Arctic Terrestrial Ecosystems and Environmental Change [and Discussion]

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Phil. Trans. R. Soc. Lond. A 1995 **352**, 259-276
doi: 10.1098/rsta.1995.0069

Arctic terrestrial ecosystems and environmental change

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The impacts of environmental change on Arctic terrestrial ecosystems are complex and difficult to predict because of the many interactions which exist within ecosystems and between several concurrently changing environmental variables. However, some general predictions can be made.

(i) In the sub-Arctic, subtle shifts in plant community composition with occasional losses of plant species are more likely than immigration of exotic species. In the high Arctic, colonization of bare ground can proceed and there are likely to be shifts in ecotypes. Major shifts in vegetation zones, such as the advance of the boreal forest, are likely to be slow and species specific responses will result in different assemblages of species in plant communities in the longer term. All changes in community structure, apart from species removal by direct extreme weather conditions (e.g. drought) will be slow because of the slow growth, low levels of fecundity and slow migration rates of plant species over large latitudinal ranges.

(ii) Mobile mammals and birds can probably adjust to changes in the distribution of their food plants or prey in the Arctic, but vertebrate and invertebrate herbivores may face problems with changes in the quality of their food plants. Non-migratory animals could be severely affected by altered winter snow conditions which affect availability of food and shelter.

(iii) Increases in primary production are uncertain and depend mainly upon the responses of soil microbial decomposer activity to changes in soil temperature, moisture and plant litter quality. Assumptions that climate warming will lead to warmer soils and increased nutrient availability to sustain higher productivity are uncertain as greater biomass may lead to reduced soil temperatures through insulation effects and increased nutrients released may be immobilized by soil microorganisms.

(iv) Changes in environmental conditions are themselves often uncertain. There is particular doubt about changes in precipitation, growing season length, cloudiness and UV-B radiation levels while such environmental changes are likely to vary in magnitude and direction between different regions of the Arctic.

(v) The large populations and circumpolar distributions typical of Arctic biota lead to a strong buffering of changes in biodiversity. Perhaps the greatest threats to Arctic biota will be imposed by the degradation of permafrost which may lead to either waterlogging or drought depending upon precipitation regimes.

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Phil. Trans. R. Soc. Lond. A (1995) **352**, 259–276
Printed in Great Britain

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1. Introduction

The interactions between Arctic terrestrial ecosystems and environmental change are receiving increasing attention (e.g. Chapin *et al.* 1992; Callaghan *et al.* 1992, 1995) for several reasons. Arctic terrestrial ecosystems cover more than 7 million km^2 and contain rich biological resources adapted to the particular environment there, together with mineral and fossil fuel resources. While biotic and abiotic resources of the Arctic are particularly important to the life support of native and immigrant peoples living there, biological processes contribute to the global carbon budget through the sequestration of large amounts of atmospheric carbon in tundra organic soils. The Arctic also contributes to the global energy balance through its relatively high albedo compared with that of the boreal forest (Dickinson & Hanson 1984).

Any change in Arctic terrestrial ecosystems is therefore, likely to have local, regional and possibly global impacts. Climate change is predicted by General Circulation Models (GCMS) to be greatest at high latitudes (Mitchell *et al.* 1990) while even small changes in temperature are likely to stimulate disproportionately large biotic responses in those organisms already close to their lower temperature limits for survival. Further, slow growth or development and low fecundity of terrestrial primary producers together with low species diversity of Arctic biota result in the fragility of Arctic ecosystems experiencing disturbance or environmental change. The degree of environmental change expected in the Arctic together with the possibility of disproportionately great impacts on the biota present a system in which early indications of environmental change can be detected, while the considerable longevity and slow response of many Arctic organisms offer a system in which the signal to noise ratio is high.

Environmental change is not new in the Arctic: plants and communities thriving in the cold period immediately before the Little Ice Age some 400–500 years ago on Ellesmere Island, now exist in a much warmer climate (Havström *et al.* 1995). Climate has even changed over the past 30 years with warming of 4.5 °C in some continental areas and cooling in others (Jones & Briffa 1992). However, it is a combination of natural environmental changes combined with numerous types of anthropogenic stresses and disturbances (e.g. greenhouse induced climate change, transboundary pollution leading to eutrophication, mining impacts, etc.) which now present particular threats to terrestrial Arctic ecosystems and a challenge for researchers aiming to predict and limit their ecological impacts.

2. Environmental characteristics of Arctic terrestrial ecosystems

(*a*) *Stress*

The Arctic is characterized by a long, dark, cold winter when water necessary for life processes is in solid form. Consequently, Arctic organisms have resting phases, migrate or are physiologically and morphologically adapted to withstand the winter. Summers with mean daily temperatures exceeding zero may be less than 6 weeks in the high Arctic but high temperatures may be experienced briefly and continuous sunlight allows some plant species to attain positive energy balances throughout the 24 hour cycle.

Precipitation is variable and soil moisture often varies from the extremes of flooding and anaerobic conditions during spring thaw to drought in arid polar regions during late summer (compare figure 3*a* with 3*c*). Topography, even at the microscale (cm) and permafrost dynamics are important determinants of soil moisture for plants, soil microbes and invertebrates and exposure is critical for plants, some birds and mammals. Soil moisture and soil and air temperature gradients can be extreme; plants can be 23.5 °C warmer than the air a short distance above (Mølgaard 1982). Such temperature differentials may lead to problems such as late winter desiccation in plants when shoots are warm and snow free but roots are frozen in the soil.

(*b*) *Disturbance and mechanical impacts*

Many tundra habitats are characterized by extreme stress and disturbance, the latter usually associated with permafrost dynamics, freeze–thaw cycles in soil and rock, and water and wind erosion. Degradation of permafrost may disturb whole landscapes, e.g. when the active layer becomes detached or during 'baidgerahk' formation (figure 3*b*). Freeze–thaw cycles produce patterning in the landscape. They disrupt plant communities and soil fauna when ice grows and hummocks, polygons, pingos and palsas form. However, such disturbance can be associated with a drying of the soil, an increase in soil temperature and an increase in biotic diversity as plant seedlings become established and rodents, foxes, wolves, snowy owls etc. inhabit the warm dry soil.

Water erosion, particularly during permafrost degradation, removes soil organic matter containing plant nutrients as well as underlying mineral soils carrying them onto the vast continental shelves of the Arctic. Disruption to plant and soil communities can be severe. Wind provides a mechanical impact on exposed organisms which have evolved to either escape or to reduce resistance in aerodynamically smooth forms such as cushion plants. Wind also erodes both substrates and plants, particularly through ice crystal abrasion during winter.

(*c*) *Snow cover*

The persistent snow cover limits the length of the active period for plants as the ground becomes snow-free first in late June or in July when the solar angle is already decreasing. However, the snow offers comparatively benign environments for plant meristems, hibernating invertebrates and winter-active small rodent herbivores in the sub-nivean space beneath the snowpack, and creates protection from larger herbivores and predators. The small rodents, common over most of the Arctic, forage in winter where snow accumulates, while large mammals, e.g. musk-oxen, caribou and dall-sheep, exploit habitats with thin snow cover.

(*d*) *Resource status*

Space shows an increasing limitation from the barren polar high Arctic deserts (figure 3*a*) to the completely vegetated shrub tundras of the low Arctic (figure 3*e*). Although plant nutrients may be locally abundant in Arctic soils, they are generally unavailable to plants (Shaver & Chapin 1980) and this resource limitation, generally more than the stresses and disturbance described above, results in low rates of primary production. Nutrient limitations of primary production usually result from low decomposer activities in cold, often anaerobic soils together with the sequestration of nutrients in microbial biomass. Low levels of primary production limit the productivity of other trophic levels dependent on the plants.

