Vitality of heather (*Calluna vulgaris*) along gradients of climate, structure and diversity in dry lowland heathland habitats of Northern Germany

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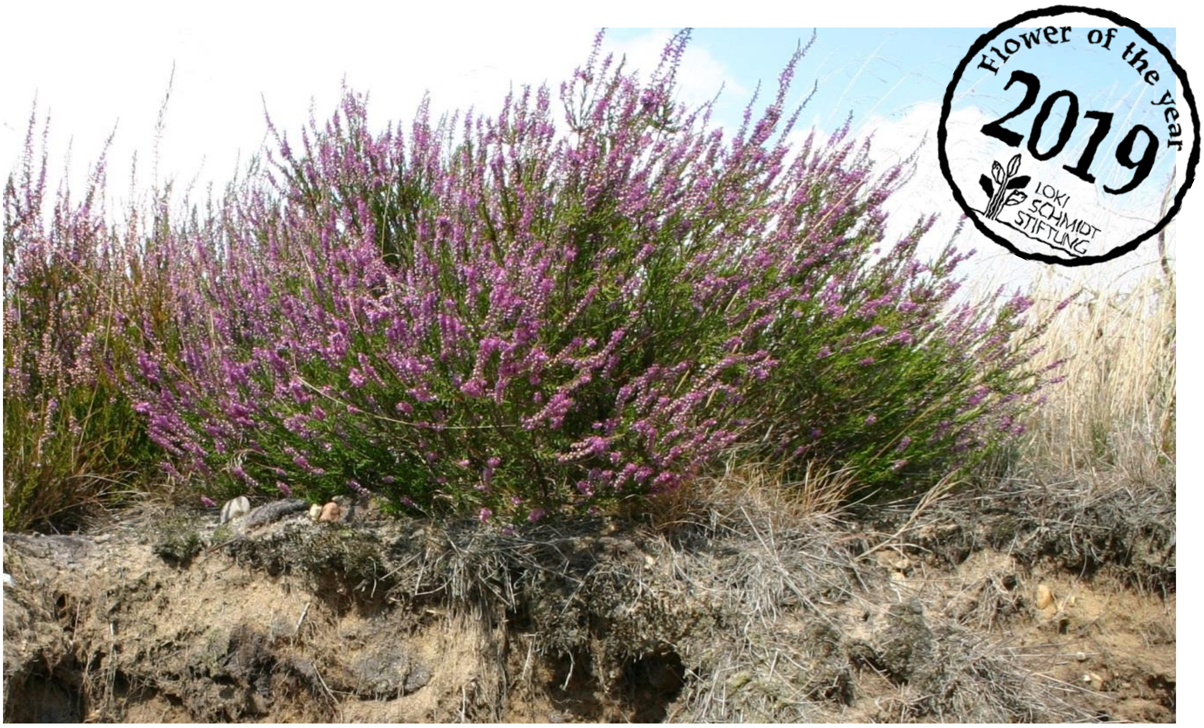

Calluna vulgaris

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List of Abbreviations

B	Building growth phase
CI_{95}	95% Confidence interval
D	Degeneration growth phase
D_2014	Scenario used in Chapter 4, representing the maximum drought conditions in 2014
ESM	Electronic Supplementary Material, see Appendix p. 140
GLMM	Generalized Linear Mixed Model
HT	Habitat type in the Natura 2000 network
K	Kotilainen's Index of Oceanicity
LMM	Linear Mixed Model
M	Mature growth phase
MaxD_10YEAR	Scenario used in Chapter 4, representing the most severe drought conditions in 2011-2020
N	Nitrogen, unless otherwise specified the airborne nitrogen load in $kg*ha^{-1}*yr^{-1}$
NoD_2014	Scenario used in Chapter 4, representing the minimum drought conditions in 2014
P	Pioneer growth phase (Chapter 3); Precipitation sum in the survey period (Chapter 4)
PL	*Calluna* plants from prostrate adventitiously rooted stems ('layering')
PS	young *Calluna* recruits germinated from seed
PR	*Calluna* plants resprouted from older ones, mostly from Mature- or Building stage plants after aboveground biomass disturbance
SD	Standard deviation
SPEI	Standardized Precipitation and Evapotranspiration Index (Chapter 4)
T	Mean air temperature (°C) in the survey period (Chapter 4)

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Summary

This thesis provides a fundamental overview to North German Dry lowland heathland vegetation composition, vegetation structures and the determinants for the vitality of the key species, *Calluna* vulgaris. It offers new insights into the complex interactions of site history-related disturbances, edaphic conditions, climate and nitrogen (N) deposition, with consequences for heathland habitat quality. The main threats protected heathland habitats are faced with are primarily related to recent management. The purpose of heathland management is to provide suitable conditions for favourable habitat diversity and structures, ensuring the long-term maintenance of the ecosystem functionality. Under changing conditions of climate and pollution, heathland management is challenged with inter- and counteracting effects of traditional management and recent threats.

Heathlands in the German Northwest are among the most nutrient-poor habitats. In historical times, heathland faming induced and maintained the nutrient poverty, as well as associated species and structures, but the invention of artificial fertilizers allowed for the cultivation of the poor sandy substrates in the early 19th century. As a consequence, the former nitrogen (N)-limited heathland ecosystems were exposed to inputs of N, either directly with fertilizers, or indirectly with airborne or fluent deposits. The fast increase in plant-available N within a century faces the recent heathlands with threats like species composition changes, fertilizing effects with boosted growth and accelerated ageing as well as reduced drought resistance. Additionally, there is a trend towards longer and more severe droughts in the study areas, as well as more imbalanced and generally lower rainfall. As a consequence, the changing climate and high N depositions are challenging efforts for heathland protection, demanding for an improved basic knowledge to heathland responses to those threats and the possibility to compensate for them.

Based upon 352 plots in 19 dry lowland heathlands, data to plant assemblages, soil conditions as well as *Calluna* age structures and vitality were collected in the years 2013 and 2014. The analysis focussed on 1) heathland plant community ecology, with a characterisation of plant composition and its determinants along dynamic heathland development pathways, 2) *Calluna* plant life history, with the revision of the *Calluna* life cycle as the central criterion for the assessment of age structures and 3) the drought susceptibility of *Calluna* recruitment under high N loads, as a determinant for post-disturbance heathland recovery with potential consequence for long-term heathland maintenance.

The analysis of plant community composition and structures revealed two edaphically distinct pathways of heathland development; 1) the psammophilous heathland pathway, which describes heathland development on poor, loose drift sands, representing early stages in the seral progression of altering soil conditions along long-term successional changes, and 2) the consolidated sand heathland pathway, representing heathland development on more developed, but still poor sandy soils. Their edaphic conditions are determined by historical and recent land use, emphasizing the character of young psammophilous heaths occurring in the North German East as a product of military training activities in the past century and the older, historical heathlands in the Northwest, with consolidated sand heaths prevailing.

Mosaic heathlands in close contact to pioneer grasslands provided highest diversity in species and structures, thus confirming the importance of early –stage conditions, providing host for many threatened species, in particular lichens.

The *Calluna* life cycle is the key criterion for determining age structures in the terms of heathland habitat nature conservation status assessments. But the established concept lacks in some detail to regeneration processes and the habitual diagnostics of regenerating plants, with consequences for management planning and the estimation of regeneration potentials. Hence, this study provides an extended life cycle, including the regeneration processes of post-distubance resprouting and layering *Calluna* plants. The study provides evidence that age-related shifts in *Calluna* vitality are determined by both, the aboveground (regeneration) age and the total plant age. Thereby, the high-vital life phase is restricted to approx. 15 years, and resprouting may induce a regrowth to a mature plant again, with another approx. 10 years of high vigour, but there was no evidence for an elongated total life by a resprouting cycle. The inability to regenerate with a high vigour and to regrow to a Mature-phase plant again was related to the shift from the primary rooting supply to de-central adventitious rooting, a process which was shown to be determined by the total plant age and hence irreversible. As a consequence, the findings of this study do not support the theory of repetitive cycling in terms of unrestricted highly vigorous resprouting and the constant layering of procumbent stems as the regeneration of older plants was confirmed as a quite stable, but often low-productive stage of degeneration.

Young *Calluna* plants had a high resistance to drought during the growing season, although growth rates were reduced and tissue damages increased under severe drought conditions. Thereby, seedlings were rather negatively affected than resprouted plants.

The results presented in this thesis clearly show that droughts under high N depositions are important post-disturbance heather regeneration determinants. Thereby, the effect of N deposition depends chiefly on the drought severity; high N loads limit *Calluna* seedlings under conditions of extreme drought on the one hand, but favour the growth of seedlings and resprouted plants under non-drought conditions on the other. Under severe drought, complete generations of young *Calluna* seedlings may get lost, especially under high N loads, and successful *Calluna* recruitment from seed may only take place in years of favourable conditions. As a consequence, heath stands that regenerate mainly from seed, e.g. after sod-cutting, are particularly vulnerable to droughts in their early regeneration stages, especially under high N load, whereas regeneration from resprouting plants provides a high resistance. However, the results presented in this study showed that high N loads reduce the competitive power of young *Calluna* plants by altering the stomatal sensitivity, with lethal consequences for seedlings, and a reduced growth for resprouted plants under drought.

With a reduction of competitive strength, not only *Calluna* cover decreases, but also general heathland plant species composition changes take place. The results of this thesis support a high N-load induced reduction of the low-productive species pool from early successional stages, such as lichens, and an increase of regeneration stages of low diversity. Mosaic stands with a high potential to harbour high species diversity become grass-dominated heathland mosaics under high N.

The results to North German dry lowland heathland species composition and their dynamics, the *Calluna* life cycle and the drought resistance of *Calluna* recruitment strengthens the biological-ecological knowledge required for informed advice on heathland management and thus provides some implication for the specification of nature conservation assessment criteria, ensuring an improved assessment of heathland habitat quality and regeneration potentials. Additionally, the findings of this thesis highlight the need for a sharpened view on the changes in dry lowland heathland ecosystems and to figure out whether managements have the potential to counteract some of the recent threats and degeneration processes induced by natural succession, but altered by changing climate and high N loads. The specific need for intensive soil disturbances to provide early-stage soil conditions was highlighted in this study, but it also pointed out that post-disturbance regenerations are prone to droughts. Hence, the challenge for future management is to weigh between trade-offs and to balance probabilities of risks and success. Thereby, high-intense, but small-scale disturbances in varying frequencies and management combinations may provide the highest probability to improve the resilience of heathland habitats to future climate changes and to ensure a high species and structural diversity in heathland landscapes for maintaining their functionality.

Zusammenfassung

Heidelebensräume des norddeutschen Tieflands sind aufgrund ihrer kulturhistorischen Bedeutung, ihrer Einzigartigkeit und ihrer vielfältigen Ökosystemdienstleistungen schützenswerte Habitate. Sie verfügen über eine Artengemeinschaft die zwar nicht durch Artenreichtum besticht, aber die sich über die letzten Jahrhunderte an nährstoffarme, menschenbeeinflusste Offenlandlebensräume angepasst hat. Durch den Verlust solcher Habitate seit der Mitte des 19. Jahrhunderts, bei denen es durch vielfältige Landnutzungsänderungen zur Wiederaufforstung, Umwandlung in Grünländer oder Äcker zum Rückgang der Lebensraumfläche insgesamt kam, sind die heute verbliebenen Flächen unter europäischem und nationalem Naturschutzrecht geschützt und die Lebensräume müssen in ihrer Artengemeinschaft und Vielfältigkeit, die die Strukturen und Funktion bestimmen, geschützt werden.

Der Erhaltungszustand von trockenen Tieflandsheiden in Mitteleuropa wird überwiegend als schlecht bewertet, maßgeblich verursacht durch fehlendes oder falsches Management. Hinzu kommen jedoch Veränderungen im Nährstoffhaushalt und dem Klima, die die Effizienz der etablierten Maßnahmen einschränken und die generelle Resistenz der Heide gegenüber ökologischen Stressfaktoren, wie Trockenheit oder Insektenkalamitäten vermindern. Langfristig bedeutet eine verminderte Vitalität der Besenheide (*Calluna vulgaris*), die als Schlüsselart maßgeblich zum Aufbau, der Struktur und den Habitatbedingungen der vorkommenden Heide-Lebensgemeinschaften beiträgt, eine Verschiebung im Konkurrenzgefüge, was zur Habitatdegradation, z.B. zur Vergrasung mit *Deschampsia flexuosa* oder *Molinia caerulea*, führt.

Zahlreiche Studien untersuchten bisher die Gründe und Ursachen vom Rückgang der Heide-Habitatqualität, mit dem Ergebnis, dass nur die Berücksichtigung sehr vieler, komplexer Zusammenhänge Erklärungsansätze bieten. Die vorliegende Arbeit versucht diese für die norddeutschen trockenen Tieflandsheiden zu untersuchen und gibt daher zunächst einen umfassenden Überblick über die Vegetation und ihren ökologischen und strukturellen Charakteristika. Aus diesen werden die historisch und/oder edaphisch bedingte Vergesellschaftungen der Arten sowie Vegetationsstrukturen herausgearbeitet und in ihren Entwicklungspotentialen bewertet. Da die Habitatqualität maßgeblich von der Vitalität und vom Lebenszyklus der *Calluna vulgaris* bestimmt wird, beschäftigt sich ein weiterer Schwerpunkt dieser Arbeit mit dem Alterungsprozess des Zwergstrauchs. Eine wichtige Frage hierbei ist, ob dieser unter den in Norddeutschland herrschenden Bedingungen an der Arealgrenze trockener Tieflandsheiden Unterschiede zu den typischen Atlantischen Vorkommen aufzeigt, ob Alterungsprozesse beschleunigt oder Regenerationsmechanismen

variieren. Weiterhin wird untersucht inwiefern vegetative Regenerationen, z.B. nach Brand, den Lebenszyklus beeinflussen. Hierbei ist von besonderem Interesse wie langlebig die einzelnen Stadien im Lebenszyklus sind, da diese direkt mit bestimmten Ökosystemdienstleistungen verknüpft sind und direkt als Bewertungsmaßstab für die Habitatqualität dienen.

Ein weiterer wichtiger Themenbereich ist die Re-Etablierung neuer Heidevegetation nach Störung, z.B. nach Mahd oder Brand, die nach aktuellem Kenntnisstand durch klimatische Veränderungen und die athmogenen Stickstoffdepositionen beeinträchtigt sein könnte. Die vorliegende Studie untersucht daher wie junge *Calluna*-Pflanzen auf die in Norddeutschland vorkommenden Bedingungen von Sommertrockenheit und Stickstoffdepositionen reagieren.

In 19 Heidegebieten, verteilt über das gesamte Norddeutsche Tiefland, wurden in den Jahren 2013 und 2014 auf insgesamt 352 Aufnahmeflächen Artenzusammensetzung und Vegetationsstruktur sowie detaillierte Parameter zum Habitus, dem Pflanzenalter, dem Jahreszuwachs sowie Schäden an Trieb- und Blattmaterial an *Calluna*-Individuen erhoben. Die daraus erstellten Klassifikationen und Modellierungen berücksichtigen jeweils eine Vielzahl an ökologischen Einflussfaktoren und ermöglichen eine Analyse des komplexen Gefüges sowie das Herausarbeiten der wichtigsten bestimmenden Parameter.

Die Analyse der Heidevegetation ergab zwei grundsätzlich unterscheidbare Entwicklungswege, die standörtlich durch Bodencharakteristika und Nutzungsgeschichte bestimmt werden. Ein Entwicklungsweg kennzeichnet psammophile Heiden auf nur sehr initial entwickelten Sandböden, oft Flugsanddecken oder Inlanddünen mit extremer Nährstoffarmut, die in engem Kontakt zum Pioniergrasland des Corynephorion vorkommen. Dementsprechend beherbergen sie eine Vielzahl der dort typischen Arten mit der Anpassung an diese sehr speziellen Lebensbedingungen und stellen die artenreichsten trockenen Heidelebensräume im Norddeutschen Tiefland dar, maßgeblich durch ihre hohe Zahl an geschützten Flechten. Diese Artenvielfalt hält sich auch über initiale Heide-Entwicklungsstadien hinaus, so dass die vorliegende Untersuchung auch aufzeigt, dass die Artenzusammensetzung und –vielfalt nicht vorrangig durch das vorherrschende Heidealter bestimmt wird, sondern eher durch edaphische und strukturelle Charakteristika.

Der zweite Entwicklungsweg kennzeichnet typische Heidelebensräume in den Gebieten mit fortgeschrittener Entwicklung der Sandböden, mit Rohhumusauflagen und einer gegenüber den reinen Sandböden verbesserten Wasserhaltekapazität und Nährstoffverfügbarkeit. Diese Heiden beherbergen eine Vielzahl der typischen Gefäßpflanzenflora, und sind sehr variabel in Artenausstattung und struktureller Diversität, sind aber generell recht artenarm. Mosaike können mit dem typischen (Gefäß-)Pflanzeninventar und guter struktureller Vielfalt auftreten, allerdings kommen auch Mosaike vor die Vergrasungsprozesse anzeigen und dann extrem artenarm sind. *Calluna*-Dominanzbestände auf konsolidierten Sandböden sind oft gleichaltrig und extrem artenarm. Sie entstehen oft als Regeneration auf Mahd- oder Brandflächen, bei denen aber Bodenentwicklung und Humusanreicherung fortgeschritten sind.

Ein Subtyp des zweiten Entwicklungsweges beschreibt die Entwicklung von Heiden auf basenreicheren Standorten, wo sie in Kontakt mit basophilen Sandtrockenrasen vorkommen und über ein sehr großes Artenspektrum verfügen können. Diese sind im Vergleich zu den azidophilen Sandheiden relativ selten oder nur kleinräumig vorhanden.

Obwohl die Artenzusammensetzung also hauptsächlich durch nutzungsgeschichtlich beeinflusste Bodenmerkmale und lokale Arteninventare bestimmt ist, zeigte sich, dass junge Entwicklungsstadien eine höhere Artenvielfalt aufweisen als ältere, begründet durch die hohe Zahl an Arten aus den Gesellschaften der am Mosaik beteiligen Pflanzengesellschaften und der Armut an tatsächlich eng nur an Heide gebundenen Arten.

In der Störungsdynamik der Tieflandsheiden kommt demnach jungen Entwicklungsstadien eine besondere Bedeutung zu. Managementmaßnahmen wie Plaggen, Brennen oder Mahd bestimmen die Intensität und Schnelligkeit der *Calluna*-Regeneration, und daraus folgend Bestandesstrukturmerkmale, wie die Dichte an *Calluna*-Individuen, die Alterszusammensetzung der regenerierenden *Calluna* und die Anteile der weiteren Arten bzw. Lebensformen, entsprechend der oben skizzierten edaphisch bedingten Entwicklungswege.

Der Lebenszyklus der Besenheide bestimmt dabei diese Dynamik entscheidend, indem z.B. die Aufwuchsgeschwindigkeit in der ersten Zeit nach der Störung entscheidend für den Konkurrenzkampf mit Gräsern, v. A. *Deschampsia flexuosa* und *Molinia caerulea*, ist. In dieser Arbeit wird gezeigt, dass der Austrieb aus wurzelhalsnahen, basalen Sprossachsen nach Störung sehr schnell erfolgt, vorausgesetzt die Pflanzen sind zur Zeit der Störung nicht älter als 15 Jahre. Dieser Wiederaustrieb ist durch eine hohe Biomasseproduktion und Blühintensität gekennzeichnet, verlängert allerdings die totale Lebenszeit der Pflanze nicht unbedingt, da diese sekundäre hochvitale Phase kürzer anhält als die typische Aufbauphase einer aus dem Samen herangewachsenen Pflanze. Die Betrachtung der altersabhängigen Veränderungen im Habitus der ober- und unterirdischen Biomasse zeigte außerdem, dass Pflanzen aus Regeneration seltener die End-Wuchshöhe von Pflanzen, die direkt aus Samen herangewachsen sind, erreichen. Weiterhin zeigte sich dass die Pflanzen aus Wiederaustrieb zwar nur über wenige Jahre eine höhere Blühintensität aufweisen, aber schneller als direkt aus Keimlingen aufgewachsene Pflanzen beginnen an niederliegenden Ästen durch Adventivbewurzelung die Versorgung mit Wasser und Nährstoffen zu dezentralisieren und auf eine stammweise Versorgung umzustellen. Dieser Prozess beginnt bei Pflanzen die direkt aus Samen aufwachsen nach ca. 15 Jahren, nach oberirdischem Biomasse-Entzug allerdings auch schon eher und wird mit dem Wiederaustrieb intensiviert. Diese Umstellung vom primären Wurzelsystem auf das dezentrale Adventiv-Wurzelsystem geht einher mit einer allmählichen physiognomischen Wuchsformänderung, bei der schließlich die basalen Sprossachsenabschnitte fortlaufend neu bewurzeln und nur der diesjährig belaubte Haupttrieb aufrecht bleibt (‚layering'). Solche Pflanzen bilden dann dicht belaubte, grüne Matten und können bei Unkenntnis dieser Regenerationsmechanismen fälschlicherweise als eine Pflanze in der Aufbauphase gehalten werden. Gegenüber einer solchen sind sie allerdings altersbedingt in ihrer Regenerationsfähigkeit stark eingeschränkt.

Der Lebenszyklus von *Calluna vulgaris* in Norddeutschen Tieflandsheiden unterscheidet sich nicht grundlegend von denen anderer Tieflandheiden im Atlantischen Mitteleuropa, z.B. im Vereinigten Königreich. Es fanden sich weder Hinweise auf eine Verkürzung der Lebensdauer noch grundlegende Unterschiede in der Persistenz der einzelnen Wuchsphasen. Es fanden sich Hinweise dass unter den im Norddeutschen Tiefland herrschenden Klima- und N-Depositionsbedingungen ein etwas schnellerer Aufwuchs zur Reifephase stattfindet, aber ohne die Lebenszeit der Pflanze zu verkürzen.

Klimaereignisse, besonders Dürreereignisse während der Vegetationsperiode, werden als limitierende Faktoren für die Verbreitung trockener Atlantischer Tieflandsheiden vermutet.

In der vorliegenden Arbeit fanden sich jedoch kaum Hinweise auf eine klimatisch begründbare floristische Unterscheidung von Atlantischer und kontinentaler Heidevegetation im norddeutschen Tiefland, auch wenn die enge Verzahnung von Heide und Silbergrasfluren im subkontinentalen Osten öfter auftraten. Nur wenige Arten, die zudem auf eher basenreicheren Standorten vorkamen, ließen eine gewisse Zunahme an Kontinentalität erahnen, deren Wirkung aber geringer ist als die deutlich überprägenden edaphischen Unterschiede und die gebietsspezifischen Nutzungsgeschichten. Auch der Lebenszyklus der Besenheide scheint nicht sehr von der abnehmenden Ozeanität beeinflusst, aber weitere Studien sind nötig um hier Gewissheit zu erlangen.

Dürre während der Vegetationsperiode beeinträchtigt die Vitalität von jungen *Calluna*-pflanzen; die Jahreszuwachsraten waren geringer und die Blätter zeigten mehr Trockenschäden. Keimlinge zeigten eine erhöhte Empfindlichkeit gegenüber Trockenheit wenn die Stickstoffeinträge bei $25kg*ha^{-1}*a^{-1}$ lagen, der hier genutzte erhöhte Depositionswert, so wie dies in vielen nordwestdeutschen Heiden der Fall ist. Im östlichen Teil des Norddeutschen Tieflandes ist die Stickstoffdeposition geringer ($10\text{-}12kg*ha^{-1}*a^{-1}$), unter solchen Bedingungen war die Vitalität zwar unter Trockenheit verringert, war aber zumeist nicht tödlich, selbst unter den modellierten stärksten Dürrebedingungen die aufgrund des 10-Jahres-Trends (2011-2020) zu erwarten sind. Diese Ergebnisse belegen dass *Calluna* generell eine sehr hohe Trockenheitsresistenz hat, auch unter subkontinentalen Bedingungen, aber dass hohe Stickstoffdepositionen diese bei Keimlingen vermindern kann. Generell zeigte sich, dass ein hoher Stickstoffeintrag die Konkurrenzfähigkeit von jungen *Calluna*-Pflanzen unter Dürre reduziert und daher eine durch Vergrasung bedingte Habitatdegradation selbst unter moderatem Trockenstress verursachen kann.

Die hier vorliegenden Ergebnisse zeigen auf, dass die Vitalität und die Lebensgeschichte der Besenheide die Artenzusammensetzung zwar nur marginal direkt beeinflusst, denn dafür sind die edaphischen Standortfaktoren sowie die gebietsspezifischen Arteninventare und Managementeinflüsse wichtiger, aber dass die Habitatstruktur und die sich daraus ergebenden Habitat-Qualitätsmerkmale stark von der altersabhängigen Vitalität determiniert werden. Außerdem zeigte sich dass die Re-Etablierung von *Calluna* nach Störungen nicht nur von der Art des Managements abhängt, sondern auch durch sommerliche Trockenheit und hohe Stickstoffdeposition beeinträchtigt ist.

Die Arbeit untermauert die naturschutzfachlich hohe Bedeutung von frühen Heide-Entwicklungsstadien, insbesondere diese mit mosaikartig verzahnten Pioniergrasländern, die die höchste Arten- und Strukturvielfalt beherbergen. Die Bedeutung der Bereitstellung von günstigen Bodenbedingungen und die Notwendigkeit der dafür notwendigen Maßnahmen wurde erneut bestätigt, zugleich aber auch die Empfindlichkeit der jungen Regenerationsstadien gegenüber ungünstigen Klimabedingungen während der frühen Re-etablierungsphase.

