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Original Research Article

Over-shading is critical for inducing a regime shift from heathland to grassland under nitrogen enrichment

G.A.K. van Voorn [a,*], B.W. Kooi [b], A.K. Bregt [c]

[a] Biometris, Wageningen University and Research Centre, Droevendaalsesteeg 1, 6708 PD Wageningen, The Netherlands
[b] Faculty of Earth and Life Sciences, VU University, de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
[c] Laboratory of Geo-Information, Science and Remote Sensing, Wageningen University, Droevendaalsesteeg 3, 6708 PB Wageningen, The Netherlands

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ABSTRACT

The mass conversion of heathland to grassland in north-western Europe the past decades is a typical example of how tipping points threaten the biodiversity and ecosystem services delivered by biota. Different explanations have been provided for this conversion, with nitrogen enrichment resulting from anthropogenic activities being a commonly supported hypothesis. Here we present a mathematical model to investigate the conditions under which the conversion of heathland to grassland can occur. The model describes indirect competition for light and nitrogen between heather dwarf shrub (*Calluna vulgaris*) and wavy hair-grass (*Deschampsia flexuosa*), while both species also over-shade each other. Nutrient co-limitation in the model is described using the Synthesizing Unit concept. Over-shading is found to play a pivotal role in the existence of alternative stable states in the model. Under constant light availability a combination of over-shading and enrichment with ammonia leads to a regime shift from heathland to grassland, while under enrichment with ammonia alone there is coexistence between the two species. These results are supported by experimental findings in the literature.

1. Introduction

A major conservation issue nowadays is the loss of biodiversity and the subsequent loss of ecosystem services provided by biota via *regime shifts* or *tipping points* (Folke et al., 2004; Scheffer et al., 2009; Boettiger et al., 2013). Regime shifts are fast and large-scale changes caused by relatively small changes in system drivers, often because of direct or indirect anthropogenic influences, resulting from the existence of nonlinear interactions and feedbacks (Scheffer and Carpenter, 2003). The complexities surrounding the conditions under which tipping points occur pose a significant challenge for future environmental policy and management but have to be considered (Folke et al., 2004; Schlüter et al., 2012).

An interesting case study in this regard may be the large-scale conversion of heathland to grassland. Heathland is an ecosystem type that provides unique ecosystem services, such as a high conservational value for biota and a high aesthetic and historical value (Alonso et al., 2001), while it historically provided grazing terrain for sheep. It has also been suggested that heathland may be used as a source of bioenergy production (Worrall and Clay, 2014). Experimental studies have suggested that the dynamics of the heathland plant community may be considered as essentially a two-species system consisting of heather dwarf shrub (*Calluna vulgaris*) and wavy hair-grass (*Deschampsia flexuosa*) (Damgaard et al., 2009). Normally heathland is dominated by *Calluna*, but since the 70s and 80s of the last century mass replacements have occurred in north-western Europe (UK, The Netherlands) of *Calluna* by *Deschampsia*, while further losses of heathland have occurred due to a combination of afforestation and poor management (Cadbury, 1992).

Several theories have been suggested to explain the mass shifts from heathland to grassland. Wavy hair-grass occurs naturally in heathland, in particular after heather dieback caused by infestation by heather beetle (*Lochmaea suturalis*). It therefore has been suggested that heathland can naturally change to grassland through beetle infestation alone (Berdowski, 1987). Nevertheless, grasses seldom outgrow *Calluna* under pre-industrial or even mildly elevated nitrogen availability levels (Alonso et al., 2001). This may perhaps be because of specific grazing by ungulates like sheep and deer (Alonso et al., 2001), which may target grasses more than *Calluna*.

The dominant view in ecological literature is that nitrogen enrichment is the main driver in heathland conversion to grassland

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[*] Corresponding author at: P.O. Box 16, 6700 AA Wageningen, The Netherlands. Tel.: +31 317484616.

E-mail addresses: george.vanvoorn@wur.nl (G.A.K. van Voorn), bob.kooi@vu.nl (B.W. Kooi).

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in the Netherlands (Heil and Bobbink, 1993) and the UK (Power et al., 1998). Replacement of *Calluna* by grasses does occur in experiments with significant nitrogen enrichment (Heil and Diemont, 1983). The concept of *critical load* has been introduced to provide threshold values above which nitrogen deposition rates start to have observable negative effects on ecosystem communities (Bobbink et al., 2011). In the UK wet deposition of nitrogen has increased from around 2–6 kg nitrogen per hectare per year in the 1900s to around 15–60 kg in the 1990s (Pitcairn et al., 1995). In the Netherlands nitrogen deposition levels are predicted to be as high as 1400–1800 mol per hectare per year over the period 2010–2030 (Velders et al., 2010), which translates to an average of ca. 22 kg per hectare per year. An exceedance by 500–1500 mol (ca. 10 kg) per hectare per year in many of the NATURA2000 areas in the Netherlands is predicted (Velders et al., 2010). Such numbers indicate at least that nitrogen deposition will have effects, although it does not directly explain a shift from heathland to grassland.

Another factor that has been suggested to be of importance is competition for light between the two species (Van der Eerden et al., 1991; Britton et al., 2003), but only under gap formation resulting from e.g. grazing (Aerts et al., 1990). Experiments with *Calluna* show that shading leads to strong reduction of flowering, etiolating of shoots, and lower shoot densities, while nitrogen enrichment leads to increased flowering (Iason and Hester, 1993). Other observations suggest that *Calluna* with an intact canopy can out-compete grasses, even at increased levels of nutrient supply (Alonso et al., 2001), while grown as seedlings *Deschampsia* always outcompetes *Calluna*. These observations could be explained by over-shading playing an important role in the inter-specific competition, possibly leading to priority effects (i.e., bistability or alternative steady states; Drake, 1991). Other experimental results suggest that (mostly) one-sided competition by grasses towards *Calluna* may indeed be associated with over-shading (Britton et al., 2003).