Atmospheric carbon dioxide, an important resource for plant photosynthesis, is increasing in concentration, particularly at high northern latitudes (Goreau 1990). However, it is unclear to what extent this resource alone limits primary production as some plant responses to elevated levels of carbon dioxide last only for weeks and whole ecosystem response is no longer observed after three years (Tissue & Oechel 1987).

Resource quality can also be an important limitation. Plants with high carbon to nitrogen ratios, for example those grown in high concentrations of atmospheric CO_2, and particularly those with secondary metabolites (e.g. those grown in high UV-B radiation), limit both rates of decomposition and rates of consumption by invertebrate and vertebrate herbivores (Bryant & Reichardt 1992).

3. Biotic characteristics

(a) *Growth and life cycle strategies of plants*

Plants generally are slow growing, long-lived and have low fecundity. Primary production rates and phytomass are low with a disproportionate amount of phytomass (up to 98%) in belowground structures. In closed vegetation of the sub-Arctic, clonal plants predominate and recruitment from seedlings is often restricted in both time and space. In the open vegetation of the high Arctic, recruitment by seedlings and viviparous propagules is more common but is often sporadic. Patchiness of habitat and resources is a dominant feature of Arctic landscapes (e.g. polygons (figure 3*c*) and hummocks (figure 3*d*)) and plant adaptations to these environments are common, for example a high degree of physiological integration between generations within a clone (Jonsdottir & Callaghan 1990). Physiological strategies have been claimed to be limited, with most plants adopting avoidance strategies or morphological and developmental adaptations. However, freeze tolerance is an obvious prerequisite for existence in the Arctic and adaptation to immediate recovery from anaerobic conditions has recently been shown to be important in relation to encapsulation in ice (Crawford *et al.* 1994). Also, photosynthetic optima are lower in Arctic plants than in their temperate counterparts.

(b) *Characteristics of Arctic animals*

Arctic lakes and ponds often have a high productivity of insects with aquatic larval stages and other invertebrates (e.g. crustaceans) that form the food source of higher aquatic or terrestrial animals. The numerous small ponds offer particularly good feeding places for several aquatic birds and for waders because some trophic levels containing predators of invertebrates, such as fish, may be absent, particularly in those shallow ponds in which water freezes to the bottom in winter. Thus, the Arctic contains abundant food and attracts migratory birds during the short summer – over 6 million North American sea birds nest in the Arctic regions of that continent while far greater numbers (mainly waders) migrate to the Siberian Arctic each summer. Most birds of the Arctic and some mammals are migratory species. A few species stay in the Arctic all year round and remain active above or below the snow during the entire winter period whereas others, as for instance most invertebrates and some larger mammalian species, enter diapause or hibernate, respectively.

(c) *Biodiversity*

Low fecundity of plants, long life spans and large latitudinal separation from biologically diverse latitudes together with the environmental filter of freezing have resulted in low species diversity among Arctic plants (figure 1). However, where sexual reproduction is more frequent in the high Arctic, subspecies diversity can be high

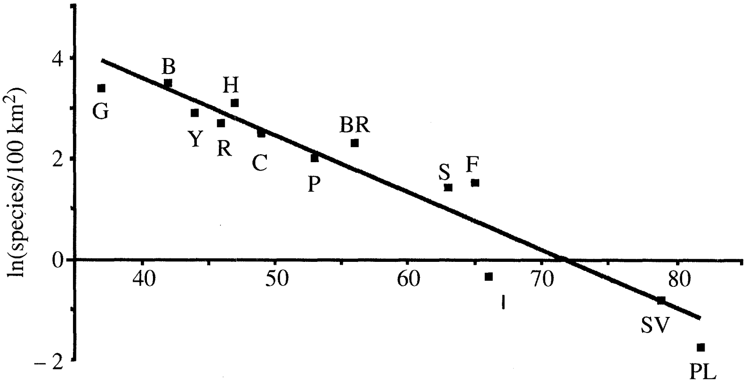

Figure 1. Biodiversity trends in vascular plants of Europe and the European Arctic. $r = 0.957$, $p < 0.001$; (G) Greece; (B) Bulgaria; (Y) Yugoslavia; (R) Romania; (H) Hungary; (C) Czechoslovakia; (P) Poland; (BR) Baltic Republics; (S) Sweden; (F) Finland; (I) Iceland; (SV) Svalbard; (PL) Peary Land, northeast Greenland. (Based on Hendry 1993 and Billings 1992.)

(Crawford *et al.* 1993). Fecundity of many birds and mammals is high although often cyclical as in rodents, which in turn also affects the reproduction of their predators. The large Arctic land masses together with the world's most extensive continental shelf, some of which might have been above sea level and ice-free during the last glaciation, have resulted in efficient dispersal of plants and animals so that many have circumpolar distributions and very large, extensive populations.

(*d*) *Population dynamics*

Life cycles of many plants and animals of the Arctic are cyclical. Lemming populations fluctuate in density on three- or four-year cycles. This cyclicity interacts with other trophic levels and results in similar population patterns for predators and for primary production which is reduced by grazing. Plants which require several years to flower, and in which flowering is followed by death of the flowering shoots, also follow cyclical patterns (Carlsson & Callaghan 1994). Invertebrates usually follow well determined life cycles with one generation per summer but opportunistic life cycles can occur although with the risk that non-resting stages of the life cycle, or non-hardened individuals may be killed by the early onset of winter (Webb *et al.* 1995). Population dynamics of migrant animals, mainly birds, depend on factors in areas other than the Arctic, such as hunting laws and changes in agriculture/land use along the migration routes and in their overwintering areas. Generally this decreases the population sizes of migrant birds, but in some cases population sizes can increase to the extent of increased grazing pressure denuding ecosystems (Jefferies *et al.* 1992).

4. Responses of the biota to environmental change

The fastest and most profound changes in Arctic biota are related to local land use and industrialization. Climate change impacts, in contrast, are likely to be more widespread and to occur over longer time scales.

(*a*) *Responses of organisms*

Environmental manipulation experiments simulating various aspects of climate change in different Arctic regions (Alaska, Swedish Lapland (figure 3*e*), Svalbard (figure 3*a*)) have shown that Arctic plant species can respond surprisingly quickly to increases in temperature and nutrient availability. Additions of nutrients have been given to plant communities to simulate the assumed increase in plant litter mineralization rates responding to higher temperatures and increasing deposition of atmospheric nitrogen. In general, nutrient addition treatments have great effects on plant performance, particularly in the most benign low altitude sub-Arctic environments (Havström *et al.* 1993). Increased temperatures stimulated the greatest plant responses at the most severe high Arctic sites (Havström *et al.* 1993; Wookey *et al.* 1993, 1995) where initial impacts of increased temperature were mostly restricted to plant development, reproduction and seed germinability (Wookey *et al.* 1993, 1995). Nichols (1995) found that spruce trees along a 1500 km transect through the Arctic tree line in eastern Canada produced pollen and cones in 1993 whereas no such production was seen 20 years before this.

Other experiments on Svalbard investigating responses of invertebrates to simulated climate change showed that, as in the plants, the response of an Arctic aphid was greatest where climate was harshest and response was apparent in the first year (Strathdee *et al.* 1994). In contrast, the responses of soil dwelling invertebrates were limited even after three years of environmental manipulation (Coulson *et al.* 1995), presumably because soils show less warming than the air (see below).

