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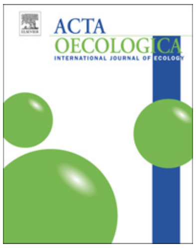

Original article

# Different responses of *Molinia caerulea* plants from three origins to $CO_2$ enrichment and nutrient supply

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ARTICLE INFO

*Article history:*
Received 31 May 2007
Accepted 2 October 2007

*Keywords:*
Global change
Growth chambers
Intraspecific responses
Phenology
Ramets
Rootstocks

ABSTRACT

The global environmental change factors eutrophication and $CO_2$ enrichment will affect carbon and nutrient cycling in plants and ecosystems. In order to study their interactions on plant performance, growth chamber experiments were performed with plants from three origins of the common but ecologically variable Purple Moor Grass (*Molinia caerulea* (L.) Moench) grown in a bi-factorial combination of two levels of nutrients (for N: 31 or 62 kg $ha^{-1}$ $year^{-1}$) and $CO_2$ (400 or 600 $\mu$mol $mol^{-1}$ $CO_2$). Plants were established from ramets with known start weights so that total biomass accumulation of each plant over time could be analysed. Plant phenology, leaf properties and the biomass of different fractions (inflorescences, leaves, stems and rootstocks) were investigated to identify treatment effects on plant development and allocation patterns. The few consistent responses identified in the plants were a significant increase in leaf biomass by doubling the nutrient supply and plants exposed to elevated $CO_2$ showing a reduced specific leaf area (SLA), an increased number of senescent leaves and increased rootstock growth. Increasing the nutrient supply had greater effects on aboveground biomass than raising the $CO_2$ concentrations but significant interactions between the two plant fertilisers were absent. The variable responses of the ramets to the addition of resources were largely modified by their phenology and their readiness to switch from vegetative to reproductive growth. We conclude that differences in phenology and ecological behaviour of ecotypes of the same plant species will largely affect their response to environmental change.

## 1. Introduction

Recent field experiments on $CO_2$ enrichment indicate that crop yield responses have been overestimated in agroecological models and that plant productivity will be modified by other global change components including tropospheric ozone and nitrogen deposition (Fuhrer, 2003; Long et al., 2005). However, interactions between $CO_2$ enrichment and other atmospheric compounds have not much been considered in experiments due to higher technical complexity. On the crop and wild plant species level climate change and $CO_2$ enrichment will probably affect food security and biodiversity but as the vegetation cover is both a source and a sink of greenhouse gases, man-made land use changes and releases of eutrophying compounds will also determine reduction potentials of these gases in the coming decades

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1146-609X/$ – see front matter
doi:10.1016/j.actao.2007.10.006

(Brouwer and McCarl, 2006). The inter-relations between net primary productivity, vegetation sink activity, temperatures and $CO_2$ fluxes in the exceptionally hot year 2003 have been demonstrated by Ciais et al. (2005), and the meta-analyses of Luo et al. (2006) and De Graaf et al. (2006) addressed C and N dynamics and the productivity of ecosystems at ambient and elevated $CO_2$. The results of both analyses suggest that globally the main driver of soil C sequestration is the input of carbon through plant growth, which largely depends on the availability of nutrients.

While such meta-analyses aim to quantify whole ecosystem effects of the long-term progressive nutrient limitation (PNL) on carbon sequestration, further field studies and experiments in controlled environments are needed to identify changes in carbon–nutrient balances in selected plant communities and single keystone plant species, especially those currently extending their ranges. In monocultures the $CO_2$ response is lower in plants grown under N limited conditions (Daepp et al., 2000; Aeschlimann et al., 2005), but in more complex communities resource use will be more efficient and some species or functional types may react stronger than others to either the $CO_2$ fertilisation or the nutrient supply (Reich et al., 2001, 2004).

Obviously, the response of plants to changes in the atmospheric composition depends much on plant–plant interactions determining the uptake of nutrients from the soil and the canopy structure determining the uptake of $CO_2$ and other gases. Nevertheless, it is the identity of a plant species, its inherent plant traits, anatomy, resource acquisition potential, ecology and phenology which will determine whether it will profit or lose following environmental changes. In the case of carbon dioxide it has been shown that plant species with a higher gas-exchange rate, i.e. the more productive plants, generally respond stronger to enhanced levels of $CO_2$ (Poorter, 1998; Poorter and Navas, 2003). It is therefore suggested that inherently fast-growing species are stimulated proportionately more in biomass by $CO_2$ enrichment and even more so if nutrients are unlimited. However, inherently slow-growing species may be more responsive to $CO_2$ under a low nitrogen supply than the fast growing species (Arp et al., 1998).