Außerdem stellt die Arbeit durch die Erweiterung des klassischen *Calluna*-Lebenszyklus um die Regenerationswege und die Beschreibung der altersbedingten, habituellen Unterschiede zwischen dem ungestörten und dem gestörten Lebenszyklus eine bessere Einschätzung der Lebenshistorie von *Calluna*-Pflanzen bereit, so dass Einschätzungen zu Regenerationspotenzialen und Altersstrukturen im Rahmen der Erhebung von Habitat-Qualitätsmerkmalen treffender vorgenommen werden können.

Chapter 1:

Introduction

1.1 A short history of North German heathlands

Dry lowland heathlands dominated by *Calluna vulgaris* (L.) Hull (hereinafter: *Calluna*) are widespread over the oceanic and sub-oceanic regions of Europe, which comprise coastal areas bordering the North Sea and the English Channel (Gimingham 1972), but also inland regions of France, the Netherlands, Belgium, Germany, Poland and the Czech Republic.
The typical stratification in Atlantic dry heathlands is characterized by the absence of trees, due to the influence of man, as in temperate Atlantic or sub-Atlantic lowlands forests always preceded heath and natural dry heathlands occur as forest understory of Oak, Pine or Birch woodlands or small-scale clearings on nutrient-poor Pleistocene sandy sediments (Gimingham 1972; Gimingham 1975; Hüppe 1993a, 1993b). They are dominated by *Calluna vulgaris* and other Ericaceae, in Germany moreover *Vaccinium myrtillus, V. vitis-idaea, Genista pilasoa, G. tictoria* and *G. anglica*, accompanied by stress-tolerant hemicryptophytes, pioneer tree species (e.g. *Pinus sylvestris, Betula pendula*) as well as cryptogams.

The landscape character of dry lowland heathlands in Mid-Western Europe is a result of the complex interaction of human impact and natural processes of the past 5000 years, induced by forest degradation and historical heathland farming, with frequent disturbances resetting successional processes in soils and vegetation (Gimingham 1975; Gimingham & de Smidt 1983; Webb 1998). This conversion of former forests and woodlands to heathlands has been subjected in many studies, for heathlands in general (e.g. Gimingham 1972), but also specifically for German lowland heathlands (e.g. Behre 2008; Graebner & v. Bentheim 1904; Graebner et al. 1925; Hüppe 1993a, 1993b). During the conversion process, which started about 3000BC, the former woodland soils became extremely nutrient-poor and acidic, first induced by the reduction of trees, but later in the 10th century intensified by the periodical removal of aboveground biomass, humus and topsoil ('plaggen'; Ellenberg & Leuschner 2010). Maximum heathland area extent in Germany was reached in the mid 19th century, with a subsequent rapid decline, predominately due to the invention of chemical fertilisers and the many fundamental changes in land use associated with it (Ellenberg & Leuschner 2010; Hooftman & Bullock 2012; Piessens et al. 2005).

The large traditionally farmed open heathlands have been shaping the landscape in the German Northwest, but they did not occur in the Eastern part of the North German Plains, or to a much lower extent (Mortensen 1941, Pott 1999). Today, nearly 75% of the recent heathlands is located there (referring to those designed as dry heathland habitat types in the Natura 2000 network, Table 1.1, p. 6, with the German East roughly corresponding to the Continental biogeographic region). The prevalence of open heathland there is a result of intensive military training activities in the past century, with the sites differing to the traditional heathlands not only in their specific origin, but also in edaphic and climatic conditions (Schellenberg & Bergmeier 2014).

For instance, their disturbance regime differed in recent historical times, with northwestern heathlands managed moreover constantly over time, providing a higher habitat continuity and a lower amplitude of disturbances, whereas the eastern heathlands are exposed to irregular, but high-intensive biomass and soil disturbances due to military training activities.

The high-frequent fires, during summer, too, in combination with intense mechanical impact, such as tank driving, are assumed to be the predominant factors for the inland dune-like, vegetation-free conditions and the high spatial differentiation of development stages, often created by chance (Ellwanger & Ssymank 2016). After the Russian troop withdrawal in the early 1990s, the neglection of the former military training sites induced a small-scale mosaic succession, resulting in a high diversity in *Calluna* age structures and species, reflecting a wide range of development stages and associated soil conditions. The positive influence of military training activities on the nature conservation status of dry lowland heaths has often been emphasized (e.g. Burkart et al. 2004), but the recent heathland maintenance with methods of mechanical management is restricted, due to unexploded ordnance (Ellwanger & Ssymank 2016).

Up to now, there are no studies to the potential differences in heathland species composition or vegetation structures among heathlands in the German Northwest and Northeast, and little is known about the role of site history and its complex consequences on species composition and diversity. Almost all heathland nature conservation assessment schemes and references, as well as management approaches are moreover based on knowledge derived from studies conducted in Atlantic, traditional dry lowland heathlands. This thesis aims to figure out species composition patterns and vegetation structures along the range of climatic and edaphic conditions in the North German Plains and their relation to historical and recent land use to identify whether the traditional heathlands of the Northwest are differing to those in the East (Chapter 2).

1.2 *Calluna vulgaris*

The ericoid sclerophyllous dwarf shrub *Calluna vulgaris* acts as the key species of dry lowland heathlands, determining heathland habit and stand structures. Although it has a world-wide distribution range, covering almost the entire boreal to meridional northern hemisphere, its role as the dominant species in Atlantic dry lowland heaths is restricted to coastal-near regions in Northwestern Europe (Floraweb 2013; Gimingham 1972: 10). The distribution limit of Atlantic dry lowland heathland is determined by oceanic climatic conditions (Gimingham 1972, Loidi et al. 2010).

The wide distribution of *Calluna* suggests an ecological profile of a broad tolerance concerning temperature and moisture conditions, but the morphological characteristics, such like the woody, dense habit and the small, convolute, sclerophyllous leaves arranged like scales, with sunken stomata and hairs point to specific adaptions to drought. Consequently, *Calluna* has a wide tolerance towards water shortage and a high resistance to drought (e.g. Albert et al. 2012; Bannister 1964a, b; Gordon et al. 1999, Haugum et al. 2021; Kongstad et al. 2012). However, this drought resistance seems to be limited to moderate drought conditions under oceanic or sub-oceanic climate conditions, and *Calluna* rather suffers under longer droughts like occasionally occurring in subcontinental regions (Marrs & Diemont 2013; Gimingham 1972; own observations in 2013 and 2018, Chapter 4).

Calluna-dominated heathlands in Germany are located partially within the main distribution areal for Atlantic dry lowland heaths, especially the German Northwest, but some areas in the North German East provide moreover subcontinental climate conditions and are therefore on the distribution rear edge (Fig. 1.1, p. 14; Table 1.2, p. 13; Gimingham 1975: 87). Under such climate conditions, *Calluna* dieback events induced by drought or winter frosts occur more often (Gimingham 1972; Marrs & Diemont 2013; Pott 1995), and especially summer droughts are assumed to determine the distribution limit (Loidi et al. 2010).

During its life, *Calluna* growth form and vitality alters, described in the life cycle concept introduced by Watt (1955) and later refined by Gimingham (1972, 1975). This concept comprises four life phases, with distinct age-related shifts in the plant's height and shape, growth rate, flowering intensity and the proportion of dead shoots (after Gimingham 1972):

1. Pioneer phase (germination – approx. 10 years)
2. Building phase (up to approx. 15 years)
3. Mature phase (up to 25 years) and
4. Degeneration phase up to plant death with approx. 30 years

Since its introduction, this life cycle is established as a key criterion for determining age structures in heathlands, providing an easy and fast estimation of heather plant age. It allows for the detection of degeneration processes indicating the need for mechanical biomass disturbances that prevent over-ageing.

However, this theoretical concept is basing on the idea of an undisturbed *Calluna* life and therefore does not reflect heathlands under conservation management, with occasional fires, mowing or sod-cutting. The probability that a *Calluna* plant in a dry lowland heath in Germany is faced with one or several of such disturbances at least once in its lifetime is very high. Although this restriction for the application of the life cycle concept have been discussed and descriptions of post-disturbance growth stages are existent (e.g. Gimingham 1988), there is still a poor knowledge whether the growth phases detection may validly represent *Calluna* age and regeneration capacities. Additionally, potential alterations of this cycle, induced by unfavourable climate conditions or high airborne nitrogen (N) loads, are assumed (e.g. Berdowski & Siepel 1988), but evidence is still sparse.

The knowledge to *Calluna* drought resistance, drought adaption potentials and their effects on plant demographics at their distribution margin is still poorly understood. This study aims to contribute to a broader understanding of the *Calluna* life cycle and potential alterations of growth, vigour and regeneration potential under gradients of climate and N deposition. *Calluna's* age-specific vigour and growth are analysed along the gradient from oceanic conditions (Coastal areas of Lower Saxony, Schleswig-Holstein and Hamburg), to sub-oceanic (Mecklenburg-Western Pomerania, northern parts of Lower Saxony and Saxony-Anhalt as well as North-West Brandenburg) and even subcontinental conditions in the south-eastern parts of Saxony Anhalt, Saxony and Brandenburg. Thereby, a special focus is on post-disturbance regeneration mechanisms (Chapter 3), as well as their drought resistance (Chapter 4).

1.3 Heathland conservation efforts

Protection facts and framework

Dry lowland heathlands play a crucial role in the traditional European landscape, providing many ecosystems services, hosting a large number of threatened species and representing a cultural heritage (e.g. Fagúndez 2013; Gimingham 1975; Wessel et al. 2004).

The heathland biotopes considered in this study are protected by European and National law (Natura 2000 Habitats Directive 92/43/EEC; §30 BNatSchG). They are assigned as Habitat type F4.2 in the EUNIS habitat classification and as either European Dry heaths (HT 4030; Habitats directive Annex I: 4030, EIONET 2021a) or Dry sand heaths with *Calluna* and *Genista* (HT 2310; Habitats directive Annex I: 2310; EC 2013, EIONET 2021b) in the Natura 2000 network. On the national scale, they are referred to as Heaths on sandy soils (40.03, Finck et al. 2017).

There is an unsharp distinction between the HT 4030 and HT 2310, based almost only on the geological substrate and weak floristic support (c.f. EC 2013; Olmeda et al. 2020). As an inconsequential result, according to the latest report to the nature conservation status of HT 2310, its distribution ends abruptly on the German frontier, with no more occurrences in the adjacent Poland (c.f. map in EIONET 2021b). Of course, it is unlikely that they do not occur in Poland, and much more likely that they are designated as HT 4030 there, due to EU member state-specific HT assessment criteria. The imprecise distinction between the HT 4030 and HT 2310 led to the decision to include sites either assigned as HT 4030 or HT 2310 in this study, representing dry lowland heathlands on sandy soils.

Table 1.1 Distribution and extent of designated Dry lowland heathland in the EU and Germany (km^2 and proportion). Calculated for HT 4030 and HT 2310, in the EU and in Germany, for Atlantic (ATL) and Continental (C) biogeographical regions, as well as pooled. Calculated after data from EIONET (2021a, 2021b), for the report period 2013-2018.

	HT 4030 European Dry heath	HT 2310 Sand dunes with Calluna and Genista
EU	1 019 710	51 019
Germany	178 205 (17.5%)	32 569 (64.0%)

	ATL	C	ATL	C
EU	590 453	429 257	33 923	17 096
Germany	39 678 (6.7%)	138 527 (32%)	15 623 (46.1%)	16 946 (99.1%)

	HT 4030 European Dry heath + HT 2310 Sand dunes with Calluna and Genista	
	ATL	C
EU	624 376	446 353
Germany	55 301 (8.9%)	155 473 (34.8%)

Dry heath is listed as ‘vulnerable’ in the Red List of European habitats (Janssen et al. 2016). On the national scale, degenerated heaths (biotope code 40.03.03) are ‘not threatened’, but those of high vitality and structure are ‘critically endangered’ (40.03.01; Finck et al. 2017).

The responsibility of Germany to contribute to the European dry lowland heathland maintenance is very high, as Germany hosts a considerable share of the total European dry lowland heathland, in particular in the Continental biogeographical region (Table 1.1). Germany has the highest number of designated 4030 sites (>400), although with a relatively low size per site (Olmeda et al. 2020).

Many of the dry heathlands, both on dunes or not, have been assessed as being in an unfavourable to bad nature conservation status, with a deteriorating future trend. The reasons are abandonment of traditional management, insufficient or wrong management, airborne nitrogen deposition, loss of specific habitat structure, fragmentation and invasive non-native species (BfN 2019, Ellwanger et al. 2020, Olmeda et al. 2020, EIONET 2021a, 2021b)

Heathland management

Heathland management purpose changed from historic to recent times. Up to the 19th century, heathlands have been primarily used as pastures, and traditional farming practices allowed for the cultivation of the poor, sandy land (Ellenberg & Leuschner 2010, Gimingham 1975). The aims of traditional heathland farming were to provide a sufficient fodder quality for the robust livestock breeds and to cultivate the poor sandy soils. This was achieved by transferring the limiting nutrient (N) from the heathland to the cereal fields by periodically removing heathland aboveground biomass and topsoil, using it as bedding for the livestock, and then bringing it to the cereal fields to enrich the poor soils with nutrients and humus. The re-establishment of heathland vegetation ensured fodder for the livestock, but the quality decreased with *Calluna* age. As a consequence, cyclical mowing or burning was applied to induce vegetative regeneration with a high fodder quality due to highly vigorous resprouting.

Nowadays the main scope of conservation measures is to optimize heathland habitat structures for maintaining the several ecosystem functions and services. The rejuvenation of heather is still the driver of vital heathland development, and mechanical disturbances are still applied with a similar aim than historically; transferring nutrients from the heath. But today, the scope changed more to providing suitable nutrient-poor conditions to re-establish typical heathland species assemblages, including the compensation of airborne N depositions.

The objectives of recent dry lowland heathland nature conservation management according to Olmeda et al. (2020) are

1) maintaining or improving the structure and the function of heathlands,
2) providing suitable conditions for the typical species inventory and plant communites, and
3) to ensure a favourable future prospect.

In the North German lowlands, the former traditional heathland sites with a long history of heathland farming were either converted into non-heath habitats or managed by the continuation or re-introduction of heather rejuvenation-inducing biomass disturbances for nature conservation purposes. Thereby, the used techniques are adopted from traditional heathland farming and comprise grazing, mechanical biomass and soil disturbances (sod cutting, 'plaggen'), as well as prescribed burning.

Mechanical managements differ widely in their intensity and extend to remove biomass and topsoil, mowing with the lowest, and a deep sod cutting ('plaggen') with the highest intensity. They attempt to restore suitable soil conditions for heathlands, thereby the effectiveness is dependent on the management type and the airborne nitrogen loads to compensate for (Jones et al. 2017; Walmsley & Härdtle 2021).

Traditional grazing in the North German lowlands is with herded robust sheep breeds, but recently, fenced grazing regimes are common as traditional shepherding is hardly economically beneficial today and is applied primarily for nature conservation and touristic purposes. There is a wide variety in used breeds, grazing intervals and stock densities (Table 1.2 p. 13). Grazing with other animals, such like robust cattle and horse breeds as year-round extensive pastures or small-scale goat grazing is less frequent. Not perceived adequately, and therefore likely underestimated in their potential positive value for heathland management, browsing activities by free ranging deer (red deer, fallow deer, roar deer) contribute to heathland dynamics wherever those animals occur in sufficient densities (Tschöpe et al. 2004, 2011; own observations).

Without a doubt, grazing is an important tool for heathland conservation management, but its advantages, disadvantages and effectiveness must be assessed on a regional, site-specific scale (e.g. Bakker et al. 1983; Bullock & Pakeman 1997; Brunk et al. 2004; Bunzel-Drüke et al. 2008; Fagúndez 2013; García et al. 2013; Gimingham 1972, 1994; Kirkpatrick & de Blust 2013; Newton et al. 2009; Vandvik et al. 2005).

A high number of studies addressed impact, efficiency, (dis)advantages, as well as possibilities and restrictions of the different heathland managements (e.g. Anders et al. 2004; Ellwanger & Ssymank 2016; Fagúndez 2013; Gimingham 1972, 1994; Olmeda et al. 2020; Walmsley & Härdtle 2021; Walmsley et al. 2021; Webb 1998), but despite some general findings, results and conclusions differ widely across regions and management types, even within one management type, due to the complex study area-specific situation determining the success or failure. Therefore, this study aims to find general determinants for *Calluna* vitality and heathland diversity rather than comparing different management types.

Threats and pressures

The main reasons for Atlantic dry lowland heathland habitat quality and distribution decline in the recent history were related to land use changes (Fagúndez 2013; Fagúndez & Izco 2016). The decrease of the economic value of traditional pastoralism and the introduction of chemical fertilizers in the mid 19th century introduced a large-scale heathland distribution decline (Ellenberg & Leuschner 2010; Fagúndez 2013; Gimingham 1972). As a consequence, many heathlands were abandoned, afforested, converted into agricultural fields, or were used for housing, mineral working and others (Olmeda et al. 2020). The establishment of nature reserves and the (re-)introduction of heathland management for nature conservation purposes prevented further habitat losses, but cannot compensate for habitat quality decline, which is the major threat today.

Heathland habitat quality depends on whether the recent management is sufficient in providing favourable *Calluna* rejuvenation and age structures, typical species compositions, edaphic conditions and habitat connections, for enabling heathland ecosystem services and functions. The management methods applied in the past and up to now are usually based on the local site-specific conditions and opportunities given. Despite the fact that sometimes frequency or intensity was too low to prevent for tree invasion or *Calluna* degradation, the overall problem may not be that there is a general uncertainty about the efficiency of the methods applied. The problem is that recent conditions of changing climate and high airborne nitrogen (N) deposition is assumed to cause inter- and counteracting effects on heathland dynamics, with a yet unclear future prospective (Diemont et al. 2013; Fagúndez 2013).

High N loads are known to be threats to nutrient-poor ecosystems, altering species composition (e.g. Diemont et al. 2013) and ecosystem functioning (e.g. Bähring et al. 2017). In the 1980s, the sensitivity of heathland ecosystems to high airborne N loads was detected, with the observation that heathland became grasslands under high N deposition (Heil & Diemont 1983). Later on, several studies detected the fertilizing effects of high N loads (e.g. Bähring et al. 2017) and vitality reduction (e.g. Krupa 2003), particularly in interaction with climatic and edaphic conditions (e.g. Gordon et al. 1999; Calvo-Fernández et al. 2018; Meyer-Grünefeldt et al. 2015, 2016). High N deposition shifts the N-limited heathlands to phosphorus limitation, causing competitive advantages for species that can use low soil phosphorus more efficiently than *Calluna*, such like *Molinia caerulea* or *Deschampsia flexuosa* (Falk et al. 2010; Härdtle et al. 2006; Grimoldi et al. 2005; Roem et al. 2002). These findings highlighted the need for disentangling counter- and interacting impacts of high N deposition, managements and disturbance-induced *Calluna* population dynamics.

The critical loads for airborne N in dry heathlands are ranging within $10\text{-}20^{kg}/_{ha*y}$ (Bobbink & Hettelingh 2011), but many regions in Europe are above that level (Diemont et al. 2013; Erisman et al. 2015; Waldner et al. 2014), including the German Northwest (Table 1.3, p. 16). As a consequence, removing N from heathland ecosystems to compensate for the airborne loads is one of the most important challenges in today's heathland management (Jones et al. 2017; Härdtle et al. 2006, 2009; Vogels et al. 2020; Walmsley & Härdtle 2021; Walmsley 2021).

European heathlands are affected by the changing climate. In the past years, severe droughts during vegetation period induced large *Calluna* dieback events in dry lowland heathlands (Marrs & Diemont 2013; own observations during the survey period 2013 and in 2018). Such droughts will occur more often in future (e.g. IPCC 2021; Schönwiese & Janoschitz 2008, Wagner et al. 2013) and may challenge *Calluna* and its high adaption potential. Recent studies showed that drought resistance is negatively affected by high atmospheric N loads (e.g. Meyer-Grünefeldt et al. 2015, 2016), thus increasing the complexity of ecological stressors and their interactions *Calluna* is faced with.

Other threats and pressures, such like invasive species or disturbances destroying typical habitat structures are moreover local threats, but may not contribute to the overall trend of declining habitat quality.

Assessing the conservation status

Several criteria are used for assessing the recent status of habitat quality and the effectiveness of nature conservation efforts, comprising parameters of habitat distribution, structure and threats. The assessment schemes are varying among the EU member states, causing difficulties in the comparability and the validity of overall European nature conservation strategy efficiency assessments. Additionally, favourable reference values, acting as target conditions, are not well defined (Olmeda et al. 2020).

In Germany, the first assessment scheme was defined in 2007, later revised for two times (2010, 2017). Heathlands with a high nature conservation value have a complete 'typical' species composition, complete 'typical' structures (*Calluna* growth phases, open soil) and no recent pressures or potential future threats, such like grass dominances, invasive species or signs of succession (BfN & BLAK 2017, assessment scheme: Appendix: Table A-1, p. 138).

Hereby, 'typical' refers to an expert rating rather than clearly defined and assessable criteria in the national assessment schemes (BfN & BLAK 2017). To improve the regional-specific assessment concerning the 'typical' plant inventory, the German Federal states provide modified lists (e.g. for Brandenburg: LfU Brandenburg 2014a, 2014b).

The assessment scheme provides some uncertainty in the determination of typical plant assemblages, *Calluna* age and their associated growth phases. According to the assessment scheme from BfN & BLAK (2017) growth phases are determined focusing on the successional context, assessed together with habitual characteristics of the prevailing *Calluna* growth form. Thereby, specific early-stage (pioneer) species compositions and later stage (degeneration) species assemblages, adapted from Gimingham (1972) and van der Ende (1993), were used to substantiate the growth stage assessment.

Several problems coincide with this. First, this approach is strongly depending on the spatial scale the habitats are mapped. In the optimum, heathlands are mosaics, comprising small-scale heathland patches of different ages, and are mapped together as one habitat, resulting in a high diversity of age structures. Mechanically managed heathlands are often patchy as well, but on a larger scale, with clear distinct patches of e.g. burnt or mowed sites and sharp borders to adjacent heathland habitats. The criteria for either combining or separating such heathland patches as one or several habitat(s) are rather imprecise, differ between the federal states and depend on the expert's decision, maybe pre-specified by the mapping customer. As a result, the validity of the assessments in the diversity of age structures and species composition depends chiefly on the mapping scale.

Second, this approach assumes that the complex edaphic changes in succession, e.g. raw humus accumulation and podsolization, are reflected by the species composition and the *Calluna* age. During my field work, I got the impression of species composition reflecting edaphic conditions rather than the aboveground age of *Calluna*, which seems not to give any informative value for the successional edaphic processes but was moreover determined by the management. Hence, one aim of this study is to analyse the interactions of species composition and edaphic conditions, and setting the findings into a context of successional heathland development on the plant community scale (Chapter 2).

Additionally, the current methodology of age structure assessment via growth phases lacks in the informative value concerning regeneration processes and the safe detection of regeneration growth phases, with yet unknown consequences for the assessment of *Calluna* vitality regeneration capacities and reproductive potential. Therefore, this study aims to refine and revise the established life cycle concept to provide a new basis for criteria adjustment, refinement and improvement (Chapter 3).

1.4 Study areas and Sampling

Study areas

The study region comprises the North German Plains, including the federal states of Lower Saxony, including coastal and inland sites in Schleswig-Holstein, Hamburg, Mecklenburg-Western Pomerania, Saxony-Anhalt, Brandenburg and Saxony (Fig. 1.1 p. 14; Fig. 2.1 p. 29).

Study areas were selected on the basis of meeting several criteria:

- Dry lowland heathland area, protected either as Natura2000 site or National Natural Heritage with protected heathland biotopes.
- Representing heathland variability in size, site history and recent managements.
- Reflecting the range of abiotic environmental conditions for heathlands in the North German plains (soils, climate, airborne nitrogen deposition).
- Hosting heathland habitats of different stages, ages and vitality.

Aim of the study design was to represent the variability of North German heathland habitats, for analyzing general characteristics, the commons and differences, but also the interplay of the complex environmental conditions under field conditions.

Some of the study areas have already been subject of studies on regional heathland plant communities and heathland ecology (e.g. Preising et al. 2012; Pott 1999; Schubert 1973), but a general study to North German dry lowland heathland communities, both the Northwestern and Northeastern part, has never been conducted so far, probably due to historical reasons. Hence, this study provides the first overview to North German Plain lowland heathland plant communities, as well as the vitality of its key species *Calluna vulgaris* along the gradients of climate, soils and management provided by the study region.

The 19 heathlands considered in this study are protected habitats within the framework of the Natura 2000 Habitats Directive (17 sites), and/or natural heritage sites with protected dry lowland heathland habitats (10 sites, Table 1.2). From small heathland patches of less than 100 ha, such like the Süderlügumer Binnendünen near the Danish frontier or the former airfield Vietmannsdorfer Heide north of Berlin in Brandenburg, study areas range in size up to more than 20,000 ha (Lüneburger Heide and the NATO military training area Bergen, both Lower Saxony, Table 1.2).