An 'individualistic' response of plants to the various environmental manipulation experiments resulted in a dampening of community productivity in Alaskan tussock tundra (Chapin & Shaver 1985) such that little variation in overall primary production occurred between treatments. However, the structure of the community changed over a decade such that graminoids showed a marked early response and then a dwarf shrub became dominant (Chapin *et al.* 1995). In the sub-Arctic, however, the compensatory mechanism of individualistic responses did not operate, and all higher plant species responded to environmental changes in the same direction (Jonasson 1992; Parsons *et al.* 1994). No species migrated into sub-Arctic birch heath experimental plots over the four years of the study.

In contrast, existing species can expand in response to environmental manipulations, particularly nutrient addition, in the most extreme environments where open ground is extensive (Fowbert & Lewis Smith 1994; Wyn Williams 1990; Wookey *et al.* 1995; figure 3*a*) and 'new' species can immigrate (C. H. Robinson, personal communication).

Data on direct responses of invertebrate and vertebrate animals to natural, rather than experimentally induced changes in temperature and moisture are rare. However, Järvinen (1994) found a significant positive correlation of increasing egg size in sub-Arctic birds, which increases survival, with temperature in the Finnish sub-Arctic and Tenow & Holmgren (1987) found a significant negative correlation between incidence of low winter temperature and insect damage during outbreaks of *Epirritia autumnata*, a moth caterpillar which defoliates sub-Arctic birch trees (figure 3*f*). In the last example, overwintering eggs were killed in cold depressions and in cold winters when temperatures dropped below −36 °C. Any increase in temperature could lead to increased survival of eggs and greater destruction of birch forests.

(*b*) *Implications of climatic change for interactions between soil microbes and plants*

Any temperature increase will have greater effects on plant growth and the activity and development of the above-ground fauna than on the activity of soil fauna

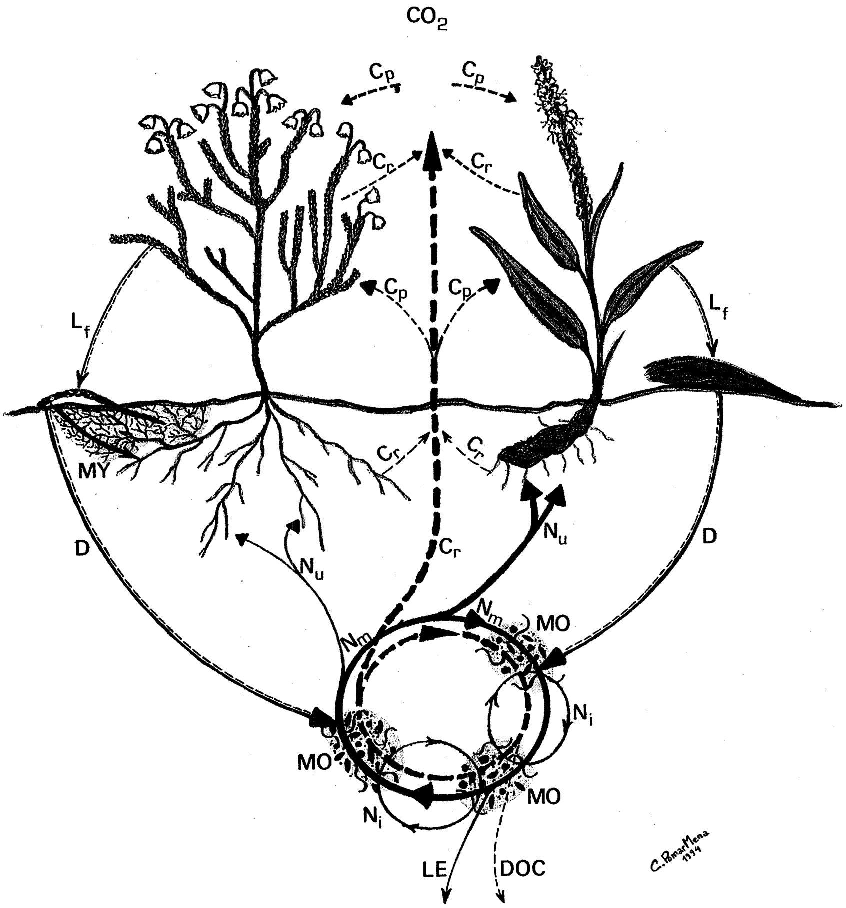

Figure 2. Schematic illustration of ecosystem carbon fluxes and nutrient circulation in tundra. Atmospheric CO_2 is fixed in the plants through photosynthesis (C_p). Dead parts of plants with organic carbon (carbon pathways with hatched arrows) and nutrients (pathways with continuous arrows) fall to the ground as litter (L_f) and go into the decomposition cycle (D) where they are transformed into soil organic matter. The organic matter with its nutrients undergo complicated transformations in the soil microbial biomass (MO) through cycles of mobilization/immobilization (N_m/N_i). Carbon is continuously lost to the atmosphere as CO_2 through microbial and plant respiration (C_r) and made available directly for plant photosynthesis or added to the atmospheric pool (CO_2). The nutrients are circulated within the microbial system of the soil or traded off and taken up by the plants (N_u). The plant species differ widely in nutrient uptake rates; here represented by *Cassiope tetragona* with slow uptake rate and *Polygonum viviparum* with high uptake rate. Some plants, e.g. *Cassiope tetragona* can circumvent the microbial mobilization/immobilization process by uptake of nutrients directly from organic matter decomposed by mycorrhizal fungi (MY) associated with their roots. Some carbon and nutrients can be lost from the system as dissolved organic matter (DOC) or nutrient leachate (LE) transported to adjacent systems. Climate change acts on the system mainly by controlling the rate of CO_2 uptake by plants and the activity of micro-organisms. Tundra ecosystems differ from others by having large stores of nutrients and carbon in the soil and microbial biomass and in having low rates of CO_2 uptake, i.e. low productivity.

and microbes, due to the insulation of the soil by plant cover and low conductivity of heat. Thus, below ground processes will be operating at lower temperature increases than those above ground. However, assuming that decomposition and mineralization rates increase after warming, fewer nutrients than anticipated may be available. Recent research (Jonasson *et al.* 1995) has shown that microbial uptake of nitrogen and phosphorus increases strongly after nutrient addition but shows little or no response after addition of a labile carbohydrate (sucrose) which is the response anticipated in most other ecosystems with energy-limited microbial communities. This suggests that any increased decomposition and mineralization rate in the Arctic may result in microbial immobilization of nutrients rather than an increased release rate of nutrients in the plant available form (Jonasson *et al.* 1993). This will proceed until the soil carbon to nutrient ratio has decreased to below the critical level for immobilization. As plant community production is usually nutrient limited, the assumption of significant soil warming and scenario of increased microbial nutrient immobilization imply that the main changes will take place in the heterotroph, belowground communities and not in the aboveground autotroph community. The result of these scenarios will be an increased emission of CO_2 from the ecosystems to the atmosphere (figure 2), but other environmental changes may act in opposite directions (see below) and soil warming may not match expectations.

In addition to the interactions between plants and decomposers, many plant species which dominate Arctic ecosystems have ericoid mycorrhizae or ectomycorrhizae that contain proteolytic enzymes which can break down complex organic, nitrogen-containing compounds (Read 1991). These species may, therefore, be supplied with nitrogen directly through their fungal symbiont and hence, circumvent the mobilization–immobilization cycle taking place in the non-symbiotic microbial community. How the mycorrhizae respond to a changing climate regime is however, poorly investigated.

