Heathland ecosystems, human impacts and time: A long term heathland trial investigating ecosystem changes that occur after exposure to climate change, elevated N deposition and traditional vegetation management practices
Kopittke, G.R.

Citation for published version (APA):
Kopittke, G. R. (2013). Heathland ecosystems, human impacts and time: A long term heathland trial investigating ecosystem changes that occur after exposure to climate change, elevated N deposition and traditional vegetation management practices

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
Chapter 6

Synthesis
1 Introduction

This synthesis aims to discuss a heathland soil under the influence of three conditions caused by human activity: heathland management practices (cyclical vegetation removal), a predicted climate change scenario (repeated annual drought) and elevated N deposition. The feedback of carbon (C) to the atmosphere is of topical interest and so this aspect has been given the most attention within the following chapter, although other ecosystem changes, such as soil acidification under ambient conditions, are also very relevant in the discussion about human influences on the environment.

The human activity of heathland management was investigated from a C perspective, to determine if an increasing Calluna vulgaris stand age resulted in increasing C storage (Chapter 2) or resulted in a change to annual CO$_2$ emissions from soil respiration (Chapter 3). A model selection procedure was used to choose an appropriate model to calculate these soil respiration emissions and, as this was discussed in detail in Chapter 3, it is not discussed further in this synthesis.

A climate change scenario was also investigated with regard to C emissions from the heathland. This human induced condition was investigated on the oldest stand of heathland to determine if a growing-season drought (repeated annually on 14 occasions) suppressed soil respiration, thus resulting in an overall suppression of the annual soil C loss (Chapter 4).

Nitrogen deposition was the third condition resulting from human activity that was investigated on the heathland soil. The long term soil chemistry was investigated under ambient rates of N deposition to determine if the decreasing trend of N emission observed across Europe had resulted in a recovery (or retardation) from soil acidification (Chapter 5). The interaction of the repeated annual drought on the soil acidification trend was also investigated (Chapter 5).

These three environmental conditions and their impact on the heathland soil (and wider system) are discussed in the following sections. As these conditions do not exist independently, the interactions are brought together within each section below, to discuss the observed results and hypothesize about the future of the heathland. To the author’s knowledge, this is the first study in which multiple environmental conditions resulting from human activity have been investigated in conjunction with a long term heathland experiment.

2 Vegetation Management

Traditional management practices produced even-aged stands of Calluna heathland and this stand age influenced ecosystem functioning, particularly in C fluxes and the aboveground C storage. As heathland communities aged from a 0 year old stand (bare
ground) to a 28 year old stand, there was a shift from predominantly soil processes contributing to the C balance, to a mix of soil and vegetation processes.

When the vegetation had been recently cut and the ground was bare (Year 0), photosynthesis ($P_c$) and root respiration ($R_a$) were zero. Therefore, the major source of C loss from the system was attributable to microbial decomposition of organic matter ($R_{hi}$) within the soil. This bare soil experienced greater extremes of temperature than the soil under Calluna and moss cover, with the overall effect that the calculated annual $R_{hi}$ values were higher than observed in older vegetated areas.

When the vegetation had been cut for 1 to 2 years and Calluna had not established, a thin layer of cyanobacteria established (Sass-Gyarmati et al. 2012). This establishment of cryptogams in the early successional stages of inland dunes is similar to that observed in other studies within the Netherlands (Sparrius et al. 2011). Low levels of $P_c$ were recorded on these cut areas and, although the data was not reported in this thesis, it is hypothesized to be associated with this cryptogam layer.

Eleven to twelve years after vegetation cutting, C had accumulated in the Calluna (stems and roots) and moss biomass. The plants were highly active in C uptake ($P_c$) and C loss through root respiration ($R_a$). Overall, the highest values for these fluxes were recorded on this Young community. Eighteen to nineteen years after vegetation cutting (Middle community), the Calluna had reached its peak biomass, but the rate of both C uptake and C loss from the plants had decreased. The oldest vegetation (27 to 28 years) was not significantly different to the Middle community, although Calluna biomass and C loss through root respiration on the Old community were slightly lower than on the Middle community. The rate of microbial decomposition ($R_{hi}$) was the same on all community ages and the shade provided by plants appeared to regulate against extremes of soil temperature.

