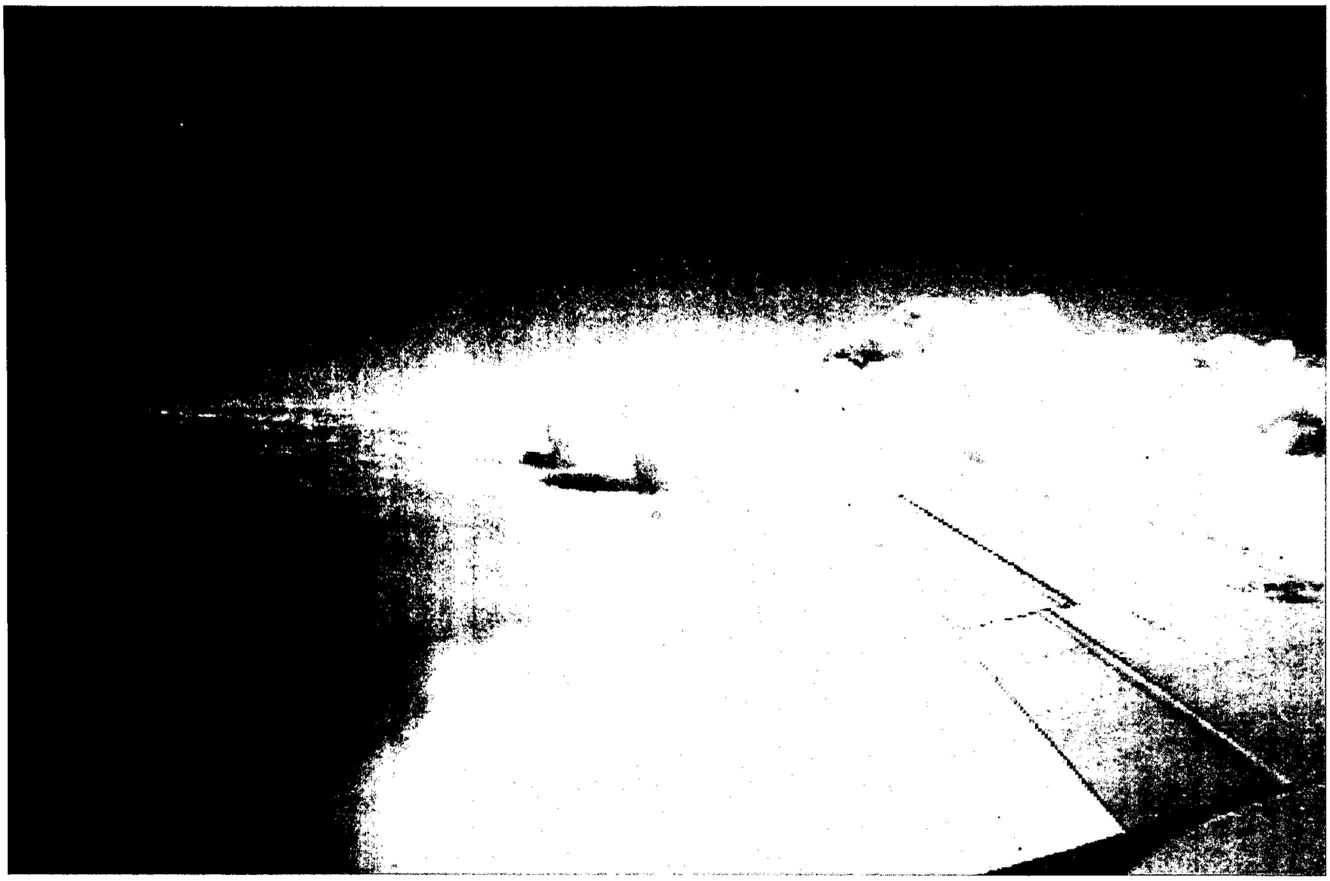

tion, can be found on the CLARA internet pages:

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Effects of global change on plant species composition

• by Wim Arp, Frank Berendse and Carolien de Kovel

Environmental conditions, such as soil type and climate, determine plant species composition and biodiversity. Global change can directly affect the environment of the plant through changes in climate, higher atmospheric CO_2 concentrations, and indirectly through changes in soil moisture and nutrient mineralisation. How will this affect the species composition of the vegetation? Growth experiments and simulation models suggest that this depends on whether the ecosystem is nutrient or water limited. Also, the different aspects of global change (temperature or CO_2 increase) can have opposing effects on plant species composition.

