

CHAPTER 10

SYNTHESIS

The descriptive ecology of the terrestrial High Arctic (Summerhayes & Elton 1928; Warren Wilson 1966; Dierßen 1996; Rønning 1996) has laid the basis for using it as a model ecosystem. Vegetation composition is simple, diversity low, abiotic factors are of seemingly overriding importance for the growth and survival of all its inhabitants, and trophic ladders are very short indeed. Venturing into the details and minutia of arctic plant ecology revealed a surprising complexity of adaptations to both obvious (coldness, length of winter) and less obvious (anoxia, radiation) environmental conditions (e.g., Crawford 1989; Lee 1999). All these may or may not affect the way plants respond to environmental changes, such as elevated temperature, increased nutrient availability or increased grazing intensity.

The High Arctic is predicted to be exposed to major climate change (IPCC 1998), and is likely to be very sensitive to the changes. However, biotic interactions within arctic ecosystems are not well enough understood to enable us to make good predictions of responses. The mutual impetus for these studies was to address the potential knock-on effects of changing climate onto plants, and through plants onto herbivores. Therefore one needs to understand the principal interactions of the natural, unperturbed system. In consequence, this synthesis first pulls together how climate, plants and herbivores are interconnected in the High Arctic, before, in a second step, aims at predicting possible effects of alterations of this situation.

SPECIES INTERACTION

Only little is known about plant-plant interactions in the High Arctic. Summerhayes & Elton (1928) already described a successional pattern of vegetation development from barren rocks with lichens, over mosses, cushion plants towards a denser turf of dwarf shrubs and herbs, but the mechanisms behind this change were, to my knowledge, never explored. Weathering of rocks, accretion of silt and clay and the build-up of organic matter continuously changes the substrate of plant growth, giving

advantage from opportunistic lichens and mosses to vascular plants. We can only presume that mosses outcompete lichens and then get themselves overgrown by higher plants, but there seems to be no experimental evidence.

Only recently have plant ecologists performed removal experiments to investigate plant-plant interactions in the Arctic (see discussion in CHAPTER 5). Moreover, only one experiment (Hobbie *et al.* 1999) included mosses in the species pool. The result (*Sphagnum* removal resulted in a positive response of birch) indicates that indeed cryptogame-phanerogame interactions are present, although in this case *Sphagnum* controls growing conditions of *Betula*, rather than exerting direct competitive influence. For higher plant-plant interactions, the shelter that plants provide for themselves and their neighbours is a factor of great importance in the Arctic (CHAPTER 4, Carlsson & Callaghan 1991). The removal of facilitation causes more stress than the release from competition can make up for, hence removal experiments more often find positive than negative plant-plant interactions (Hobbie *et al.* 1999; Shevtsova *et al.* 1997). Using a different experimental approach, this problem can be solved, as demonstrated in CHAPTERS 4 and 5: even in the High Arctic plants do compete with one another, making competition an important factor in structuring plant communities. One important consequence of this finding is that we need to quantify the importance of competition and facilitation compared with abiotic checks on plant performance. This will require more sophisticated field experiments, which manipulate competition without manipulating facilitation, which look at the effect of plant density (of both neighbours and target species) on growth and, of course, an investigation into the mechanisms of facilitation and competition. In small pilot experiments, I could find no immediate temperature benefit for *Salix polaris* in stands of *Luzula confusa* or for it finding an associational refuge (Hay 1986) from grazing.

In comparison with plant-plant competition, herbivory in the High Arctic has been much more intensively investigated. However, due to the lack of long-term herbivore exclosures (but see Bazely & Jefferies 1986; Jefferies *et al.* 1994; Virtanen *et al.* 1997) we are still only beginning to understand the consequences of grazing in this ecosystem. Moreover, even for the most important food plants data are scarce. The best investigated example surely is the case of grazing by snow geese in La Perouse Bay, Canada, where due to a dramatic increase in bird numbers the system changed

from a grazed to a “ploughed” salt marsh, with virtually no vegetation remaining (Bazely & Jefferies 1986; Hik *et al.* 1992; Jefferies *et al.* 1994; Cargill & Jefferies 1984).

On Svalbard, vegetation development is influenced by reindeer (Van der Wal & Brooker, in prep.). Grasses in particular profit from the trampling and grazing of mosses, which otherwise hinder soil warming, thereby impeding the growth of vascular plants (Van der Wal *et al.* 2001b). In the data set from their survey, however, no correlation of *Salix polaris* abundance and grazing intensity could be detected (René van der Wal, pers. comm.), suggesting no lasting effect of reindeer grazing on that particular species. In CHAPTER 7, I suggest that this is must not be the case. The experimental exclusion of reindeer was a drastic measure, leading to a shift in the female-male-ratio, increased growth rates and increased allocation to secondary compounds. These may have long-term consequences, from pollination bottlenecks, through altered vegetation composition to reduced nutrient cycling due to less degradable leaf litter (Hobbie 1992). On the other hand, nutrient turnover by decomposition is extremely slow in the Arctic, taking decades to centuries (Dowding *et al.* 1981; Chapin *et al.* 1988). Hence, this is the time scale we would expect indirect effects of altered nutrient cycling to be detectable in the vegetation.

Furthermore, herbivores may influence the quality of their forage. Work especially from Scandinavia on Mountain Birch (*Betula tortuosa*) has shown the importance of (delayed) induced resistance for further usage of the same tree by the moth *Epirrita autumnata* (Haukioja & Neuvonen 1985; 1985a; 1985b). Our data from a simulated browsing experiment indicate a very fast increase in phenolics (within 15 minutes), but no resistance over a longer term (CHAPTER 7). On the contrary, phenolic levels were actually *reduced* in grazed plots compared to those where grazing was excluded for three years (CHAPTER 6). This ties in with the data of Chapin *et al.* (1985), who also reported a lack of inducible resistance for three Alaskan woody species. Thus, in our system, continuous grazing seems to maintain higher food quality (as reflected in the selection of clipped plots over controls: CHAPTER 7), hinting at maintenance of forage grounds by ungulate herbivores (“cyclic grazing”, as reviewed in Drent & Van Der Wal 1999).

