecology* **5**: 187-193

Kummerow J, McMaster GS, Krause DA. 1980. Temperature effect on growth and nutrient contents in *Eriophorum vaginatum* under controlled environmental conditions. *Arctic and Alpine Research* **12**: 335-342.

Kummerow J, Russell M. 1980. Seasonal root growth in the arctic tussock tundra. *Oecologia* **47**: 196-199.

Kutzbach L, Wagner D, Pfeiffer EM. 2004. Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry* **69**: 341-362.

Limbach WE, Oechel WC, Lowell W. 1982. Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. *Holarctic Ecology* **5**: 150-157.

Loya WM, Johnson LC, Kling GW, King JY, Reeburgh WS, Nadelhoffer KJ. 2002. Pulse-labeling studies of carbon cycling in arctic tundra ecosystems: contribution of photosynthates to soil organic matter. *Global Biogeochemical Cycles* **16**: 1101.

Maessen O, Freedman B, Nams MLN, Svoboda J. 1983. Resource allocation in High Arctic vascular plants of differing growth form. *Canadian Journal of Botany* **61**: 1680-1691.

Malmer N & Wallén B. 1986. Inorganic elements above- and belowground in dwarf shrubs on a subarctic peat bog. *Oikos* **46**: 200-206.

Marion GM, Miller PC, Black CH. 1987. Competition for tracer ^{15}N in tussock tundra ecosystems. *Holarctic Ecology* **10**: 230-234.

Marion GM & Kummerow J. 1990. Ammonium uptake by field-grown *Eriophorum vaginatum* roots under laboratory and simulated field conditions. *Holarctic Ecology* **13**: 50-55.

McConnell NA, Turetsky MR, McGuire AD, Kane ES, Waldrop MP, Harden JW. 2013. Controls on ecosystem and root respiration across a permafrost and wetland gradient in interior Alaska. *Environmental Research Letters* **8**: 045029.

McGraw JB, Chapin FS. 1989. Competititive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* **70**: 736-749.

McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA *et al*. 2002. Resource-based niche provide a basis for plant species diversity and dominance in arctic tundra. *Nature* **415**: 68-71

Michelsen A, Quarmby C, Sleep D, Jonasson S. 1998. Vascular plant ^{15}N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* **115**: 406-418.

Michelsen A, Schmidt IK, Jonasson S, Quarmby C, Sleep D. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. *Oecologia* **105**: 53-63.

Miller OK. 1982. Mycorrhizae, mycorrhizal fungi and fungal biomass in subalpine tundra at Eagle Summit, Alaska. *Holarctic Ecology* **5**: 125-134.

Miller PC, Mangan R, Kummerow J. 1982. Vertical distribution of organic matter in eight vegetation types near Eagle Summit, Alaska. *Holarctic Ecology* **5**: 117-124.

Miller PC, Miller PM, Blakejacobson M, Chapin FS, Everett KR, Hilbert DW, Kummerow J, Linkins AE, Marion GM, Oechel WC *et al*. 1984. Plant–soil processes in Eriophorum vaginatum tussock tundra in Alaska: A systems modeling approach. *Ecological Monographs* **54**: 361-405.

Nadelhoffer K, Shaver G, Fry B, Giblin A, Johnson L, McKane R. 1996. ^{15}N natural abundances and N use by tundra plants. *Oecologia* **107**: 386-394.

Nams MLN, Freedman B. 1987. Phenology and resource allocation in a high arctic everygreen dwarf shrub, Casiope tetragona.

Holarctic Ecology **10**: 128-136.

Nowinski NS, Trumbore SE, Schuur EAG, Mack MC, Shaver GR. 2008. Nutrient addition prompts rapid destabilization of organic matter in an arctic tundra ecosystem. *Ecosystems* **11**: 16-25.

Olsrud M, Christensen TR. 2004. Carbon cycling in subarctic tundra; seasonal variation in ecosystem partitioning based on *in situ* ^{14}C pulse-labelling. *Soil Biology & Biochemistry* **36**: 245-253.

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC *et al*. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**: 361-364.

Pavlova EB. 1969. On the plant mass of tundras of the western Taimyr. *Vestnik of the Moscom University*, *Biology Series* 5: 62-67. (In Russian.)

Ping CL, Bockheim JG, Kimble JM, Michaelson GJ, Walker DA. 1998. Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. *Journal of Geophysical Research-Atmospheres* **103**: 28917-28928.

Ping CL, Michaelson GJ, Packee EC, Stiles CA, Swanson DK, Yoshikawa K. 2005. Soil catena sequences and fire ecology in the boreal forest of Alaska. *Soil Science Society of America Journal* **69**: 1761-1772.

Read DJ, Leake JR, Perez-Moreno J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany* **82**: 1243-1263.

Segal AD. 2013. *Root and microbial respiration dominate CO_2 efflux in an arctic ecosystem.* MS thesis, University of Alaska, Anchorage, USA.

Shaver GR, Billings WD. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. *Ecology* **56**: 401-409.