(*c*) *Implications for interactions between plants and animals*

A more benign climate in the Arctic is likely to decrease mortality in most animal groups during summer which could increase herbivory. Increased herbivory is also likely to occur as a side-effect of increased plant growth, during which extra carbohydrates dilute the nutrient concentration in forage. In these circumstances, the herbivores must increase food intake to compensate for its lower nutrient concentration. Such a temperature dependent decline of forage quality has, indeed, been observed in plants during naturally occurring warm summers (Jonasson *et al.* 1986). Also higher levels of atmospheric carbon dioxide and UV-B radiation can decrease plant tissue ‘quality’ and adversely affect dependent organisms such as various invertebrate groups (Fajer *et al.* 1989; Couteaux *et al.* 1991) and fungal decomposers (Gehrke *et al.* 1995).

In contrast, winter mortality can increase in non-migrating mammals if winter temperatures – and particularly if the frequency of events with temperatures above zero – increases. Such thawing and freezing events could result in ice crust formation in the snow, and possibly formation of an ice-crust on the soil. This prevents larger mammals (reindeer, musk-oxen) from reaching the vegetation below the snowpack and small rodents living in the subnivean space from utilizing the vegetation encrusted in the ice.

(*d*) *Changes in distributions of organisms and communities*

The general stimulation of plant reproductive development by increased temperatures is likely to assume greatest significance in those areas with open, disturbed ground which can be colonized, e.g. high Arctic deserts and polar semi-deserts (figure 3*a*), Arctic fellfields, thermokarst landscapes (figure 3*b*), and areas disturbed by man around settlements, industries, mines, oil wells, roads, etc. (Forbes 1995).

Tundra ecosystems are characterized by a mosaic of habitats with different communities, e.g. polygonal tundra with moist, low-centred polygons, dry polygon ridges and wet polygon troughs (figure 3*c*). Latitudinal distances between major geographical vegetation zones on the other hand tend to be large (hundreds of km). Thus the slow migration rates of species along extensive latitudinal gradients is likely to result in only longer term changes in communities whereas the colonization of changing habitats by species from neighbouring habitats is likely to be a faster process. However, exceptions may occur in those areas acting as 'refugia' for species with a southerly distribution, e.g. pockets of trees in the tundra (Landhausser & Wein 1994) and erect shrubs along river valleys in mid Arctic tundras. Such refugia with local favourable microclimates might provide 'innocula' for the invasion of extensive areas when the general climate changes. In the high Arctic (e.g., figure 3*a*), the initial changes in communities might be more subtle as ecotypes of species such as *Saxifraga oppositifolia* from microclimatically favourable microhabitats displace those from less favourable sites during climate warming (Crawford *et al.* 1993). Other exceptions to the expected gradual change in distribution of organisms occur where corridors for migration are created by human activities (Forbes 1995).

Animals, with their greater mobility than plants, can change their distributions rapidly and this phenomenon has been used to infer rapid changes in climate during the Holocene from changes in distributions of *Diptera* (Coope 1975).

The mechanisms for change in plant community structure are likely to be competitive exclusion of northern species by southern species or faster growing neighbouring species and ecotypes (Callaghan & Jonasson 1995). This has been inferred from the sensitivity of many Arctic plant species to shade yet their general ability to grow in more southerly latitudes when competitors are artificially excluded. Some Arctic species, particularly those with large below-ground biomass, may however, suffer an adverse carbon balance in warmer climates.

Assuming a doubling of atmospheric CO_2, and no constraints on the migration of species, Emanuel *et al.* (1985) and Leemans (1989) calculated that tundra areas would decrease in extent by between 20 and 32% because of the northwards expansion of the boreal forest biome (figure 3*e*). However, tree migration rates are slower than predicted rates of climate shift. For example, a warming of 2 °C could result in a 4–5° latitude northward shift of the climate zone currently associated with the taiga of Eurasia (Velichko *et al.* 1990), i.e. a shift of 400–500 km by the year 2020. If the taiga could migrate at the same rate, tundra would be totally displaced from the Eurasian mainland by 2020. However, the migration rates of taiga trees are only about 10–300 $\mathrm{m\,a^{-1}}$ for conifers (Nichols 1967; Chertovskij *et al.* 1987 quoted in Razzhivin 1995) to 130 to 1000 $\mathrm{m\,a^{-1}}$ for deciduous alder and birch (Velichko *et al.* 1990; Chertovskij *et al.* 1987 quoted in Razzhivin 1995).

The inequality in rate of climate and vegetation shift will subject large areas of vegetation to supra-optimal climate regimes where damage from extreme weather, fire, pests etc will increase. It is likely that the individualistic responses of plant species to climate change will result in the disintegration of current communities and the formation of new assemblages of plants.

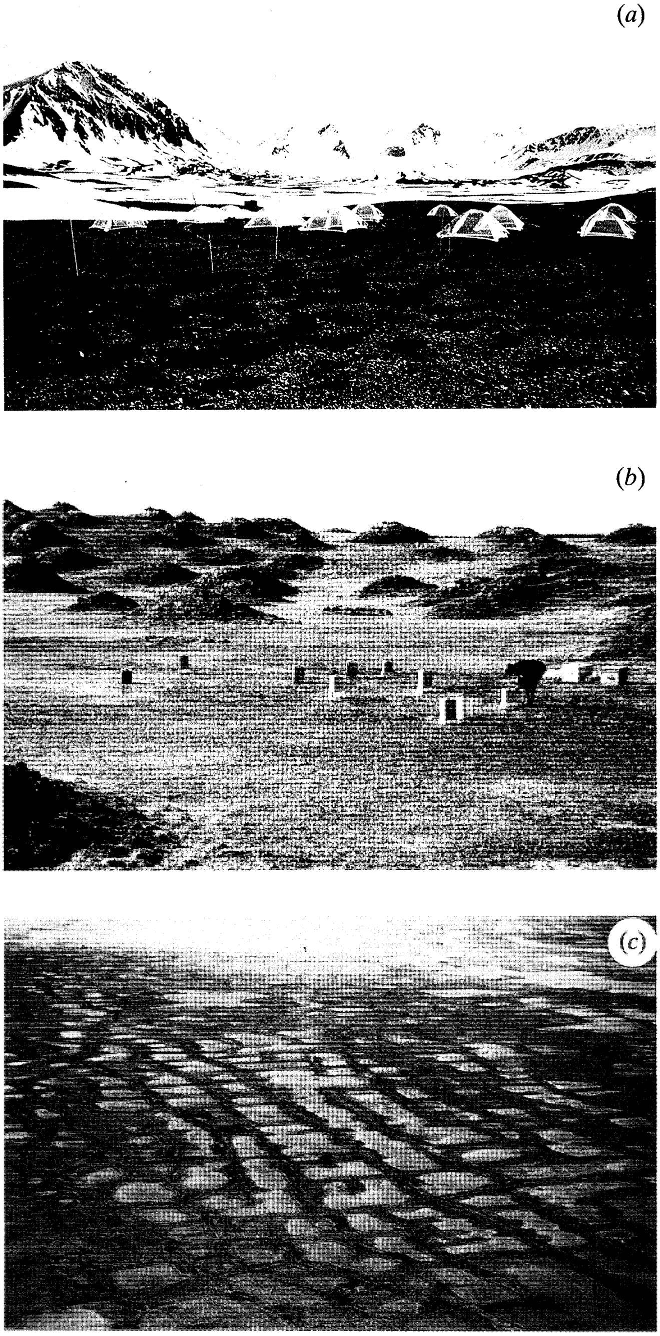

Figure 3. Arctic landscape types. (*a*) High Arctic polar semi-desert near Ny Ålesund, Svalbard showing temperature manipulation experiments on scattered *Dryas octopetala* vegetation. Photo credit: T. V. Callaghan. (*b*) High Arctic vegetation and thermokarst scenery dominated by 'baidgerakhs', i.e. raised polygon centres accentuated by rapidly thawing polygon troughs, Ostrov Faddeyevskiy, New Siberian Islands. Measurements of methane fluxes are in progress. Photo credit: S. E. Jonasson. (*c*) Polygonal/tetragonal coastal tundra, Olenekskiy Bay, North-central Siberia, showing sunken and flooded polygon centres, raised polygon rims and polygon troughs. Photo credit: T. V. Callaghan.