IMPACT OF GLOBAL CLIMATE CHANGE ON TERRESTRIAL HIGH ARCTIC ECOSYSTEMS

In which way will environmental changes influence the functioning of arctic ecosystems, especially a) the growth of plants and the interactions between b) plants and plants and c) plants and herbivores? CHAPTER 2 reviews the results of field experiments carried out in the Arctic, investigating the effects of elevated temperature, increased UV-B, etc. The general result is that, as nutrient limitation is limiting to plant growth in most circumstances, all treatments that alleviated this limitation had a significant impact on plant growth (such as fertilisation, elevated temperature and shading). Plant responses to manipulations were highly individualistic (species specific), but grasses and shrubs seem to be the plant types gaining most from the climate of the future. This was indeed observed in an experiment manipulating air temperature (CHAPTER 5), where the deciduous shrub *Salix polaris* increased biomass in warmed plots, while the wood rush *Luzula confusa* did not (the interaction between these two species are discussed below).

However, some factors, such as season length, winter conditions, have been neglected in experimental approaches, although there is first evidence that they are indeed important (Van der Wal *et al.* 2000c; Walsh *et al.* 1997; Galen & Stanton 1999). Season length was also a significant determinant of the abundance of *Polygonum viviparum* plants along a snowmelt gradient (CHAPTER 3), although it had no effect on the actual biomass of the plants. But, as biomass was negatively correlated with soil water content, and soil water content decreased with earlier snowmelt, season length may have indirect effects on the performance of *Polygonum viviparum*. These data serve also as test of the idea that the high within-species, ecotypic diversity provides a buffer against environmental change: the two tested genotypes of *Polygonum viviparum* did not differ in temperature-dependence of their germination, nor did soil water content affect them differently (CHAPTER 3). This by no means rejects the principle idea of intraspecific variability buffering species against environmental change. However, the first reliable data supporting this notion are still to be produced. Predictions of the resilience of species and communities to global change are of great interest to science and society, and work of this type (i.e. linking a species' variability to its resilience) should be encouraged.

Plant-plant interactions

Only a handful of arctic studies tried to assess the impact of altered environments on interactions between plant species: Jonasson (1992) factored fertilisation with neighbour removal and found no interaction between these factors, indicating that facilitative effects are equally strong in fertilised and control plots. This is in line with the conclusions of Hobbie *et al.* (1999), who "... found no significant interactions between warming and species removal, suggesting that increased temperature per se will not alter the intensity of species interactions." (p.417). In contrast Shevtsova *et al.* (1997) found various cases where neighbour removal altered the response of plant species to warming or watering, but not always increased growth: *Empetrum nigrum* grew worse in warmed plots when its dominant neighbour *Vaccinium vitis-idaea* was removed. A similar result was obtained in the study of Hobbie & Chapin (1998a), where *Populus tremuloides* showed a reduced biomass in warmed plots with neighbours removed, while it responded positively to warming when the surrounding vegetation was left intact.

The results of the experiment presented in CHAPTER 5 support the latter conclusions: in mixed stands under elevated temperatures, *Salix polaris* outperformed *Luzula confusa* when compared to ambient temperatures. This change in competitive balance might have repercussions on the reindeer, which prefer *Salix* over *Luzula*, as well as on the nutrient cycling in the tundra, as *Salix* leaves decompose faster than those of *Luzula*, which remain attached to the plant for two or more years. However, this is the first study to show a change in *competition* rather than a change in *facilitation*. Hence the interplay of facilitation and competition in tundra ecosystems has to be incorporated into experiments and predictive models of vegetation change in the Arctic (see also CHAPTER 4).

Plant-herbivore interactions

Herbivores alter plant-plant interactions, as well as plant competition alters the effects of herbivory (CHAPTER 9). This simple statement hides the complexity of the connections and interrelationships that competition and herbivory have. In most studies of one factor the other is neglected, although presumably all plants experience both factors at some point in their life. Often enough, field experiments on competition delivered spurious results, because herbivory was not considered (Reader 1992). It is well documented that herbivory can cause shifts in competitive

dominance (CHAPTER 9, Crawley 1983), alter vegetation composition and ecosystem properties (Milchunas & Lauenroth 1993). Similarly, competition is regularly invoked as the ultimate cause of plant species replacement during succession (Glenn-Lewin & van der Maarel 1992). The simultaneous and synergistic action of competition and herbivory however deserves more consideration, especially by field experiments (see, e.g., Bonser & Reader 1995; Dormann *et al.* 2000; Van der Wal *et al.* 2000a). The simple modelling approach performed in CHAPTER 9 illustrates how complex the results of interacting biotic agents can be (e.g. leading to amplifications or damping of another factor, depending on the intensity of both), and how complex the environment is that plants are evolving into. Including facets of the abiotic environment in the model can be a first step to estimate the effect of changes in this environment. Not all changes, say in temperature, will effect plant-plant or plant-herbivore interactions, while others might tip the balance between dominance and extinction.

As mentioned in the introduction, so far only two field studies have tried to address the consequences of climate change on Arctic ungulate herbivores. Both (Walsh *et al.* 1997; Van der Wal *et al.* 2000c) manipulated the timing of snowmelt, simulating different season lengths, and their results are complementary, finding reindeer/caribou utilising early snowmelt patches more than late snowmelt patches, as biomass is higher there, independent of higher C/N-ratios. Plant defence (measured as phenolics in Van der Wal *et al.* 2000c) were similarly high throughout the experiment and hence could not serve as selection clue.