These changes in C fluxes over time correlated to the growth phases of Calluna plants, as described by Gimingham (1985), in which biomass accumulated in the Calluna plants with time since cutting. This indicated that plant C fluxes and quantity of plant stored C related to the frequency of the management cycle. However, there was no significant difference in the total C stored in the ecosystem. Therefore, the C stored in the soil and the soil microbial C fluxes were not noticeably related to the frequency of vegetation management.

This could be partially attributable to uneven deposition of leaf and root litter, resulting in highly variable C accumulation, thus obscuring any landscape C storage pattern. However, it is also hypothesized that as the vegetation aged (post-12 years) and C uptake rates decreased, there was a shift to net C loss which negated any earlier C accumulation that had occurred.

In addition, the heathland did not consist of Calluna alone, with mosses also contributing to C fluxes. This study did not quantify the separate contributions of moss and Calluna to
the overall photosynthetic rates; however, based on the preliminary data from in a trial in May 2012, the Young Calluna plants were approximately 2.5 times more photosynthetically active than the Middle and Old Calluna. The contribution of the moss to other ecosystem functions other than photosynthesis should not be overlooked, as moss has been shown in this study and in others to moderate soil temperature throughout the year and influence soil moisture in between rainfall events (Startsev et al. 2007).

Within the last 50 years, the cutting, burning and grazing cycles on heathlands have not occurred as frequently or as regularly as during the intensive agricultural periods of past centuries (Webb 1998). This thesis has shown that the length of time since the last vegetation cutting influences the C fluxes from the ecosystem and the C stocks in the vegetation. From the perspective of optimizing C uptake and minimizing C output, having an understanding the C dynamics of these ecosystems allows us to determine the optimum time to cut the vegetation, thus contributing to global C emission mitigation measures. A preliminary assessment of C balances for the ages of vegetation was undertaken and is presented in a following section and a hypothesis presented for optimizing cutting cycles and maximizing ecosystem C storage.

The C fluxes and balances in each stand age were also affected by other anthropogenic influences. These interactions will be further discussed in the following sections.

3 Climate Change

Drought reduced C loss from soil respiration after 14 annual treatment periods. This suppression was observed across all the year, although the effect was most obvious during the actual drought period. Root respiration was affected more than microbial respiration by the application of the repeated annual drought and the modeling process identified that different processes were occurring between treatments.

Although C loss from root respiration decreased under Drought conditions, there was no significant reduction in the C stored in the Calluna biomass and the plants exposed to the repeated drought had an overall greater C uptake \( (P_G) \) rate. This was unexpected, as plants exposed to drought conditions commonly reduce their enzymatic activity or close stomata to minimize water loss, which decreases photosynthesis and respiration rates (Chaves et al. 2002, van der Molen et al. 2011).

Two processes are hypothesized to have contributed to this difference observed between treatments: moss cover increases and plant root adaptations. The moss cover increased on both treatments, with greater increases on the Drought than the Control. Moss thickness and moss biomass was also greater (although not significantly) on the Drought treatment than the Control. This greater Drought moss cover and thickness is likely to result in greater precipitation interception and water holding capacity, particularly if rainfall events were small and moss holding capacity was not exceeded; thus enhancing
the drought effect on Calluna roots. Additionally, both Calluna and moss plants contributed to $P_G$, while only the Calluna root systems contributed to $R_A$. Mosses have many adaptations to drying, including a high water holding capacity (up to 1400% of their dry mass), ability to intercept atmospheric water, such as fog or dew, and can achieve maximum photosynthesis rate within 30 seconds of rewetting (Glime 2007). Preliminary studies in May 2012 indicated that mosses contribute significantly to $P_G$ in this heathland (between 30–60% of total $P_G$ for Control), but these C uptake rates have not yet been determined for either the Drought treatment or across different seasons.

Secondly, plant roots have been shown to respond to drought by increasing the relative allocation of photosynthates to root growth, ultimately resulting in higher root:shoot ratios and a greater capacity to absorb water and nutrients (Chaves et al. 2003, Kozlowski and Pallardy 2002). The soil moisture results indicated that the Drought plants were able to extract more moisture from the mineral soil than the Control plants. This suggests that more roots of Drought plants grew below the organic layer into the mineral soil to search for moisture.