In this paper we investigate under which conditions heathland can change to grassland by looking at the combined effects of competition for nitrogen and light between *Calluna* and *Deschampsia* on the respective species populations. For this we develop a mathematical model consisting of a set of ordinary differential equations which is based on stylized facts that have been put together from various literature sources. The competition for light and nitrogen is indirect and incorporated by describing co-limitation of light and nitrogen sources (ammonium, nitrate) available to *Calluna* and grass by making use of the *Synthesizing Unit* formulation (Kooijman, 2010). Light availability is constant but for the two species it is affected by over-shading. Phosphorus limitation has been suggested to be of relevance as well, but experiments with nitrogen and phosphorus enrichment of *C. vulgaris* have not indicated a clear phosphorus limitation (Von Oheimb et al., 2010), hence we do not include phosphorus in the model.

The paper is organized as follows. In Section 2 we provide the description of the conceptual model and discuss the stylized facts (in Table 1) and important assumptions and simplifications (in Table 2). In Section 3 the mathematical model is given, which is a set of ordinary differential equations. The derivation of the functional responses of the model based on the *Synthesizing Unit* concept is given in Appendix A. The model is analyzed in Section 4 by primarily using bifurcation analysis. Section 5 presents the discussion and conclusions.

2. Conceptual model

The model describes *Calluna* and grass which are co-limited by light and nitrogen (ammonium and nitrate). The graphical depiction of the conceptual model is given in Fig. 1. Conceptually the system resembles a food web model consisting of resources and consumers. For the development of the conceptual model we make use of various stylized facts that are based on observations and experimental findings published in the peer-reviewed literature. These can be found in Table 1.

Table 1
Stylized facts about heather and grass taken from literature.

No.	Short description and source
I	*Deschampsia* significantly affects *Calluna* but not the other way around. However, intra-specific competition for *Deschampsia* occurs at planting densities above 29 plants m^{-2}, while *Calluna* does not show clear intra-specific competition (Britton et al., 2003)
II	*Calluna* is slow-growing but evergreen and with an intact canopy can outcompete grasses, even at increased levels of nutrient supply (Alonso et al., 2001). When grown as seedlings *Deschampsia* always outcompetes *Calluna*
III	*Calluna* competes best on sandy soil, where the shoot biomass ratio is greatest (Britton et al., 2003)
IV	Grasses (including *Deschampsia*) typically utilize surface water and surface nitrogen, which is ammonium. Shrubs (including *Calluna*) typically utilize deeper water and deep soil nitrogen, which is (leached) nitrate (Gherardi et al., 2013)
V	Shrubs have a higher nitrate uptake rate than grasses, while their ammonium uptake rates are similar (Gherardi et al., 2013)
VI	Young *Calluna* and grass individuals respond only significantly to soil type (peat vs. sandy soil), and not to nitrogen additions or watering regimes (Britton et al., 2003)
VII	*Calluna* seedling germination depends highly on damp conditions (Britton et al., 2003 and references therein)
VIII	*Calluna* canopy is most dense if the individuals are of medium age; young *Calluna* still needs to grow, while older *Calluna* shows gaps in its canopy (Alonso et al., 2001)
IX	Fencing (which prevents grazing by deer and sheep) increases the height of *Calluna*; *Calluna* typically has a height of 0.2–2 m (Alonso et al., 2001)
X	Fencing and experimental nitrogen addition both roughly equally contribute to increase in *Deschampsia* height (Alonso et al., 2001)
XI	Grazing seems to occur mostly at the rim of *Calluna* canopy. Grazers prefer grass because of the higher palatability as compared to *Calluna*, which contains relatively many phenolics (Alonso et al., 2001)
XII	Ammonium barely leaches, although there are some losses through volatilization. Ammonium is nitrified to nitrite and nitrate by microorganisms. Nitrate, in turn, easily leaches to surface or deeper soil waters (Ri and Prentice, 2008)

Table 2
Overview of the main assumptions and simplifications of the food web model of heather and grass.

No.	Short explanation
1	All nitrogen deposition in natural areas is in the form of ammonia, i.e., there is no appreciable influx of nitrate
2	Any chemical side-effects from nitrogen deposition are ignored in the regime shift, like soil acidification and the mobilization of toxic compounds such as aluminium
3	There is no limitation in the processes resulting from microbial activity, i.e., nitrate formation from ammonium and re-mineralization of dead biomass
4	There is no distinction between different soil layers. The fact that *Calluna* extracts nitrogen mainly from deeper layers (in the form of nitrate) is represented by a higher uptake rate for nitrate
5	Light intensity (L) cannot change and is homogeneous, hence L is not a dynamic state variable but a parameter in the model
6	Nitrogen is the only limiting element, and hence all (bio)masses are expressed in terms of N-mol. There is a fixed ratio assumed of carbohydrates-to-nitrogen in the creation of biomass, i.e., there is a fixed conversion factor of light
7	Grazing by herbivores and infestation by heather beetle are ignored
8	Any stoichiometric differences between dead material from grasses and *Calluna* are ignored, i.e., dead material consists of only one type. Hence the re-mineralization of dead material is perfect, and there is no distinction between labile and recalcitrant components
9	Water is not a limiting factor