Table 1.2 Study area characteristics: Location, size, protection status, site history and recent management.

Nr in map . Fig. 1.1	Study area	Meters above sea level	size [ha]		Federal state	Site history and recent management	Natural Heritage	Natura 2000 site	Plots sampled
			Area	Heathland area 4)					
1	Tinner Dose	21	19480	360	Lower Saxony	military training with high-frequent fires, intense mowing	no	yes	**11**
2	Cuxhavener Küstenheiden	10	1279	360	Lower Saxony	former military training area (until 2003), now year-round extensive grazing with cattle/horses or sheep grazing (fenced), sometimes mowing, scrub clearing on pastures	yes	yes	**10**
3	Süderlügumer Binnendünen	16	303	<100	Schleswig-Holstein	old inland dune area, sheep and goat grazing (fenced)	no	yes	**5**
4	Fischbeker Heide	11	773	155	Hamburg	traditional heathland area; sheep grazing (herded), mechanical measurements (sod cutting, mowing)	no	yes	**11**
5	NATO training area Bergen-Hohne	70	28702	3100	Lower Saxony	military training area with high-frequent fires and mechanical disturbances due to tanks and other military vehicles; mowing and scrub clearing	no	yes	**60**
6	Lüneburger Heide	92	23286	4700	Lower Saxony	traditional heathland area; party former military training, sheep grazed (herded), mechanical measurements (sod cutting, burning, mowing), scrub clearing	no	yes	**91**
7	Nemitzer Heide	26	1061	360	Lower Saxony	accidental fire in 1971; sheep grazing (herded), sod cutting, mowing 5)	no	yes	**11**
8	Leussower Heide	40	6205	1000	Mecklenburg-Western Pomerania	former military training (until 2013); no management since then	yes	yes 3)	**15**
9	Marienfliess	72	1082	150	Mecklenburg-Western Pomerania 1)	former military training area (until 1991); sheep grazing (fenced) and burning	yes	yes	**10**
10	Kyritz-Ruppiner Heide	75	12871	1000 2)	Brandenburg	former military training area (until 1991); burning, mowing, high deer browsing activity	yes	yes 3)	**20**
11	Oranienbaumer Heide	75	3331	350	Saxony-Anhalt	former military training area (until 1991); year-round extensive grazing with horses/cattle, scrub clearing, mowing	yes	yes	**10**
12	Rüthnicker Heide	45	3957	120	Brandenburg	former military training area (until 1991); mowing	yes	-	**10**
13a /b	Kleine Schorfheide / Vietmannsdorfer Heide	60/ 55	3620/ 1675	1000/ <100	Brandenburg	former military training area/ airfield (until 1991); sheep grazing (fenced) and mowing	no	yes	**20**
14	Glücksburger Heide	85	2812	550	Saxony-Anhalt	former military training area (until 1991); mowing, sheep grazing (fenced, started after survey)	yes	yes	**14**
15	Bundeswehr training area Jägerbrück	20	8813	1000	Mecklenburg-Western Pomerania	active military training with high-frequent fires and mechanical soil disturbances due to driving activities	no	yes	**20**
16	Prösa	118	3732	200	Brandenburg	former military training area (until 1991); mowing, sheep grazing (herded)	yes	yes	**12**
17	Zschornoer Wald	110	2148	200	Brandenburg	former military training area (until 1991); burning, mowing	yes	no	**12**
18	Daubaner Wald	140	3531	225	Saxony	former military training area (until 1991); mowing, sheep grazing (herded)	yes	yes	**10**

1) only partly sampled in Mecklenburg-Western Pomerania. 2) area only partly sampled; only southern part in ownership of Sielmann foundation. 3) in parts. 4) heathland area calculated and rounded, based on rough digitalisation of identifiable heathland on satellite maps of study areas in QGIS. This rough estimation was used for determination of amount of samples per area. 5) Nemitzer Heide was assigned as 'traditional heathland site' in this study, because it was a traditional heathland up to the mid 19th century, then afforested, and then again open heathland due to an accidental burning 1971. This Table was modified after a table provided in the electronic supplement to Chapter 2.

It is difficult to determine which of the study areas can be considered as ‘historical’ heathland, as the term “heath” is used in varying senses, often with regional differentiations (Ellenberg & Leuschner 2010, Hüppe 1993a, b; Schellenberg & Bergmeier 2014). However, in this study, I roughly distinguished between heathlands under active military training (n = 10; e.g. NATO training area Bergen, Lower Saxony (No. 5 in Fig. 1.1) and the Bundeswehr training area Jägerbrück, Mecklenburg-Western Pomerania (No. 15 in Fig. 1.1)), those with a traditional heathland farming history (n = 4; e.g. Lüneburger Heide, Lower Saxony (No. 6 in Fig. 1.1); Fischbeker Heide, Hamburg (No. 4 in Fig. 1.1)) and those shaped by military training activities in the past century, but now under nature conservation management (n = 4; former military training areas, e.g. Kyritz-Ruppiner Heide, Brandenburg (No. 10 in Fig. 1.1), Glücksburger Heide, Saxony-Anhalt (No. 14 in Fig. 1.1; Table 1.2)).

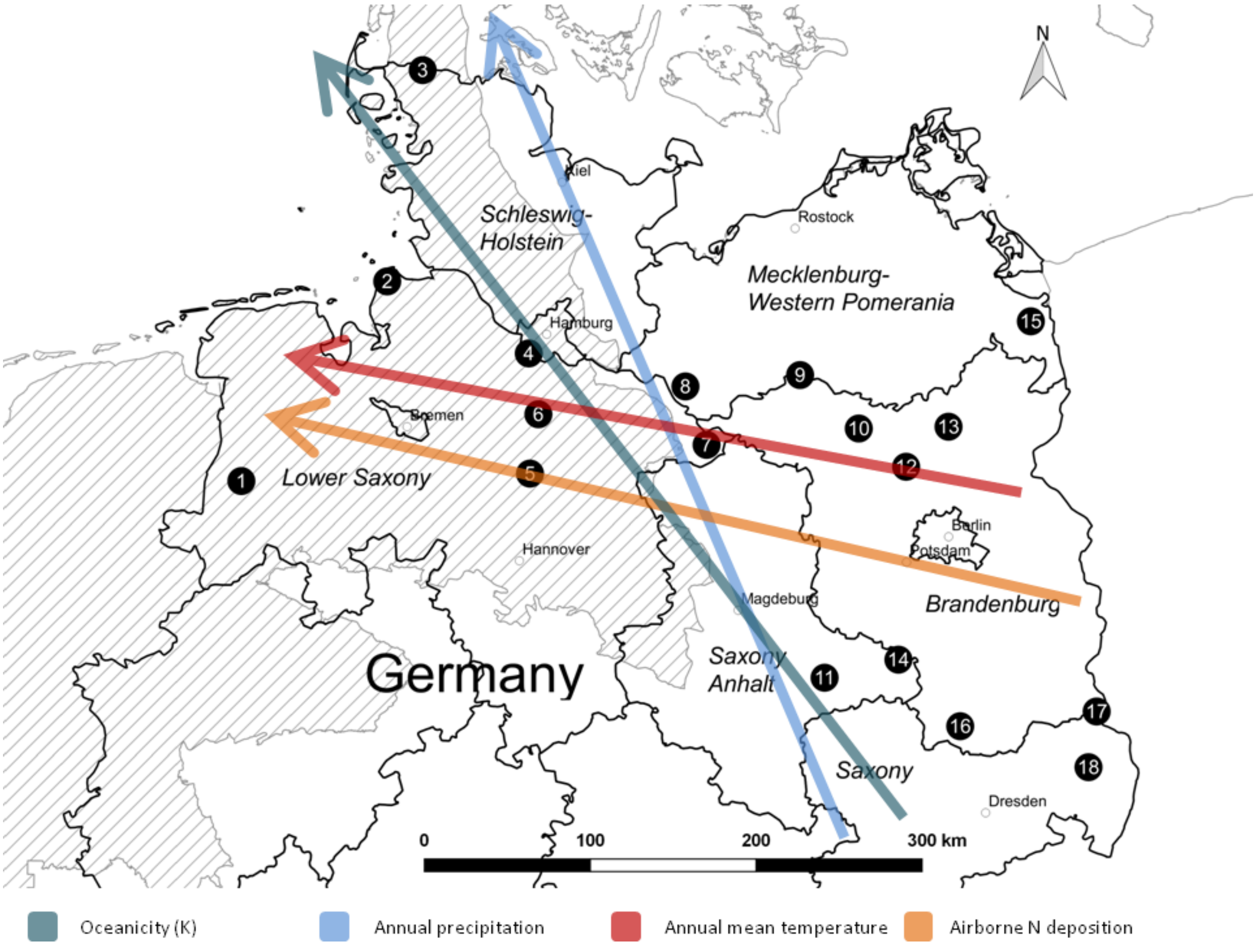


Fig. 1.1 Map of study area locations and the gradients of Climate (Oceanicity, Annual precipitation and mean temperature) and N deposition. Arrows indicate in which directions the gradient is increasing, but they are only roughly corresponding to the values given in Table 1.3 for showing the general patterning. Biogeographic regions (EEA 2016): Atlantic, grey hatched; Continental, white. For study area names 1-18 see Table 1.2 or Table 1.3. Administrative boundaries © Bundesamt für Kartographie und Geodäsie, Frankfurt 2011.

North German lowland heathlands are exposed to climatic conditions varying from oceanic, coastal areas in the Northwest, over suboceanic to even subcontinental properties in the East and Southeast (Table 1.3; Fig. 1.1; Schellenberg & Bergmeier 2014: 113). As a measure of Oceanicity, the Kotilainen's Index (K)was used, reported to provide the best correlation of climatic conditions and biological phenomena (Godske 1944):

$$\mathrm{K} = \frac{\mathrm{N} * \mathrm{dt}}{100\Delta}$$

with N = yearly precipitation in mm, dt = number of vernal or autumnal days with mean temperatures ranging from 0°C – 10°C and Δ = difference between the mean temperature of the warmest and coldest month. For the calculation of K, daily observations of the reference period from 1980-2010 was used (DWD 2015; Table 1.3). For the coastal heathlands in Norway, K ranges roughly from 100 to 300, with some peaks (>400) but also regions with K < 100 (Godske 1944). There were similar ranges in the Scottish upland heaths (Poore & McVean 1957), but with no values K < 100. In contrast, none of our study areas reached a K > 100 (Table 1.3), they moreover ranged from 40 (Glücksburger Heide and Oranienbaumer Heide, No. 11 and No. 14 in Fig. 1.1, both in the southern Saxony-Anhalt) to 85 (Süderlügumer Binnendünen, Schleswig-Holstein, near the coast and the Danish frontier, No. 3 in Fig. 1.1).

Heathlands in the North German Plains stock on acidic Pleistocene sandy sediments of varying thickness and development stage (Härdtle et al. 1997). The substrates are determined by the age of the sediments, the site history and the climate. In the German Northwest, the sandy sediments are older, and under the Atlantic climate, podsolization and raw humus accumulation rates are higher (Lache 1979, Härdtle 1997). Eastern the river Elbe, sandy sediments are younger. Although they were stocked with woodland before the military training activities started, the specific and high-intense disturbances caused by accidental fires throughout the whole year, tree and scrub clearings as well as tank driving resulted in an exposition of bare sands, often inland dune-like (e.g. the drifting dune in the Leussower Heide). In contrast to surrounding sites, the military training areas have never been subject to fertilizing or soil improvement for agricultural purposes, a factor which favoured erosion to bare, exposed and extremely nutrient-poor sands (Burkart et al. 2004).

Hence, the sandy soil development stages, with varying raw humus accumulation and podsolization intensity differ across the regions, with potential influences on the recent heathland plant composition and heathland dynamics, thus not have been subject for any studies up to now.

Table 1.3 Study area characteristics: Climate conditions, location above sea level and annual N deposition (UBA 2019, basing on the PINETI-3 model for the reference period 2013-2015, Schaap et al. 2018). Kotilainen's Index of Oceanicity is calculated after Godske (1944): Kotilainen's Index of Oceanicity and the climate data are basing on the reference period 1981-2010 (DWD 2015, stations used see Appendix: Table A-2).

	m asl	Annual N deposition [kg*ha^{-1}*yr^{-1}]	Kotilainen's Index of oceanicity	Annual precipitation [mm]	Days without precipitation	Mean annual temperature	Annual amplitude of daily mean temperature
1 - Tinner Dose	21	23	71.4	797	168	10.0	33.1
2 - Cuxhavener Küstenheiden	10	18	79.2	882	171	9.6	30.0
3 - Süderlügumer Binnendünen	16	17	84.6	855	157	8.5	31.2
4 - Fischbeker Heide	11	18	68.7	710	173	9.6	33.7
5 - NATO training area Bergen-Hohne	70	15	56.7	771	173	9.6	35.3
6 - Lüneburger Heide	92	15	68.6	812	171	9.0	34.8
7 - Nemitzer Heide	26	12	45.2	611	187	9.2	35.6
8 - Leussower Heide	40	15	51.6	610	179	9.0	34.6
9 – Marienfliess	72	12	51.7	621	179	8.8	35.3
10 - Kyritz-Ruppiner Heide	75	11	41.4	574	198	9.2	35.4
11 - Oranienbaumer Heide	75	11	40.1	525	194	9.4	37.2
13a - Kleine Schorfheide	60	10	43.1	582	196	8.6	37.2
13b - Vietmannsdorfer Heide	55	10	45.0	624	188	9.0	37.2
14 - Glücksburger Heide	85	11	40.1	525	194	9.4	37.2
15 - Bundeswehr training area Jägerbrück	20	11	45.7	536	190	8.8	35.8
16 - Prösa	118	11	41.9	615	220	9.2	37.6
17 - Zschornoer Wald	110	10	42.5	683	189	9.2	38.8
18 - Daubaner Wald	140	11	45.0	691	182	9.2	39.2

Sampling

Depending on the study area size and the diversity in managements a total of 352 plots was selected, each a 25m^2 quadrat with a randomly generated GPS coordinate as Southwestern corner (Fig. 1.2, using QGIS versions 2.1-2.8, 2013-2017). The sampling took place in two survey periods, with the first survey period focusing on species composition and vegetation structure (May-August 2013), and the second on *Calluna*-individual plant vitality attributes (August-September 2014, field protocols: ESM1_1).

In 2013, the data for the vegetation classification (Chapter 2) was collected, with vegetation structures and topsoil samples gathered in the 25m^2 plots and a vegetation relevé conducted on the 4m^2 subplots (Fig. 1.2). Two of the 352 plots have been recently sod-cut with an initial regrowth of only *Calluna*, and have been therefore excluded from the plant community analysis in Chapter 2.

In 2014, freshly sod-cut or burnt sites were excluded, as they provided no valuable plant material for the vitality attribute analysis. Additionally, area or plot accessibility problems reduced the dataset to 319 plots. The sampled vitality data on individual *Calluna* plants within the 25m^2 plot in 2014 was used for the analysis of age-dependant changes in plant habit and vigour (Chapter 3) as well as for the analysis of drought susceptibility (Chapter 4). In the latter, only up to three-year old plants were selected from this dataset, from 259 plots.

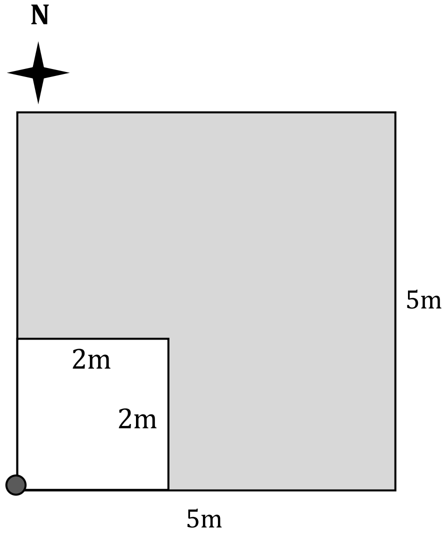


Fig. 1.2 Schematic Sampling Design for the survey periods 2013 and 2014. The 4m^2 quadrat was used for the vegetation relevé, the 25m^2 quadrat for the collection of structure and vitality data. The lower left corner (=Southeast corner, shown as grey dot) is the randomized GPS coordinate.

1.5 Dry Lowland heathland ecology: Gaps of knowledge to cover

Heathland plant species composition and vegetation structures

The present study aims to assess overall commons, patterns and differences in species diversity and composition of North German dry lowland heathlands. To the best of my knowledge, such a study has never been conducted in the North German lowlands, neither with the complexity nor with the spatial extent. The existing studies are often focussing on phytosociological analyses, often with a limited spatial scope (e.g. Berg 2004; Preising et al. 2012; Schubert 1973, 1974), providing fundamental community descriptions and ecological profiles of the plant assemblages in the specific regions addressed. They do not allow for a direct comparison of plant community species composition over the entire North German plains, due to different analysis methods, publishing times and subjective interpretations of the different authors.

The interplay of species composition, species diversity and heathland development stage is still insufficiently understood. The theory of heathland development phases, determined by the prevailing *Calluna* growth phase with its associated species (c.f. Gimingham 1972, van der Ende 1993) is the basis of our heathland dynamics understanding and status assessment, but its application lacks in some details.

First, this idea was introduced and approved for unmanaged stands in North-East Scotland (Gimingham 1972). German (and of course many other) dry lowland heathlands are usually managed, with their development describing a seral change of communities after disturbances. Thereby, the type and intensity of the disturbance determines the starting point for the succession, either starting from ‘real’ early-stage conditions (e.g. bare sands after sod-cutting) or only early *Calluna* growth phase conditions (e.g. after mowing or burning). As a consequence, the idea of growth-phase specific plant assemblages may only be valid for sites with a ‘real’ reset to early-stage edaphic conditions, and an undisturbed *Calluna* life cycle. This shows that the assumption of specific heathland plants associated with each *Calluna* growth phase may be invalid for frequently managed stands, where the species composition of sod-cut sites is probably different to those on mowed or burnt sites, although with the same *Calluna* growth phase prevailing.

Second, an even-aged, dense stand with prevailing Building-phase plants, e.g. after mowing, provides other microclimatic conditions for e.g. cryptogams than an open mosaic heath with

Calluna in the Building phase, e.g. after burning. Hence, heathland plant community changes along successional gradients cannot be analysed without considering 1) edaphic conditions and 2) the vegetation structures. I assume both to play a central role in the species composition along heathland development paths.

Therefore, an aim of the study presented in Chapter 2 is to improve the understanding of heathland community dynamics and the role of regional patterning. More specifically, it tries to identify species and structures that allow for a valid estimation of the successional stage, reflecting soil and vegetation dynamics as well as restoration potentials.

Additionally, the study asks for the importance of ecological key factors determining the species composition and the vegetation structure, whether it is the site history or climate (oceanic vs. subcontinental conditions), and how high airborne N loads alter species composition and heathland dynamics.

Derived from those findings, the study aims to assess the potential nature conservation value of the heathland plant communities by using the established criteria for determining nature conservation status in the mapping of Natura 2000 protected habitat types. Thereby, the criteria were critically revised and potential specifications to improve their informative value concerning heathland habitat quality assessment were provided.

Calluna life cycle as the determinant for heathland dynamics

The established *Calluna* life cycle concept with its distinct four growth phases is the basis for determining heathland age structures, one of the key criteria for nature conservation status assessment. This cycle refers to an undisturbed *Calluna* life and although regeneration processes have been mentioned to alter it ('post-fire regeneration'; Gimingham 1988; Wallen 1980), the recent usage does not distinguish between plants of different life histories.

Calluna has generally a very high potential for vegetative regeneration (e.g. Gimingham & Mohamed 1970), a trait which allowed for the establishment on sites frequently disturbed by man. Two mechanisms are typical for the *Calluna* vegetative regeneration after disturbance, the resprouting, resulting in vigorous clusters of new shoots from stem bases or axillary dormant buds, and the layering, where procumbent shoots are rooting adventitiously. Resprouting is the prevailing vegetative regeneration of younger plants, whereas layering occurs in older plants. The resprouting capacity is limited to young plants of up to 15 years, due to the secondary xylem growth reducing the capacity of buds to resprout (Miller & Miles 1970; Mohamed & Gimingham 1970).

The assumption that any heather regeneration may entry a new *Calluna*-typical life cycle again, like assumed in the 'repetitive cycling' theory, lacks in evidence-based research, as well as the assumption that any regeneration may improve heathland vitality and *Calluna* is immortal (Wallen 1980; Webb 1986). Some studies already indicated that older plants have a restricted regeneration capacity, but there is no study that aims to track the further development of regenerated plants, their persistence in post-disturbance growth phases, their longevity and general vigour. In the second chapter of this thesis, vitality attributes that are known to alter with age have been analysed, considering plants of different age and life history. I aimed to disentangle effects of the total plant age, the regeneration age, the plant life history, management, climate, and N deposition. The aim was to detect potential differences in age-related vitality between the plants grown from seeds (PS), plants resprouting from buds near stem base (PR) and those growing from rooted stems lying on the ground (PL). The persistence of PS, PR and PL in the physiognomically determined growth phases was assessed and compared to find potential differences in their regeneration potential. Additionally, this study aimed to answer the question whether there is evidence for 'repetitive cycling' processes, i.p. whether recurring regeneration cycles produce highly vigorous plants independent from the total plant age, and whether *Calluna* plants are immortal or not.

Furthermore, I asked whether the *Calluna* life cycle in North German lowland heathlands shows evidence for any alteration compared to other regions, and whether those may be explained by high N depositions or the conditions of climate in the marginal distribution range.

Drought susceptibility of young *Calluna* plants under changing climate and high N loads

Although *Calluna* has a wide tolerance towards water shortage and a high adaption potential to regional ecological conditions (c.f. 1.2 *Calluna vulgaris*), field observations show that extreme droughts, as in 2018, caused lethal damages on both, adult and young *Calluna* plants (University Hasselt 2021; own observations). It is hitherto unknown whether these damages indicate that the physiological drought tolerance limit is simply already reached under those severe drought conditions, thus supporting the drought limitation of *Calluna*-dominated dry lowland heathland distribution (Loidi et al. 2010), or whether the ability to withstand severe drought is potentially reduced by other, external factors, such like high N depositions or the frequency of severe droughts, or other ecological stressors. This is of specific interest for young *Calluna* plants, as they are rather sensitive to drought than older plants (Meyer-Grünefeldt et al. 2015). As a consequence, young post-disturbance regeneration phases are prone to suffer from severe droughts, but are highly important for a successful heathland re-establishment after management.

The fourth chapter of this thesis focusses on the young *Calluna* plant establishment after biomass disturbances, such as mechanical managements, and asks for the influences of drought and N deposition. More specifically, I asked how young *Calluna* plants react to drought, referring to the drought conditions of the survey year 2014 and modelled their response to the most severe drought conditions that occurred in the years 2011-2020. Furthermore, I aimed to analyse whether seedlings are rather affected by drought than resprouted plants, as the latter may profit from their already developed rooting systems and are supplied by stored reserves in the post-disturbance remaining biomass. Additionally, I analysed how high N depositions potentially altered the young *Calluna* plant responses to drought, and whether high N loads increased drought susceptibility, like evident in recently published studies (Meyer-Grünefeldt et al. 2015, 2016). Thereby, I asked whether the influence of high N on drought susceptibility may differ between seedlings and resprouting plants.

Chapter 2:

Heathland plant species composition and vegetation structures reflect soil-related paths of development and site history

Schellenberg J, Bergmeier E (2020) Heathland plant species composition and vegetation structures reflect soil-related paths of development and site history. Appl Veg Sci 23: 386–405. https://doi.org/10.1111/avsc.12489

Abstract

Questions: To improve our knowledge on how environmental conditions determine the development of high-value *Calluna vulgaris* heathland habitats, we studied the floristic and structural characteristics of heathland plant communities across North Germany and how they are influenced by edaphic, climatic and management factors. We ask how heathland development is related to these factors and what are the implications for conservation management and restoration.

Location: North German Plain.

Methods: We collected 350 relevés in 18 dry *Calluna* heathland areas. Plant communities were classified using Isopam, RDA determined effects of environmental conditions. Potential pathways of development and the nature conservation status of the communities were identified on a multifactorial basis.

Results: We found nine floristically and structurally distinct heathland plant communities. Heathland vegetation showed distinct patterns along *Calluna* age development stages and environmental conditions. Soil conditions and related effects of long-term site history and recent management turned out to be the predominant factors influencing species composition and diversity, resulting in three potential heathland succession pathways. Mosaic-like communities with particularly high taxonomic diversity and conservation value occurred on early-successional inland dunes or as regeneration stage growing on nutrient-poor sandy soils without humus accumulation.

Conclusions: The study reveals fundamental differences between historically farmed heathland in the oceanic Northwest and former military training areas mainly in northeastern Germany with consequences for restoration ecology. Present nature conservation criteria turned out to be insufficient in predicting habitat quality, as lichens are frequently disregarded. Our findings highlight the need for intense soil disturbance to maintain early-stage soil conditions and a diverse *Calluna* growth phase composition, as these factors essentially determine species richness in lowland heaths.