The effects of a change in environmental conditions on biodiversity can be separated into two components. The first is the 'short term' effect caused by the 'change' itself. Any disturbance usually results in a decrease in biodiversity because the present species composition is no longer in balance with its environment, and adaptation of the vegetation to the new environment may require the establishment of new species. A change in climatic conditions might force species to move from other climatic zones over large distances. Depending on the ability of species to distribute and on the availability of corridors, it may take a long time before a new equilibrium is reached.

The second component is how the changed environment determines species composition and biodiversity in the 'long term' equilibrium situation.

The main question in our research programme is how global change might have a long-term effect on species composition, succession and possibly on biodiversity. The focus is on the effects of CO_2 enrichment and temperature increase on growth and turnover of plant species in nutrient poor environments. Important aspects are the effects of global change on nitrogen availability and water supply, which affect the vegetation indirectly.

Table 1

Species used:	Nutrient rich sites: (fast growing species)	Intermediate:	Nutrient poor sites (slow growing species)
	Arrhenatherum elatius (false oat-grass)	*Molina caerulea* (purple moor-grass)	*Calluna vulgaris* (heather)
	Rumes obtusifolius (broad-leaved dock)	*Vaccinium myrtillus* (bilberry)	*Erica tetralix* (bog heather)

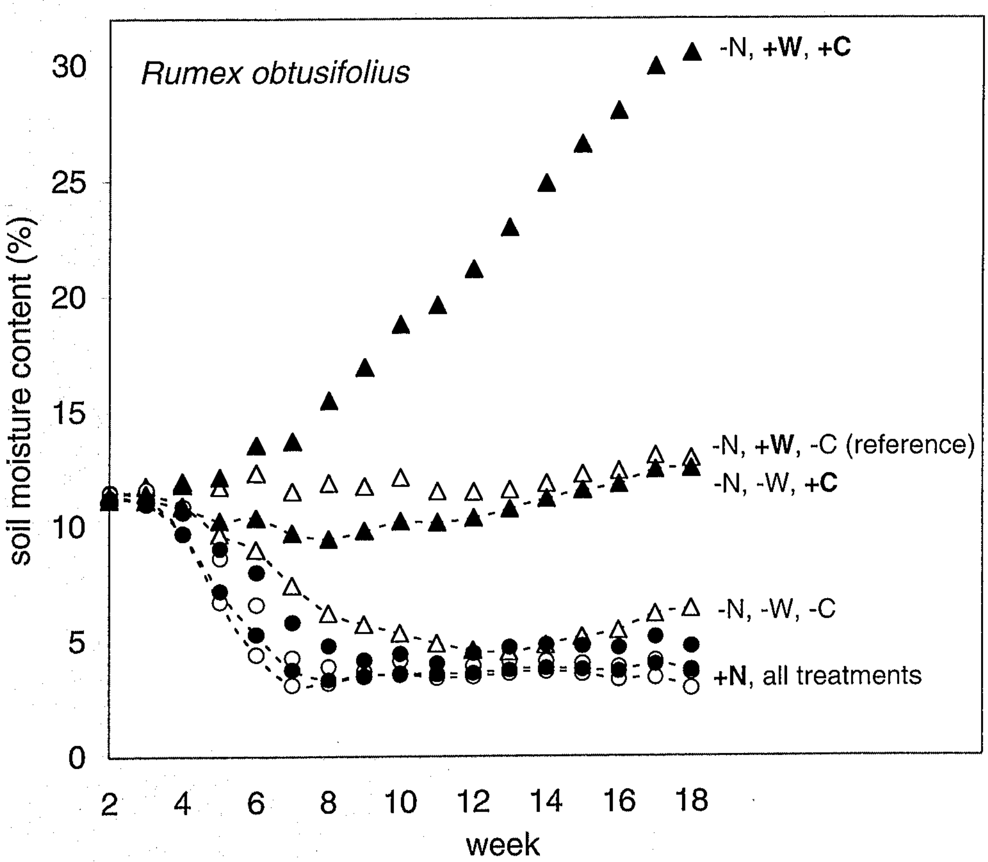
Nutrient limited ecosystems often harbour a high biodiversity. High levels of nitrogen deposition currently threaten to reduce this biodiversity by enabling species adapted to nutrient rich sites to replace the existing vegetation. It has been suggested that these faster growing species may also benefit more from a higher CO_2 concentration. We have tested how elevated CO_2 and temperature affect species from nutrient limited and nutrient rich ecosystems using field and greenhouse experiments. Computer simulation models were created to assess the effects of global change on ecosystem processes and plant species composition.