If one accepts that plant-herbivore interactions in boreal and arctic systems are at least partly determined by secondary compounds (Bryant & Kuropat 1980; 1981; 1991b; 1991a), then changes in secondary chemistry are among the most likely effects of altered climate to affect herbivore population dynamics. The carbon-nutrient balance hypothesis (Bryant *et al.* 1983) predicts decreases in plant defence compounds with increases in the relative availability of limiting nutrients (e.g. nitrogen). This was indeed the result of a two year shading \times fertilisation experiment (CHAPTER 8). Independent of the mechanism of alteration of the C/N-balance (i.e. either by increasing the N uptake and keeping C-assimilation constant, or by decreasing C-assimilation and keeping N uptake the same), *Salix* secondary compounds decreased linearly with increasing N-content of leaves. However, the fertilisation and shading levels required to produce a significant change in leaf-N are

dramatic, and beyond the most extreme predictions for arctic climate change. Elevated temperature, on the other hand, although increasing plant growth, did not alter the C/N-ratio of the leaves and accordingly had no detectable effect on plant defence chemistry (CHAPTER 8). Thus, judging from this short-term (two years) experiment, global climate change is unlikely to cause major bottom-up benefits or restrictions to the reindeer population.

FUTURE CHALLENGES

Although some features, such as plant growth, of arctic ecosystems have received much attention, quite some are still only insufficiently known. The recent rise in publications investigating **soil processes in the context of global climate change** (Nadelhoffer *et al.* 1991; 1997; Jonasson *et al.* 1993; 1999; Schmidt *et al.* 1999) is a promising step towards understanding the "hidden two-thirds" of terrestrial arctic ecosystems. However, all ecosystem processes are extremely slow in the Arctic, thus requiring long-term (>10 years) research, sensitive methods (e.g. isotope analysis, Robinson 2001) and the support of modelling approaches. The latter are especially rare for tundra ecosystems (Reynolds & Leadley 1992), and some vegetation change models still treat the soil as a black box (e.g. Epstein *et al.* 2000). On the other hand, as CHAPTERS 5 and 9 indicate, biotic interactions are at least partly driven by resource availability. In how far alterations of nutrient cycling will affect plant competition or plant-herbivore interactions is at present beyond our understanding. In a first step, determination of *in situ* decomposition rates for litter of different plant species may give us some idea as to which plants will have the biggest influence on nutrient cycling. Such experiments are underway in the Low Arctic (Hans Cornelissen, University of Amsterdam, personal communication), but need to be extended to the much harsher conditions of the High Arctic. In a next step, fertilisation experiments with *low* levels of nitrogen and phosphorus addition can be used to estimate the impact of altered nutrient availability on plant species composition. At present, fertilisation experiments employ much too high doses to mimic nutrient cycling processes (see CHAPTER 2).

The gaps in our knowledge of ecosystem processes are not restricted to soil processes. We only begin to unravel the **impact of grazing** on plant growth, nutrient cycling, vegetation composition, vascular-non-vascular plant interactions and so forth (Zimov *et al.* 1995; Milchunas & Lauenroth 1993; Manseau *et al.* 1996; De

Mazancourt *et al.* 1999; Olofsson *et al.* 2001; Van der Wal & Brooker 2001). Moreover, herbivory often interacts with plant-plant-competition in other ecosystems (Reader 1992; Dormann *et al.* 2000), making it a factor acting on multiple levels of the system. In the low arctic salt marsh at La Perouse Bay, where 80 to 100% of the net primary productivity is consumed by geese, nutrient cycling through faeces allows plant to overcompensate for grazing off-take (Belsky 1987; Hik & Jefferies 1990). In the case of mammalian grazing, off-take is usually much lower, and faeces deposition less homogenous. Clearly, the impact of reindeer grazing on productivity and species composition in tundra ecosystems needs further investigation. At the same time, both direct and indirect grazing effects might alter plant-plant interactions with long-term consequences for plant population dynamics (Mulder & Ruess 2001).

If we want to use the **tundra as a model ecosystem**, we have to understand what it has in common, and in which respects it differs from other ecosystems. For example, Are the factors limiting plant growth comparable?, Are seasonal effects of importance for ecosystem functions?, Does grazing affect the tundra more or less than temperate or tropic systems?, What are the roles of competition and facilitation between plants in shaping the vegetation and hence the primary productivity? Field experiments are a crucial part in the answering of these questions, they provide the parameters for ecosystem models, and they open our eyes for further hypotheses and ideas. One important step taken was the foundation of the International Tundra Experiment (ITEX), which tries to integrate research across the Arctic, with similar experimental protocols and objectives. Similar networks e.g. for mountainous areas in Europe (GLORIA, etc.) are providing first steps towards a comparison across latitudinal gradient. To allow a synthesis of these experiments, simple common approaches, such as the competition experiments of CHAPTER 4, herbivore exclosures (CHAPTER 7) and nutrient availability measurements (CHAPTER 5), need to be employed.

Finally, **long-term monitoring**, e.g. by aerial photography or satellite imagery plus permanent plots in the field, can provide useful data on two processes that are usually beyond the time scale of experimentation: soil formation/erosion and catastrophic events. Arctic soils display constant mixing due to frost heave (cryoturbation). This is more pronounced in wet than in dry tundra, and it acts over decades (Kuntze *et al.* 1994). As a consequence, soil is constantly destroyed, eroded and reborn, and plant life has to adapt to an unstable ground, as arctic plants can life

decades to centuries (Crawford 1989). Equally important might be catastrophic events like heavy erosion, snow-free winters or grazing destruction. The implications of these rare catastrophes are utterly unknown.

