Trophic interactions in gradients of primary productivity

van de Koppel, Johan

SUMMARY

In this thesis, we studied a number of systems from which the dynamical behaviour deviates from that predicted by conventional exploitation theory. Most studies deal with the changes in community structure along primary productivity gradients found on the island of Schiermonnikoog, The Netherlands. Two studies deal with the mechanisms behind dramatic vegetation changes in grazing systems in (semi-arid) savannas and arctic salt marshes. In this final chapter, I summarize my findings and briefly discuss mechanisms that may account for patterns of species abundances or species interactions found in these systems.

The first part of this thesis deals with the grazing of hare, rabbit and geese along the primary productivity gradient found on the salt marsh of the island of Schiermonnikoog. Field data revealed that the grazing by these herbivores, measured as the amount of dung produced within a year, was most intense at parts of the salt marsh with intermediate levels of primary productivity. Furthermore, we found that exploitation by geese, expressed as the proportion of the maximum standing crop that is consumed, was maximal at low primary productivity. Both exploitation by geese and exploitation by lagomorph species decreased as primary productivity increased. These findings are in strong contradiction with conventional exploitation theory.

We hypothesized that the low numbers of herbivores found on the more productive parts of the salt marsh were caused by a low foraging efficiency of these herbivores in vegetation with a high plant standing crop. This hypothesis was tested using captive barnacle geese that were allowed to forage on vegetation dominated by *Festuca rubra*. We investigated whether the foraging efficiency of barnacle geese, in terms of both consumption and growth, was lower on high biomass vegetation compared to low biomass vegetation of *Festuca*. Daily consumption by the geese, measured as the amount of dung produced, was significantly higher on low biomass vegetation compared to high biomass vegetation, supporting our hypothesis. No differences in growth of geese were found. Four potential mechanisms may account for the decrease in foraging efficiency of geese in dense vegetation. An increase of plant standing crop may result in a decrease in plant quality due to maturation of plant tissue, may lead to decreased short-term intake rates due to for instance an increase in the proportion of standing dead, or may lead to an increase in the time spend on spotting potential predators, and thus to a decreased time spend on foraging. Finally, it may result in a shift to plant species adapted to competition for light, which are generally less favourable for herbivores. In our experiment on *Festuca*-dominated vegetation, a low bite rate in high biomass vegetation, caused by high densities of plant litter intermingled with the food items, seems to be the most likely cause of the low foraging efficiency of geese in dense vegetation. On the scale of the salt marsh, however, plant species replacement may be of greater importance.

A low herbivore foraging efficiency in vegetation of high standing crop may have large implications for the dynamics of plant-herbivore systems. We examined plant-herbivore models where the growth of herbivores decreases in dense vegetation, and analysed the behaviour of this model along a gradient of primary productivity. In systems of intermediate productivity, two stable states are found. In one state, the herbivore maintains a low standing crop. The other state is dominated by dense vegetation unsuitable for herbivore grazing. In systems of high productivity, the herbivore is unable to maintain a short sward and a dense vegetation without herbivores develops. The model supports our hypothesis that foraging limitations are the cause of low herbivore numbers on the more productive parts of the salt marsh. However, neither conventional exploitation theory, nor the model described above explains the decrease in exploitation intensity found along the productivity gradient. We argue that the exploitation patterns we found result from the ability of herbivores to move and exploit a large variety of patches available on the salt marsh. Local abundance of herbivores within a single patch of vegetation would not be determined by growth and mortality, as in conventional models, but rather by movement of herbivores in and out of the patch. We present a theoretical analysis which shows that herbivore mobility may explain the exploitation patterns found along the salt-marsh productivity gradient. In the analysis, exploitation intensity is found to decrease with increasing productivity for a wide spectrum of parameter values, independent of the type of relation between migration and plant standing crop. Other patterns, such as increasing or alternating exploitation intensity with increasing productivity, however, are also feasible. The model reveals that patchy systems with mobile herbivores may have multiple stable states. The occurrence of multiple stable states depends on the relation between plant standing crop and herbivore migration, and on the productivity of the vegetation.

Most natural ecosystems harbour multiple herbivore species. The extent to which foraging is limited in vegetation of high standing crop will differ among these herbivores. In order to investigate the dynamic implications of multiple herbivore species in systems in which herbivore foraging efficiency is maximal at intermediate plant standing crop, we analysed a plant-herbivore model that contains two herbivores. One of these herbivores, labelled as 'small', is unable to survive on vegetation of high standing crop, whereas the other, labelled as 'large', can survive on such vegetation. At high plant standing crop, the large herbivore may facilitate the small herbivore by reducing vegetation biomass. Competition between both herbivores will prevail at low standing crop. This may have large consequences for the dynamics of herbivore-dominated systems, especially in systems where humans have had little impact on herbivore diversity. We argue that interactions between 'small' herbivores such as impala or buffalo and 'large' herbivores such as elephant may explain dynamic transitions between (high biomass) savanna woodlands and (low biomass) grasslands in Africa. Literature dealing with competitive interactions between elephants and other herbivores supports this hypothesis. Equilibrium models may not apply to such systems.

Conventional grazing theory predicts that per capita plant growth is enhanced when herbivore pressure is increased. We review studies from grazing systems in semi-arid savannas and arctic salt marshes where increases in herbivore grazing have resulted in an irreversible collapse of the vegetation. A number of empirical studies indicate that plant-soil feedbacks are the dominant cause of the collapse of vegetation in these systems. In semi-arid savannas in Africa, a reduction of plant standing crop led to a decreased infiltration of rainwater, followed by surface runoff. This, in turn, led to soil erosion and loss of nutrients. Both water and nutrients are vital for plant growth in semi-arid savannas. In arctic salt marshes along the Hudson Bay, enhanced herbivore grazing and grubbing for roots led to salinisation of the top soil, which had a negative effect on plant growth. Hence, in both systems, degradation of soil resulted in reduced plant growth. This led to positive feedback between reduced plant density and deteriorated soil conditions, which ended in the observed destruction of the vegetation.

The studies described above examined specific interactions or rather small food webs. To investigate the effects of productivity changes on more complex food webs, we studied changes in soil food webs found along a productivity gradient in the dunes of Schiermonnikoog. We focussed on whether changes that occur in the soil food web could be explained

by current models of food chains. The number of functional groups in the food web and the average length of food chains increased with the productivity at the base of the food web, conforming with the predictions of food chain theory. Contrary to food chain models, we found that the first trophic level reached a plateau at sites with high productivity, whereas the second and third trophic level showed a more continuous increase with productivity. Individual functional groups showed a strongly varying response to increased productivity: a number of functional groups increased with productivity, whereas others levelled off, suggesting they were limited by predation. These patterns did not show any relation with the trophic position of functional groups. Our results indicate that the complexity of soil food webs may limit the predictions of models based on food chains.

In an additional chapter a system for photographing within 8 × 8 cm minirhizotrons is described, that uses a telescopic lens instead of an endoscope. This system is designed especially to operate under field conditions; it is portable, shockproof, cheap, easily repaired, and can be operated by a single person. Furthermore, it provides photographs of superior quality as compared to those produced by the conventional endoscope system. The system proved to be a valuable tool in the field study on soil food webs presented in chapter seven.

In the systems described in this thesis, interactions between trophic levels appeared relatively complex compared to the more simple interactions that are the basis of conventional exploitation theory. Using minimodels, we showed that these complex interactions may invoke positive feedbacks that lead to dramatic changes in community structure. Although models based on simple interactions between trophic levels aid in guiding studies on community function, incorporating these complex interactions in ecological theory is essential in fully understanding the behaviour of ecological systems.