In a greenhouse we exposed a wide range of plant species to different combinations of CO_2 concentration, nitrogen supply, and drought stress. No difference in relative response to CO_2 was found between species, although the absolute biomass increase was larger for the potentially fast growing species under the high nitrogen supply (see table 1).

A large interaction between CO_2 and nitrogen was found: when nitrogen was added, CO_2 enrichment resulted in a large stimulation of biomass production, but no reduction in water use. The relative effects of CO_2 on biomass were larger when water supply was limited. When no nitrogen was supplied, CO_2 had no effect on biomass, but water use was reduced, which resulted in a higher soil moisture.

Figure 1 shows the soil water content for the different treat-

Figure 1. Soil moisture content of Rumex obtusifolius pots during the course of the experiment.
Closed symbols: high CO_2, open symbols: ambient CO_2; circles: high N, triangles: low N; solid lines: high water, dashed lines: low water. All other species showed comparable results.



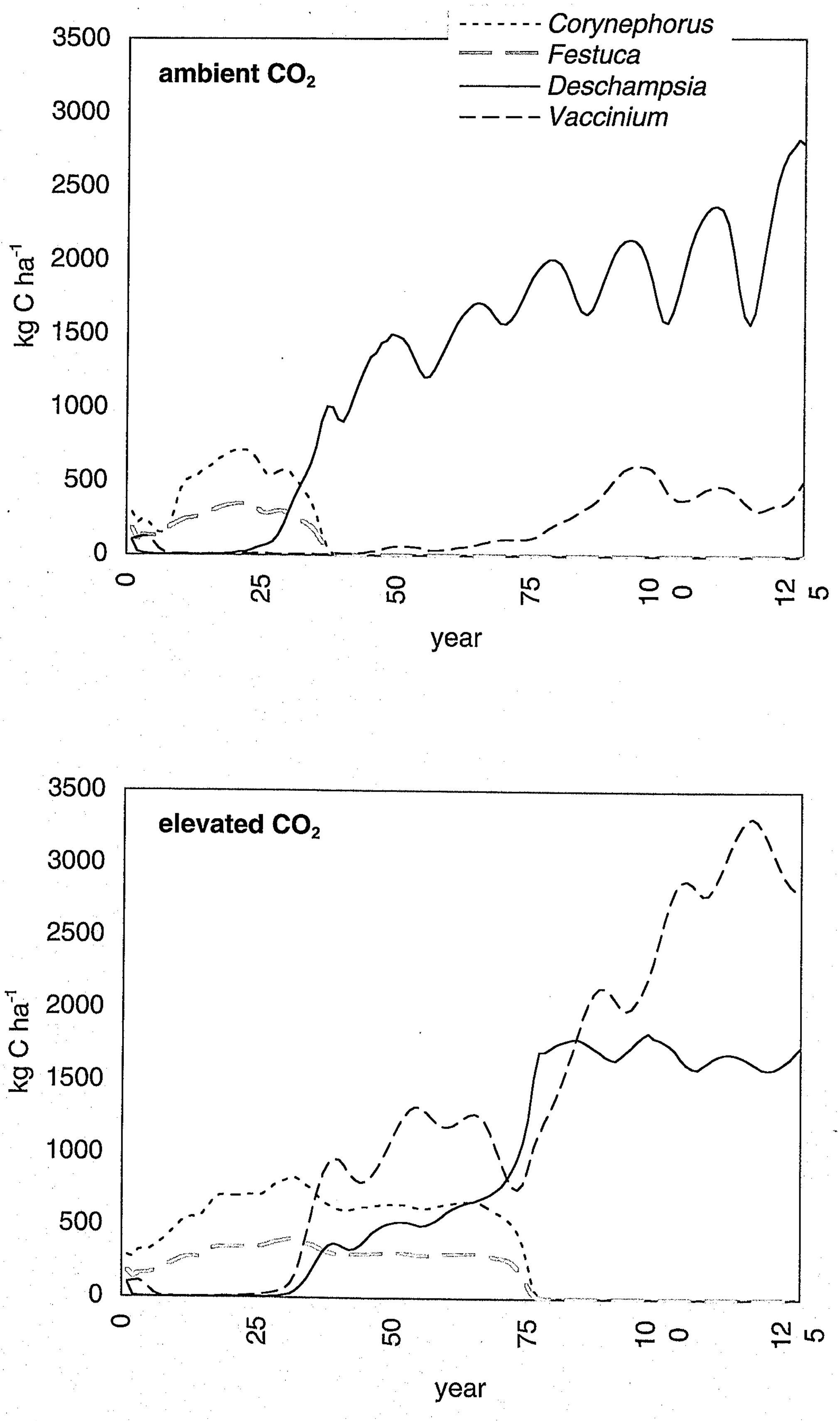


Fig. 2. Simulation results at ambient (350 ppm) and elevated (600 ppm) CO_2 for understorey species of a developing mixed forest on dry and nutrient poor substrate. Corynephorus canescens = gray hair-grass; Deschampsia flexuosa = wavy hair-grass; Festuca ovina = sheep's fescue; Vaccinium myrtillus = blueberry.