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APPENDIX

Table A 1 Response variables and there grouping for analysis.

group	Response parameter measured	
Biomass-group	1 total biomass (g)	7 apical abovegr. growth (g·m ²)
	2 aboveground biomass (living tissue) (g)	8 shoot growth (g)
	3 below-ground biomass (g)	9 stem growth (g)
	4 total above-gr. biomass (dead + live) (g)	10 relative stem growth (g·y ⁻¹)
	5 individ. leaf or shoot biomass (g)	11 leaf growth (g·y ⁻¹)
	6 total leaf mass (g)	
Chemistry-group	1 N-pool aboveground (g·m ⁻²)	14 Mn-content of leaves (mg·g ⁻¹)
	2 P-pool aboveground (g·m ⁻²)	15 B-content of leaves (mg·g ⁻¹)
	3 K-pool aboveground (g·m ⁻²)	16 sugar content of leaves (mg·g ⁻¹)
	4 Ca-pool aboveground (g·m ⁻²)	17 polysaccharide content of leaves (mg·g ⁻¹)
	5 Mg-pool aboveground (g·m ⁻²)	18 protein N content of leaves (mg·g ⁻¹)
	6 N-content of leaves (mg·g ⁻¹)	19 amino acid N content of leaves (mg·g ⁻¹)
	7 P-content of leaves (mg·g ⁻¹)	20 soluble organic P content of leaves (mg·g ⁻¹)
	8 K-content of leaves (mg·g ⁻¹)	21 sol. phenolic content of leaves (mg·g ⁻¹)
	9 Ca -content of leaves (mg·g ⁻¹)	22 condensed-tannin content of leaves (mg·g ⁻¹)
	10 Mg-content of leaves (mg·g ⁻¹)	23 total chlorophyll content of leaves (μmol·g ⁻¹)
	11 Zn-content of leaves (mg·g ⁻¹)	24 carotinoids content (g·m ⁻²)
	12 Cu-content of leaves (mg·g ⁻¹)	25 UV-B compounds (mg·g ⁻¹)
	13 Fe-content of leaves (mg·g ⁻¹)	26 leaf total non-structural carbon (mg·g ⁻¹)
leaf-group	1 leaf area (mm ² ·tiller ⁻¹)	4 leaf area (cm ² ·leaf ⁻¹)
	2 shoot or leaf length (mm)	5 relative leaf growth rate (cm·y ⁻¹)
	3 leaf width or thickness (mm)	6 specific leaf area (m ² ·g ⁻¹)
reproduction-group	1 length of prefloration period (d)	8 fruit or bulbil dry weight/flower or spike (mg)
	2 inflorescence density (nr.·m ⁻²)	9 fruit fresh weight (mg)
	3 seed setting flowers (m ⁻²)	10 fruit density (nr.·m ⁻² or plant ⁻¹)
	4 flowering (%)	11 fruits (flower ⁻¹)
	5 nr. of seeds or bulbils (per flower or spike)	12 spike or pedicel length (cm)
	6 capsule volume (mm ³)	13 allocation to seeds (%)
	7 fruit or bulbil dry weight (mg)	14 germination rate (%)
physiology-group	1 leaf δ ¹³ C (‰)	11 carboxylation efficiency (%)
	2 meristems active (%)	12 N-uptake (g·m ⁻² ·y ⁻¹)
	3 CO ₂ -uptake rate (μmol·m ⁻² ·s ⁻¹)	13 P-uptake (g·m ⁻² ·y ⁻¹)
	4 transpiration rate (mg·m ⁻² ·s ⁻¹)	14 nitrate reductase activity (μmol·gFW ⁻¹ ·h ⁻¹)
	5 area net photosynthesis (μm·m ⁻² ·s ⁻¹)	15 ascorbate peroxidase act. (nkat·mg protein ⁻¹)
	6 weight net photosynthesis (μm·g ⁻¹ ·s ⁻¹)	16 glutathione reductase act. (nkat·mg protein ⁻¹)
	7 N net photosynthesis (μmol·gN ⁻¹ ·s ⁻¹)	17 phosphatase activity (μmol·g ⁻¹ ·h ⁻¹)
	8 P net photosynthesis (μmol·gP ⁻¹ ·s ⁻¹)	18 exocellulase activity (μmol·g ⁻¹ ·h ⁻¹)
	9 light saturation rate (Amax: μmolCO ₂ ·m ⁻² ·s ⁻¹)	19 endocellulase activity (μmol·g ⁻¹ ·h ⁻¹)
	10 apparent quantum yield (molCO ₂ ·mol photon ⁻¹)	

Table A 2 Studies incorporated in the database, showing which data were used (response variables: for coding see Table A1). "Year" refers to the duration of the experiment when measurements were taken. "Factors" are: acid = simulation of acid rain, CO₂ = elevated CO₂, F = fertilisation, L = shading, N = nitrogen addition, P = phosphorus addition, removal = selective species removal treatment, UV-B = increased UV-B radiation, T = elevated temperature, W = watering; + and × indicate treatments combined additively or factorially, respectively.

location	references	experi- ment	factors	year	species	response variable	
Ellesmere Island, Canada 78,9°N 30 m a.s.l. (?)	Henry <i>et al.</i> 1986	1	F, W	2	<i>Carex membranacea</i>	biomass-2,4	
					<i>Eriophorum angustifolium</i>	biomass-2,4	
					<i>Cassiope tetragona</i>	biomass-2,4; reproduction-2	
					<i>Dryas integrifolia</i>	biomass-2,4; reproduction-2	
					<i>Eriophorum angustifolium</i>	biomass-2,4; reproduction-2	
					<i>Juncus biglumis</i>	biomass-2,4; reproduction-2	
					<i>Luzula arctica</i>	biomass-2,4; reproduction-2	
					<i>Papaver lapponicum</i>	biomass-2,4	
					<i>Polygonum viviparum</i>	biomass-2,4; reproduction-2	
500 m a.s.l.	Stenström <i>et al.</i> 1997	2	T	1	<i>Saxifraga oppositifolia</i>	reproduction-2,11,12	
					2	<i>Saxifraga oppositifolia</i>	reproduction-2,11,12
					3	<i>Saxifraga oppositifolia</i>	reproduction-2,11,12
30 m a.s.l. Barrow, Alaska	Jones <i>et al.</i> 1997	3	T	1	<i>Salix arctica</i>	biomass-5; leaf-2; reproduction-1,10,11	
					4	T	1
Eagle Creek, Alaska 65°26'N 145°30'W 730 m a.s.l.	Shaver & Chapin 1986	5	F	3	<i>Eriophorum vaginatum</i>	biomass-1	
					<i>Carex bigelowii</i>	biomass-1	
					<i>Vaccinium uliginosum</i>	biomass-1	
					<i>Betula nana</i>	biomass-1	
					<i>Rubus chamaemorus</i>	biomass-1	
					<i>Vaccinium vitis-idaea</i>	biomass-1	
					<i>Empetrum nigrum</i>	biomass-1	
					<i>Andromeda polifolia</i>	biomass-1	
total	biomass-1						