Keywords

Calluna vulgaris, heath development, heather, heathland, heathland history, historical heathland, lowland heath, military training, phytodiversity, succession, vegetation classification, vegetation dynamics

2.1 Introduction

Dry open to semi-open dwarf-shrub heathland dominated by heather, *Calluna vulgaris* (L.) Hull (hereinafter: *Calluna*), occur in the oceanic and suboceanic, cool-temperate parts of Northwest Europe. They show a wide variety of plant assemblages along edaphic, geographical and climatic gradients (Berg 2004; Bridgewater 1981; Preising et al. 2012; Schubert 1973, 1974; Stortelder et al. 1996). With the exception of some coastal and montane habitats, they are formed and maintained by animal and human influences (Gimingham 1972; Hüppe 1993b; Webb 1986). In Germany, sheep farming with heathland burning and sod-cutting was practiced in the oceanic northwestern part of the country (Leuschner & Ellenberg 2017). Further east, grazing and litter raking was practiced, but no sod-cutting or similarly severe interference took place. The establishment of open heathlands in these northeastern regions of Germany are chiefly the result of military training activities in the 20th century (Ellwanger & Ssymank 2016; Schellenberg & Bergmeier 2014).

Within the entire Northwest of Europe merely a fraction of the formerly vast heathland areas still exist, mainly due to changes in land use (fertilisation and agricultural intensification, afforestation, abandonment, nitrogen deposition) or other adverse effects. Dry lowland heathlands considered in this study are protected biotopes in the nature conservation network of Natura 2000, assignable to the habitat type (HT) 4030 - European dry heaths and HT 2310 - Dry sand heaths with *Calluna* and *Genista* (EC 2013). In Germany, both HT are widely distributed over the northern lowlands, corresponding to two biogeographical regions (EEA 2016); the Atlantic region (A) in the North and Northwest and the Continental region (C) in the East and Southeast. Both HT have larger extensions in the eastern, 'Continental', part of the country (HT 4030 A: 165 km^2; C: 325 km^2; HT 2310 A: 10 km^2; C: 27 km^2; BfN 2019). The recent conservation status especially for HT 2310 has been assessed as being unfavourable (BfN 2019), and for the EU member states dry heath has been rated as 'vulnerable' in the European Red List of habitats (Janssen et al. 2016). The principal reasons for heathland habitat quality decline are abandonment of traditional management, insufficient or wrong management, airborne nitrogen deposition, loss of specific habitat structures and invasive non-native species (BfN 2019). At present, nature conservation management measures which attempt to imitate the effects of historical farming practices are in place in most of the remaining heathland areas.

For an assessment of nature conservation value, including habitat quality and the effectiveness of conservation efforts, the current conservation status is defined by using criteria of structural and floristic diversity (BfN 2019). Additionally, potential threats or conditions reducing habitat quality are considered. For structural diversity, *Calluna* age structures and composition of heathland-typical life form groups are used. For *Calluna* age structure, a categorical model commonly distinguishes four phases for describing patterns in heathland dynamics: Pioneer, Building, Mature, and Degeneration (Gimingham 1972; Watt 1955). Plant life form group composition is assumed to be instructive for indicating favourable (e.g. presence of lichens) or unfavourable conditions (e.g. tree invasion or grass dominances, NLWKN 2012; LfU 2014a, 2014b). In terms of floristic diversity, the heathland-typical species assemblage is defined for each HT, comprising both, typical, highly-frequent and rare species.

Using these assessment criteria, we aim to identify heathland plant communities of high nature conservation value and to derive plant-community-wise threats and development potentials. To test for habitat quality variation between potential pathways of heathland development we relate the *Calluna* growth patterning to species composition and edaphic conditions. The key processes underlying heathland development are favourable soil conditions and cyclical regeneration of heather, but a broader approach to disentangle these relationships in the European subatlantic-subcontinental region using local-scale data does not exist. However, when attempting to predict the vegetation dynamics and heather regeneration potential of historically young heathlands in the Northeast German lowland in particular, questions of transferability and long-term site development may arise.

In this study we provide a basic overview of the entire North German dry lowland heath plant communities and relate their floristic traits to edaphic, climatic and management conditions. Based on this, we attempt to disentangle complex developmental processes in heathlands, thus helping to understand successional pathways and regeneration potentials. Hence, this study may serve as a basis for conservation management decision-making and predicting heath development.

Specifically, we attempt to answer the following questions:

(1) What are the floristic and structural characteristics of dry lowland heath plant communities in Germany?

(2) How do gradients of edaphic conditions, climate, management and/or site history shape these characteristics?

(3) Do specific environmental conditions result in different pathways of heathland development?

(4) Which types of heathland vegetation are of particular nature conservation concern and what conservation management implications can be derived from the results of this study?

2.2 Methods

Study sites

We surveyed dry heathlands of the HT 4030 and HT 2310 throughout North Germany. In the federal states of Lower Saxony, Schleswig-Holstein, Mecklenburg-Western Pomerania, Brandenburg, Saxony-Anhalt and Saxony, eighteen study sites were selected located along a northwestern to southeastern gradient of decreasing oceanicity (Fig. 2.1). Field data were collected in May to August 2013.

The heathlands were not influenced by groundwater, the mean annual precipitation ranged from approximately 500 mm in the subcontinental parts of eastern Germany up to 900 mm in coastal areas in the Northwest (DWD, 2015). Oceanicity (K) was calculated based on daily weather data from the period 1980-2010 (DWD, 2015; Fig. 2.1), using an algorithm proposed by Godske (1944).

Airborne nitrogen deposition ranged between 23 kg N ha^{-1}*yr^{-1} in the Northwest and 10-11 kg N ha^{-1}*yr^{-1} in the East (UBA 2019, ESM2_1: Table S1-1). All heathlands were on sandy soils, differing in soil development and depth.

The study sites were either long-term heathlands with a traditional farming history or military training areas, abandoned or active, with or without recent management, thus reflecting the most important management types of heathlands in the North German Plain (study site details: ESM2_1). Multiple management categories, e.g. burning and subsequent grazing, were each considered separately (see Table 2.1 for a list of all management categories).

Sampling Design

At each study site randomly chosen plot locations were stratified according to recent management using QGIS (versions 2.1-2.8, 2013-2017). The total sample comprised 350 quadrates of 5 m × 5 m = 25 m^2 for measuring structural data and 4 m^2 (2 m × 2 m) in the lower left corner for recording floristic and species abundance data (vegetation relevés). The sample plot size for floristic data was consensual for sampling vascular plants and cryptogams (Dierschke 1994; Chytrý & Otýpkova 2003). All species of vascular plants and epigeal bryophytes and lichens were recorded; lichens, if not identified on-site, were collected for identification using chemical properties. Cover values of each species were assessed using the 7-level Braun-Blanquet scale (Dierschke 1994; Nomenclature for vascular plants: Buttler et al. 2018, Bryophytes: Caspari et al. 2018, Lichens: Wirth et al. 2011).

Table 2.1 Environmental variables and their attributes used to relate species composition to site history, recent management and soil conditions.

Variable	**Attribute/levels**	**Characteristics, effects**
Site history (past and present land use)		
	Active military training	Long-term and frequent disturbances of varying spatial scale and intensity, with or without characteristics of historical farming. Distributed throughout North Germany.
	Former military training	Long-term and frequent disturbances of varying spatial scale and intensity in the recent past now abandoned and often advanced in succession, without characteristics of historical farming. Distributed mainly in the eastern part of the North German Plain.
	Historical-farming heathland	Characterized by long-term historical farming; with or without temporary military use in the more distant past. Distributed mainly in Northwest Germany.
Recent management (incidents in the past five years)		
Intensive managements	Burning	Intensive management: prescribed or accidental; (almost) complete destruction of aboveground plant material, ash deposition; of varying intensity.
	Mowing	Intensive management: plants cut in 5-10cm height, often with soil surface disturbances and removal of mowed plants and litter.
	Sod cutting	Intensive management: removal of humus and uppermost mineral soil, together with aboveground plant parts, only a few rootstocks may survive; of highest intensity.
	none	No intense management such as burning, mowing or sod cutting in the past five years; former incidents likely especially in active military training areas and historical-farming heathlands.
Grazing	Deer grazing	Browsing mainly by red deer and fallow deer, not enclosed, year-round; of varying impact on phytomass and soil
	Horse and cattle grazing	Grazing mainly non-intensive by Konik horses and Heck cattle in spacious enclosures, year-round; of varying but overall moderate impact on phytomass and soil, with small-scale disturbance
	no grazing	No grazing impact become known or observed but non-intensive deer grazing cannot be ruled out
	sheep enclosure	Intense sheep grazing over periods of varying length and with variable sheep density in temporarily fenced sites; overall high-intensity browsing and trampling
	sheep herded	Traditional sheep herding, not enclosed; high spatial heterogeneity in browsing and trampling.
	sheep pen	Daily concentration of herded sheep and trails; very high browsing and trampling intensity.
Edaphic conditions		
Humus layer	layer thickness [cm]	thickness of accumulated undecomposed or partly decomposed humus above, not permeated in the mineral topsoil.
Soil organic matter	rich (1) / poor (0)	Organic matter content of upper 10 cm topsoil assessed visually as rich (1) or poor (0, comparable to pure sand)
Soil texture	Loamy sand (1) / pure sand (0)	Sands with marked fraction of clay or silt, often humus-rich, or pure sands.
Airborne nitrogen deposition	kg/ha^{-1}*a^{-1}	Data from UBA (2019)
Climatic conditions		
Oceanicity	Kotilainen´s Index for Oceanicity	Calculated after Godske (1944).
Calluna age structures	%	Cover of plants in the 4 growth phases P – Pioneer, B – Building, M-Mature and D-Degeneration

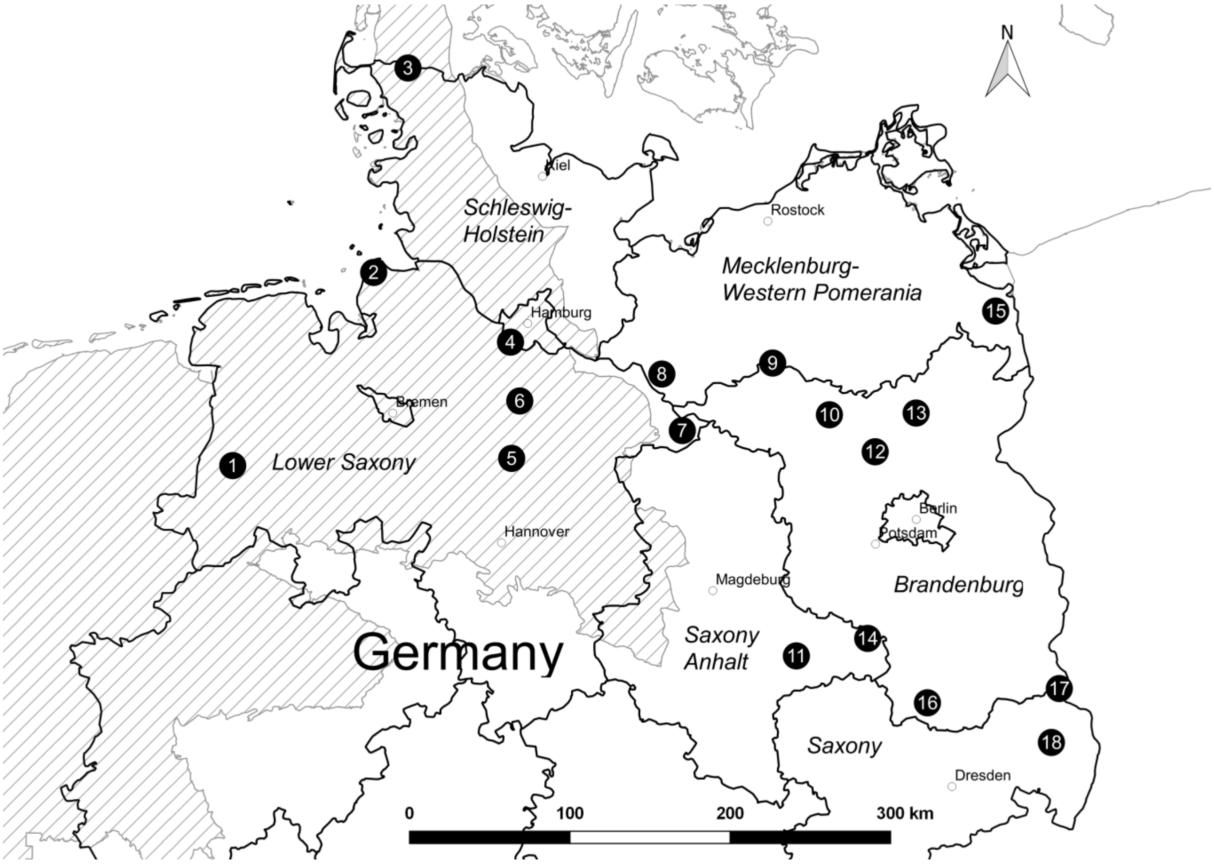


Fig. 2.1 Study areas 1-18 (black dots) in northern Germany, in the legend with full names, sample size (n) and oceanicity K - Kotilainen's Index of Oceanicity (Godske 1944). Biogeographic regions (EEA 2016): Atlantic, grey hatched; Continental, white. Slightly different K values within study area 13 refer to 'Kleine Schorfheide' and 'Vietmannsdorfer Heide', 8 km away. For details on study areas see ESM2_1.

Administrative boundaries © Bundesamt für Kartographie und Geodäsie, Frankfurt 2011.

	Study area	**n**	***K***
1	Tinner Dose	**11**	71.4
2	Cuxhavener Küstenheiden	**10**	79.2
3	Süderlügumer Binnendünen	**5**	84.6
4	Fischbeker Heide	**11**	68.7
5	NATO training area Bergen-Hohne	**60**	56.7
6	Lüneburger Heide	**89**	68.6
7	Nemitzer Heide	**11**	45.2
8	Leussower Heide	**15**	51.6
9	Marienfließ	**10**	51.7
10	Kyritz-Ruppiner Heide	**20**	41.4
11	Oranienbaumer Heide	**10**	39.9
12	Rüthnicker Heide	**10**	40.9
13	a) Kleine Schorfheide / b) Vietmannsdorfer Heide	**20**	43.1/ 45.0
14	Glücksburger Heide	**14**	40.1
15	Bundeswehr training area Jägerbrück	**20**	45.7
16	Prösa	**12**	41.9
17	Zschornoer Wald	**12**	42.5
18	Daubaner Wald	**10**	45.0

Structural diversity was measured as the cover of six life-form groups (trees, heather, graminoids, non-graminoid herbs, bryophytes, lichens) as well as bare sand per 25 m^2 plot. The tree cover was assessed on a 100 m radius around the plot's initial GPS coordinate in order to assess the structural context of the plot.

Age structures of heather were evaluated by noting the life history stage covers of *Calluna*, with designing plants to one of the four growth phases (Watt 1955; Gimingham 1972):

(1) Pioneer phase is defined as the timespan between germination and switching from monopodial to sympodial growth of the heather plant,

(2) Building phase comprises the ageing of the plant up to maximum size and vitality,

(3) Mature phase is the optimal to slightly degenerating status with continuing growth, but ageing in the central plant parts, stems beginning to prostrate and start adventitious (cauline) rooting, until in the

(4) Degeneration phase only adventitiously rooted stems are still alive, the plant is generally of decreasing vitality and eventually dies.

For the designation of a plant to one of these four growth phases, we used visual attributes such as growth form (monopodial or sympodial growth), habit (proportion of (sub)erect branches and adventitious roots, total plant height and width) as well as vitality (flowering intensity, leafless branches).

Humus layer thickness and soil texture were determined by finger test and by visual inspection at 3-4 random points per 25 m^2 plot.

Statistical analysis

For classification, Braun-Blanquet species cover values were translated to cover percentages (r = 0.01%, + = 0.5%, 1 = 3%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%) and the latter arcsine transformed. Rare species in the dataset (fewer than 3 occurrences) were excluded prior to classification to reduce noise.

Among several classification methods tested (Kmeans, TWINSPAN, PAM), the results of a non-hierarchical Isopam were the most clearly interpretable (Schmidtlein et al. 2010). In our empirical classification approach, floristic-based results of 6- to 9-group non-hierarchical Isopam were compared in terms of their validity in representing structural differences between plant communities. Partial Isopam was performed to test further group separation to improve floristic and/or structural distinctness.

For validation on floristic level, silhouette plots (Rousseeuw 1987) were used for numerical clustering goodness measurement. Fidelity and differential taxa were used to interpret the compositional pattern in synoptic tables. Differential taxa were calculated by implementing the algorithm of Tsiripidis et al. (2009) to a function into R (package 'goeveg', Goral &

Schellenberg 2019). The fidelity measure phi (Φ) after Sokal & Rohlf (1995) was implemented in 'goeveg' to calculate species fidelity per cluster.

For validation of significant structural differences between Isopam clusters, cover of *Calluna*, life form groups and open soil were compared cluster-wise using non-parametric multiple Mann-Whitney U tests with Bonferroni correction for different sample sizes.

Redundancy Analysis (RDA) was used to determine effects of site history, recent management, climate, *Calluna* age structure and edaphic conditions on plant composition. To this effect, a subset of only diagnostic species with a minimum percentage frequency of 20% in the synoptic table and without *Calluna* was used. The final model for best explaining environmental influences on species composition was selected by 'ordistep' function, starting from null model with multiple forward/backward selections (Oksanen et al. 2019). Tested numerical constraints were scaled with the scale()-function in R in advance of RDA model selection. The final model was checked for variance inflation to detect collinearity of included predictors. Significant influences of the final model predictors were tested with a post-hoc ANOVA with 999 permutations.

Gross and net effects of environmental variables were calculated by using partial RDA (pRDA). Gross effects were assessed by setting up models for each single predictor, without considering any covariables. For detecting net effects, a single predictor was tested with all other final model predictors included as covariables to partial out their effects.

As the study sites as such had a considerable influence on species composition, likely to suppress measureable effects of history, climate and other site-related factors, two final models were set up; one with site as conditional term (RDA+s), the other without it (RDA-s). Site-specific pseudoreplication effects bias was judged by quantifying remaining area-specific parts of explained variance in net area model, where all predictors of the final model were used as covariables.

For assessing plant species richness, species alpha-diversity (total species richness per 4 m^2 plot) was calculated. Threatened species occurrences per life form group were counted based on the most recent national red lists (vascular plants: Metzing et al. 2018; bryophytes: Caspari et al. 2018; lichens: Wirth et al. 2011; ESM2_4: Table S4-1 includes a list of all red list species).

For the purpose of rating the plant communities with respect to their nature conservation value, they were assessed in their heathland-typical species composition as well as their typical structures and threats, according to the criteria for nature conservation assessment of European dry heaths (HT 4030) and Dry sand heaths (HT 2310) (NLWKN 2012; LfU 2014a, 2014b). The criteria given in the national mapping instructions were extrapolated for application at the community scale (see definition of modified criteria ESM2_4: Table S4-2).

Following the mapping instructions, the rating categories range between A – favourable, B – unfavourable and C – unfavourable-bad.

Statistical analyses and plots were performed in statistical software R (R Core Team, www.rproject.org Version 3.4.1). We used the packages 'isopam' (Schmidtlein 2014) for Isopam clustering, 'cluster' (Maechler et al. 2018) for calculating silhouette widths, 'goeveg' (Goral & Schellenberg 2019) for creating synoptic Tables, calculating diagnostic species and fidelity Φ, and 'vegan' (Oksanen et al. 2019) for calculating RDA, pRDA and ordination plots.

2.3 Results

Main characteristics of North German dry heathland plant communities

The classification revealed nine floristically and structurally distinct heathland plant communities (Table 2.2, Fig. 2.2). The identified communities belong to the Genisto pilosae-Callunetum Braun 1915 (syn. Genisto anglicae-Callunetum Tüxen 1937), represented by communities 1-6 and 8-9, and the Euphorbio cyparissiae-Callunetum vulgaris Schubert 1960, approached by community 7. The main floristic differences are roughly related to vascular-plant richness (units 1,4,7), lichen richness (units 2,4,5) or generally species poverty (3,6,8,9). For phytosociological and floristic detail, complete synoptic tables and fidelity values see ESM2_2.

The nine communities were grouped into three heathland development stages, according to their dominant *Calluna* growth phase:
1) early-stage regeneration, from Pioneer to early Mature stage (3 communities);
2) Late Building up to Mature stage (4 communities); and
3) Late Mature up to Degeneration stage (2 communities).
Additionally, the communities showed distinct patterning in two types of *Calluna* cover characteristics (stand mosaic structure vs. *Calluna* dominance). Generally, mosaic communities (1, 4, 6, 7, 9) showed lower *Calluna* cover, but high cover of vascular non-ericoid plants, whereas *Calluna* dominance stands (2, 3, 5, 8) have simple stand structure with dense *Calluna* canopy and an understory of cryptogam mats (Fig. 2.3). Hence, vascular plant diversity was clearly related to mosaic structure (communities 1, 4, 7), whereas lichen diversity was potentially high in *Calluna* dominance stands as well (community 5, Fig. 2.3, ESM2_4: Fig. S4-1).

Factors shaping species composition and structures

The RDA revealed that species composition was explained best by humus layer thickness and cover of mature heather, irrespective of whether site effects have been included (RDA+s) or not (RDA-s), Table 2.3). These two factors, along with related environmental conditions, span two of the three main gradients shaping compositional patterns in the ordination diagram (Fig. 2.2).

The first gradient describes the shift of edaphic soil conditions along a successional gradient, expressed by decreasing bare sand and increasing humus layer thickness along the first axis (Fig. 2.2a). Floristic diversity, as well as cover of herbs and lichens was related to open stands of early successional stage (Fig. 2.2c), more specifically in communities with early-successional edaphic conditions rather than in communities with early-stage regeneration of heather (Fig. 2.2d).

The second gradient was characterized by a change of structural components along the second axis, explaining 4.8% of variance. Open, grass-rich stands differ clearly from those dominated by *Calluna*, reflecting the structural attributes of *Calluna* cover characteristics reported above.

Calluna age structure explained 3.5% (RDA+s) or 3.8% (RDA-s) of diagnostic species composition, with the major share explained by cover of mature heather plants (Table 2.3). It was only marginally reduced when including site effects, thus validating its general effect on heathland species composition.

Calluna age structures and their changes along the gradient could be related to recent and historical management, because disturbances directly affect heather growth. Recent management explained 7.1% of total species composition variance (RDA-s), with highest explanation power of grazing regimes (2.8%, $p \leq 0.01$), while intensive management (2.1%, $p \leq 0.001$) and site history (1.1%, $p \leq 0.001$) showed weaker explanatory power.

Cryptogam-rich regeneration (community 2) often occurred after burning, whereas the vascular-plant rich or species-poor regeneration stages (communities 1 and 3) developed more frequently after mowing (ESM2_3). The high vascular plant diversity of community 7 was strongly related to horse- and cattle-grazing, the other plant assemblages showed a rather weak pattern concerning grazing regimes (ESM2_3).

Table 2.2 Synoptic table of heathland plant communities in the North German Plain. Species with a minimum frequency of 20% and a diagnostic character in one of the identified plant groups are listed. Frequencies highlighted in grey refer to positively differentiating species. Frequency values ≥ 25% are in bold type. Asterisks are indicating diagnostic fidelity values (Φ > 0.3). Life form groups: *s* – shrubs and dwarf shrubs, *h* – non-graminoid herbs, *g* – graminoids, *m* – bryophytes, *l* – lichens, *t* – trees. Silhouette width s(i) is a measure of Isopam clustering validity, with values ranging from 0 (low structure) to 1 (optimum clustering structure). Not included species of high frequency, but low diagnostic value: *Calluna vulgaris, Carex pilulifera, Deschampsia flexuosa, Rumex acetosella, Hypnum cupressiforme, Pinus sylvestris, Brachythecium rutabulum*. A table of all species and fidelity values is presented in ESM2_2. Table continues on the next page.