Both the increasing atmospheric concentration of carbon dioxide and the eutrophication of ecosystems (e.g. by the deposition of nitrogen and other nutrients) will have stimulating effects on some plant species, whilst others, presumably the slow growing, less competitive species will not be able to profit from the fertilisation. It is postulated that the changing competitive balances in semi-natural vegetation by the ongoing global fertilisation will lead to the extinction of rare plant species and the spread of invasive, ruderal species which possess traits that confer high resource acquisition (Ellenberg, 1985; Chapin et al., 1993; Diekmann and Falkengren-Grerup, 2002). In productive crops, the increased availability of carbon may require a higher supply of nutrients in order to compensate for nutrient imbalances and changes in crop quality. While agriculture will be able to adapt fertilisation practices, nutrient imbalances might arise in unmanaged vegetation. On the other hand, we would expect stronger responses to $CO_2$ in those regions where long-lasting and pronounced nutrient deposition has lead to increased nutrient availability. Furthermore, Reich et al. (2006) hypothesise that limitations to productivity resulting from the insufficient availability of nutrients in both unmanaged and managed vegetation will be an important constraint on global terrestrial responses to elevated $CO_2$.

Although a great number of chamber and field experiments have been established in which single plants and communities have been exposed to $CO_2$, the question whether different sub-species and ecotypes of the same species respond uniformly to changes in the atmospheric composition has not much been addressed. In trees intraspecific differences in growth sensitivity to $CO_2$ and N have been shown to be considerable (Spinnler et al., 2003), but in herbaceous plants and grasses such responses have not been studied much to date. An exception is Jablonski (1997) who investigated the response of vegetative and reproductive traits of three cultivars of *Raphanus sativus* and the wild relative *R. raphanistrum* to $CO_2$ at varying supply of nitrogen. Enhancements in vegetative biomass due to $CO_2$ and nitrogen fertilisation did not correlate with the reproductive response, which points to the necessity to perform detailed studies on the reproductive phase to understand the effects of plant fertilisers. Like the varied responses in different taxa to atmospheric changes, the ecotypic variation in sensitivity to air pollutants and presumably $CO_2$ enrichment will also be associated with the origin of the plants, their different phenology, growth rates and leaf characteristics. It can thus be expected that the ecological context of a plant and its phenotypical plasticity determine responses to changes in air quality and nutrient supply.

In the present study, we studied the responses of a common European grass species to a factorial combination of different levels of nutrients and $CO_2$. The species *Molinia caerulea* (L.) Moench was chosen because it has increased in frequency throughout North-Western Europe in different plant communities in past decades (van Breemen and van Dijk, 1988; Aerts and De Caluwe, 1989; Hogg et al., 1995). Strongest increases of the grass species have been reported in those dry and wet heathland regions, in which nitrogen deposition is high. Many of these sites are no longer N- but P-limited so that grasses like *Molinia* may get an advantage over herbs and shrubs (Ruthsatz and Holz, 1994; Kirkham, 2001). In Norway and in the Northern UK, however, *Molinia* did not show changes in frequency (Nygaard and Odegaard, 1999; Stevens et al., 2004) even in those regions with high N deposition. According to the review of Taylor et al. (2001) *Molinia caerulea* is a "very variable species owing to a combination of phenotypic plasticity and genetic variation". Morphological plasticity of the grass is mainly expressed as variation in overall size and in the length and width of leaves. The Euro-Siberian boreotemperate species grows in altitudes ranging from the sea level to the mountains and it has a bimodal pH distribution with peaks of abundance on both highly acidic and calcareous soils. It is common in wet and dry heaths, grasslands and oak-birch forests. This wide variation and range of habitats of *Molinia* reveal the species as particularly useful in studying ecological variation and adaptation of different origins to specific environments (Salim et al., 1995). We thus found it interesting to investigate the responses of a highly mutable species to the two important global change components $CO_2$ enrichment and eutrophication using material from different origins.

In order to address the variability of responses of *Molinia caerulea* to increased availability of nutrients and $CO_2$, we