Kurapuk Ridge, Alaska 68°37'N 149°18'W 917 m a.s.l.	Shaver & Chapin 1986	6	F	3	<i>Petasitis frigidus</i>	biomass-1
					<i>Polygonum bistorta</i>	biomass-1
					<i>Pyrola secunda</i>	biomass-1
					<i>Saxifraga punctata</i>	biomass-1
					<i>Calamagrostis spec.</i>	biomass-1
					<i>Eriophorum vaginatum</i>	biomass-1
					<i>Carex bigelowii</i>	biomass-1
					<i>Vaccinium uliginosum</i>	biomass-1
					<i>Betula nana</i>	biomass-1
					<i>Salix pulchra</i>	biomass-1
					<i>Rubus chamaemorus</i>	biomass-1
					<i>Vaccinium vitis-idaea</i>	biomass-1
					<i>Ledum palustre</i>	biomass-1
					<i>Cassiope tetragona</i>	biomass-1
					<i>Empetrum nigrum</i>	biomass-1
					total	biomass-1
	<i>Calamagrostis spec.</i>	biomass-1				
	<i>Poa arctica</i>	biomass-1				
	<i>Eriophorum vaginatum</i>	biomass-1				
	<i>Carex bigelowii</i>	biomass-1				
	<i>Betula nana</i>	biomass-1				
	<i>Salix pulchra</i>	biomass-1				
	<i>Salix reticulata</i>	biomass-1				
	<i>Vaccinium vitis-idaea</i>	biomass-1				
	<i>Ledum palustre</i>	biomass-1				
	<i>Cassiope tetragona</i>	biomass-1				
	<i>Empetrum nigrum</i>	biomass-1				
	total	biomass-1				
Sagwon, Alaska 69°37'N 148°40'W 388 m a.s.l.	Shaver & Chapin 1986	7	F			
					<i>Calamagrostis spec.</i>	biomass-1
					<i>Eriophorum vaginatum</i>	biomass-1
					<i>Carex bigelowii</i>	biomass-1

					<i>Betula nana</i>	biomass-1
					<i>Salix pulchra</i>	biomass-1
					<i>Vaccinium vitis-idaea</i>	biomass-1
					<i>Ledum palustre</i>	biomass-1
					<i>total</i>	biomass-1
Toolik Lake	Shaver & Chapin 1986	8	F	5	<i>Polygonum bistorta</i>	biomass-1
68°38'N 149°34'W					<i>Calamagrostis spec.</i>	biomass-1
760 m a.s.l.					<i>Eriophorum vaginatum</i>	biomass-1
					<i>Carex bigelowii</i>	biomass-1
					<i>Vaccinium uliginosum</i>	biomass-1
					<i>Betula nana</i>	biomass-1
					<i>Salix pulchra</i>	biomass-1
					<i>Rubus chamaemorus</i>	biomass-1
					<i>Vaccinium vitis-idaea</i>	biomass-1
					<i>Ledum palustre</i>	biomass-1
					<i>Cassiope tetragona</i>	biomass-1
					<i>Empetrum nigrum</i>	biomass-1
					<i>total</i>	biomass-1
LTER, Toolik Lake, Alaska	Chapin & Shaver 1985 [1]	9	L, T, F	1	<i>Eriophorum vaginatum</i>	biomass-1,3,5,8; chemistry-1,2,6,7; chemistry-16-22 [3]
68°38'N, 149°39'W	Shaver, Chapin & Gartner 1986 [2]			2	<i>Aulacomnium turgidum</i>	biomass-5 [1]
760 m a.s.l.	Chapin, Shaver & Kedrowski 1986 [3]				<i>Betula nana</i>	biomass-5 [1]
					<i>Carex aquatilis</i>	biomass-5 [1]
					<i>Carex bigelowii</i>	biomass-5 [1]
					<i>Empetrum nigrum</i>	biomass-5 [1]
					<i>Eriophorum angustifolium</i>	biomass-5 [1]
					<i>Eriophorum vaginatum</i>	biomass-5 [1]; biomass-1,3,8; chemistry-1,2,6,7; chemistry-16-22 [3]
					<i>Ledum palustre</i>	biomass-5 [1]
					<i>Polygonum bistorta</i>	biomass-5 [1]
					<i>Rubus chamaemorus</i>	biomass-5 [1]
					<i>Salix pulchra</i>	biomass-5 [1]
					<i>Vaccinium vitis-idaea</i>	biomass-5 [1]
	Chapin <i>et al.</i> 1995 [1]	10	L, T, F	3	<i>Aulacomnium spec.</i>	biomass-2,7 [1]