		I Early-stage regeneration heathland			**II Late Building and Mature stage**				**III Late Mature and Degeneration stage**	
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
association		**Genisto pilosae-Callunetum typicum,** vascular plant-rich regeneration stage	**Genisto pilosae-Callunetum cladonietosum,** cryptogam-rich regeneration stage	**Genisto pilosae-Callunetum typicum,** species-poor regeneration stage	**Genisto pilosae-Callunetum cladonietosum,** *Corynephorus* variant, cryptogram-rich open sand grass-heathland	**Genisto pilosae-Callunetum cladonietosum,** Mature-stage cryptogam-rich open sand heathland	**Genisto pilosae-Callunetum danthonietosum,** consolidated dry sand heath	**Euphorbio cyparissiae-Callu-netum vulgaris,** subcontinental dry grass-heathland on base-containing ground	**Genisto pilosae-Callunetum typicum,** moss-rich degeneration stage	**Genisto pilosae-Callunetum typicum,** *Deschampsia flexuosa*- and moss-rich degeneration stage
Sample size		*41*	*21*	*32*	*40*	*53*	*23*	*8*	*55*	*77*
s(i)		*0.02*	*0.03*	*0.05*	*0.07*	*0.08*	*0.06*	*0.14*	*0.11*	*0.11*
	Life form group									
I Early stage regeneration heathland										
Placynthiella oligotropha	*l*	7	**38***	9	5	13	0	0	2	1
Betula pendula	*t*	7	**24**	12	2	4	9	12	15	4
Molinia caerulea	*g*	**37**	**52**	**34**	0	6	**22**	0	16	**23**
Cladonia pyxidata	*l*	**32**	**48**	**22**	**35**	**55**	**22**	12	5	5
Cladonia macilenta ssp. macilenta	*l*	10	**29**	9	**22**	**21**	0	0	4	3
Campylopus introflexus	*m*	12	**38**	16	0	**21**	0	0	5	8
Ceratodon purpureus	*m*	**41**	**86***	3	**30**	17	17	**25**	7	4
Placynthiella icmalea	*l*	**41**	**62**	**34**	**28**	**30**	13	0	0	0
Cephaloziella divaricata	*m*	**32**	**57**	**41**	**60**	**74***	0	**25**	9	5
Cladonia coccifera	*l*	**27**	14	**22**	**68***	**45**	4	0	5	4
Corynephorus canescens	*g*	**24**	0	0	**58***	4	**35**	12	0	1
Festuca filiformis	*g*	**29**	**38**	3	5	4	**52**	0	9	8
Hypochaeris radicata	*h*	**32**	5	0	**25**	2	**70***	12	2	4
Nardus stricta	*g*	20	0	6	2	4	**22**	0	9	17
Hieracium pilosella	*h*	**41**	19	0	**32**	8	**91***	**75**	5	1
Agrostis capillaris	*g*	**59**	5	3	**35**	9	**74***	**75**	9	14
Agrostis vinealis	*g*	**29**	5	0	**22**	4	**22**	**62**	4	9
Polytrichum piliferum	*m*	**71**	**43**	**31**	**98***	**57**	**70**	12	7	3
II Mature-stage										
Open sand grassland group										
Spergula morisonii	*h*	12	0	0	**50***	9	4	0	5	1
Cladonia furcata	*l*	7	0	0	**28**	19	13	0	5	5
Trapeliopsis granulosa	*l*	5	19	6	**28***	6	0	0	0	0
Cetraria aculeata	*l*	0	5	0	**25***	9	0	0	0	1
Cladonia pleurota	*l*	2	0	3	20	11	0	0	0	0
Cladonia uncialis	*l*	5	0	0	20	11	4	0	4	4
Cladonia subulata et rei	*l*	**39**	**52**	19	**92***	**87***	**39**	**25**	18	12
Cladonia ramulosa	*l*	20	10	6	**48**	**49***	0	0	4	5
Cladonia cervicornis s.l.	*l*	5	10	9	**35**	**28**	0	0	2	3
Cladonia gracilis	*l*	2	5	3	**30**	**28**	0	0	2	3
Pohlia nutans	*m*	5	**29**	19	**32**	**45***	4	12	7	4
Cladonia fimbriata	*l*	10	**24**	9	**35**	**64***	17	**38**	**24**	16
Cladonia portentosa	*l*	2	14	3	12	**32**	0	0	11	9
Cladonia coniocraea	*l*	2	5	3	10	**23**	0	0	11	3
Dicranum polysetum	*m*	2	0	3	8	**23**	0	0	11	9

Continued on next page

Table continued from previous page

		I Early-stage regeneration heathland			**II Late Building and Mature stage**				**III Late Mature and Degeneration stage**	
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
	association	**Genisto pilosae-Callunetum typicum,** vascular plant-rich regeneration stage	**Genisto pilosae-Callunetum cladonietosum,** cryptogam-rich regeneration stage	**Genisto pilosae-Callunetum typicum,** species-poor regeneration stage	**Genisto pilosae-Callunetum cladonietosum,** *Corynephorus* variant, cryptogam-rich open sand grass-heathland	**Genisto pilosae-Callunetum cladonietosum,** Mature-stage cryptogam-rich open sand heathland	**Genisto pilosae-Callunetum danthonietosum,** consolidated dry sand heath	**Euphorbio cyparissiae-Callunetum vulgaris,** subcontinental dry grass-heathland on base-containing ground	**Genisto pilosae-Callunetum typicum,** moss-rich degeneration stage	**Genisto pilosae-Callunetum typicum,** *Deschampsia flexuosa*- and moss-rich degeneration stage
	Sample size	*41*	*21*	*32*	*40*	*53*	*23*	*8*	*55*	*77*
	s(i)	*0.02*	*0.03*	*0.05*	*0.07*	*0.08*	*0.06*	*0.14*	*0.11*	*0.11*
	Life form group									
Dense grass-heathland plant group										
Carex arenaria	*g*	12	0	6	15	4	**22**	12	4	3
Festuca ovina	*g*	15	0	3	**42**	17	**30**	**62**	9	17
Hypericum perforatum	*h*	12	10	0	8	2	**35**	**75***	4	1
Danthonia decumbens	*g*	2	5	0	8	0	13	**88***	5	1
Genista tinctoria	*s*	0	0	0	0	0	0	**62***	0	0
Luzula campestris	*g*	5	0	3	5	6	**30**	**50**	9	9
Potentilla argentea	*h*	0	0	0	0	0	4	**50***	0	0
Koeleria macrantha	*g*	4	0	0	0	0	0	**38***	0	0
Polygala vulgaris	*h*	0	0	0	0	0	0	**38***	0	0
Campanula rotundifolia	*h*	0	0	0	0	0	0	**25***	0	0
Thymus serpyllum	*s*	0	0	0	2	0	0	**25***	0	0
Subcontinental grass-heathlands on base-containing sands										
Calamagrostis epigejos	*h*	17	0	0	10	6	0	**100***	11	10
Galium verum	*h*	0	0	0	0	0	0	**50***	0	0
Helichrysum arenarium	*h*	2	0	0	0	0	4	**50***	0	0
Leucanthemum ircutianum	*h*	0	0	0	0	0	0	**50***	0	0
Plantago lanceolata	*h*	2	5	0	0	0	13	**50***	0	1
Euphorbia cyparissias	*h*	0	0	0	0	0	4	**38***	0	1
Viola riviniana	*h*	0	0	0	0	0	0	**38***	0	3
Achillea millefolium	*h*	2	0	0	0	0	9	**25**	2	0
Anthoxanthum odoratum	*g*	0	0	0	0	2	4	**25**	0	3
Centaurea jacea	*h*	0	0	0	0	0	4	**25***	0	0
Centaurium erythraea	*h*	0	0	0	0	0	0	**25***	0	0
Dianthus deltoides	*h*	2	0	0	0	0	0	**25***	0	0
Disturbed sites										
Populus tremula	*t*	2	0	3	2	4	0	**38**	5	4
Tanacetum vulgare	*h*	0	0	0	0	0	9	**38***	0	0
Taraxacum sec. Ruderalia	*h*	0	0	0	0	0	0	**25***	2	0
III Mature and late mature-stage plants										
Hypnum jutlandicum	*m*	**22**	10	**25**	**60**	**89**	17	12	**93***	**73**
Dicranum scoparium	*m*	15	19	12	**35**	**55**	0	0	**29**	**57**
Pleurozium schreberi	*m*	2	0	6	**22**	**51**	4	0	**51**	**71***
Galium saxatile	*h*	15	0	0	0	2	13	0	4	**32***

Table 2.3 Gross and net effects of environmental factors on species composition (% of explained variance). Gross effects given for all tested constraints, but net effects only calculated for those included in the final model. Final models given for the version with including site effects, were site was included as covariable (conditional term and for the model version without considering site effects (RDA without site). Net effects were calculated using one predictor of the final model and the others as covariables. Asterisks show effect significances in the net model (*** p<0.001).

		RDA with site as covariable			**RDA without site**		
			final model			**final model**	
	constraint explained variance [%]		10.4***			19.7***	
	unconstrained variance [%]		74.0			80.3	
	tested potential constraints	**gross effects**	**net explained variance**	**pooled net variance**	**gross effects**	**net explained variance**	**pooled net variance**
	study site	15.7	12.7	12.7	15.7	8.2	8.2
climatic/ edaphic factors	**Oceanicity [K]**	0.0	-	3.7	2.2	-	5.3
	Nitrogen deposition	0.0	-		2.0	0.8***	
	humus-rich soils	1.1	-		2.0	0.4*	
	pure sands	0.7	-		1.7	-	
	mineral-rich soil	0.3	0.4*		0.8	0.6***	
	humus layer thickness	4.1	3.4***		5.0	2.4***	
land use/ management	**site history**	0.0	-	1.6	4.0	1.1***	7.1
	grazing	2.2	-		4.6	2.8**	
	intense management	2.5	1.6***		3.5	2.1***	
Calluna age structures	**cover of Pioneer *Calluna* plants [%]**	0.8	-	3.5	0.9	-	3.8
	cover of Building *Calluna* plants [%]	1.0	1.3***		0.9	1.4***	
	cover of Mature *Calluna* plants [%]	2.2	2.8***		2.1	3.1***	
	cover of Degeneration *Calluna* plants [%]	0.4	0.5**		0.4	0.5*	

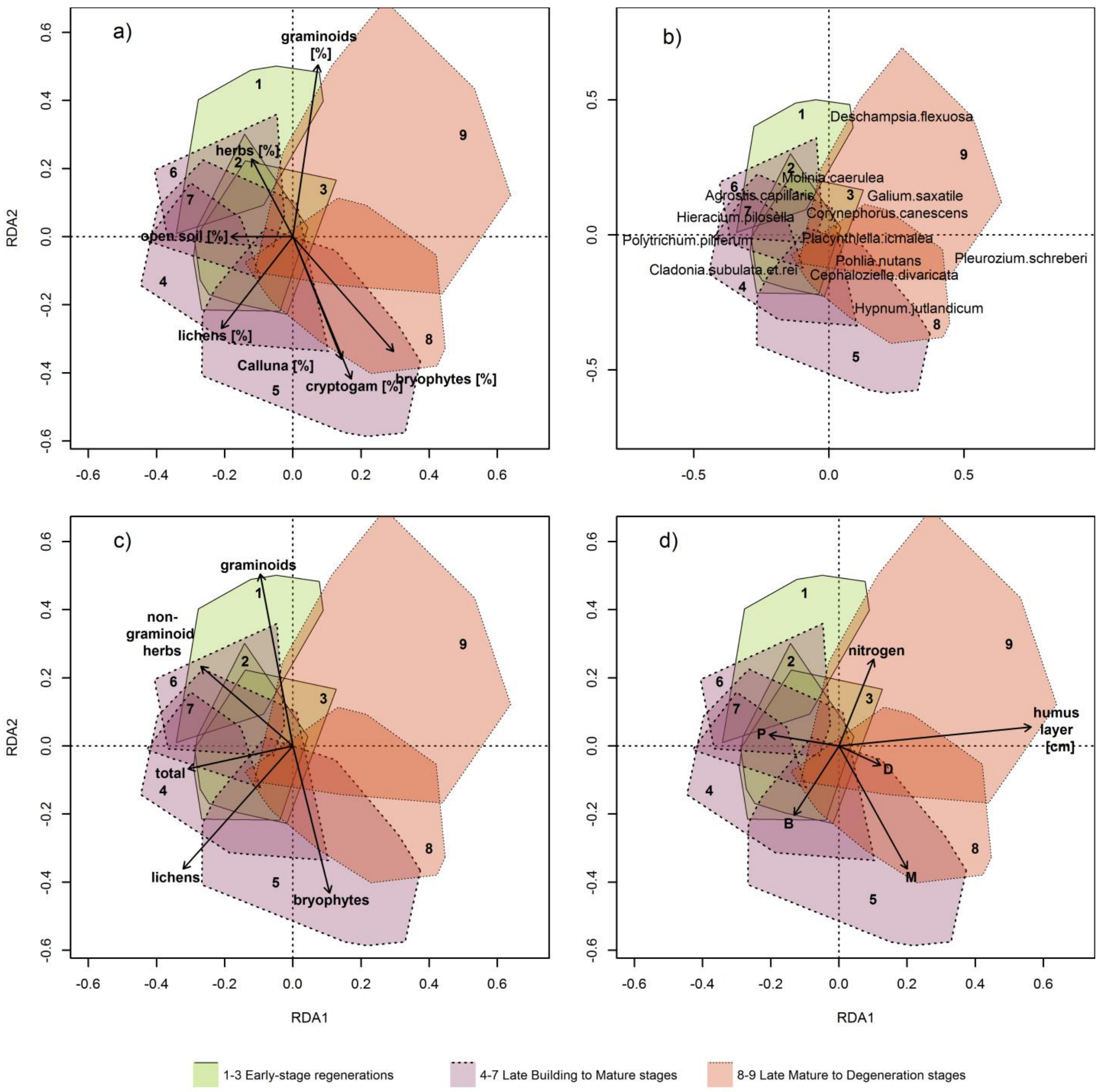


Fig. 2.2 Redundancy Analysis (RDA) of species composition, with envelopes around samples (plots) representing groups of identified plant communities. RDA without site (RDA − s) used for creating ordination diagrams. RDA axis 1 explained 7% of total variance, RDA axis 2 explained 4.8%. The nine plant communities differ in aspects of vegetation structure (a), species composition (b), species richness (species/[4 m2]; c), and the linear constraints identified in RDA − s for explaining species composition differences (d). Constraints were age structure of heather (% of cover; P, Pioneer; B, Building; M, Mature; and D, Degeneration, explaining all together 3.8%), airborne nitrogen deposition (0.8% exp. variance) and humus accumulation (2.4%). For species composition (b), only the 10% of the species fitting best to the RDA ordination and the 70% most abundant species were displayed using the ordiselect()-function in R (Goral and Schellenberg, 2019). Three main gradients shaping heathland species composition were identified: (1) along the first axis: shift of edaphic soil conditions along a successional gradient, with early stages at the left and later ones on the right part of the diagram; (2) along the second axis: structural gradient with open, grass-rich stand in the upper part of the diagram and dominance, but bryophyte- and lichen-rich stands at the bottom; (3) climate and airborne nitrogen deposition, with sub Atlantic/subcontinental sites with low nitrogen deposition at the lower left quadrant of the diagram and higher nitrogen loads and Atlantic-subatlantic sites in the upper right quadrant.

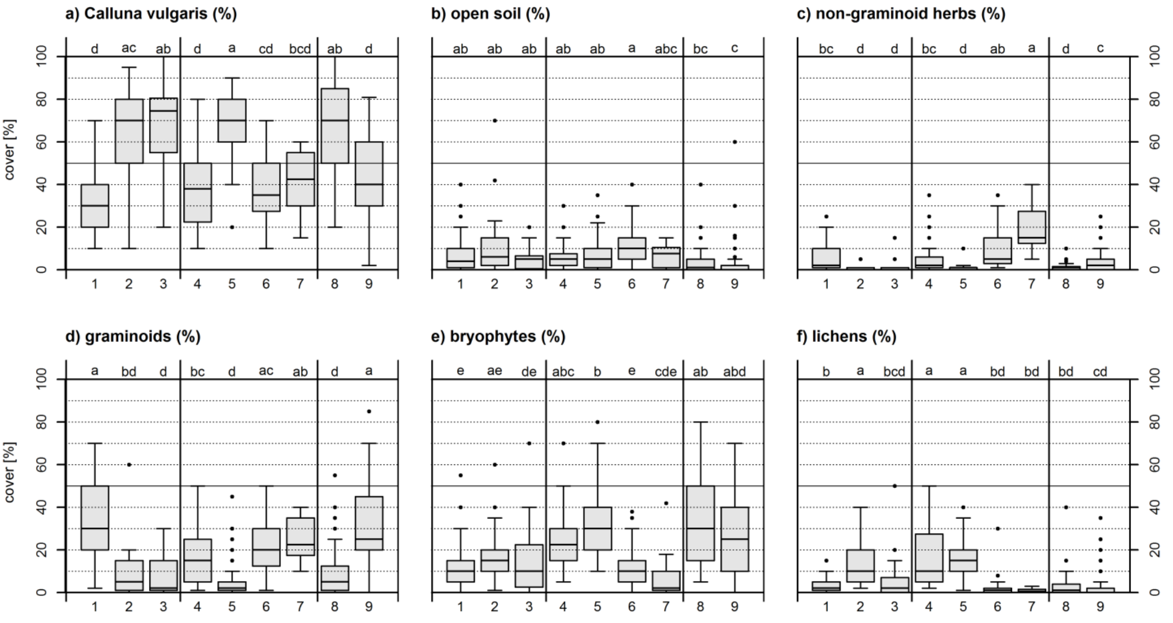


Fig. 2.3 Heathland plant community cover proportions (%) of a) *Calluna vulgaris*, b) open soil, c) non-graminoid herbs, d) graminoids, e) bryophytes and f) lichens. 1-3 Early-stage regeneration heathlands; 4-7 Late Building to Mature stages; 8-9 Late Mature and Degeneration stages. For names of plant communities 1-9 see Table 2.2. Single letters at the boxplot top are indicating significant group differences (<0.05).

The third gradient is encoded in the strongly coupled factors of climate, nitrogen deposition and site history. Former military training areas included in our study are distributed in the subatlantic-subcontinental eastern and southeastern part of the German Lowland, showing rather low oceanicity, with lower airborne nitrogen loads (Fig. 2.2d, ESM2_1: Table S1-1, ESM2_3). Communities there provide potentially higher lichen cover and diversity, the cryptogam-rich bare sand grass-heathland (community 4) is strongly restricted to those conditions.

In contrast, the grass-rich communities 1 and 9 are old traditional heathlands or active military training sites of the Atlantic biogeographic region, exposed to higher nitrogen loads.

Site effects caused a strong patterning, overlaying effects of management, climate and edaphic conditions (cf. explanatory power of predictors RDA+s vs. RDA-s, Table 2.3). Management effect was strongly reduced by including site effects in the model as covariates (1.6% in RDA+s vs. 7.1% in RDA-s, Table 2.3). A weaker reduction was found for climatic and edaphic conditions (3.7% in RDA+s vs. 5.3% in RDA-s). This indicates site-specific management and climate inseparable from general site effects and may involve pseudocorrelation issues. To reduce this uncertainty, we calculated the remaining net explained variance by area when the explanatory power of final model constraints was factored out. We interpreted this as the component of site effects not explainable by the factors included in the model but by pseudocorrelation. With 12.7% of explained net variance in RDA+s and 8.2% in RDA-s, effects of site-specific species pools and composition appeared to be strong.

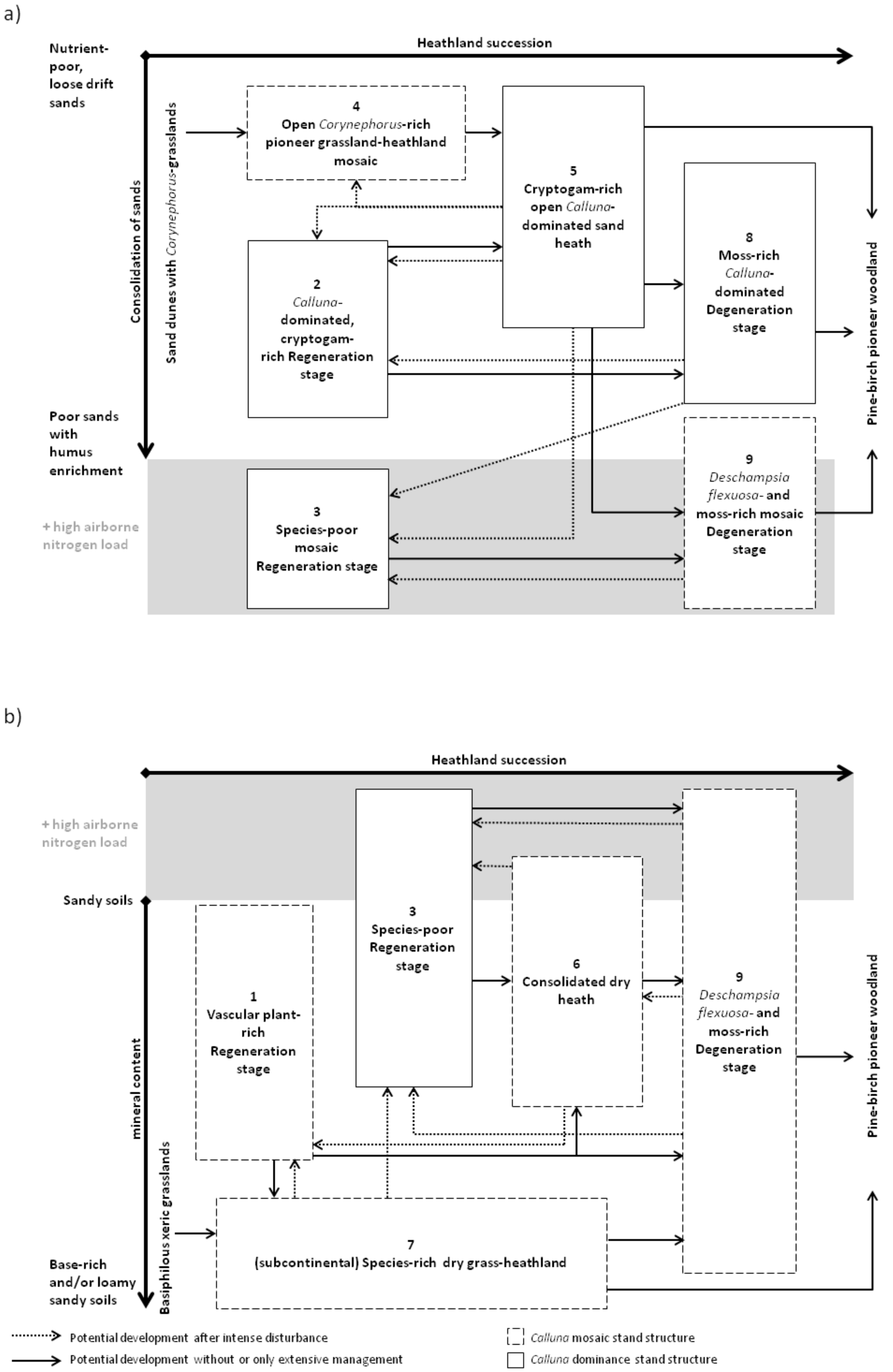
Pathways of heathland development

The interplay of the RDA gradients interpretation of the conditions shaping community-specific plant assemblages allowed for an identification of two edaphically driven successional pathways, each with specific plant communities involved and characteristic plant species turnover (Fig. 2.4):

(1) Psammophilous heathland pathway: Initial Corynephorion pioneer grassland is invaded by *Calluna*, forming an open sand grassland-heathland mosaic (community 4). With increasing heather cover and soil development, two-layered stands of tall Mature-phase dominant heather plants with regrowth in the understory and a highly diverse cryptogam layer develops (community 5, cryptogam-rich bare sand heath). Cryptogam synusial assemblages show clear successional turnover, with an early-stage species group indicating exposed sand dune conditions (e.g. *Cladonia furcata, Trapeliopsis granulosa, Cetraria aculeata*), followed by assemblages of humus- (or wood-)dwelling lichens demanding relatively high humidity, such as *Cladonia fimbriata, C. coniocraea* and *C. portentosa*. Intense management leads to cryptogam-rich regeneration stages (community 2). With lack of management, they develop towards moss-rich degeneration stage (community 8) or to moss-rich heath-woodlands.

This pathway is linked to very poor sandy soils and to former military training areas, where frequency and intensity of soil disturbances used to be very high in the past, but are now absent for at least 5 years. Due to the fact that military training sites occurred mainly in the eastern part of Germany, this pathway is also linked to rather low oceanicity.

Under conditions of high airborne nitrogen deposition, a cryptogam-poor regeneration stage (community 3) or grass- and moss-rich degeneration stages (community 9) may occur.


a)
Heathland succession
Nutrient-poor, loose drift sands
Poor sands with humus enrichment
+ high airborne nitrogen load
Consolidation of sands
Sand dunes with *Corynephorus*-grasslands
4 Open *Corynephorus*-rich pioneer grassland-heathland mosaic
5 Cryptogam-rich open *Calluna*-dominated sand heath
2 *Calluna*-dominated, cryptogam-rich Regeneration stage
8 Moss-rich *Calluna*-dominated Degeneration stage
3 Species-poor mosaic Regeneration stage
9 *Deschampsia flexuosa*- and moss-rich mosaic Degeneration stage
Pine-birch pioneer woodland
b)
Heathland succession
+ high airborne nitrogen load
Sandy soils
mineral content
Basiphilous xeric grasslands
Base-rich and/or loamy sandy soils
3 Species-poor Regeneration stage
1 Vascular plant-rich Regeneration stage
6 Consolidated dry heath
9 *Deschampsia flexuosa*- and moss-rich Degeneration stage
7 (subcontinental) Species-rich dry grass-heathland
Pine-birch pioneer woodland
Potential development after intense disturbance
Potential development without or only extensive management
Calluna mosaic stand structure
Calluna dominance stand structure

<< Fig. 2.4 Succession schemes of German dry lowland heathlands, (a) Psammophilous heathland pathway (ht 2310 – Dry sand heaths with Calluna and Genista) and (b) Consolidated heathland pathway (ht 4030 - European dry heath). Potential pathways in heathland succession were determined by edaphic conditions and related site history and climate. Numbers of units refer to plant communities in Table 2.2. Potential development under high airborne nitrogen load (approx. >15kg N/ha-1*a-1) is shaded in grey.

(2) Consolidated sand pathway: This heathland succession pathway was found on acidic, more or less nutrient-poor sands which are more fine-grained, humus-rich and consolidated than in the preceding pathway. The typical form, involving communities 1, 3, 6 and 9, results in fairly species-poor heathlands of varying structure, but often with *Calluna* dominance; regeneration stages of the Genisto-Callunetum typicum (community 3) generally had less than 10 species per 4 m^2. Further succession leads to species-poor variants of the Genisto-Callunetum danthonietosum with high *Calluna* cover (community 6), but also directly towards a moss-rich degeneration stage (community 9), without a species-rich mature stage. Although generally poor in species, the communities along this successional pathway represent heathlands with a typical vascular plant composition but rather low structural diversity.