Therefore, the greater moss cover with a greater water holding capacity may have resulted in an elevated $P_G$ on the Drought treatment, whilst also enhancing the drought effect on Calluna roots (and further reducing annual $R_A$). The drought adaptation of Calluna root systems would provide resilience to periods of low rainfall, but root activity is still likely to be suppressed when exposed to prolonged drought periods (i.e. reduced $R_A$).

A change in root depth and distribution in the Drought treatment would also have other consequences, such as better extraction of nutrients and cations from the mineral soil and a reduction in cations lost through leaching. Retention of cations then impacts on other processes occurring in the ecosystem, such as the retardation of acidification which is discussed further in the following section. It is interesting to consider here too, that the Calluna roots in the Control treatment are currently dealing with an increasingly acidic soil, which may have caused root damage at depth and resulted in the Calluna plants being less able to withstand natural drought conditions. This may have suppressed $P_G$ rates, in comparison to the rates observed on the Drought treatment.

When vegetation management (i.e. cutting) was applied to a portion of the Drought plots, the C fluxes were different from the cut areas of the Control plots. One to two years after cutting, soil respiration remained lower on the Drought than the Control; however, $P_G$ from the cryptogam layer (including cyanobacteria) was not significantly different between the treatments in any season. This is unusual because cyanobacteria are physiologically active only when wet (Lange 2001) and therefore, cyanobacteria would be expected to have lower $P_G$ under a drought treatment. Potentially, the elevated N deposition rates at the site (particularly in the Control) may have led to negative responses in the cryptogam soil crust. Cryptogam layers have been reported to experience ammonium toxicity (Glime 2007) and, although no data is available for cyanobacteria, this may have resulted in differences between the cryptogam growth on the Drought
treatment (which had less N deposition) and the Control treatment. Information on the biomass of the cryptogam layer is not currently available for the trial treatments.

The regrowth of Calluna plants on these cut areas would be interesting to study. On the Drought treatment, the number of days in which soil moisture does not limit seed germination or root establishment is reduced. In contrast, on the Control treatment, the plants must establish on an increasingly acidic soil which may limit root growth into the mineral soil.

4 Elevated N Deposition

This ecosystem is subject to high bulk N deposition rates, which were measured at 10.7–37.4 kg N ha\(^{-1}\) year\(^{-1}\) over the 13 years of the long term trial (1999–2011). Nitrogen deposition exceeded the lower critical limit (10 kg N ha\(^{-1}\) year\(^{-1}\); Bobbink et al. (2010)) in all years, while the upper critical limit (20 kg N ha\(^{-1}\) year\(^{-1}\)) was exceeded in 55% of years. In 45% of years, the N deposition actually exceeded 30 kg N ha\(^{-1}\) year\(^{-1}\), at which levels there is evidence to suggest that heathlands on sandy podzols are seriously threatened, as the typical lichen rich vegetation does not develop anymore (Sparrius 2011).

The deposition of these anthropogenic N compounds in the Calluna heathland resulted in soil acidification over the 13 years of monitoring. Under ambient deposition conditions, N was the main contributor to the acidification process, with N transformations rather than S transformations generating the majority of the protons in the soil. This continual addition of protons gradually protonated the conjugate bases at the previous proton levels, leading to a pH decrease in the soil. More acidic rainfall in 2010/2011 may have accelerated this process. These results suggest that acidification continues to be of ecological concern at sandy podzol sites where N deposition exceeds critical loads.

When the ambient deposition conditions were examined in conjunction with a Drought climate treatment, it was found that the soil acidification trend was retarded, even under the more acidic rainfall in 2010/2011. The repeated annual drought resulted in a long-term change in the underlying mechanisms: N transformations became less important while the generation of protons from S transformations became relatively more important (or more observable) in the Drought treatment and / or the S atmospheric deposition had increased (unlikely).