Chapin & Shaver 1996 [2]					<i>Betula nana</i>	biomass-2,7 [1]; biomass-5; chemistry-6,7; physiology-6 [2]
					<i>Carex bigelowii</i>	biomass-2,7 [1]
					<i>Eriophorum vaginatum</i>	biomass-2,7 [1]; biomass-5; chemistry-6,7;11,12; physiology-6 [2]
					<i>Hylocomium splendens</i>	biomass-2,7 [1]
					<i>Ledum palustre</i>	biomass-2,7 [1]; biomass-5; chemistry-6,7; physiology-2,6 [2]
					<i>Rubus chamaemorus</i>	biomass-2,7 [1]
					<i>Sphagnum spec.</i>	biomass-2,7 [1]
					<i>Vaccinium vitis-idaea</i>	biomass-2,7 [1]; biomass-5; chemistry-6,7; physiology-2 [2]
					total	biomass-2,7; chemistry-1-5; physiology-12,13 [1]
				9	<i>Aulacomnium spec.</i>	biomass-2,7 [1]
					<i>Betula nana</i>	biomass-2,7 [1]
					<i>Carex bigelowii</i>	biomass-2,7 [1]
					<i>Eriophorum vaginatum</i>	biomass-2,7 [1]
					<i>Hylocomium splendens</i>	biomass-2,7 [1]
					<i>Ledum palustre</i>	biomass-2,7 [1]
					<i>Rubus chamaemorus</i>	biomass-2,7 [1]
					<i>Sphagnum spec.</i>	biomass-2,7 [1]
					<i>Vaccinium vitis-idaea</i>	biomass-2,7 [1]
					total	biomass-2,7; chemistry-1-5; physiology-12,13 [1]
Shaver <i>et al.</i> 1998	11	L, F×T		6	<i>Carex cordorrhiza</i>	biomass-1; chemisty-6,7
					<i>Carex rotundata</i>	chemisty-6,7
					<i>Eriophorum vaginatum</i>	chemisty-6,7
					<i>Trichophorum caespitosum</i>	biomass-1
					moss	biomass-1; chemisty-6,7
					graminoids	biomass-1; leaf-4
					total	biomass-1-3; chemisty-1,2; ecosystem-1-3
Tissue & Oechel 1987	12	CO ₂ , CO ₂ +T		1	<i>Eriophorum vaginatum</i>	chemistry-26; leaf-1,5; physiology-3,4
Moorhead & Linkins 1997	13	CO ₂ , water Table			<i>Eriophorum vaginatum</i>	physiology-14,19
					<i>Betula nana</i>	physiology-14,17-19
Molau & Shaver 1997	14	T, F		9	<i>Eriophorum vaginatum</i>	reproduction-3,9
Hobbie & Chapin 1998	15	T		1	<i>Alnus crispa</i>	reproduction-14
					<i>Betula papyrifera</i>	reproduction-14
					<i>Picea glauca</i>	reproduction-14

				<i>Populus balsamifera</i>	reproduction-14
				<i>Populus tremuloides</i>	reproduction-14
			2	<i>Alnus crispa</i>	biomass-8
				<i>Betula papyrifera</i>	biomass-8
				<i>Picea glauca</i>	biomass-8
				<i>Populus balsamifera</i>	biomass-8
				<i>Populus tremuloides</i>	biomass-8
Hobbie <i>et al.</i> 1999 [1]	16	T × removal	1	<i>Carex bigelowii</i>	leaf-2 [1]
Hobbie & Chapin 1998A [2]				<i>Eriophorum vaginatum</i>	leaf-2 [1]
				<i>Betula nana</i>	leaf-2 [1]
				<i>Ledum palustre</i>	leaf-2 [1]
				<i>Vaccinium vitis-idaea</i>	leaf-2 [1]
				<i>Hylocomium splendens</i>	leaf-2 [1]
				<i>Sphagnum</i> spp.	leaf-2 [1]
			2	<i>Carex bigelowii</i>	leaf-2 [1]
				<i>Eriophorum vaginatum</i>	leaf-2 [1]
				<i>Betula nana</i>	leaf-2 [1]
				<i>Ledum palustre</i>	leaf-2 [1]
				<i>Vaccinium vitis-idaea</i>	leaf-2 [1]
				<i>Hylocomium splendens</i>	leaf-2 [1]
				<i>Sphagnum</i> spp.	leaf-2 [1]
			3	<i>Rubus chamaemorus</i>	biomass-4 [1]
				<i>Vaccinium uliginosum</i>	biomass-4 [1]
				<i>Betula nana</i>	biomass-4 [1]
				<i>Andromeda polifolia</i>	biomass-4 [1]
				<i>Cassiope tetragona</i>	biomass-4 [1]
				<i>Empetrum nigrum</i>	biomass-4 [1]
				<i>Ledum palustre</i>	biomass-4, reproduction-5,8 [1]
				<i>Vaccinium vitis-idaea</i>	biomass-4, reproduction-5,8 [1]
				<i>Carex bigelowii</i>	biomass-4, reproduction-5,8 [1]
				<i>Eriophorum vaginatum</i>	biomass-4 [1]
				<i>Pedicularis</i> spp.	biomass-4 [1]
				<i>Polygonum bistorta</i>	biomass-4 [1]

					<i>Aulacomnium turgidum</i>	biomass-1 [1]
					<i>Dicranum</i> spp.	biomass-1 [1]
					<i>Hylocomium splendens</i>	biomass-1 [1]
					<i>Sphagnum</i> spp.	biomass-1 [1]
					lichens	biomass-1 [1]
					total	biomass-4 [1]
		17	T	4	<i>Eriophorum vaginatum</i>	biomass-2,3; chemistry-1; physiology-13 [2]
					<i>Carex bigelowii</i>	biomass-2,3; chemistry-1; physiology-13 [2]
					<i>Betula nana</i>	biomass-2,3; chemistry-1; physiology-13 [2]
					<i>Rubus chamaemorus</i>	biomass-2,3; chemistry-1 [2]
					<i>Vaccinium uliginosum</i>	biomass-2,3; chemistry-1 [2]
					<i>Vaccinium vitis-idaea</i>	biomass-2,3; chemistry-1; physiology-13 [2]
					<i>Ledum palustre</i>	biomass-2,3; chemistry-1; physiology-13 [2]
					<i>Cassiope tetragona</i>	biomass-2,3; chemistry-1 [2]
					<i>Empetrum nigrum</i>	biomass-2,3; chemistry-1 [2]
					<i>Andromeda polifolia</i>	biomass-2,3; chemistry-1 [2]
					<i>Pedicularis</i> spp.	biomass-2,3; chemistry-1 [2]
					<i>Polygonum bistorta</i>	biomass-2,3; chemistry-1 [2]
					<i>Sphagnum</i> spp.	biomass-5; chemistry-1; physiology-13 [2]
					<i>Aulacomnium turgidum</i>	biomass-5; chemistry-1; physiology-13 [2]
					<i>Dicranum</i> spp.	biomass-5; chemistry-1; physiology-13 [2]
					<i>Pleurozium schreberi</i>	biomass-5; chemistry-1 [2]
					<i>Polytrichum</i> spp.	biomass-5; chemistry-1 [2]
					<i>Tomenthypnum nitens</i>	biomass-5; chemistry-1 [2]
					<i>Ptilium crista-castrensis</i>	biomass-5; chemistry-1 [2]
					lichens	biomass-5; chemistry-1; physiology-13 [2]
					total	biomass-2,3 [2]
Eagle Summit, Alaska	McGraw 1985	18	N, P, L, W	3	<i>Dryas octopetala</i>	biomass-2
65°26'N 145°30'W					forbs	biomass-2
1050 m a.s.l.					graminoids	biomass-2
					shrubs	biomass-2
					total	biomass-2
Disko Island, Greenland	Mølgaard & Christensen 1997	19	T	1	<i>Papaver radicum</i>	biomass-2, reproduction-5