A base-rich subtype in Young Drift landscapes in subcontinental eastern Germany is characteristic of slightly more favourable sandy soils with considerable humus and base content where heaths rich in vascular plants and generally low cryptogam diversity develop. Within stands containing a mosaic structure, suitable management often leads to species-rich regeneration stages with high structural diversity (community 1). Mature stages with these conditions were restricted to only one site in our study (community 7, Oranienbaumer Heide), where the Euphorbio cyparissiae-Callunetum vulgaris represents a local grass-heathland mosaic.

High nitrogen deposition rates may favour grass-rich subtypes, thus explaining grass-dominated species-poor regeneration (community 3) or degeneration stages (community 9).

Conservation value of heathland plant communities

The nature conservation status of plant communities varied widely, ranging from a quite good (A-B) to an unfavourable status (B-C, Table 2.4). Specifically, when applying heathland-typical structures as criterion mosaic communities (1, 2, 4) provided a higher potential value for favourable conservation status than dominance stands (communities 3 and 5). Degeneration stages, if prevailing, generally had low potential for favourable structural conditions.

In terms of the second criterion of ‘heathland-typical species composition’, vascular-plant-rich mosaic communities of early regeneration to mature stage qualified for grade A.

Although generally rich in threatened lichen taxa, cryptogam-rich communities often achieved only a grade B due to the fact that these communities were often deficient in vascular plant composition.

We found 191 species in total, with 57 of them nationally red-listed. The majority of red-listed species were lichens or non-graminoid herbs (see ESM2_4 for more details). The majority of red-list bryophytes and vascular plants were category V, corresponding approximately to IUCN category 'Near Threatened', whereas most of the lichens were listed as 'Vulnerable', 'Endangered' or even 'Critically Endangered'.

Applying the third conservation value criterion, 'threats such as unfavourable grass dominances, tree or neophytes/ruderals invasions', generally resulted in low quality assessment, but some communities appeared to be more vulnerable than others. The regeneration stage rich in vascular plants (community 1) was found to be subjected to a high risk of grass encroachment by *Molinia caerulea* or *Deschampsia flexuosa*. However, mature stages were assessed as being subjected to only low to moderate risk of grass prevalence. The vascular-plant rich and structurally diverse Euphorbio-Callunetum (community 7) often suffered from invasion by grasses (*Calamagrostis epigejos*) and ruderal plants. Neophytes were found regardless of specific patterning. *Campylopus introflexus,* an invasive acrocarpous moss, *Erigeron canadensis*, a summer-annual or biennial herb, and *Prunus serotina*, a rapidly regenerating shrub or small tree, were the most frequent and locally abundant neophytes. On degeneration-stage plots, neophytes were usually absent. Ruderal plants occurred only on base-rich sands in the Euphorbio-Callunetum (community 7, ESM2_2: Table S2-1).

Taken together, three communities were rated to be of high nature conservation value; the mosaic heaths of the Genisto-Callunetum typicum, including its species-rich regeneration stage (communities 1 and 6) and the *Corynephorus* variant of the Genisto-Callunetum cladonietosum (community 4).

Table 2.4 Assessment of potential nature conservation status, based on national criteria, considering heathland-typical species inventory, structures and threats (according to mapping instructions for the monitoring of Natura 2000 habitat types 2310/4030 (NLWKN 2012, LfU 2014a & 2014b). Highest values are highlighted in bold. Nature conservation status: A – Favourable, B – Unfavourable - inadequate, C – Unfavourable - bad.

		Early-stage regeneration			**Late Building to Mature heathland**				**Late Mature to Degeneration stage**	
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
habitat-typical structures	typical relief	high	high / moderate	moderate	high	moderate	high / moderate	high	low	low
	open sand [%]	high	high	moderate	high	high	high	high	moderate	low
	beneficial *Calluna* age structures	high	high	moderate	high	high / moderate	high / moderate	moderate	low	moderate
	typical structures grade	**A**	**A**	**B**	**A**	**B**	**A-B**	**A-B**	**C**	**B-C**
heathland-typical species composition	***vascular plants***									
	mean frequency of typical vascular plants [4m^2]									
	ht 2310	5.1	2.4	2.2	4.4	2.2	6.2	**6.8**	2.6	3.6
	ht 4030	5.6	3	2.8	4.9	2.5	6.4	**6.6**	3	4.3
	mean frequency of red list vascular plant species/4m^2	0.5	0.2	0.3	0.7	0.2	0.6	**3.9**	0.3	0.3
	vascular plant interim grade	**A**	**B**	**B**	**A**	**B**	**A**	**A**	**B**	**A-B**
	cryptogams									
	mean frequency of typical mosses	1.2	1.0	1.0	2.2	**2.8**	1.0	0.5	2.1	2.2
	mean frequency of typical lichens	2.1	3.1	1.5	5.7	**4.9**	1.0	0.4	0.6	0.6
	endangered cryptogam species [per community]	13	11	12	21	**24**	5	1	11	16
	mean occurence of endangered cryptogam species/4m^2	0.7	1.1	0.7	**3.1**	2.9	0.3	0.1	0.5	0.5
	cryptogams interim grade	**B**	**B**	**B**	**A-B**	**A-B**	**B-C**	**B-C**	**B-C**	**B-C**
	total red list species									
	total endangered species	24	15	16	28	**29**	12	12	19	25
	mean occurence of endangered species/4m^2	1.2	1.3	0.9	3.8	3.2	0.9	**4.0**	0.8	0.9
	species composition grade	**A**	**B**	**B**	**A**	**A-B**	**A**	**A**	**B**	**A-B**
threats	potential risk of unfavourable dominating grasses (<30% cover)	high	low	low	low	low	moderate	moderate	low	high
	neophyte/ruderal occurences	low	moderate	moderate	low	moderate	moderate	high	low	low
	tree invasion	low	moderate	moderate	moderate	high	low	high	high	high
	threats grade	**A-B**	**B**	**B**	**A-B**	**B**	**A-B**	**B-C**	**B**	**B-C**
Total nature conservation status potential (total rating)		**A-B**	**B**	**B**	**A-B**	**B**	**A-B**	**B**	**B-C**	**B-C**

2.4 Discussion

Floristic and structural characteristics of dry lowland heathlands

Our analysis of heathland plant communities, their structures and species composition as well as their relationship to climate, soil and management provided valuable insights into the complex conditions governing the ecology and appearance of heathlands in northern Germany. The important role of the dwarf shrub *Calluna vulgaris* as the key species of Northwest European dry lowland heath could be verified. *Calluna* determines stand structure and developmental stages by growth phase composition and plant canopy cover. Furthermore, we show that considering *Calluna* age structures and the life form group composition improves the floristic-based classification in terms of ecological information value considerably. In this study, we linked its versatile growth habit directly to patterns of species diversity and composition.

The total cover of *Calluna* determines the stand character as rather dense *Calluna* dominance heath or a more open grass-heather mosaic. This confirms the general concept of heathland formations described by Gimingham (1972). Mosaic stands can be ‘typically’ three-layered with *Calluna* canopy, herbaceous plant layer (incl. graminoids) and cryptogam layer (Leuschner & Ellenberg 2017). We showed that such a typical heathland structure does not coincide with high species diversity nor with high conservation value and presence of red-listed taxa. The mosaic-type dry grass-heathland on base-rich sands (community 7) lacks a cryptogam layer, but shows high vascular plant diversity. In contrast, the lichen-rich open *Calluna*-dominated heath (community 4) is structurally simple but includes many red-list lichen species.

The dominant *Calluna* growth phase determines the heathland development stage, along with characteristic species turnover and shift of soil conditions. It is noteworthy that the pattern formation (dominance, mosaic) is not strongly related to heathland development stages. Richness patterns of vascular plants and lichens are directly determined by edaphic conditions and *Calluna* density and age, resulting in distinct lichen-rich, vascular-plant-rich or generally species-poor assemblages. Generally, we found heathland-typical vascular plant diversity to decrease towards the East and Southeast, where more grassland species contribute to the general heathland plant composition, supporting findings of Schubert (1973).

Environmental conditions determining heathland vegetation

The drivers of heathland biodiversity are known to be complex and characterized by several, interacting factors (Fagúndez 2013). We showed that additive effects of *Calluna* age structures and site history, recent management, edaphic and climatic factors are shaping heathland vegetation patterns and stand structures, and their interaction may further strengthen these effects. The two identified soil-related pathways of heathland development confirmed that floristic patterns may be explained primarily by soil conditions (De Graaf et al. 2009) and by stand-internal structural features.

During heathland succession the proportions of organic matter and clay in the sands enhance nutrient and water supply, favouring vascular plants (De Graaf et al. 2009; Heil & Diemont 1983; Mitchell et al. 2000, Sevink & de Waal 2010). In our study, this process, involving consolidated, somewhat more nutrient-rich sandy soils, was found to result in higher vascular plant cover and diversity. The edaphic tipping point between the lichen-rich and the vascular-plant-rich pathway appears to depend on soil texture and the amount of nutrient and water supply. Additionally, differences in herb and lichen diversity between heathlands were found to be determined by grazing and nitrogen deposition. Whereas the absence of sheep grazing does not adversely affect lichen diversity and cover (nor is it necessarily favourable for lichens), heathland grazing with horse and cattle inhibits high cryptogam diversity, either directly through trampling and nutrient enrichment or indirectly in that cattle and horse pastures are inherently more nutrient-rich.

Management affects heathland plant assemblages; either directly by shaping *Calluna* growth or indirectly by site-history effects forming soil conditions. Heathlands, both on former military training and historically farmed areas, depend on intense disturbance but they differ considerably in the continuity and amplitude of anthropogenic impacts. On long-term farmed heathlands, regularly though not pervasively disturbed, originated a fairly stable vegetation with low-amplitude successional cycle. In contrast, military training areas are characterized by irregular high-amplitude disturbances. The military training regime with frequent fires and intense mechanical disturbance leads to sparsely vegetated areas or to locally bare drift sand flats. These dune-like areas provide habitat conditions with poor water supply, towards the East enhanced by subcontinental droughts and low relative humidity during the vegetation period. After abandonment, which generally took place in the 1990s, natural succession took over, resulting in small-scale habitat variation with diverse structure and species composition (Ellwanger & Ssymank 2016).

Direct effects of climate appear to be of minor importance, probably influencing individual plants, but not (yet) entire assemblages. We found no evidence for the occurrence of more drought-tolerant taxa in subcontinental than in oceanic heathlands – except for lichens, which showed a tendency to higher diversity and cover values in suboceanic-subcontinental regions, no doubt supported by favourable edaphic (early-stage inland dune) conditions and lower airborne nitrogen deposits.

Heathland succession pathways

We found that species composition differed across edaphic conditions rather than along heathland development stages, supporting the scheme of two distinct heathland successional pathways:

(1) The psammophilous heathland pathway, often with pronouncedly lichen-rich communities, on dune-like habitats of bare acidic drift sands show floristic relations to Corynephorion canescentis pioneer grasslands on sand dunes, persistent only with continued micro-scale erosion or other frequent and adequate disturbance events (Schubert 1974). Contrary to some reports, e.g. Lache (1976), there was no interim stage with dominating *Festuca* spp. in the subcontinental East of northern Germany. On a few occasions were *Agrostis* grasslands or a direct encroachment to dense heathland or pine woodland observed. The latter development has been reported to be typical for succession on sand drift areas (Ketner-Oostra et al. 2010; Sevink & de Waal 2010). This pathway is related to the HT 2310 (EC 2013), especially in the eastern German lowlands typical for many former military training sites.

(2a) The consolidated sand heath succession pathway occurs as two subtypes. One subtype represents the typically species-poor variant of the HT 4030 on dry Old Drift sands. The heath structure as even-aged *Calluna* dominance stands may be related to fast vegetative regeneration, favoured by mowing and burning. These stands have a rather rudimentary, but relatively stable species composition. To provide suitable habitats for vascular plants, nutrient-poor conditions of the consolidated sands should be maintained, although this is difficult in areas of high loads of airborne nitrogen such as in northwestern Germany.

(2b) The subtype of the consolidated dry heath pathway on base-rich sands includes heaths rich in vascular plants with generally low cryptogam diversity. Not uncommon in Young Drift landscapes in eastern Germany, this pathway culminates in a subcontinental form of HT 4030 and also encompasses mosaics with xeric base-rich sand grasslands (HT 6120).

Conclusions and implications for conservation management

Heathland habitats are of high nature conservation value if they contain many heathland-typical species and structures. Three of our identified communities met these criteria, whereas the other six suffered mainly from unfavourable structures and/or imminent threats, rather than incomplete species composition. As adverse impacts are mainly related to insufficient or failed management, the bleak future perspective for HT 2310 and 4030 (BfN 2019) indicates that knowledge on how to efficiently and successfully manage such systems is urgently needed in order to improve the long-term stability and restoration of heathlands. The findings of the present study provide several implications relevant for heathland conservation management:

(1) Our study showed that species richness patterns and occurrences of rare species are related to soil conditions and long-term site history. Communities with the highest diversity of (rare) species were those of early successional stage, with high bare-sand proportions and without notable humus accumulation. Hence, maintaining or restoring heathland successfully requires suitable soil conditions, in particular nutrient-poor early-stage sandy soils for European dry heaths (HT 4030; De Graaf et al. 2009) or even bare dune-like conditions for inland sand dune heathlands (HT 2310; Ketner-Oostra et al. 2010).
Our study suggests that heaths where humus accumulated and has not been removed may provide *Calluna* age structural diversity after disturbance, but they are often of low floristic diversity. In practice, sufficiently profound soil disturbance may sometimes be problematic due to management obstacles, e.g. unexploded ordnance on active and former military training sites (Ellwanger & Ssymank 2016; Goldammer et al. 2016).

(2) Among the differences in species composition explained by edaphic conditions, there is only relatively little species turnover or structural change from the pioneer through to the mature stage. This indicates a species pool already existent at early *Calluna* regeneration stages. Hence, the floristic regeneration potential is predetermined during early heathland development stages. With heathland ageing and degeneration structural diversity decreases. However, there is also a continuous and substantial loss of species diversity. Older development stages provide only a reduced restoration or regeneration potential. Maintaining typical heathland of high nature conservation value in the long term means the provision of refugia for rare heathland-typical species in Building and Mature-phase dominated stages, so as to migrate to adjacent, currently intensively managed heathland sites. Hence, in areas where intense management possibilities are restricted (e.g. former military

training areas) the focus should be to preserve the local species pools rather than maintaining typical structures in order to prevent a gradual depletion of species diversity.

(3) Mosaic heaths provide higher floristic and structural diversity compared to dominance stands. Therefore, management should target restoring mosaic-structured open heathlands. Locally intensive management practices such as sod-cutting or military training may favour such structures. In contrast, mowing tends to promote even-aged dense dominance stands.

(4) Heaths in former military training areas in the subcontinental eastern part of northern Germany differ in species diversity and heath development pathway from historically farmed heathlands in the northwestern part of the country. A high proportion of the former are moreover psammophilous heaths (Sevink & de Waal 2010), generally poorer in heathland-typical vascular plants but richer in cryptogams, floristically similar to inland drift sand vegetation or to steppe-like heathland (c.f. Ketner-Oostra 2010; Schubert 1974). Therefore, site-specific management schemes should be developed that respect different local species pools and heathland successional pathways.

(5) The *Calluna* growth phases and life cycle concept (Gimingham 1972) need to be critically re-assessed, taking into account (multiple) regeneration cycles and age-dependant vitality of heather. *Calluna* growth phases should be considered at three different scales: (1) individual plant life history scale, (2) mid-term heathland development, reflected by the dominant heather growth phase in the stand (stand scale), and (3) the mid- to long-term site-history scale, where edaphic conditions change in the course of heathland succession. Heather life history often determines stand stage, but not necessarily site history stage as well. Disturbances, e.g. burning, may cause a reset of early-phase *Calluna* plants by regeneration, but not necessarily a reset to early-stage soil conditions. Additionally, age-dependant resprouting capacities are likely to determine post-disturbance stand habit. Hence, the growth-phase derived mid- and long-term development potential requires further research.
Furthermore, successful rejuvenation of heather is known to be influenced by the predominant type (generative reproduction or vegetative regeneration), management and favourable (micro-)climatic conditions (Henning et al. 2017; Miller & Miles 1970; Mitchell et al. 1998). Applicability of the established *Calluna* life cycle concept throughout its range may also be constrained by high airborne nitrogen loads and subcontinental weather events affecting adversely *Calluna* plant vitality and heathland health (Fagúndez 2013, Meyer-Grünefeldt et al. 2015).

(6) High floristic diversity is not necessarily linked to high structural diversity. This reveals interpretation deficits of vegetation maps focussed on vascular plant composition and contradicts the common belief that only highly structured heaths can provide high species diversity, which is true for vascular plants, but not for lichens. Therefore, structural diversity is an important proxy for habitat quality but should not be overinterpreted with regards to its ability to predict floristic diversity or rare species occurrences.

(7) The lists of species considered heathland-typical (NLWKN 2012; LfU 2014a, 2014b) need adjustment. Species instructive for conservation status and heathland development stage need to be diagnostic for specific favourable or unfavourable habitat conditions. We showed that determining factors are mainly soil conditions; hence species related to specific soils are of particular informative value. In our study, lichens turned out to be diagnostic for both favourable soil conditions and species richness. In contrast, many 'typical' vascular plants being almost always present, even in species-poor communities, were indicators for more consolidated sands, and they were less informative concerning floristic diversity.

We found that cryptogam synusial patterns turned out to be most instructive for heathland development stages. In contrast to studies where lichen-richness is considered to be characteristic of young pioneer or old degeneration stages (e.g. Gimingham 1972), the present study establishes that vital lichen stands of remarkable diversity, as typical communities of the psammophilous heath development pathway (Ketner-Oostra et al. 2010), may also occur in heath stages dominated by Building and Mature phase heather. Typical synusial changes along succession gradients as suggested by Coppins & Shimwell (1971) and Daniels et al. (1993) can be confirmed for the most part, although our findings suggest variation in floristic detail. Hence, general patterning of cryptogam assemblages are highly indicative for assessing heathland development stages. This highlights the need for valuing both lichens, mosses and vascular plants in their contribution to 'typical' heathland species assemblage.

Electronic Supplementary Material

ESM2_1: Additional information to study sites and community distribution.

ESM2_2: Floristic and phytosociological remarks. Text and Synoptic Tables.

ESM2_3: Additional results. Figures for *Calluna* growth phase composition, site history, climate, edaphic conditions, grazing regimes and intense managements in heathland plant communities.

ESM2_4: Nature conservation status additional information. Tables of rare species and nature conservation status assessment criteria applied.

ESM2_5: R source codes and original data Tables.

Chapter 3:

The *Calluna* life cycle concept revisited: implications for heathland management

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Abstract

Heather, *Calluna vulgaris*, is a key species of European dry heath and central determinant of its conservation status. The established *Calluna* life cycle concept describes four phases – pioneer, building, mature, and degeneration – distinguishable by growth and vitality characteristics of undisturbed plants grown from seeds. However, little is known about the life cycle and ageing of plants subjected to severe disturbance, although measures to this effect (burning, mowing) are common in heathland management. We studied the vitality of over 400 heather plants by examining multiple morphological (plant height, long shoot and inflorescence lengths, flowering activity), anatomical (growth rings) and environmental (management, nitrogen deposition, climate) attributes. We found *Calluna* vitality to be mainly determined by the aboveground stem age, and that severe disturbances promote vigorous vegetative regeneration. Ageing-related shifts in the habit and vitality of plants resprouting from stem-base buds is similar to that of seed-based plants, but the former revealed higher vitality when young, at the cost of a shorter life span. In contrast, plants originating from decumbent stems resemble building-stage plants but apparently lack the capacity to re-enter a cycle including stages other than degeneration-type. As a consequence, we supplemented the established heather life cycle concept with a post-disturbance regeneration cycle of plants derived from resprouting. We conclude that management of dry lowland heathlands should include rotational small-scale severe disturbance to support both seed germination and seedling establishment as well as vegetative regeneration chiefly of young heather plants capable of resprouting from buds near rootstock.

Keywords

Calluna vulgaris, degeneration, disturbance, growth phase, heathland conservation, heather vitality, life cycle, plant age.

3.1 Introduction

Calluna vulgaris (L.) Hull (henceforth referred to as *Calluna* or heather) is the dominant species of European dry heath and inland dune heath (European Union Habitats Directive Annex 1 habitat types 4030 and 2310, EC 2013). It is an evergreen small shrub of rarely more than 60 cm, multiple-stemmed and much-branched with numerous axillary short shoots and erect long shoots terminating in long raceme-like inflorescences. It is of hemispherical shape when young and mature, and with age develops decumbent or horizontal stems rooting by adventitious buds when in ground contact (Gimingham 1972).

The vast majority of lowland dry heath in Northwest Europe is anthropogenic, semi-natural and disturbance-driven, forming an often century- if not millennia-old landscape (Behre 2008; Ellenberg and Leuschner 2010). As such, it is an important cultural heritage and protected habitat for biodiversity (Chatters 2021). Throughout the last century dry heathlands have been suffering serious habitat loss, mainly due to land use change and succession coupled with ageing of heather, and degradation resulting from nitrogen deposition and perhaps also climate change (Ellenberg and Leuschner 2010; Fagundez 2013). The ongoing loss of heathland habitat in temperate Europe requires vitality monitoring of heather to assess habitat quality, guide management planning, and estimate heath restoration and regeneration potential. Most widely used in this context is the life cycle concept of heather conceived by Watt (1955) and refined by Gimingham (1972; 1975). This concept defines development phases centred on age-related attributes such as plant height and shape, growth, flowering intensity and the proportion of dead shoots. It involves the pioneer (in British upland heathlands plants aged up to 10 years), building (to 15 years), mature (to 25 years) and degeneration phases (plants aged to 30–40 years; Gimingham 1975, Webb 1986). The early stages of development up until the young mature phase are the ones with highest biomass production and flowering intensity, whereas late mature and degenerating heather is characterized by a decrease in flowering intensity and an increase in bare, non-flowering shoots, especially on stems in the plant centre, and a shift from erect or ascending stems to decumbent growth. Variations in growth form with dense compact prostrate stems with short internodes have been reported to be caused by stress, such as exposure to wind at high altitudes or heavy grazing pressure (Gimingham 1975).

In former times, heathland farmers aimed to maintain or improve fodder quality for their livestock by burning and cutting, thereby enhancing rejuvenation (García et al. 2013; Gimingham 1972; Webb 1998). Then as now, *Calluna* ageing and heath succession make it mandatory to periodically reset heather to retain habitat functions and biodiversity. To this effect, severe measures such as burning, cutting or sod cutting are carried out periodically, e.g., every 10-20 years for burning and 20-30 years for sod cutting (pers. comm. by heathland managers in North-German lowland heaths; Härdtle et al. 2009). Additionally, scrub and tree management may become necessary in order to retard or prevent succession (Marrs and Diemont 2013). Grazing is another important management factor as it delays the senescence of heather plants and enhances seed germination by moderate soil surface disturbance through trampling (Henning et al. 2017; Kirkpatrick and de Blust 2013).

Successful heathland recovery after severe disturbance depends on both seed germination followed by seedling establishment and the vegetative regeneration of plants that survived the disturbance. The rate of sexual reproduction success and asexual regeneration depends on climate (Velle and Vandvik 2014), management type and plant age (Mohamed and Gimingham 1970). In a subcontinental lowland heath, the amount of seed production and germination was similar to more oceanic sites, but seedling establishment was very low (Henning et al. 2017; Ibe et al. 2020). Favourable microclimatic conditions, such as sufficient water supply and humidity are critical for successful seedling establishment (Gimingham 1972; Henning et al. 2017). These findings indicate that the role of seed production and vegetative regeneration of heather varies along climatic gradients of oceanicity.

The conditions of cyclical regeneration in heathlands have been much discussed (Gimingham 1988; Marrs and Diemont 2013), particularly whether *Calluna* rejuvenation requires periodic disturbances or not. According to Watt (1955), undisturbed late mature or degeneration-stage heath can enter 'repetitive cycling' whereby *Calluna* plants rejuvenate vegetatively in gaps. This was affirmed by Wallen (1980) who reported repetitive regeneration cycles in long-term stable heathlands without severe disturbances, and by Webb (1986) who assumed potential immortality of *Calluna*. Gimingham (1988) concluded that repeated vegetative regeneration occurs as long as succession through trees or grasses is prevented. The hypothesis of repetitive rejuvenation would presume constant vitality of the individual plants, with ageing affecting aboveground biomass only. This repetitive cycling hypothesis was, however, not addressed in more than a theoretical way up to now, probably because it is hard to identify individual plants' life histories by other than long-term or genetic studies. Nevertheless, our study attempts to challenge the hypothesis and aims to provide evidence for either vegetative regeneration capacities being constrained by plant age, or for unlimited vegetative regrowth and thus potential immortality of individual plants.