Shaver GR, Billings WD. 1977. Effects of daylength and temperature on root elongation in tundra graminoids. *Oecologia* **28**: 57-65.

Shaver GR, Chapin FS III. 1991. Production: Biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs* **61**: 1-31.

Shaver GR, Chapin FS, Billings WD. 1979. Ecotypic differentiation in Carex aquatilis on ice-wedge polygons in the Alaskan coastal

tundra. *Journal of Ecology* **67**: 1025-1046.

Shaver GR, Chapin FS III, Gartner BL. 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *Journal of Ecology* **74**: 257-278.

Shaver GR, Cutler JC. 1979. Vertical distribution of live vascular phytomass in cottongrass tussock tundra. *Arctic and Alpine Research* **11**: 335-342.

Shaver GR, Laundre JA, Giblin AE, Nadelhoffer KJ. 1996. Changes in live plant biomass, primary production, and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research* **28**: 363-379.

Shaver GR, Johnson LC, Cades DH, Murray G, Laundre JA, Rastetter EB, Nadelhoffer KJ, Giblin AE. 1998. Biomass and CO_2 flux in wet sedge tundras: Responses to nutrients, temperature, and light. *Ecological Monographs* **68**: 75-97.

Sloan VL. 2011. *Plant roots in arctic ecosystems: stocks and dynamics, and their coupling to above-ground parameters.* PhD thesis, University of Sheffield, UK.

Sloan VL, Fletcher BJ, Press MC, Williams M, Phoenix GK. 2013. Leaf and fine root carbon stocks and turnover are coupled across Arctic ecosystems. *Global Change Biology* **19**: 3668–3676.

Sorensen PL, Clemmensen KE, Michelsen A, Jonasson S, Strom L. 2008. Plant and microbial uptake and allocation of organic and inorganic nitrogen related to plant growth forms and soil conditions at two subarctic tundra sites in Sweden. *Arctic, Antarctic, and Alpine Research* **40**: 171-180.

Stoner WA, Miller P, Miller PC. 1982. Seasonal dynamics and standing crops of biomass and nutrients in a subarctic tundra vegetation. *Holarctic Ecology* **5**: 172-179.

Ström L, Tagesson T, Mastepanov M, Christensen TR. 2012. Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. *Soil Biology & Biochemistry* **45**: 61-70.

Sullivan PF, Arens SJT, Chimner RA, Welker JM. 2008. Temperature and microtopography interact to control carbon cycling in a high arctic fen. *Ecosystems* **11**: 61-76.

Sullivan PF, Sommerkorn M, Rueth HM, Nadelhoffer KJ, Shaver GR, Welker JM. 2007. Climate and species affect fine root production with long-term fertilization in acidic tussock tundra near Toolik Lake, Alaska. *Oecologia* **153**: 643-652.

Sullivan PF, Welker JM. 2005. Warming chambers stimulate early season growth of an arctic sedge: results of a minirhizotron field study. *Oecologia* **142**: 616-626.

Tye AM, Young SD, Crout NMJ, West HM, Stapleton LM, Poulton PR, Laybourn-Parry J. 2005. The fate of ^{15}N added to high Arctic tundra to mimic increased inputs of atmospheric nitrogen released from a melting snowpack. *Global Change Biology* **11**: 1640-1654.

van der Wal R, van Lieshout SMJ, Loonen M. 2001. Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology* **24**: 29-32.

van Wijk MT, Williams M, Gough L, Hobbie SE, Shaver GR. 2003. Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? *Journal of Ecology* **91**: 664-676.

Väre H, Vestberg M, Eurola S. 1992. Mycorrhizae and root-associated fungi in Spitsbergen. *Mycorrhiza* **1**: 93–104.

Vare H, Vestberg M, Ohtonen R. 1997. Stifts in mycorrhiza and microbial activity along an oroarctic altitudinal gradient in northern Fennoscandia. *Arctic and Alpine Research* **29**: 93-104

Vikhireva-Vasilkova VV, Gavrilyuk VA, Shamurin VF. 1964. Aerial and underground mass of some dwarf shrub communities of Koryak Land. *Problemy Severa* 8: 130-147. (In Russian.)

Visser EJW, Bogemann GM, Van de Steeg HM, Pierik R, Blom CWPM. 2000. Flooding tolerance of Carex species in relation to field distribution and aerenchyma formation. *New Phytologist* **148**: 93-103.

Wallén B. 1986. Above- and belowground dry mass of the three main vascular plants on hummocks on a sub-arctic peat bog. *Oikos* **46**: 51-56.

Wang B, Qui Y-L. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* **16**: 299-363.

Webber PJ. 1977. Belowground tundra research – commentary. *Arctic and Alpine Research* **9**: 105-111.

Wein RW, Bliss LC. 1974. Primary production in Arctic cottongrass tussock tundra communities. *Arctic and Alpine Research* **6**: 261-274.

Wielogolaski FE. 1972. Vegetation types and plant biomass in tundra. *Arctic and Alpine Research* **4**: 289-306.