The acidification retardation by the Drought treatment was hypothesized to be primarily associated with the reduction in rainfall resulting in lower drainage rates. The lower drainage rates have led to greater retention (or reduced mobilization) of base cations and Al\(^{3+}\), thus resulting in a long term reduced lowering of the long term acid neutralizing capacity (ANC) of the soil. In addition, the Drought treatment excluded a portion of the wet N deposited when the rainfall was excluded. This resulted in less N input and less N transformations / proton formation occurring within the soil. But it is unlikely that this completely explains the retardation effect observed.
Atmospheric N or leaching N will not be available for N transformations if it is intercepted by mosses prior to reaching the soil or by plant roots within the soil. Increases in plant N storage (such as with increasing biomass following vegetation management) would indicate if a net N uptake from the soil had increased. Calluna N storage was estimated for the Control treatment and this indicated that N storage had generally increased from 1999 to 2002 when the plant community was aged between 14 and 18 years and was in a ‘net biomass gain’ phase of growth. After 2002, there were no further increases in N storage as the Calluna plants aged into the ‘net biomass loss’ phase. This indicated there was negligible change in the N uptake by Calluna plants in either the Control or Drought treatments for the majority of the study period. However, N storage in the mosses increased over the 13 years of monitoring and estimates indicated that the moss layer filtered atmospheric deposition at a rate of approximately 8 kg ha\(^{-1}\) year\(^{-1}\) (Control) and 12 kg ha\(^{-1}\) year\(^{-1}\) (Drought). This pattern of increasing moss biomass observed over the 13 years of the long term trial was not observed on the ‘Young-Middle-Old’ chronosequence. This indicated that the increasing biomass of the dominant moss species (*Hypnum cupressiforme*: a pollution tolerant species) was not associated with increasing community age. The reasons for moss biomass increase on the site since 1999 is not known, nor is it possible to determine if the ratio between moss and lichen species has changed, as bryophyte identification was only undertaken once, in 2011. It is unlikely that moss biomass can continue increasing at this rate and therefore, it is likely that future moss N filtration rates will further increase.

All three chronosequence communities were subjected to the same rates of N deposition and the effect of varying the N deposition rate was not assessed in this thesis. However, other studies have identified that elevated N deposition has direct and indirect effects on ecosystems through increased succession rate, increased C allocation, increasing the decomposition rates of easily degradable organic material and decreasing decomposition rates of recalcitrant organic matter (Bobbink et al. 2010, Fog 1988, Sparrius et al. 2012). Indirectly, leaf chemistry and litter quality can change under elevated N deposition, thus leading to an accelerated decomposition rate (Kozovits et al. 2007, Nierop and Verstraten 2003). Root respiration rates have also been observed to increase under elevated N deposition (Burton et al. 2012). The reduction of N deposition through reduction in rainfall during drought periods may have indirectly led to some of these changes occurring within the Drought treatment. However, for example, root respiration rates and litter decomposition rates in the Drought treatment were suppressed in comparison to the Control treatment rather than elevated, and therefore it is hypothesized that moisture reduction was the dominant process affecting plant responses in this drought affected heathland.
5 Carbon Feedback

This thesis has investigated a number of conditions caused by humans which affect a Calluna heathland. From the data presented within this thesis and other information available from the long term research trial, a C balance has been calculated for each of the chronosequence sites (Figure 1). The C stocks and C fluxes are based on results obtained from August 2011 – July 2011, where the heathlands at the time were aged: Year 0 (Chapter 3: ‘Trenched’ plots), Year 2 (Chapter 4), Year 12 (Chapter 2 and 3), Year 19 (Chapter 2 and 3), Year 28 (Chapter 2 and 3), Year 28: Drought (Chapter 4), and Year 2: Drought (Chapter 4). The separate contribution of Calluna or moss to either $P_G$ or $R_P$ is unknown, and therefore only the net flux value has been included. In addition, the root:shoot allocation patterns of photosynthates in these Calluna heathlands with moss interactions are also not known and have not been included.

The C balance estimates indicated that all the investigated ages of heathland were sources of C to the atmosphere, with the exception of the 12 year (Young) vegetation. To the author’s knowledge, there have not been any other C balance chronosequence studies for heathlands and so these results cannot be directly compared to other aging heathlands. However, a study undertaken in Denmark indicated that a six year old Calluna heathland was a C sink of approximately 0.29 kg C m\(^{-2}\) year\(^{-1}\) (Larsen et al. 2007). This heathland was in a ‘net biomass gain’ phase of growth, and the overall C balance corresponds to the Oldebroek Young vegetation, which was in this same phase of growth.

However, heathlands are not isolated points in time, but rather are on a continuous timelines. Based on the chronosequence C balances in Figure 1, it is possible to hypothesize about the cumulative C balance across these phases of growth.