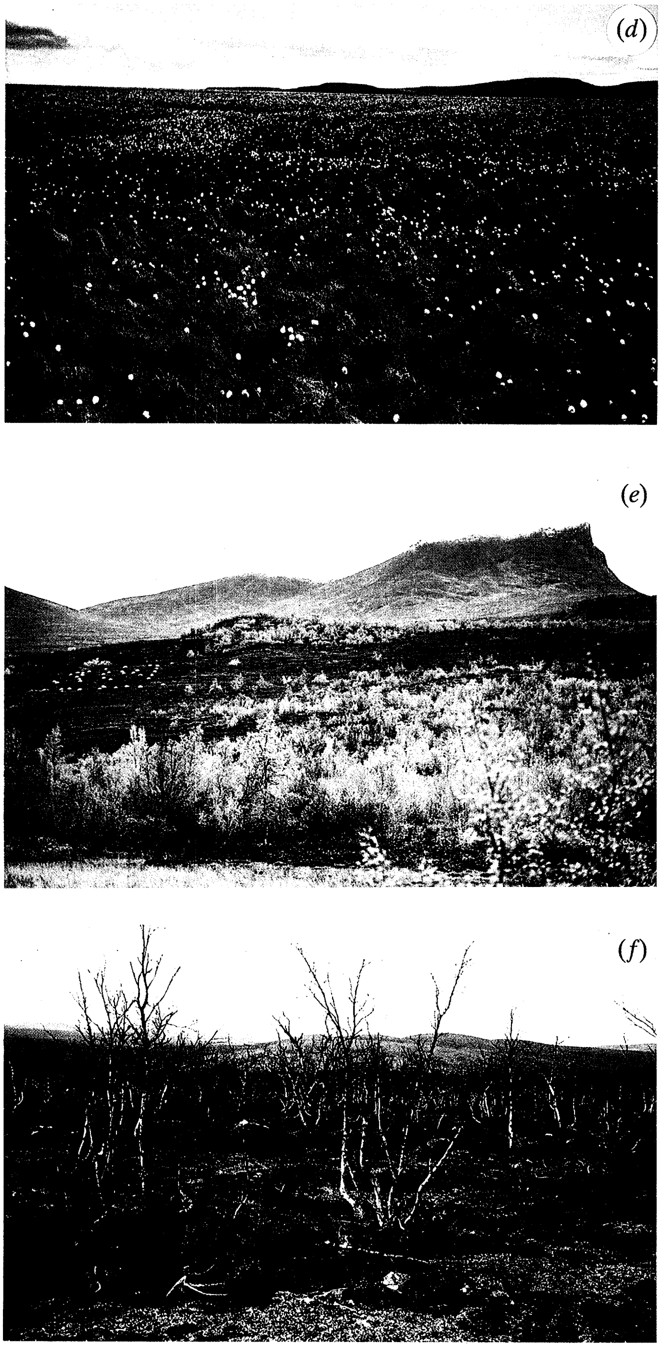

Figure 3. (*d*) Mid-Arctic tussock tundra dominated by *Eriophorum vaginatum* near the Yana Delta, east of the Taimyr Peninsula, North Siberia. Photo credit: S. E. Jonasson. (*e*) Sub-Arctic tundra/taiga ecotone dominated by mountain birch trees (*Betula* pubescence ssp *tortuosa*) and dwarf shrub heath vegetation, near Abisko, Swedish Lapland. A randomized block temperature enhancement experiment can be seen beyond the tree line. Photo credit: J. Busch. (*f*) Sub-Arctic mountain birch forest destroyed by the defoliating moth caterpillar *Epirrita autumnata* near Kevo, Finland. Pest outbreaks are currently controlled by low winter temperatures which kill eggs. Photo credit: T. V. Callaghan.

5. Feedback from Arctic terrestrial ecosystems to global environmental change

(a) Carbon cycling

(i) *Carbon stocks, trace gas fluxes*

The large stock of carbon stored in the tundra soils, estimated to be about 11% of that stored in soils globally (Schlesinger 1984), is a potential important source of greenhouse gases (CO_2 and CH_4) to the global atmosphere. Carbon dioxide is formed by autotrophic and heterotrophic respiration and is consumed and converted into organic carbon by autotrophic photosynthesis (figure 2). Methane (CH_4) is formed by bacterial degradation of organic matter in anaerobic environments and can be consumed by aerobic bacteria. Its direct contribution to changes in carbon pool sizes in the atmosphere and biosphere is probably rather limited, but methane has a particular significance as a greenhouse gas as its radiative forcing is about 30 times that of CO_2.

(ii) *Carbon sink–source relationships*

The tundra will act as an atmospheric source of carbon if plant and soil respiratory processes release more carbon per unit time than that fixed in plants (figure 2). This will occur if below-ground processes are stimulated more by changes in temperature and/or moisture than plant productivity. Such a scenario is possible in systems where low nutrient availability limits both plant and microbial growth (see above). The temperature-stimulated turnover of soil organic matter would lead to increased emission of CO_2 at the same time as the microorganisms immobilize the nutrients and prevent any substantial increase of plant production. On the other hand, the Arctic can act as a sink for atmospheric carbon if plant productivity is enhanced by increasing atmospheric CO_2 concentrations, or by increased availability of nutrients from decomposition and nutrient mineralization (figure 2), i.e. in cases when microbial nutrient immobilization is low. The Arctic could also act as a sink for carbon if waterlogging occurred as a result of permafrost thawing or increased precipitation as these conditions decrease microbial decomposition. In general, it has been suggested that the tundra of Alaska acted as a net sink for carbon throughout the Holocene by sequestering atmospheric carbon in organic soils and peat (Oechel *et al.* 1993).

Experiments by Billings *et al.* (1982; 1983) on soil microcosms from Alaska show that a drying and warming of tundra soils will lead to the increased emission of carbon. A 4 °C temperature increase could increase loss of carbon by 60–80 $\mathrm{g\,m^{-2}}$ if the water table is 5 cm below the surface and by 130–160 $\mathrm{g\,m^{-2}}$ with an 8 °C temperature increase if the water table is at a depth of 10 cm. An increase of 4 °C could therefore, increase decomposition rates and the evolution of soil carbon by 1 Pg in tundra areas and 0.5 to 2 Pg in boreal areas (Lashof 1989). In wet tundra and boreal areas which currently emit about 40 Tg methane per year to the atmosphere, a 4 °C increase in mean annual temperature could increase methane evolution by 45–65% (Melillo *et al.* 1990).

Due to the large regional and local variations over the Arctic, it seems realistic to assume that the sink–source relationship will probably vary on both a local basis (e.g. plant community, ecosystem or landscape) and regionally across the latitudinal extent of the Arctic. This has indeed been suggested for Alaskan tundra. Oechel *et al.* (1993) reported a recent change from sink (see above) to source status of the

Alaskan tundra, particularly the wet coastal tundra in comparison to the inland mesic tussock tundra.

Given the predictions of increased plant productivity in the Arctic if the climate warms (Melillo *et al.* 1994), and the proportionately low carbon stores in the high Arctic, the high Arctic will probably become a net sink for atmospheric CO_2. In contrast, the tundra in the middle Arctic with a closed vegetation cover will probably increase its sink action marginally, or possibly act as a source of CO_2 due to increased microbial respiration but little increase in productivity. The southern dwarf shrub and tall shrub tundra, bordering the boreal forest may, again, act as sinks because they have a high potential for carbon fixation even under nutrient limited conditions due to a high production of woody tissues with low nutrient content.