69°17'N 53°45'W				2	<i>Papaver radicum</i>	biomass-2, reproduction-5
				3	<i>Papaver radicum</i>	biomass-2, reproduction-5
				4	<i>Papaver radicum</i>	biomass-2, reproduction-5
Abisko, Sweden	Johanson <i>et al.</i> 1995 [1]	20	UV-B (15%)	1	<i>Empetrum hermaphroditum</i>	biomass-9,10 [1]
68°21'N 18°49'E	Taulavuori <i>et al.</i> 1998 [2]				<i>Vaccinium myrtillus</i>	biomass-9,10 [1]
360 m a.s.l.	Gehrke 1999 [3]				<i>Vaccinium uliginosum</i>	biomass-9,10 [1]
					<i>Vaccinium vitis-idaea</i>	biomass-9,10 [1]
					<i>Hylocomium splendens</i>	biomass-8, leaf-2, chemistry-25[3]
					<i>Polytrichum commune</i>	biomass-8, leaf-2, chemistry-25[3]
				2	<i>Empetrum hermaphroditum</i>	biomass-9,10; leaf-3,4 [1]
					<i>Vaccinium myrtillus</i>	biomass-9,10; leaf-3,4 [1]
					<i>Vaccinium uliginosum</i>	biomass-9,10; leaf-3,4 [1]
					<i>Vaccinium vitis-idaea</i>	biomass-9,10 [1]
					<i>Hylocomium splendens</i>	biomass-8, leaf-2 [3]
					<i>Polytrichum commune</i>	biomass-8, leaf-2 [3]
				3	<i>Empetrum hermaphroditum</i>	biomass-5 [1]
					<i>Vaccinium myrtillus</i>	biomass-5, leaf-3,4 [1]
					<i>Vaccinium uliginosum</i>	biomass-5, leaf-3,4 [1]
					<i>Vaccinium vitis-idaea</i>	biomass-5, leaf-3,4 [1]
					<i>Hylocomium splendens</i>	biomass-5,8, leaf-2,3, chemistry-23-25[3]
					<i>Polytrichum commune</i>	biomass-5,8, leaf-2,3, chemistry-23-25[3]
360 m a.s.l.	Gwynn-Jones <i>et al.</i> 1997	21	CO ₂ × UV-B	7	<i>Vaccinium myrtillus</i>	chemistry-25; physiology-15,16 [2]
				1	<i>Empetrum hermaphroditum</i>	leaf-2
					<i>Vaccinium myrtillus</i>	leaf-2; reproduction-10
				2	<i>Empetrum hermaphroditum</i>	leaf-2
					<i>Vaccinium myrtillus</i>	leaf-2; reproduction-10
				3	<i>Empetrum hermaphroditum</i>	leaf-2
					<i>Vaccinium myrtillus</i>	leaf-2,3; reproduction-10
					<i>Vaccinium vitis-idaea</i>	leaf-3
380 m a.s.l.	Karlsson 1985	22	W, F+W	1	<i>Vaccinium uliginosum</i>	biomass-7; chemistry-6-8, leaf-4
					<i>Vaccinium vitis-idaea</i>	biomass-7; chemistry-6-8, leaf-4
				2	<i>Vaccinium uliginosum</i>	biomass-7; chemistry-6-8, leaf-4
					<i>Vaccinium vitis-idaea</i>	biomass-7; chemistry-6-8, leaf-4

	Wookey <i>et al.</i> 1995 [1]	23	T × W × F	1	<i>Empetrum hermaphroditum</i>	biomass-2,8,9,11 [2]; reproduction-7,10 [1]
	Parsons <i>et al.</i> 1994 [2]				<i>Vaccinium vitis-idaea</i>	biomass-2,8,9,11 [2]
	Parsons <i>et al.</i> 1995 [3]				<i>Vaccinium uliginosum</i>	biomass-2,8,9,11 [2]
	Potter <i>et al.</i> 1995 [4]				<i>Vaccinium myrtillus</i>	biomass-2 [2]
	Press <i>et al.</i> 1998 [5]			2	<i>Calamagrostis lapponica</i>	biomass-2; leaf-2; reproduction-4 [3]
					<i>Empetrum hermaphroditum</i>	biomass-2,6,7,9 [2]
					<i>Vaccinium vitis-idaea</i>	biomass-2,6,7,9 [2]
					<i>Vaccinium uliginosum</i>	biomass-2,6,7,9 [2]
					<i>Vaccinium myrtillus</i>	biomass-2,6,7,9 [2]
				3	<i>Calamagrostis lapponica</i>	biomass-2; leaf-2; reproduction-4 [3]
					<i>Hylocomium splendens</i>	biomass-2; leaf-2 [4]
					<i>Polytrichum commune</i>	biomass-2; leaf-1 [4]
				5	shrubs	biomass-2 [5]
					herbs	biomass-2 [5]
					grasses	biomass-2 [5]
					ferns	biomass-2 [5]
					bryophytes	biomass-2 [5]
					lichens	biomass-2 [5]
450 m a.s.l.	Havström <i>et al.</i> 1993 [1]	24	L × F, F × T (2 levels)	3	<i>Cassiope tetragona</i>	biomass-5; leaf-2 [1]
	Michelsen <i>et al.</i> 1996 [2]			5	<i>Cassiope tetragona</i>	biomass-2; chemistry-6,23; physiology-1 [2]
	Graglia <i>et al.</i> 1997 [3]				<i>Empetrum hermaphroditum</i>	biomass-4; chemistry-6,23; physiology-1 [2]
	Jonasson <i>et al.</i> 1999 [4]				deciduous shrubs	biomass-4, chemistry-1,2,6,7 [4]
					evergreen shrubs	biomass-4, chemistry-1,2,6,7 [4]
					herbs (grasses & forbs)	biomass-4, chemistry-1,2,6,7 [4]
					mosses	biomass-4, chemistry-1,2,6,7 [4]
				6	<i>Arctostaphylos alpina</i>	biomass-5; leaf-1 [3]
					<i>Betula nana</i>	biomass-5; leaf-1 [3]
					<i>Rhododendrom lapponicum</i>	biomass-5; leaf-1 [3]
					<i>Vaccinium uliginosum</i>	biomass-5; leaf-1 [3]
					<i>Empetrum hermaphroditum</i>	biomass-5; leaf-1 [3]
					<i>Vaccinium vitis-idaea</i>	biomass-5; leaf-1 [3]
					<i>Salix polaris x herbacaea</i>	biomass-5; leaf-1 [3]
981 m a.s.l.	Stenström <i>et al.</i> 1997	25	T	2	<i>Saxifraga oppositifolia</i>	reproduction-1,5,10,11