A possible scenario for a smoothed timeline over the 28 years of heathland development could be: Year 0 as bare soil, Year 1 with a cryptogam layer, Years 2 to 5 with germinated Calluna producing approximately half the C fluxes measured on the Young community, Year 6 to 16 in ‘net biomass gain’ phase (i.e. Young community), Years 17 to 19 transitioning to the ‘net biomass loss’ phase (i.e. Middle community) and Years 20 to 28 in the ‘net biomass loss’ phase (i.e. Old community). Note: C fluxes in Years 2 to 12 could be highly variable; however, in the absence of this information, ‘half rates’ from the Young community are used as a proxy for Years 2 to 5 and ‘full rates’ from the Young community are used for Years 6 to 16. This hypothesized timeline and C balance trajectory is represented in Figure 2.

Using this possible scenario, the cumulative balance of the C uptake and C output for the heathland was calculated. Over the first 12 years, the cumulative calculation indicated approximately 1.9 kg C m\(^{-2}\) was stored within the ecosystem. The actual C stock measured in the plants (including root estimates) of the Young vegetation was 1.0 kg C m\(^{-2}\), which indicated a portion of the C is likely to have accumulated in the soil.
Figure 1 Carbon balances for a Calluna heathland subjected to various vegetation management time periods and a Drought climate treatment (August 2011 to July 2012). The diagram shows C stocks (grey boxes) and C fluxes (black arrows), where the fluxes are gross photosynthesis ($P_G$), photosynthate allocation to stems ($A_S$), photosynthate allocation to roots ($A_R$), plant respiration ($R_P$), leaf litter ($L_L$), root litter ($L_R$), autotrophic soil respiration ($R_A$), heterotrophic soil respiration ($R_H$), and Dissolved Organic Carbon (DOC) deposition or leaching. Numbers in italics were estimated, while a question mark indicates the value is unknown and could not be estimated.
A similar accumulation calculation for Years 13 to 19 indicated that total C storage increased in the heathland by approximately 0.6 kg C m\(^{-2}\) over the seven year period. Measured plant C stocks (including roots) on the Middle community had increased by 0.4 kg C m\(^{-2}\) over the same seven year period, which suggested that the majority of the C that accumulated in this time was stored in the plants, with the remainder in the litter and soil.

From Years 20 to 28, the C accumulation calculation indicated that 1.3 kg C m\(^{-2}\) was lost (respired) from the heathland over the nine year period. The plant C stocks in this time had not changed significantly (-0.06 kg C m\(^{-2}\)) and so it is hypothesized that the C loss predominantly originated from the soil in this nine year period. The overall cumulative balance for the 28 years indicates there was a net C gain of 1.2 kg C m\(^{-2}\).

If C emission mitigation is one of the ecosystem services valued by society, then these C balances indicate that relatively shorter cycle lengths would be required to optimize C uptake and minimize C loss from the ecosystem.

Figure 2  Annual Net Ecosystem Exchange of C (Ecosystem Respiration + P\(_G\)) for a Calluna heathland from 0 to 28 years following vegetation cutting (August 2011 – July 2012). Squares with bars represent means ± SEM (n=3) and the dotted grey line represents a hypothesized timeline of annual C balances. Positive values indicate a C source ecosystem and negative values indicate a C sink. A possible scenario for repeated annual drought is shown in brown, where the Drought treatment was applied 17 years after cutting.

When a repeated annual drought was applied, there were reductions in C loss. The above scenario was amended with the assumption that the drought-exposed plants gradually developed resilience over the first five years of drought exposure and then the subsequent eight years showed the same annual C feedback as the Drought treatment. With this assumption, the cumulative C calculations indicated that 0.6 kg C m\(^{-2}\) would have
been lost (respired) from the heathland over the nine year period. This is approximately half of the C that was lost from the non-drought system.

When vegetation was removed from the drought areas, the heathland at Year 2 after cutting was a source of C to the atmosphere but had lower C loss than the Control cut areas. However, it is possible that these drought conditions may result in delays to Calluna plant establishment, and longer periods of time without the higher rates of Calluna photosynthesis.

6 What if Vegetation Management Intensity Increased?

Within the last 50 years, the cutting, burning and grazing cycles on heathlands have not occurred as frequently or as regularly as during the intensive agricultural periods of past centuries (Webb 1998). Management of heathlands is required to maintain these cultural landscapes and in past times this management occurred on a four year cycle in some locations (Webb 1998). Currently, this cycle length has extended or is non-existent (Diemont and Heil 1984, Wessel et al. 2004).