Production and emission of methane, which is a second process by which the soil and the atmosphere exchange carbon, occur principally in water-saturated areas of the tundra, for instance in the wet sedge tundra bordering the northern coasts of Siberia and Alaska. Methane is, on the other hand consumed by CH_4-oxidising bacteria in drier tundra areas. Both the quantity of methane produced over the tundra areas and the balance between methane production and consumption is poorly known. However, measurements of methane fluxes at regular intervals along the coast of the Siberian tundra (Christensen *et al.* 1995) have indicated that net emission is generally restricted to entirely water-saturated soils, e.g. low centres of tundra polygons (figure 3*c*). Mesic sites, e.g. rims of the same polygons (some 15–20 cm higher) generally showed no net emission and could even consume methane.

(*b*) *Albedo*

The Arctic currently cools the earth by reflecting more incoming solar radiation than it absorbs. Ice and snow have the greatest reflectance and tundra vegetation has higher reflectivity (albedo) than dark, coniferous boreal forests. A result of intensive warming at high latitudes will be an eventual decrease in the extent of snow and ice on land and a northward shift in the boreal forest zone. This positive albedo feedback will be greater than that of the emissions of carbon from the biosphere and will increase the inequality of warming between the poles (mainly the Arctic) and the equator (Lashof 1989).

In conclusion, responses of individual plant species to single environmental factors are relatively well known, but impacts of environmental change on Arctic animals are less well known. At the ecosystem level, the impacts are particularly complex and difficult to foresee. The main reasons for this are the many interactions which exist within ecosystems and between several concurrently changing environmental factors.

We are indebted to the Swedish Polar Secretariat and the Swedish Royal Academy of Sciences for enabling our participation in the Russian Swedish Tundra 94 Expedition which broadened the representativeness of this contribution. We are also grateful to the Danish Natural Environment Research Council, the Swedish Environmental Protection Agency and the UK NERC Arctic Terrestrial Ecology Special Topic Programme for grants enabling our participation in Arctic ecological research. It is a pleasure to thank all of our co-workers for their collaboration and we would like to thank Christina Pomar for drawing figure 2 and Jonathan Kirkham for preparing figure 1.

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Discussion

H. Nichols (*Department of EPO Biology, University of Colorado, USA*). Previous commentary of mine on the sensitivity of the Arctic tree-line to climatic change referred to palaeoclimatic data and meteorological records to argue that this vegetation boundary has been one of the most responsive ecotones to register environmental change. Palynological evidence demonstrates mid-Holocene (hypsithermal) movements of the Canadian Arctic tree-line of up to 400 km into the tundra, in response to a natural (Milankovitch) warming cycles, locally of about +4 °C mean July temperatures (i.e. +1 °C mean = 100 km advance of tree-line). Estimates of woodland advances into Arctic tundra are approximately 300 m a^{-1} under climatic warming comparable to a full-scale $2\times CO_2$ greenhouse effect (about 3–4 °C increased mean summer temperatures). Since the global warming predicted from the anthropogenic greenhouse effect includes a strong polar warming scenario, we have sought to re-visit the sites of Nichols's 20-year old expeditions to record pollen and cone production at the boreal forest-tundra ecotone. In 1972 and 1973 a transect of pollen sampling sites was studied, from the northern woodland edge and into the Keewatin tundra, passing through clumps of mature dwarf spruce trees. At that time trees were barren, with no consistent pollen release or cone formation, indicative of then prevailing summer climatic limitations. In June and July 1993 several of the 1972–73 sites plus additional locations were visited, forming an east–west transect of about 1500 km in the Northwest Territories of Canada, from inland (west) of Hudson bay to an area north of the Great Bear Lake, south of the Arctic Ocean coastline. Eight locations were spaced along this transect, and in late June-early July Nichols set out pollen traps at each site to record regional pollen fallout from the forest to the south as well as that from the isolated groups of spruce trees. This design mimicked the 1972–73 project, the aim being to distinguish 'spikes' of local spruce pollen production from the isolated tree groups, from the background forest pollen deposition.

This east–west transect of sampling sites was repeated later in July, and as a result spruce pollen release was observed at a number of sites which did not produce pollen in 1972 and 1973. Even more impressive was the observation that at all the sites, from the whole length of the transect of 1500 km, cones were being formed on spruce trees where 20 years ago the trees were barren. At sites 150 miles (250 km) from the woodland edge, out into the tundra, dwarf spruce less than one metre high were bearing this year's (1993) cones, along with those from previous years. There is no proof that this is due to anthropogenic warming (it could be a natural 'flickering' of climate), but it is a phenomenon which would have to be observed if polar warming due to the greenhouse effect were to be credible. It is important in this respect to continue these observations to identify a trend of continuing cone production versus a return to barrenness on the part of these marginal trees.

T. V. Callaghan. Prof. Nichols has described an interesting study. The isolated trees beyond the latitudinal treeline could play a particularly important role in providing foci for the expansion of the boreal forest in a warmer climate. I agree that more frequent observations are necessary, particularly as what you have described cannot, on the basis of two observations periods, be separated from the innate cyclicity in biological phenomena in the Arctic which we have described in our paper.

R. B. Heywood (*British Antarctic Survey, UK*). Could temperate (plant) species have considerably faster reproductive processes than contemporary Arctic species. Has Professor Callaghan considered the effect on community structure of the former 'leap-frogging', as it were, the latter during colonization of regions made less hostile by the effects of global warming.

T. V. Callaghan. The process of temperate plants 'leap-frogging' into Arctic plant communities during climate warming usually depends on the availability of sites for establishment and efficient dispersal, assuming that climatic conditions are appropriate for subsequent survival. Available sites and dispersal are associated in particular with human disturbance. Thus, the greatest probability of observing this process occurs where roads and pipelines have been constructed and industrialization has disturbed or destroyed natural Arctic plant communities. Under natural conditions, the vast latitudinal distances separating temperate plants form the Arctic and the dominance of closed vegetation in the more southerly regions of the Arctic, together constrain the process of 'leap-frogging'.

R. B. Heywood. The influence of isolation cannot be ignored in any discussion in the level of endemism in polar marine ecosystems. Most marine organisms are shallow water species. The Arctic Ocean has vast areas of shallow coastal seas which are continuous with the coastal waters of all the Northern Hemisphere continents. There is no impedance to migration in and out of the Arctic Ocean. In contrast the narrow coastal waters of Antarctica are separated from those of the Southern Hemisphere continents by the vast distances of the very deep Southern Ocean.

T. V. Callaghan. Dr Heywood has underlined the essential role for the geography of the Arctic in controlling endemism and trends in biodiversity in general, and that this is equally important in marine and terrestrial ecosystems.

P. A. Wookey (*Department of Biological Sciences, University of Exeter, UK*). Professor Callaghan emphasizes early in his paper the large storage of global soil carbon in tundra ecosystems (around 11–14% of the total) and the potential for release of substantial quantities of this to the atmosphere as a result of soil warming and accelerated decomposition processes. This could indeed act as a positive feedback to climate change if assimilation of atmospheric CO_2 by plants is less than that released by heterotrophic respiration processes in the decomposition subsystem. The likelihood of such a large net efflux of CO_2 from tundra ecosystems to the atmosphere may, however, be called into question in view of the palaeoecological record of rates of carbon accumulation during the Holocene climatic optimum (6900–4800 BP): these records suggest that carbon accumulation rates in Arctic Alaskan ecosystems were highest when the climate was some 2–4 °C warmer than at present (see Marion & Oechel 1993). What is the likely explanation of this apparent paradox?