1150 m a.s.l.	Havström <i>et al.</i> 1993 [1] Michelsen <i>et al.</i> 1996 [2] Graglia <i>et al.</i> 1997 [3] Jonasson <i>et al.</i> 1999 [4]	26	L x F, F x T	3	<i>Saxifraga oppositifolia</i>	reproduction-1,5,10,11
				3	<i>Cassiope tetragona</i>	biomass-5; leaf-2 [1]
				5	<i>Cassiope tetragona</i>	biomass-2; chemistry-6,23; physiology-1 [2]
					deciduous shrubs	biomass-4, chemistry-1,2,6,7 [4]
					evergreen shrubs	biomass-4, chemistry-1,2,6,7 [4]
					herbs (grasses & forbs)	biomass-4, chemistry-1,2,6,7 [4]
					mosses	biomass-4, chemistry-1,2,6,7 [4]
				6	<i>Arctostaphylos alpina</i>	biomass-5; leaf-1 [3]
					<i>Betula nana</i>	biomass-5; leaf-1 [3]
					<i>Rhododendrom lapponicum</i>	biomass-5; leaf-1 [3]
	<i>Vaccinium uliginosum</i>	biomass-5; leaf-1 [3]				
	<i>Empetrum hermaphroditum</i>	biomass-5; leaf-1 [3]				
	<i>Vaccinium vitis-idaea</i>	biomass-5; leaf-1 [3]				
	<i>Salix polaris x herbacaea</i>	biomass-5; leaf-1 [3]				
Latnjajaure, Sweden	Abisko, Jones <i>et al.</i> 1997	27	T	1	<i>Salix herbacea</i>	reproduction-1,10,11
68°21'N 18°30'E	Welker <i>et al.</i> 1997	28	T	1	<i>Dryas octopetala</i>	reproduction-9,12
981 m a.s.l.	Alatalo & Totland 1997	29	T	2	<i>Silene acaulis</i>	reproduction-1,9-11
				1	<i>Eriophorum vaginatum</i>	reproduction-1,9
				2	<i>Eriophorum vaginatum</i>	reproduction-1,9
	Stenström & Jónsdóttir 1997	31	T	3	<i>Eriophorum vaginatum</i>	reproduction-1,9
				1	<i>Carex bigelowii</i>	leaf-2,3; reproduction-1,4,5,12
				2	<i>Carex bigelowii</i>	leaf-2,3; reproduction-1,4,5,12
	Molau 1997	32	T	1	<i>Cassiope tetragona</i>	leaf-2; reproduction-1,11
				1	<i>Ranunculus nivalis</i>	leaf-2,3; reproduction-1,5,9,11
				2	<i>Cassiope tetragona</i>	leaf-2; reproduction-1,11
				2	<i>Ranunculus nivalis</i>	leaf-2,3; reproduction-1,5,9,11
				3	<i>Cassiope tetragona</i>	leaf-2; reproduction-1,11
				3	<i>Ranunculus nivalis</i>	leaf-2,3; reproduction-1,5,9,11
	Shevtsova <i>et al.</i> 1997	33	T x W x acid removal	x 2	<i>Empetrum nigrum</i>	leaf-5
				2	<i>Vaccinium vitis-idaea</i>	leaf-5
				3	<i>Empetrum nigrum</i>	biomass-5,7-10; leaf-2,5

Ny-Alesund, Svalbard, Havström <i>et al.</i> 1993 Norway	34	F x T x L	3	<i>Vaccinium vitis-idaea</i>	biomass-5,7-10; leaf-2,5,6
			2	<i>Cassiope tetragona</i>	biomass-5; leaf-2
78°56'N 11°50'E 22 m a.s.l.	35	F x T x L	1	<i>Dryas octopetala</i>	reproduction-2,3 [1]; biomass-5,6; chemistry-6; physiology-1 [2]
			2	<i>Polygonum viviparum</i>	biomass-1; leaf-2,3,4,6,; reproduction-5,7,8,12-14 [3]
			3	<i>Dryas octopetala</i>	biomass-2; chemistry-6-8; leaf-6; reproduction-2,5,8,12-14; physiology-5-8 [4]
Baddeley <i>et al.</i> 1994	36	N x P	1	<i>Cassiope tetragona</i>	biomass-2; chemistry-6,7; physiology-7-11
			1	<i>Dryas octopetala</i>	biomass-2; chemistry-6,7; physiology-7-11
			1	<i>Salix polaris</i>	biomass-2; chemistry-6,7; physiology-7-11