Table 2:
Possible effects of CO_2 and temperature on nutrient poor ecosystems

	ambient temperature	elevated temperature
ambient CO_2:		
soil moisture	--	⇩
plant production	--	⇧
species diversity	--	⇩
elevated CO_2:		
soil moisture	⇧	?
plant production	0	⇧⇧
species diversity	⇧	⇩⇩

ments throughout the experiment for one of the species. At high nitrogen levels, all water in the pots was rapidly consumed, but at low nitrogen levels, CO_2 enrichment increased the soil moisture content.

This experiment shows that the effects of elevated CO_2 on plants depend on the environmental conditions. Biomass may increase when nitrogen is available, and this may favour the species from rich sites which show a larger absolute growth stimulation. The negative effects of increased nitrogen deposition on species composition and diversity, which is occurring in nutrient poor ecosystems, will in this case be stimulated by high CO_2. When nitrogen availability is low, the main effect of CO_2 will be on water use and soil moisture, although CO_2 may also stimulate growth under drought stress. Many nutrient limited, wet ecosystems in the Netherlands are currently experiencing a long term drought, which is having a negative effect on species composition and biodiversity. A higher CO_2 concentration could have a direct positive effect on the preservation of existing biodiversity if CO_2 reduces this drought stress. A higher soil moisture content may also enhance the chance of survival of seedlings in dry environments (see table 2).

Another aspect of global change is the expected temperature increase. This will have a different effect on nitrogen limited ecosystems than the increase in CO_2 concentration. While no effect of CO_2 on biomass is expected when nitrogen is severely limiting growth, a higher temperature will stimulate the turnover of nitrogen in the soil, resulting in a higher nitrogen availability to the plants. This effect alone, but especially in combination with higher CO_2 levels, may result in growth stimulation. Such a positive growth response was observed in the CLIMEX experiment. In this large scale experiment a nutrient poor ecosystem in southern Norway is exposed to elevated temperature and CO_2 concentration. In 1995, after only two years of treatment, the biomass of heather and blueberry had increased in this system. This biomass increase appears to be correlated with an increased availability of nitrogen.

Is this positive effect on growth permanent, or will it disappear in a few years? This will depend on whether the increase in nitrogen availability can be maintained over the long term through accelerated nutrient cycling. If this is the case, then these conditions may enable species from more nutrient rich sites to compete with the existing species, resulting in a change in species composition.

Computer simulation models show how global change (CO_2 and temperature increase) could affect plant growth, ecosystem processes, and possibly the succession (the development of a natural vegetation with time) and species composition. Preliminary results for a succession series from drift sand to forest show the following effects of CO_2 enrichment:

- The effects of climate change depend strongly on nutrient and water availability. At early stages of succession in a nutrient poor and dry system high CO_2 may accelerate succession since water stress is reduced. At intermediate stages succession is delayed because early successional species, adapted to low nutrient environments, can coexist longer with the later successional species.
- In the later stages nitrogen availability is increased because of a change in species composition. An increased proportion of the grass Deschampsia flexuosa relative to the pine tree (Pinus sylvestris) results in litter which is more easily decomposed.

Figure 2 shows simulation results for 125 years of succession at either ambient or elevated CO_2 concentration. At the high CO2 concentration early successional species are able to persist for a longer period and more species can coexist together.

How global change affects species composition depends largely on existing environmental factors, especially the availability of nitrogen and water. These factors are in turn indirectly affected by climate change. Elevated CO_2 increases soil moisture at low nitrogen, which may reduce the decline in plant species diversity that occurs in wet environments due to a lowering of ground water levels. Raised CO_2 levels, especially in combination with a climate change leading to a higher nitrogen availability, may result in a stimulation of the growth of species adapted to more nutrient rich sites. This could reinforce the decline in diversity caused by increased nitrogen imports. Higher temperatures will counteract the positive effects of elevated CO_2 on soil moisture, and are expected to have negative effects on the biodiversity of wetland ecosystems.

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