Apart from the hitherto poorly known conditions of cyclical rejuvenation in *Calluna*, the role of heather regeneration in heathland dynamics is as yet insufficiently understood. In general, the plant has two strategies of vegetative regeneration, (1) resprouting from dormant buds near stem base in a short timespan after biomass loss through disturbance, and (2) layering, where older decumbent stems form dense mats by adventitious rooting, often around centres of senescent *Calluna* plants (Gimingham 1972). Although mentioned repeatedly (e.g., Marrs and Diemont 2013; Mohamed and Gimingham 1970), the role of the regeneration strategies in the plant's life history and in the cyclical dynamics of *Calluna* has not yet been covered in depth. Moreover, existing criteria for determining *Calluna* growth phases do not distinguish between plants grown from seeds, stem-base buds or from layering plants. Hence, potential age-dependent vitality reduction cannot easily be assessed in the field, unless by keen experts. In this study, we aim to formulate more readily accessible criteria for determining heather plant age and growth phase.

Heather plant age at the time of disturbance (Mohamed and Gimingham 1970) and post-disturbance *Calluna* regeneration capacity have often been studied, post-fire (Grau-Andrés et al. 2019; Velle and Vandvik 2014) as well as after cutting and grazing (Henning et al. 2017). Nevertheless, the processes and traits associated with ageing of regenerating plants remain unclear. Little is known about how heather plants with different life histories, whether grown from seeds, derived from resprouting or from layering, differ in ageing and life span. Further, it is not known whether vitality attributes, such as flowering intensity and yearly increment, differ among plants of the same age but with different life histories. A complex set of environmental conditions may counter- or interact with age-dependent and life history effects, interrelationships that are insufficiently understood yet: (1) management; (2) climate, e.g. vitality-reducing droughts, and (3) nitrogen deposition (e.g. Meyer-Grünefeldt et al. 2015).

The overall aim of our study is to revise and refine the established *Calluna* growth phase and life cycle concept (Gimingham 1975) so as to improve the validity of vitality-based heath conservation status assessments and to strengthen the biological-ecological knowledge required for informed advice on heathland management. Therefore we studied vitality attributes in plants of different age and investigated (1) which parameters influence heather vitality most: plant age, life history, management, climate, or nitrogen deposition; and (2) how vitality attributes change with age. Specifically, we address the question whether there are (3) differences in age-related vitality between plants grown from seeds (PS), plants resprouting from buds near stem base (PR) and those growing from rooted stems lying on the ground (PL).

3.2 Methods

Study areas and sampling

We examined a total of 445 *Calluna* plants in 319 plots of 25 m^2, randomly placed by QGIS coordinate generation in 19 study areas across the North German lowlands (for location and details see ESM3_1: Fig. 1, Tables 1 and 2; see also Schellenberg and Bergmeier 2020). Up to 8 representative plants were collected on each plot, two of each development phase (ESM3_1: Table 3). Plants in pioneer phase were disregarded, as they usually had no or few flowers and their measured parameters turned out to be not comparable to those of older plants.

For age determination, growth ring samples were taken from the rootstock just below the soil surface (analysed to reveal the plant age) and in stems at heights of 10–15 cm (stem age). The stem pieces of 3–6 cm length were examined by counting the growth rings on a fresh-cut diameter surface using a binocular microscope (20–50×). In some cases, where rings were hard to identify, cut surfaces were sprayed thinly with white interior paint. After cleaning, white pigment particles remaining in the xylem cell lumina enabled better visibility of the rings. All complete circular rings were counted as growth rings, incomplete ones were assumed to be stress-induced, e.g. by drought during the growth period (Webb 1986). Counts on very young *Calluna* plants showed that in the first two years no growth rings are developed, so the approximate age of the plant was assessed to constitute its rootstock growth ring number plus 2, and the stem age plus 3, respectively.

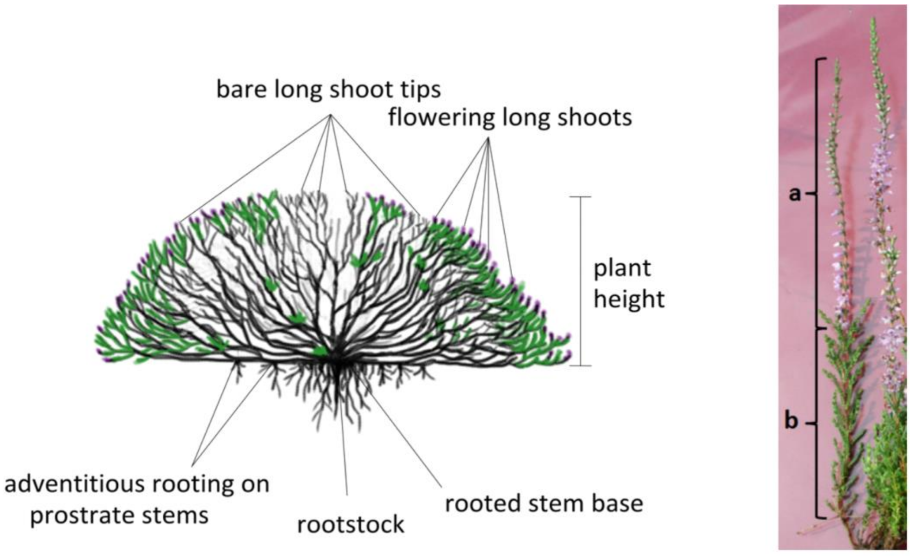


Fig. 3.1 *Calluna* habit and plant morphological terms used in this study. The yearly increment (a+b) of a long shoot is made up of the length of the inflorescence (a) and the length of the non-flowering part with foliate short shoots (b)

To understand the life history and development phases, we examined the plants' habit, adventitious rooting, and considered known management events to assess whether or not the plant had suffered severe disturbance-induced damage so far. By comparing the growth ring numbers of the rootstock and the stems we determined whether the aboveground plant directly grew from seed (PS) or developed by vegetative regeneration through resprouting from stem bases (PR) or from prostrate adventitiously rooted stems, whether or not still connected to the original plant (PL). As it turned out that in many plants the original rootstock was lacking or rotten to such a degree that growth rings were no longer identifiable, two datasets were created, one containing all plants with complete growth ring counts including rootstock used for total plant age analysis (n = 218, $\text{data}_{\text{root}}$), and another containing all plants, used for stem age analysis (n = 445, $\text{data}_{\text{stem}}$). Despite smaller sample size in $\text{data}_{\text{root}}$, both datasets showed similar patterns of growth ring numbers across development phases (ESM3_2: Fig. 2).

The trait data collected for age-dependent vitality analysis were associated either with flowering (flower density, proportion of long shoots with inflorescences, flowers per plant, length of inflorescence) or with vegetative growth (proportion of bare long shoots, yearly increment) (Table 3.1).

Table 3.1 *Calluna* vitality attributes.

Vitality attribute	Description	Unit	Numbers of plants examined In $\text{data}_{\text{root}}$ / $\text{data}_{\text{stem}}$
Flower density	Mean number of flowers per cm inflorescence	count	218 / 421
Flowering long shoots	Proportion of long shoots with inflorescences	%	218 / 445
Flowers per plant	Estimate of flowers per plant	number	218 / 445
Length of inflorescence	Mean length of inflorescence per plant (Fig. 3.1: a)	cm	218 / 445
Bare long shoots	Proportion of dead terminal long shoot tips	%	212 / 426
Relative yearly increment	Yearly increment (long shoots) as proportion of total plant height	%	206 / 414
Total yearly increment	Annual growth: Total length of this year's long shoot (Fig. 3.1: a+b)	cm	218 / 445
Plant height	Maximum plant height	cm	207 / 415

The study areas are situated along a climate gradient from oceanic conditions in the Northwest (annual precipitation about 880 mm) to subcontinental in the Southeast (annual precipitation about 520 mm, ESM3_1: Table 2). Soils were sandy or sandy-loamy, the topsoils more or less enriched by decomposed organic matter.

Information on management necessary for the determination of the plant life history was gathered by questionnaires returned from site managers as well as through personal observations during fieldwork (August-September 2014). The two management categories used in this study can be classified as intensive, comprising measures severely affecting aboveground plant biomass in the five years preceding fieldwork, in particular sod cutting, low-cutting (mowing at 5-10 cm height) and burning (both accidental and prescribed), and the less intensive grazing. Grazing regimes included reported and observed grazing and browsing (ESM3_2: Fig. 7, Fig. 8).

Airborne nitrogen rates were extracted from the interactive map service to airborne nitrogen deposition in Germany (UBA 2019; ESM3_1: Table 2), ranging from 10 $^{kg}/_{ha*y}$ up to 23 $^{kg}/_{ha*y}$. Oceanicity was calculated using the algorithm of Godske (1944), see ESM3_1: Table 2.

Statistical Analysis

All analyses were carried out and visualized in R (Rproject.org, Version 4.0.0). In an initial analysis, we inspected the data for patterns that may disturb age-related effects or may cause bias due to unbalanced sampling. An overview of the initial analysis results is given in ESM3_2. For flower density, a correction for the sampling date turned out to be necessary ($\rho = 0.36$). Therefore, we set up a simple linear model (lm() function) with the flower density as the response and the sampling date as the predictor and then corrected for the sampling date effect by centering the residuals around the predicted model mean.

To detect the main determinants for *Calluna* vitality, referring to research question (1), we used a subset of $data_{root}$ (n = 206) with all vitality attributes as response variables and checked the gradient length with a Detrended Correspondence Analysis (DCA, package ‘vegan’, Oksanen et al. 2019). The length of the first DCA axis was 1.82 SD, suggesting a linear multivariate model approach (Lepš and Šmilauer 2003). Hence, Redundancy Analysis (RDA, package ‘vegan’) with an automatic model selection (ordistep function, package ‘vegan’) was used to detect the main factors determining *Calluna* vitality, out of growth ring numbers, life history, management, oceanicity, and nitrogen deposition (RDA_{all}). Then, we set up three RDA with different groups of predictors: (1) RDA_{env} included only severe management, grazing and nitrogen deposition as predictors to identify their effects without considering any age-related effects; (2) RDA_{root} and RDA_{stem} with rootstock or stem age and life history as responses, respectively, and grazing, severe management as well as area as conditional terms to quantify explanatory power of growth ring numbers and life history; (3) RDA_{area}, where we used study area as fixed term to assess area-related effects on vitality that are not detected by age and life history, set here as conditional terms (= remaining spatial autocorrelation). In all RDA, post-hoc test for variance inflation (Zuur et al. 2009) was performed to prevent collinearity effects.

For the analysis of age-related effects on the specific eight vitality parameters (research questions (2) and (3)), we used linear mixed models (LMM, lmer-function of package 'lme4', Bates et al. 2015; for model diagnostics: 'lmertest', Kuznetsova et al. 2017; 'multcomp', Hothorn 2008), with each vitality parameter as a dependent variable and growth ring counts of rootstock ($data_{root}$) and of stems ($data_{stem}$) as predictors. If necessary, response variable was square-root transformed to account for better linear model assumptions. Model selection was conducted with a start model containing only the vitality response depending on the growth ring count and study area as random term to account for spatial autocorrelation. If the initial analysis revealed significant difference(s) in the vitality response variable between severe management or grazing categories, we included it in the model setup as random term in order to partial out its effect, as we aimed to focus on age-related effects only. We did not include oceanicity and nitrogen deposition, as both variables were study-area specific (ESM3_2: Fig. 2 & Fig. 3). We then checked whether there is a linear or a unimodal (2nd order polynomial) response of the vitality parameter to growth ring number, with visually checking their relation in a scatter plot and comparing the resulting models. Additionally, we tested whether the inclusion of the *Calluna* life history (PS, PR or PL) improved the model significantly. To detect improvement, we compared the models using AIC-statistics and post-model ANOVA of residuals. Plausibility checks of predictions and of the functional relationship between vitality and age prevented probable overfitting and influenced the selection of the final model. Final model diagnostics included a visual check of residuals according to Zuur et al. (2009). Partial R^2 of growth rings, life history, management and grazing – as far as included – were calculated by using the 'r2beta()'-function (package 'r2glmm', Jaeger 2017).

For modelling age-related differences in vitality and revising the life cycle concept, addressing our research questions (2) and (3), we used a dataset with all combinations of category levels and values of terms included in the single vitality parameter models and then calculated predictions with the 95% confidence interval using predictInterval-function (package 'merTools', Knowles and Frederick 2020). We extrapolated the prediction range for up to 60 years for modelling ageing processes over the entire hypothetical *Calluna* life span. Age of plants at date of disturbance was calculated by subtracting the branch age from total plant age. Results from modelling and observations of the author in the field were used for illustrating the life cycles for PS and PR, manually drawn using the Sketchbook software (Version 8.7.1 2019, https://sketchbook.com/).

3.3 Results

Determinants of heather vitality

RDA_{all} revealed the strongest constraining effect of stem age and life history, which together explained about 26% of total inertia (Table 3.2). In contrast, RDA_{env} with nitrogen deposition, severe management and grazing as fixed terms explained together only 5.6% in constrained terms, with grazing explaining the majority of it (ESM3_3). In this model, nitrogen was included as it explained vitality better than the highly collinear factor oceanicity ($\rho = 0.92$). Study area explained about 9–10% of total inertia (RDA_{area}), with the effects of age and life history considered as conditional terms (ESM3_3). Hence, this variance explained by area is the spatial autocorrelation effect in vitality not explained by age, but probably study area-specific differences in managements, nitrogen and oceanicity (ESM3_2: Fig. 1, Fig. 3, Fig. 5).

The clear, significant influence of age on *Calluna* vitality in RDA_{root} and RDA_{stem} explained about 13–23% of total variation, whereby the explanatory power of rootstock age was lower than that of stem age (Table 3.2). RDA_{stem} revealed a significant influence of life history and branch age on *Calluna* vitality ($p \leq 0.01$, Table 3.2). In contrast, life history did not contribute significantly in explaining vitality constrained to total plant age (RDA_{root}), indicating that life history-related vitality is somewhat masked when focusing on total plant age. However, relating the single attributes to age revealed some clear differences in age-dependent vitality between PS, PR and PL, for both total plant age and branch age (Table 3.3: partial R^2 for lh – life history; Fig. 3.4).

In both RDA age models as well as in RDA_{env}, management during the past five years and nitrogen deposition contributed together only about 6% to explained total inertia, indicating that age explained vitality rather than recent management activities and nitrogen loads (Table 3.2). In LMM vitality attribute models, there was a broad confidence interval which reflects the variability of original data, explained by random terms or remaining unexplained. As study area was set to random, this random variance can be partly interpreted as area-specific effects of oceanicity and/or nitrogen deposition (ESM3_2: Fig. 1, Fig. 3, Fig. 5). If grazing and/or severe management were included as random terms, they, too, explain parts of the variability (effect sizes: Table 3.3, ESM3_2: Fig. 5, Fig. 6, Fig. 7, Fig. 8). However, severe management had hardly any explanatory power if included, and grazing had only marginal effects on the relative yearly increment (Table 3.2, Table 3.3). Nonetheless, we detected some relevant effects of climate, nitrogen deposition and management in the initial analysis by applying simple group mean comparisons visualized as boxplots (ESM3_2). Total yearly increment was positively correlated to nitrogen deposition ($\rho = 0.28$ for both $data_{root}$ and $data_{stem}$), as well as the relative yearly increment ($\rho = 0.27$ for $data_{root}$, not evident in $data_{stem}$) and the inflorescence length ($\rho = 0.22$ in $data_{root}$, $\rho = 0.23$ in $data_{stem}$). Relations to oceanicity showed a similar pattern, due to the high correlation between oceanicity and nitrogen deposition as a sampling effect, but at a weaker level (ESM3_2: Fig 3, Fig. 5). We found a remarkable inverse correlation of rootstock age with nitrogen deposition ($\rho \leq -0.35$), indicating that *Calluna* plants in areas with higher airborne nitrogen loads have a shorter life span, or the rootstock dies early (ESM3_2: Fig. 2a,d,g).

Table 3.2 Proportion of explained inertia of RDA_{root} and RDA_{stem} on the vitality parameters presented in Table 3.1. Rootstock age or stem age (growth rings) as well as plant life history were included as constraining terms, grazing, severe management and nitrogen deposition were included as conditional terms. Asterisks indicate significance of parameters, from a post-hoc ANOVA of residuals with 999 permutations (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, n.s. = not significant).

	Growth rings	Plant life history (primary/secondary)	Constrained terms	Grazing + Management + Nitrogen deposition	Unexplained
RDA_{root}	0.13***	$0.02^{n.s.}$	0.15	0.06	0.79
RDA_{stem}	0.23***	0.03*	0.26	0.06	0.69

Table 3.3 Age-dependent vitality results from LMM for each of the vitality attributes and their response transformation (. = no transformation, sqrt = square-root transformation), fixed terms included (lh - life history (seed-grown (PS), resprouted (PR) or layering plant material (PL)) as additive term (lh) or as interaction to growth ring count (*lh), total model R^2, partial R^2 for the included fixed terms and relative explained variance for random terms (total variance = 1). Severe management and grazing were only included if there was a significant detection of category level differences in the initial analysis, see Online Resources 2 for details. R^2 value of model is for marginal effects, partial R^2 values are given for each of the fixed term. All R^2 values are highlighted in bold when R^2/partial $R^2 > 0.10$ and with grey font colour when R^2/ partial $R^2 < 0.05$. For fixed terms, t-test based p-values from model summary were included as asterisks (*** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05, n.s. not significant). In the case of non-linear relation of response and growth ring count, the R^2 and p-values are given for the linear term (1st order polynomial) as well as the quadratic term (2nd order polynomial).

	Model			**Partial R^2 for fixed terms**			**Random terms** (relative explained variance, total variance = 1)		
	Response transformation	Fixed terms (random terms)	R^2	Growth rings	Life history	Interaction terms	Study area	Severe management	Grazing
a) Growth rings of rootstock									
Flower density	.	lh (area)	0.04	.	0.04**	.	< 0.01	.	.
Proportion of flowering long shoots	.	lh (area)	**0.18**	**0.12*****	**0.10*****	.	< 0.01	.	.
Flowers/plant	sqrt	(area)	**0.18**	**1st: 0.14*****/2nd: 0.05**	.	.	0.02	.	.
Length of inflorescence	sqrt	lh (area) (man)	0.06	0.05**	0.02*	.	0.07	< 0.01	.
Proportion bare long shoot tips	sqrt	*lh (area)	**0.58**	**0.53*****	<0.01$^{n.s.}$	lh:RA 0.09***	< 0.01	.	.
Relative yearly increment	sqrt	lh (area) (man) (grazing)	**0.34**	**1st: 0.31*****/2nd: 0.05***	0.09***	.	0.05	< 0.01	0.08
Total yearly increment	sqrt	lh (area) (man) (grazing)	**0.12**	**0.11*****	0.04**	.	**0.11**	< 0.01	0.02
Plant height	sqrt	*lh (area)	**0.43**	**1st: 0.39*****/2nd: <0.01$^{n.s.}$	**0.11*****	lh:RA 1st: 0.09***/2nd: <0.01$^{n.s.}$	< 0.01	.	.
b) Growth rings of stems (10-15cm of plant height)									
Flower density	.	*lh (area)	**0.10**	0.07***	0.06***	lh:AAA 0.03***	0.03	.	.
Proportion of flowering long shoots	.	lh (area)	**0.17**	1st: 0.05***/2nd: 0.05***	0.08***	.	0.05	.	.
Flowers/plant	sqrt	lh (area)	**0.31**	**1st: 0.28*****/2nd:0.03***	0.02**	.	0.03	.	.
Length of inflorescence	sqrt	*lh (area) (man)	**0.13**	1st: 0.07***/2nd: 0.03***	0.03***	lh:AAA 1st: 0.02**/2nd: <0.01$^{n.s.}$	0.09	0.03	.
Proportion bare long shoot tips	sqrt	lh (area) (man)	**0.21**	**0.12*****	0.09***	.	0.03	0.01	.
Relative yearly increment	sqrt	(area) (man) (grazing)	**0.36**	**1st: 0.36*****/2nd: 0.02**	.	.	**0.11**	< 0.01	0.04
Total yearly increment	sqrt	*lh (area) (man) (grazing)	0.08	0.03***	0.07***	lh:AAA 0.02**	**0.15**	< 0.01	< 0.01
Plant height	sqrt	(area)	**0.53**	**1st: 0.52*****/2nd: 0.04***	.	.	0.02	.	.

Burning supported vitality in the short-term, with growth rates (length of inflorescences, total and relative yearly increment) significantly higher on burned sites compared to mowed sites or those without any such severe management (ESM3_2: Fig. 5, 6). In contrast to mowing, burning effectively reduced the amount of bare long shoot tips. Grazing affected the annual increment, the length of inflorescences and therefore, albeit only slightly, total growth rate (ESM3_2: Fig 7, Fig. 8).

The strength and specificity of age-dependent vitality effects in the LMMs varied between attributes, lower R^2 values indicated weaker relationships between the original data and model predictions, resulting in only marginal effects of age on the total yearly increment ($R^2 \leq 0.11$, Table 3.3), the length of inflorescence ($R^2 \leq 0.13$), on flowering long shoots (%, $R^2 \leq 0.18$) and on flower density ($R^2 \leq 0.10$). In contrast, clear age-related effects were found for the total number of flowers per plant, the relative yearly increment and plant height, which responded specifically to branch age ($R^2 = 0.31$, $R^2 = 0.36$, $R^2 = 0.53$, respectively). The strongest response to total plant age was found for the proportion of bare long shoot tips ($R^2 = 0.58$).

Calluna vitality depends on age and life history

The oldest plant examined was 26 years old (i.e., with 24 growth rings counted), but the majority of the rootstocks ($data_{root}$) were younger than 17 years (with 15 growth rings). PS rootstocks showed the widest age range, PR the narrowest; the majority of PR with still existent rootstock were only 9–14 years old (Fig. 3.2a, b).

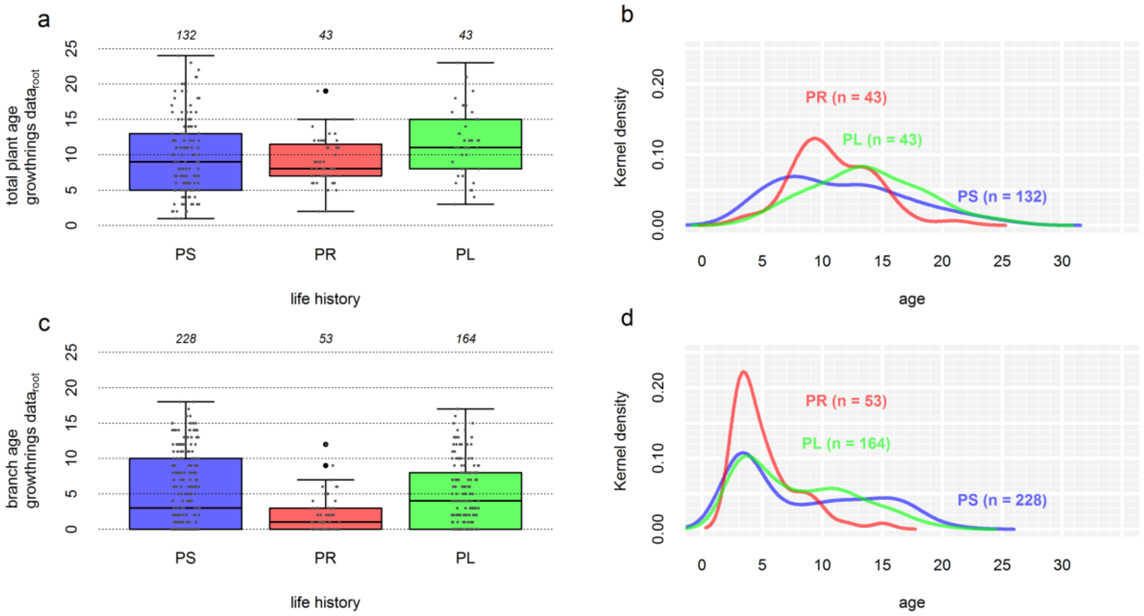


Fig. 3.2 Age of the individual plant (a, b) and the stems (c, d), for plants grown from seed (PS), from resprouting (PR) and from layering (PL).

After severe biomass disturbance, resprouting from rootstock-near stem bases was associated with adventitious rooting of the stems, followed by degeneration of the rootstock. Layering started when plants were between 7 and 15 years old, but the total age of PL was not accessible as the original rootstock was often already rotten in degenerating plants or not identifiable due to the intertwining of decumbent stems of several plants. In general, we found *Calluna* stems older than 10 years were uncommon (Fig. 3.2c, d), in particular in plants originating from re-sprouting (PR). Erect PS stems rarely reached an age of more than 20 years. PR regenerated from plants that were largely 5-15 years old at the time of disturbance (Fig. 3.3).

Fig. 3.3 *Calluna* plant age at the time of severe disturbance (which commonly prompts resprouting). Calculated as the frequency of the difference between total plant age (measured on rootstock) and stem age of resprouted plants (n = 43)

The age of plants derived from stems lying on the ground (PL) depended on their distance to the original plant's centre. If adventitiously rooted close to it, old stems were ascending and lying on the ground only at their bases, therefore PL were relatively old. If prostrate stems rooted adventitiously along their length, PL were younger. The majority of the plants derived from layering stock were younger than 9 years old, indicating that they originated from stems of fully prostrate habit rather than from older ascending stems.