From the perspective of optimizing C uptake and minimizing C output, having an understanding the C dynamics of these ecosystems allows us to determine the optimum time to cut the vegetation, thus contributing to global C mitigation measures. Based on the estimated cumulative C balance scenario presented in the previous section, a cutting frequency of 12 to 14 years would provide peak C accumulation in the ecosystem. Cutting more frequently than this, for example after six to seven years when the plants were aged between three to four years (and cut biomass is removed), there would be an overall zero C balance in the ecosystem. Cutting less frequently than this, for example after 27 years (and cut biomass is removed), would also result in a net zero balance. This indicates that management of these cultural landscapes should occur on relatively shorter cycle lengths (~12 years) if C emission mitigation is of concern.

Increasing the intensity of vegetation management would have other flow-on effects however, as removal of vegetation impacts the cation balances of the ecosystems. Removal of woody biomass has been identified as an important acidifying factor in forest ecosystems (Hruška and Cienciala (2003) in Dahlgren and Driscoll 1994, Hédl et al. 2011) where the loss of cations reduces the acid neutralizing capacity of the ecosystem. The heathland soil has already been shown to acidify over the past 13 years, due to the deposition of anthropogenic compounds, protonation of bases and subsequent loss of cations through leaching. Removal of vegetation from the heathland is likely to accelerate this acidification process.

Changing the type of vegetation management to a continuous system, such as animal grazing, would result in a continual ‘cutting’ regime and a mixed aged vegetation stand. It is hypothesized that the continual regeneration of plant biomass would generally result in more active plants with higher $P_G / R_A$ rates. In addition, the soil would not be exposed
following the removal of cut vegetation (Year 0). The absence of Year 0 and the early cryptogam years would cumulatively result in a reduction in C loss from the ecosystem. Therefore, these differences are hypothesized to produce an ecosystem with a C balance somewhere between the Young and Middle communities (i.e. a C sink). This management form would also result in increased C and N input from animal urine and manure, although the effects of these on the overall C balance are not unknown.

This discussion has been presented from the perspective of mitigation of C emissions. However, changes to the vegetation management regime may impact on other heathland services of a successional ecosystem that are important to preserve, such as species composition, and this should be taken into consideration when developing heathland management plans.

7 What if Precipitation Increased?

This thesis investigated the scenario of a repeated annual drought, i.e. decreased rainfall in the growing season every year. However, if the predicted change in precipitation patterns led to increased rainfall rates in Europe rather than reduced rainfall as tested here, the underlying mechanisms found in this study allow us to hypothesize that the soil acidification trend would increase at this site. Although the inputs of N wet deposition would be diluted, the total N input would remain the same and the overall output in the soil solution would increase leading to increased loss of cations (and therefore loss of ANC) from the soil.

Additionally, increasing the precipitation rates would impact the C fluxes of the heathland. Soil respiration was suppressed on the Drought treatment due to reductions in soil moisture. Therefore, it is hypothesized that increases in soil moisture would increase the microbial respiration ($R_H$) rates, particularly if the frequency of precipitation events increased rather than total precipitation alone. The sandy podzol soil at this site is free-draining and increasing the frequency of rainfall events would increase the number of days in which the soil moisture was optimal for microbial respiration. Additional precipitation may also increase plant growth and C allocation patterns; however, Calluna heathlands are generally nutrient limited. Therefore, the nutrient limitations are likely to restrict plant growth leading to no overall change in plant $P_G$ or root $R_A$ rates. Thus, it is hypothesized that increased precipitation would result in the current ecosystem (which already has positive C feedback) becoming a greater source of C to the atmosphere.