T. V. Callaghan. As you noted, gaseous carbon flux from the biosphere to the atmosphere and the converse organic carbon storage in soils, result from the balance between primary production and decomposition. It is possible to envisage increased rates of primary production responding to higher temperatures during the Holocene climatic optimum but decreased rates of decomposition responding to cooler soils insulated by higher biomass, or wetter soils if the climatic optimum was also a wetter period. More problematic, however, is how increased primary production could be sustained with reduced nutrient availability associated with slower decomposition.

Additional references

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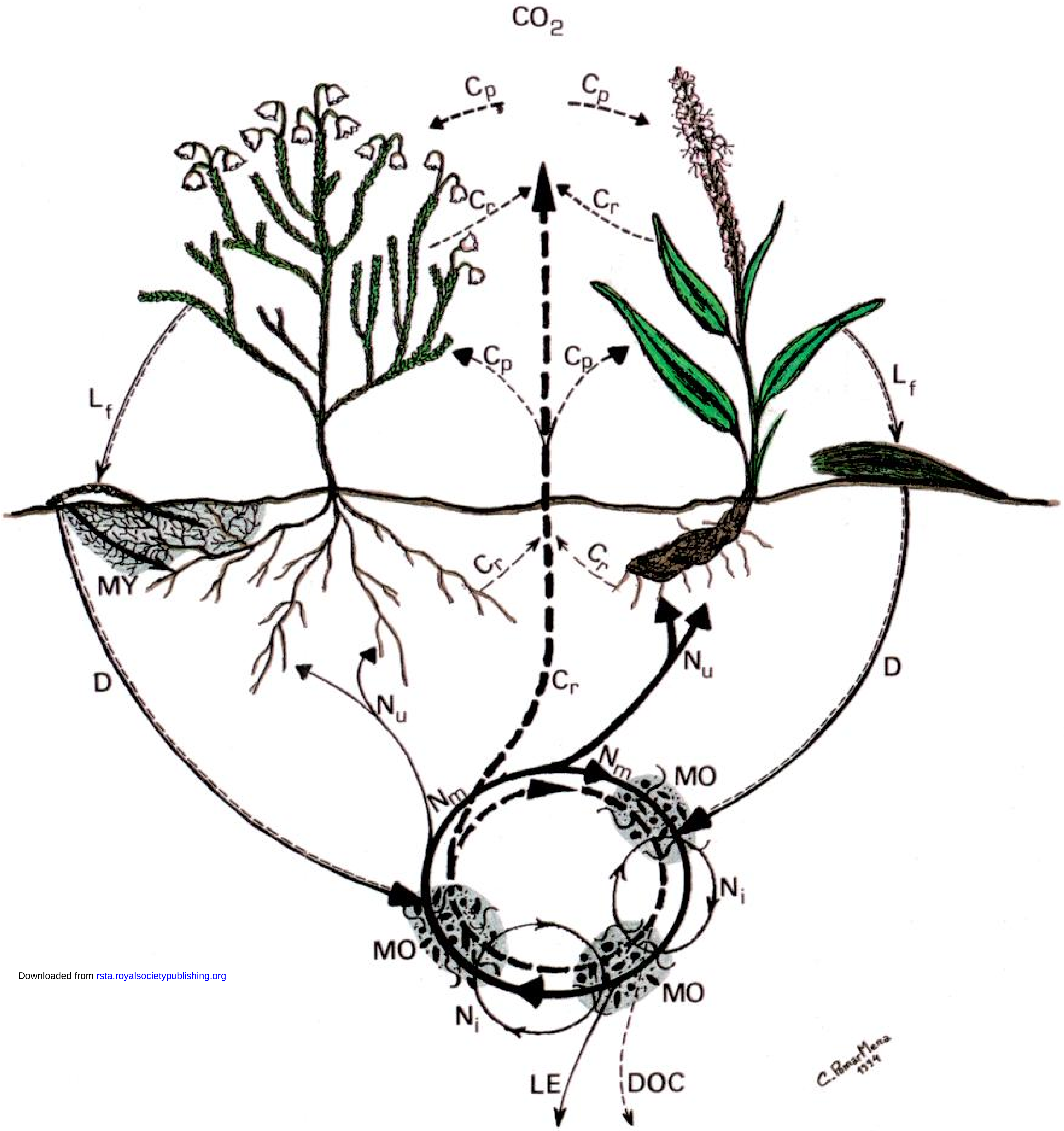
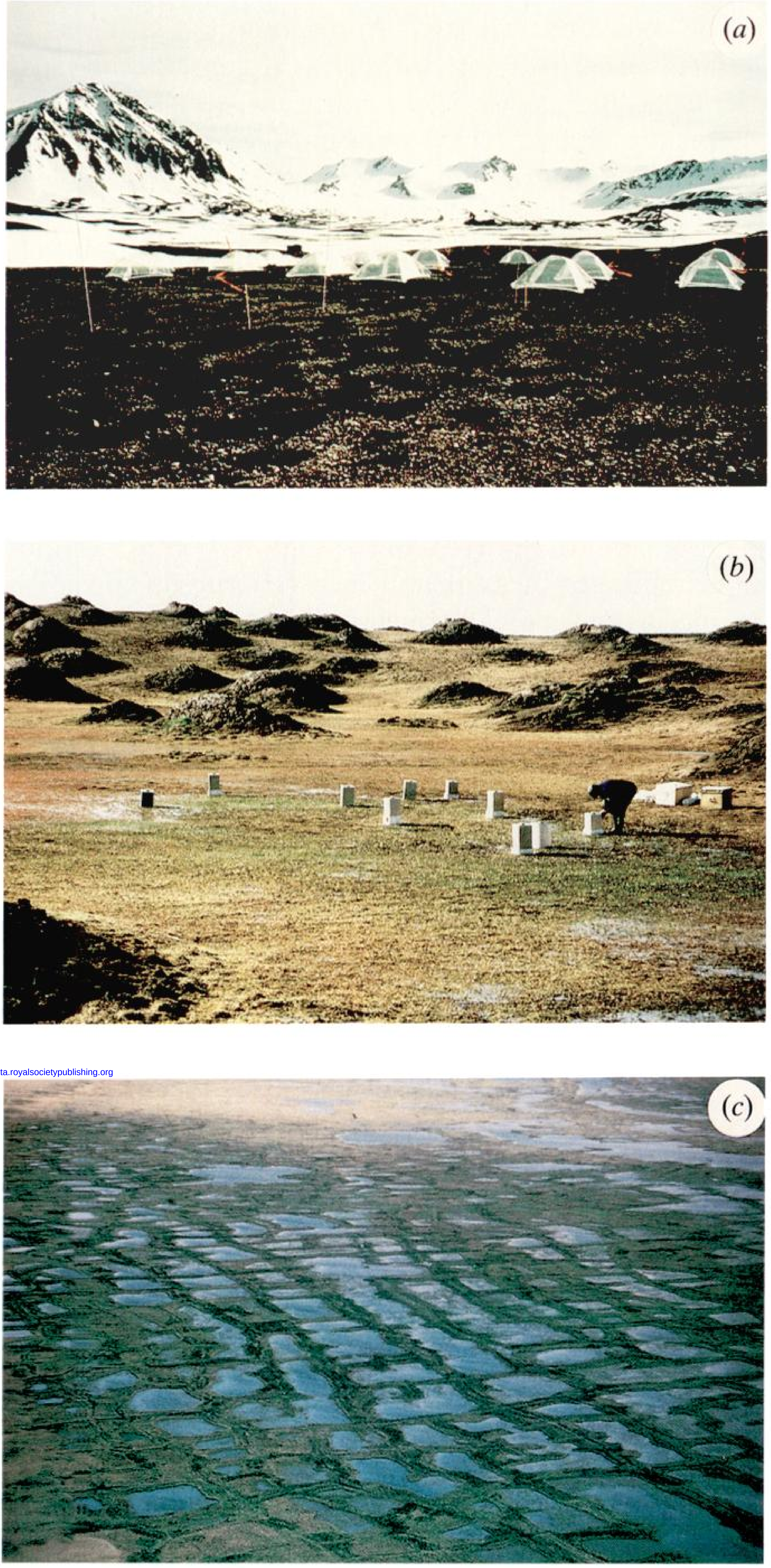
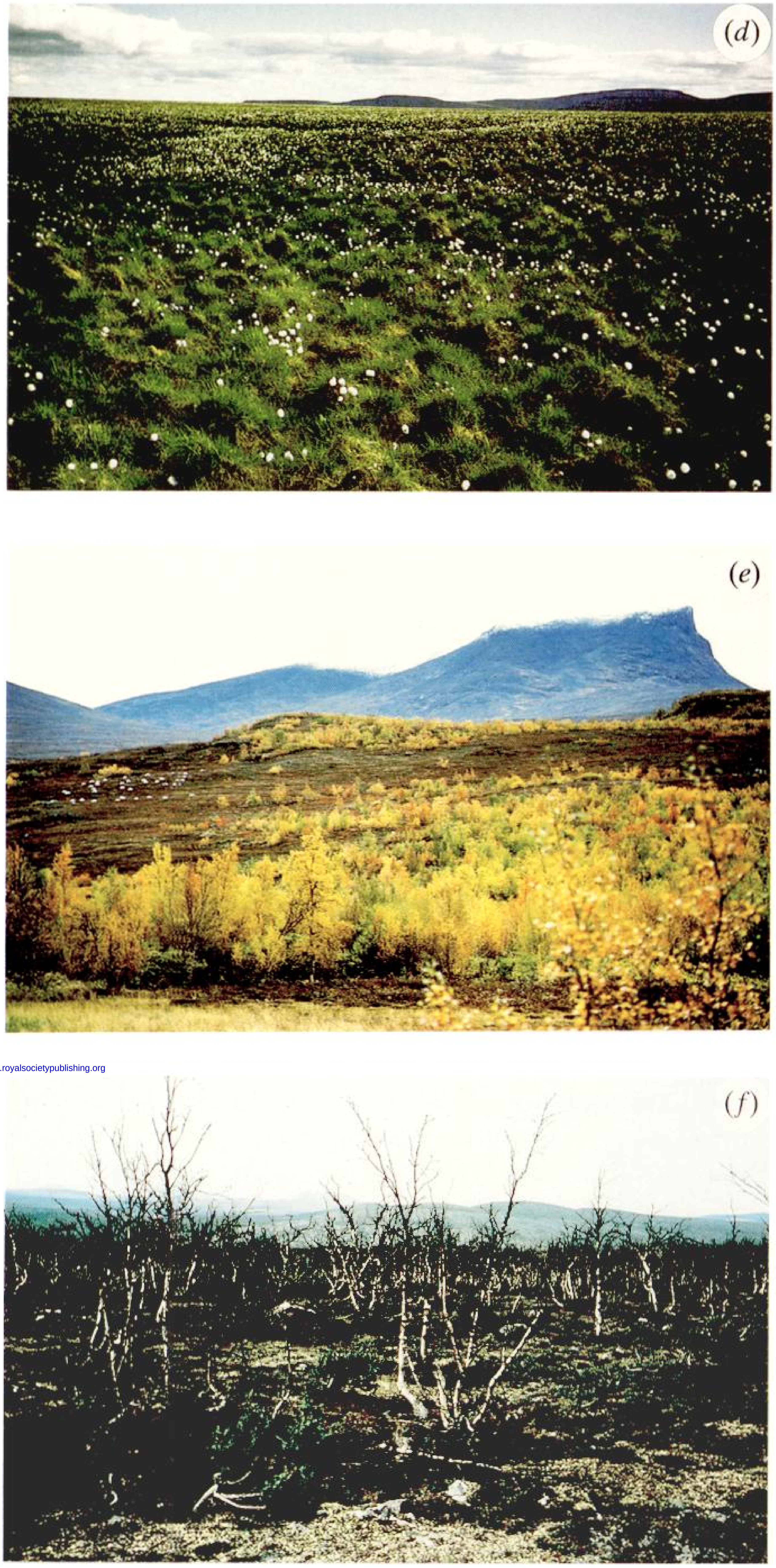


Figure 2. Schematic illustration of ecosystem carbon fluxes and nutrient circulation in tundra. Atmospheric CO_2 is fixed in the plants through photosynthesis (C_p). Dead parts of plants with organic carbon (carbon pathways with hatched arrows) and nutrients (pathways with continuous arrows) fall to the ground as litter (L_f) and go into the decomposition cycle (D) where they are transformed into soil organic matter. The organic matter with its nutrients undergo complicated transformations in the soil microbial biomass (MO) through cycles of mobilization/immobilization (N_m/N_i). Carbon is continuously lost to the atmosphere as CO_2 hrough microbial and plant respiration (C_r) and made available directly for plant photosynthesis or added to the atmospheric pool (CO_2). The nutrients are circulated within the microbial system of the soil or traded off and taken up by the plants (N_u). The plant species differ widely in nutrient uptake rates; here represented by *Cassiope tetragona* with slow uptake rate and *Polygonum viviparum* with high uptake rate. Some plants, e.g. *Cassiope tetragona* can circumvent the microbial mobilization/immobilization process by uptake of nutrients directly from organic matter decomposed by mycorrhizal fungi (MY) associated with their roots. Some carbon and nutrients can be lost from the system as dissolved organic matter (DOC) or nutrient leachate (LE) transported to adjacent systems. Climate change acts on the system mainly by controlling the rate of CO_2 uptake by plants and the activity of micro-organisms. Tundra ecosystems differ from others by having large stores of nutrients and carbon in the soil and microbial biomass and in having low rates of CO_2 uptake, i.e. low productivity.



igure 3. Arctic landscape types. (*a*) High Arctic polar semi-desert near Ny Ålesund, Sval-
ard showing temperature manipulation experiments on scattered *Dryas octopetala* vegetation.
hoto credit: T. V. Callaghan. (*b*) High Arctic vegetation and thermokarst scenery dominated by
baidgerakhs', i.e. raised polygon centres accentuated by rapidly thawing polygon troughs, Os-
rov Faddeyevskiy, New Siberian Islands. Measurements of methane fluxes are in progress. Photo
redit: S. E. Jonasson. (*c*) Polygonal/tetragonal coastal tundra, Olenekskiy Bay, North-central
iberia, showing sunken and flooded polygon centres, raised polygon rims and polygon troughs.
hoto credit: T. V. Callaghan.



igure 3. (*d*) Mid-Arctic tussock tundra dominated by *Eriophorum vaginatum* near the Yana elta, east of the Taimyr Peninsula, North Siberia. Photo credit: S. E. Jonasson. (*e*) Sub-Arctic undra/taiga ecotone dominated by mountain birch trees (*Betula* pubescence ssp *tortuosa*) and warf shrub heath vegetation, near Abisko, Swedish Lapland. A randomized block temperature nhancement experiment can be seen beyond the tree line. Photo credit: J. Busch. (*f*) Sub-Arctic nountain birch forest destroyed by the defoliating moth caterpillar *Epirrita autumnata* near evo, Finland. Pest outbreaks are currently controlled by low winter temperatures which kill ggs. Photo credit: T. V. Callaghan.