8 What if N Deposition Decreased?

The rate of N deposition has decreased across Europe since the 1990s (EEA 2012). In 2008, the European Union (EU) committed to further reduce its greenhouse gas emissions by 20% by 2020 (European Commission 2010). If this 20% reduction in emissions equated to a 20% reduction in N deposition at the trial site, then the range of N deposition between
1999 and 2011 would have been 8.5–29.9 kg N ha\(^{-1}\) year\(^{-1}\) (rather than the recorded 10.7–37.4 kg N ha\(^{-1}\) year\(^{-1}\)). Critical loads of N deposition for dry heathlands have been calculated to be 10–20 kg N ha\(^{-1}\) year\(^{-1}\) (Bobbink et al. 2010). Even with a 20% reduction in deposition, the N deposition rates in 85% of the years would still have exceeded the lower critical limit (10 kg N ha\(^{-1}\) year\(^{-1}\)) and 45% of years would still have exceeded the upper critical limit (20 kg N ha\(^{-1}\) year\(^{-1}\)). However, deposition in all years would have been below 30 kg N ha\(^{-1}\) year\(^{-1}\), which is the critical threshold above which sandy podzol heathlands are seriously threatened, where the typical lichen rich vegetation does not develop anymore (Sparrius 2011).

Decreases in N deposition could affect C storage but only if N became limiting to plant and microbial activity. In ecosystems where N is limited, atmospheric N deposition can increase C production / accumulation in plants and soils (de Vries et al. 2009, Gorissen et al. 2004, Oulehle et al. 2011, Treseder 2008). If a 20% decrease in N deposition occurred, the critical levels are still exceeded in most years and, therefore, it is not likely that a plant N limitation (or associated change in C storage) will develop in the near future.

Any decrease in N deposition will result in lower proton formation in the soil and should retard soil acidification trends at the site. However, while N deposition continues to exceed critical limits, an acidification trend is expected to continue. These results suggest that greater reductions in emissions are required to bring N deposition rates below critical limits and to retard acidification trends on sandy podzol heathlands.

9 Conclusions and Future Research

This series of studies on a Calluna vulgaris heathland focused on investigating changes associated with the environmental conditions that result from human activities. Human activities impact on our environment but they do not impact independently from each other. Therefore, where possible, these interactions were linked to explain the observed results. This research showed that C fluxes on heathlands are influenced by drought and vegetation age and an optimum cutting frequency can be determined from the perspective of optimizing ecosystem C storage. The aboveground C storage is also affected by vegetation age, and this storage rate is likely to have been influenced by the long term N deposition that has occurred at rates exceeding critical levels. This same N deposition has resulted in a soil acidification trend, although this was retarded by the repeated annual drought.

Many of the findings were interesting and remarkable when considering the hypotheses and the results of other studies. For example, a soil acidification trend was measured even with the reduced N emissions that have been reported across Europe. Further, any C storage changes that occurred in the aboveground vegetation with increasing stand age were negligible when considering the changes to (or variability in) soil C storage. At the plot-scale, only soil temperature was found to significantly explain soil respiration.
(although conditional on soil moisture for the drought treatment) and measures of plant activity did not seem to influence the modeling results for total (and also therefore, root) respiration.

The modeling process also identified a number of interesting outcomes which were not directly associated with the initial soil-related hypotheses. In the course of searching for a suitable plant activity measure for soil respiration modeling, the gross photosynthesis and biomass results were used as explanatory variables. These aboveground variables showed further paradoxical results, in which drought did not reduce the C storage in the drought-plants but elevated the ecosystem photosynthetic activity. Another incidental outcome of the research was the recognition of the moss contribution to ecosystem functions such as C storage, N filtration, soil insulation (temperature and moisture) and photosynthesis. The role of mosses had previously been underestimated within the heathland.

This research has answered a number of questions about heathlands which contribute to understanding ecosystems processes at similar shrubland sites in Europe. However, this research has also raised additional questions which would benefit from further research. The major questions that have arisen are related to the possible adaptations of Calluna plants growing under annually repeated drought conditions. Why has photosynthesis increased in this ecosystem? Has plant root depth increased as plants search for water? Is there a different plant shoot:root ratio or leaf area index under drought conditions? And do these plant measures improve soil respiration models if included as a descriptive variable?

Additionally, this research identified that mosses had not previously been included in many heathland C stock assessments, which may have led to C stock underestimations. Defining moss contribution to other C processes across an entire year, such as $P_G$ and $R_P$, would assist in understanding the role of mosses in heathland C balances and may assist in explaining differences between the Drought and Control treatments.

Further, the cryptogam layer was shown to contribute to C uptake on both the Control and Drought treatments. Additional investigation of the biomass of this layer and the processes occurring during the drought periods would contribute to our understanding of the C balances of successional heathlands which are exposed to changed climatic conditions.