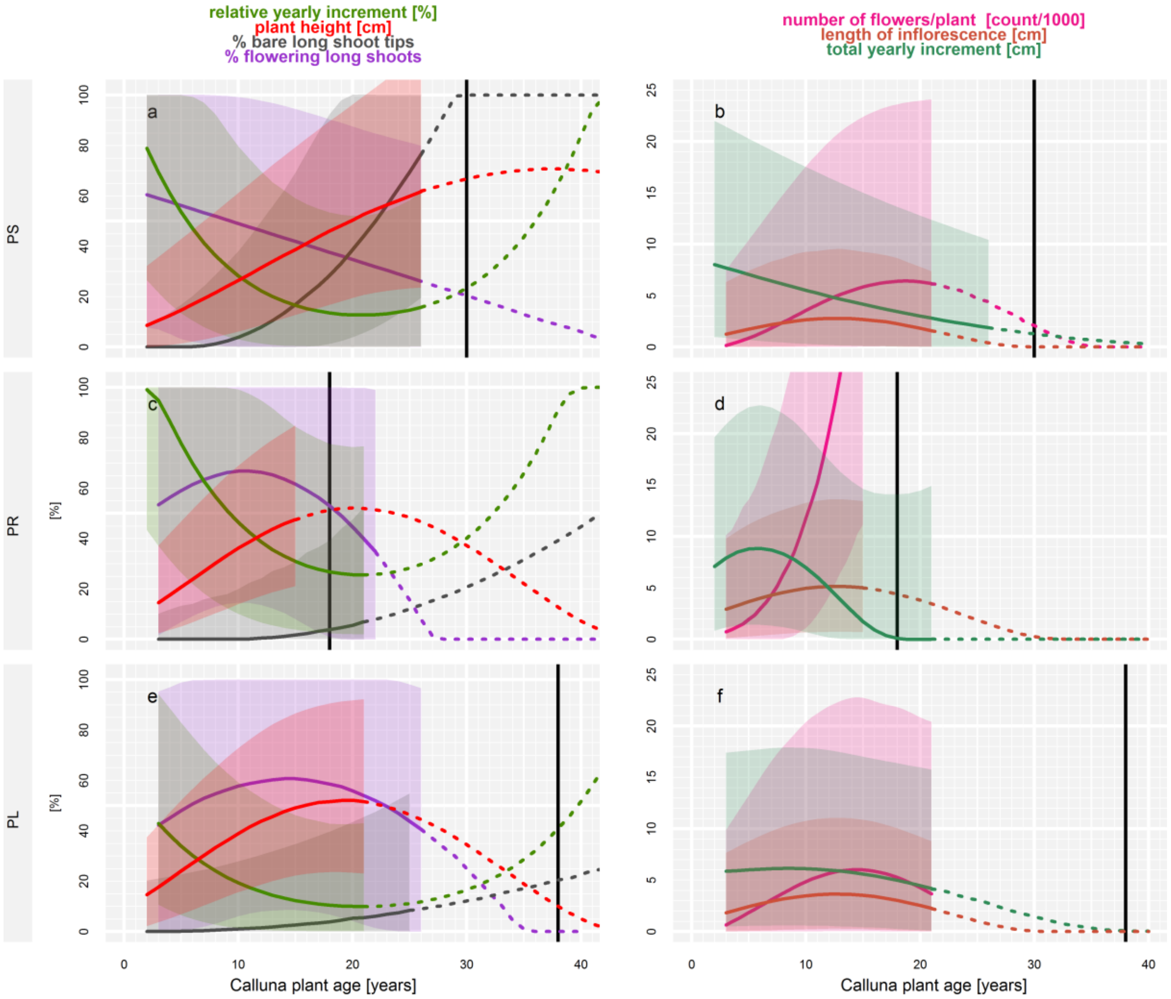


Fig. 3.4 *Calluna* vitality attributes over the plants' life span, (a, b) for plants grown from seed (PS), (c, d) for plants derived from re-sprouting near stem bases (PR), and (e, f) for plants derived from prostrate, adventitiously rooted old branches (PL). Solid lines and coloured areas mark the original data range; dashed lines are extrapolated mean predictions. Translucent coloured areas show 95% confidence intervals around predicted means. The predictions shown here are based on the single vitality parameter LMMs for rootstock age (a-b) and branch age (c-f, Table 3.3). The black vertical line indicates the hypothetical plant death when either bare long shoot tip proportion becomes 100%, or yearly increment is 0 cm

All vitality parameters –except flower density– showed a response to age (growth rings, Table 3.3, Fig. 3.4, Fig. 3.5). PS yearly increment showed a linear decrease with age, the same pattern was observed for the proportion of flowering long shoots. Plant height and the proportion of bare long shoot tips increased strongly with plant age. Attributes associated with flowering showed a unimodal response to plant age, with the longest inflorescences observed in plants of 10-15 years, but a maximum of flowers per plant found in plants of 17-22 years. The model predicted death of PS at a mean of about 30 years, when all long shoot tips of the plant become bare (Fig. 3.4a, b). Branches of PS still flowering after 20 years had a reduced growth rate and flowering. These old stems, lying on the ground but connected to the PS plant centre, counted as PS.

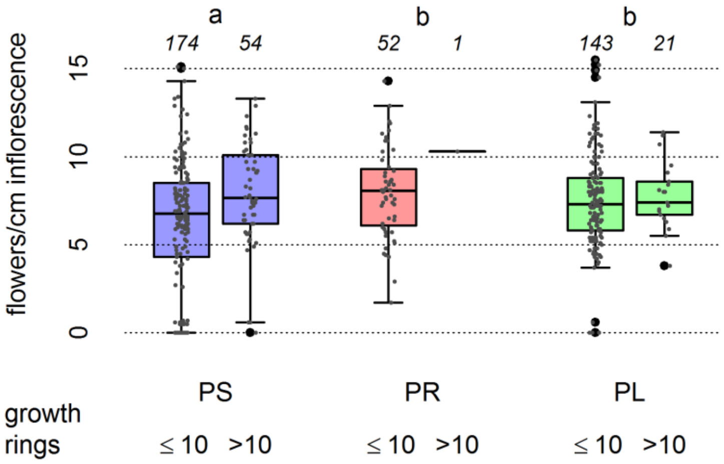


Fig. 3.5 Flower density differed significantly between PS (blue), PR (red) and PL (green). Although there was no linear response to age detected in LMM, younger plants (<10 years) tend to have a lower flower density than older ones. Original data points were shown as grey points. Sample size (n) is given above the boxes. Letters above the boxes indicate significant differences between PS, PR and PL based on a post-hoc Tukey multiple comparisons of means test. (*** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05, n.s. = not significant)

PR showed similar responses to age in plant height, relative yearly increment, but with a shift to younger plant age, resulting in a predicted plant death after no more than 18 years (Fig. 3.4c-d). In contrast to PS, plants derived from resprouting exhibited a higher proportion, density and length of inflorescences, as well as a greater number of flowers per plant of the same aboveground age. The relative yearly increment was higher and the proportion of bare long shoot tips significantly lower (Table 3.4). The number of flowers increased strongly and linearly with age, at a much higher level than PS and PL, but parts of this prediction may be biased due to very rich-flowering post-fire plants, observed especially in sites of high nitrogen deposition (Fig. 3.4d). The mean prediction for total yearly increment showed a peak in the first 10 years of growth after disturbance, but PR stopped growing at an age of approx. 18 years, an age where the other vitality attributes do not show distinct signs of senescence (Fig. 3.4c, d). This indicates an abrupt death of PR after an accelerated life cycle, or a shift towards layering, which starts earlier in PR than in PS, which was observed at about 5–10 years after resprouting. These findings suggest a persistence time of PR to be restricted to a maximum age of approx. 18 years (c.f. Fig. 3.2b).

PL vitality responses to age were similar to those of PR in terms of plant height and proportions of flowering and bare long shoots, but more similar to those of PS in terms of the total number of flowers, total yearly increment and inflorescence length. PL had significantly higher relative and total yearly increments than PS, but a significantly lower proportion of bare long shoot tips, though with high plant longevity (predicted to die after about 38 years), even if at low level of vitality (Fig. 3.4e, f). The inflorescence length and the total number of flowers per plant was significantly lower in PL compared or PR (Table 3.4).

Table 3.4 Vitality differences between life history categories: PS = plants grown from seed, PR = plants resprouted from stem base, PL = plants growing from prostrate stems adventitiously rooting, for data$_{root}$ (lefthand columns) and data$_{stem}$ (righthand columns). Mean estimated differences and their significances between the groups from post-ANOVA Tukey HSD test (. = life history not included in model, n.s. = difference was not significant, *** p ≤ 0.001, ** p ≤ 0.01, * p ≤ 0.05). Significant differences are highlighted in bold font.

	PS - PL	PR - PL	PR - PS	PS - PL	PR - PL	PR - PS
Flower density	-1.21$^{n.s.}$	-0.09$^{n.s.}$	1.12$^{n.s.}$	**-0.96****	1.37$^{n.s.}$	**2.33***
Proportion flowering long shoots	**-11.57***	5.77$^{n.s.}$	**17.34*****	**-14.39*****	8.63$^{n.s.}$	**23.02*****
Flowers/plant	.	.	.	**84***	**1602*****	**2417*****
Length of inflorescence [cm]	-0.03$^{n.s.}$	0.04$^{n.s.}$	**0.14***	**-0.06****	**0.13****	**0.36*****
Bare long shoot tips	-1.95$^{n.s.}$	-1.63$^{n.s.}$	0.01$^{n.s.}$	**2.71*****	-0.09$^{n.s.}$	**-3.77*****
Relative early increment	**-0.73***	0.42$^{n.s.}$	**2.26*****	-0.03$^{n.s.}$	0.28$^{n.s.}$	**0.48***
Total yearly increment	-0.11$^{n.s.}$	0.04$^{n.s.}$	**0.29****	**-0.15*****	0.00$^{n.s.}$	0.19$^{n.s.}$
Plant height	**0.43***	0.12$^{n.s.}$	**0.95****	.	.	.

The flower density (flowers per cm inflorescence) was significantly higher in PR and PL compared to PS. There was no influence of rootstock age on inflorescence density, and only a marginal influence of branch age, hence flower density is determined by life history or other influences rather than by age (Fig. 3.5, model details: Table 3.3). However, splitting PS, PR and PL in two data subsets, one containing all growth ring numbers <10, the other all observations with >10 growth rings, reveals a clear tendency towards higher flower densities with higher age, especially for PS (Fig. 3.5).

3.4 Discussion

Determinants for heather vitality and its dependence on age

Calluna vitality is influenced by plant age and life history rather than by the type of management. Visual attributes of *Calluna* vitality are determined by stem age rather than by rootstock age, indicating that aboveground regeneration compensates for total plant age-related vitality loss. Further, our results revealed that PR show even higher vitality than PS, but only in early phases of development after disturbance up to a stem age of about 15 years. In comparison to young PS of the same age, PR may benefit from a fully developed root system, which allows for better water and nutrient supply (Meyer-Grünefeldt et al. 2015).

With *Calluna* stem age identified as the major determinant for plant vitality, successful heathland management depends on whether the measures support sufficient aboveground regeneration of heather plants. According to our results, burning and mowing, and in case of surviving belowground plant material also sod cutting, induce resprouting from buds at rootstock or stem base level, thus fostering *Calluna* vitality in the subsequent regeneration. Additionally, we found a positive short-term effect of burning on the yearly increment, possibly due to improved nutrient supply after fire (Mohamed et al. 2007, Green et al. 2013). In contrast to severe management measures, grazing does not seem to trigger vegetative regeneration from the plant base, although resprouting is common in terminal branches. Grazing influenced inflorescence length and yearly increment, both highly variable between study areas, indicating that these vitality attributes were also affected by area-specific factors such as climate or nitrogen deposition. Our results show a clear decline in *Calluna* vitality after 10–15 years, irrespective of grazing activities, indicating that grazing alone is insufficient to ensure longer-term *Calluna* vitality (Kirkpatrick and de Blust 2013). On the other hand, frequent grazing may promote layering even in pre-degenerate plants, leading to dense mats formed by shoots with short internodes and low proportions of flowering long shoots (own observations; Gimingham 1975).

Regeneration ability of heather after severe disturbance is known to decline with age, due to reduced regeneration capacities by buds at stem bases and branches in older plants (Hobbs et al. 1984; Mohamed and Gimingham 1970). Hence, severe management measures may induce vigorous regeneration, but only in plants disturbed at an age of younger than 15 years (Mohamed and Gimingham 1970), a fact supported by our findings. Older plants may regenerate only by building new leading long shoots from decumbent stems. Further, we found evidence for an aboveground biomass turnover rate of about 15–20 years, with high vitality restricted to the first 15 years. These findings suggest either cyclical, highly vigorous regeneration after disturbance or generally stable vitality conditions by constant regeneration via rooting of stems lying on the ground, albeit at a lower level of vitality.

The role of climate (oceanicity) and nitrogen deposition for *Calluna* vitality remains somewhat unclear, since the age structure of heath stands differs between study areas for historical reasons, blurring possible effects of oceanicity and nitrogen load. Several study areas with a subcontinental climate are abandoned military training sites under ongoing succession, in contrast to oceanic, mostly continuously managed historical heathland farming sites. Nevertheless, vitality of heather is likely to differ in oceanic and subcontinental climates, as periods of drought or insect calamities causing heather dieback to occur more commonly in subcontinental than in Atlantic heathlands (Marrs and Diemont 2013). We found evidence for this in the potentially high rate of bare long shoot tips, suggesting reduced vitality at young ages in PS. This indicates that PS might be more susceptible to unfavourable growth conditions than PR and PL, which showed in general a lower number of bare long shoots per plant. Seedling establishment under subcontinental climate is also hampered (Henning et al. 2017). We found evidence that layering is common in lowland heathlands, and that they may stabilize heathlands suffering from dieback and low seedling establishment.

The yearly increment lengths found in our study (about 10 cm up to the sampling date) are comparable to values found in Atlantic upland heathlands such as in Northeast Scotland, where 11 cm/year have been documented (Mohamed and Gimingham 1970). We found that growth rates in PS declined soon after seedling establishment, whereas PR peaked in growth rate at about 5-7 years after resprouting. Other studies reported similar values (e.g. Webb 1986, p. 93).

Growth rates were influenced by nitrogen deposition rather than by oceanicity. In our initial analysis, we detected fertilizing effects by nitrogen deposition, in particular increasing total growth rate and longer inflorescences. Additionally, we found symptoms of accelerated ageing and a shorter life span of heather plants under high nitrogen loads, findings supported by several authors (Berdowski and Siepel 1988; Calvo-Fernández et al. 2018; Diemont et al. 2013; Meyer-Grünefeldt et al. 2015), although our results may also be influenced by site-specific management, heather age structure and oceanicity. Additionally, the effects of nitrogen loads on the growth of *Calluna* may further be complicated by other soil characteristics and water supply (Diemont et al. 2013).

The life cycle concept

A vital finding of our study is the age-dependent loss of *Calluna* vitality cannot be interpreted without considering the plant's life history. Our study revealed life history-related differences in the longevity, vitality and persistence of *Calluna* plants. To illustrate our findings, we supplement the primary (undisturbed) life cycle of a plant that germinated from seed with a secondary life cycle ('regeneration cycle') for plants regenerating after severe disturbance (Fig. 3.6).

In approximation, the life cycle of a *Calluna* plant grown from seed and without severe disturbance comprises three parts, (1) the pioneer and building phase, comprising 10–15 years, when the plant grows to maximum size at high vitality, (2) the mature phase, lasting a further 10–15 years, with plants retaining their vitality or at least their height, and (3) the degeneration phase characterized by a constant loss of vitality, biomass production and plant size, again comprising 10–15 years. We distinguish typical mature from late mature plants, the latter being characterized by the beginning of distal stem layering often followed by the death of rootstock and opening of the plant centre (own observations). This shift in habit, which takes place at an age of 12–20 years, may be used to assess the regeneration capacity, as is can be interpreted as the maximum age for high resprouting capacity in case of severe disturbance. While the shift from late mature to degeneration stage by definition of habitual characteristics remains somewhat unclear in the *Calluna* life cycle concept established by Gimingham (1972), we define the end of the late mature stage when the plant's nutrient and water supply shifted from the primary root system (near stem base) to adventitious roots. The persistence of plants at degeneration stage remains unclear, as many of the examined plants derived from adventitiously rooted lying stems were disconnected from the original rootstocks. Nevertheless, from what we found, layering may occur for 5–15 years, resulting in a total life span of 30–45 years (Fig. 3.6), which is similar to the life span of *Calluna* reported for British upland heaths (Gimingham 1972, Webb 1986). Our models revealed that the first plants die after 20 years, occasionally even earlier. This pre-mature ageing in PS may be caused by unfavourable external factors such as periods of drought (Marrs and Diemont 2013).

After severe disturbance by high-impact management such as sod-cutting, mowing or burning surviving heather plants may regenerate asexually from buds just below ground, near stem bases or at decumbent or procumbent stems (Mohamed and Gimingham 1970; 'post-fire-phases', Webb 1986). In contrast, moderate grazing supports resprouting from buds on the ends of browsed long shoots or last year's short shoots (Mohamed and Gimingham 1970). We found that severe aboveground biomass loss of up to 15-year-old *Calluna* plants may trigger a secondary life cycle with high-vitality (Fig. 3.6), as opposed to less intensive biomass disturbances, such as grazing. In our study, the majority of plants that resprouted from buds at soil surface or just belowground derived from plants of 10 years at the time of disturbance, usually an age of high vitality, where the plant is at the end of the building or in an early mature stage. Post-disturbance resprouting prompts a fast regrowth to early mature-stage plants within 10–15 years, under exceptionally favourable conditions on burnt sites already after 3–4 years (own observations). Such vigorous resprouting after fire is supported by a higher nutrient supply due to ash deposition, but also to the fast post-fire recovery of microbial communities, i.e. ericoid mycorrhizal fungi (Green et al. 2013). The latter allows for a very efficient nutrient uptake under the conditions of high acidification and aluminium toxicity (Shaw & Read 1989), hence providing a competitive advantage for *Calluna* (Vogels et al. 2020).

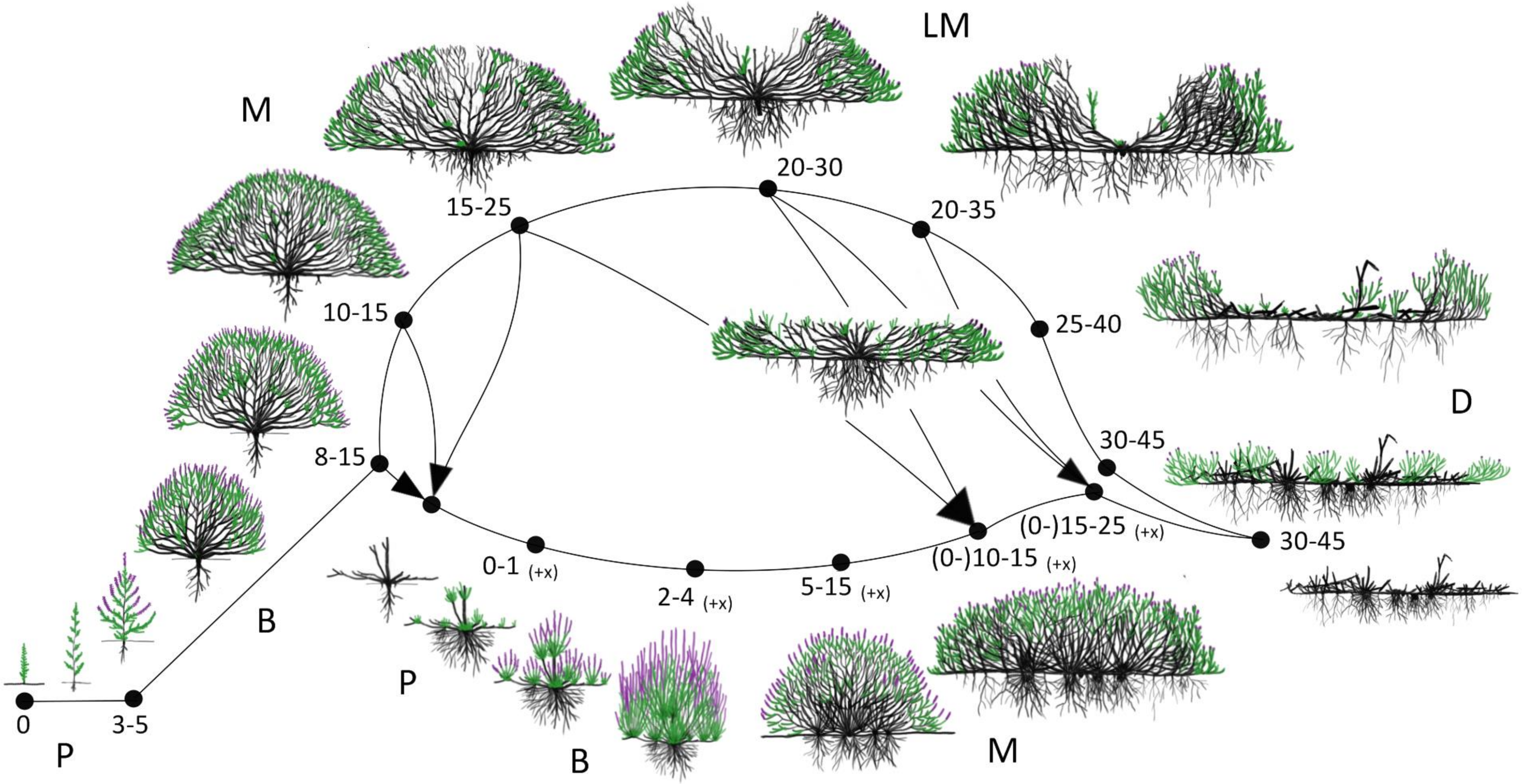


Fig. 3.6 *Calluna* life cycle, with the undisturbed growth of plants growing from seeds (PS, upper line), and below after severe biomass disturbance, indicated by arrows. Young plants in the mature stage resprout vigorously, as long as plants are sustained through functioning rootstock and stem base. Later, regeneration leads to dense, but not persistent mature-stage plants of a maximum height of 50-60cm. Growth phases: P – pioneer, B – building, M – mature, LM – late mature, D – degeneration. Age spans given indicate the approximate plant age or the age of regenerating plants after disturbance with x = age of plant at disturbance time

In general, PR turned out to be more vigorous than PS of the same age. Compared to PS, PR was less susceptible to external stress factors, such as drought, as shown by lower rates of bare long shoot tips which are beneficial, particularly in climates where periods of drought occur more frequently. Nutrients available due to ash deposition may be used more effectively by an extant root system. We observed intensified adventitious rooting after fire, which also favours nutrient uptake. As another consequence, intensified rooting leads to a shift in plant nutrient supply via rootstock to stem base roots, probably resulting in PS rootstock decay and layering to occur earlier in PR of the same aboveground biomass age (Fig. 3.6). While both PS and PR are highly vital up to 10–15 years, PR then show a strong decline in vitality, and a shift from the majority of stems in the plants' centres towards more adventitiously rooting stems. We showed that the turnover time of resprouted plants is about 10–15 years and found no evidence of stems with longer persistence. Layering processes become dominant in plants about 15–20 years of age after disturbance, with vitality similar to seed-based plants with decumbent stems. In contrast to the life cycle of undisturbed plants, resprouted plants perform an accelerated regeneration cycle, reaching building, mature, late mature and degeneration stages earlier than PS of the same aboveground age. The plant habit of PR can imitate the PS-typical hemispherical growth in the first years after resprouting, but the stems are usually generated by multiple resprouting buds near the rootstock, which is why the habit of PR is often denser. Plants at the end of the building stage began layering, flatten or become diffuse in shape, especially in dense regeneration stands as earlier as 10–15 years after disturbance. The reduction of yearly increment and the layering limits the plant height to max. 50–60 cm, even at mature stage. Hence, the mature stage of a regeneration cycle lacks high-growing distinct *Calluna* bushes, and is characterized by dense, rather flat cushions. We found no signs of the total life span of resprouted *Calluna* being extended, but resprouting prolongs the plant's high-vitality life phase.

We showed that layering plants in both the primary and the regeneration cycle are part of the degeneration stage of *Calluna*, with low vitality, as far as flowering traits are concerned, and the inability to achieve 'repetitive cycling', i.e. to become a mature plant again. Moreover, we could show that layering can be a quite stable and resilient growth form of degenerating *Calluna* plants. Unlike Gimingham (1975), who described stems lying on the ground as a characteristic of the degeneration phase persisting about 5–8 years or as a specific modification of wind-exposed plants, e.g., at high altitudes, or under high grazing pressure, we found this phase to persist for a third or more of the *Calluna* life cycle, i.e. for at least 15 years. Wallen (1980) found lying stems from regeneration not older than 13 years but, under the impression that heather had existed much longer in that site, he concluded there must be also older plants lying on the ground. In fact, our results confirmed the age determination by

Wallen (1980), though not his assumption, as the vast majority of our layering stems were indeed younger than 15 years. Wallen (1980) reported that a valid determination of the growth phase and age of plants was impossible, a fact we confirmed in our study, as total plant ages were often not determinable due to rotten rootstocks.

Due to their low height, the dense growth as well as the high proportion of non-flowering long shoots, these plants regenerating from decumbent stock resemble, and may easily be mistaken for, "building phase" plants. As a result, one may fail to recognize them as what they actually are: plants originating from degenerating plants. Nonetheless, our results show that plants consisting of stems lying on the ground are often older than 15 years. A false designation of such plants as "building phase" may result in an overestimation of regeneration capacities after severe disturbance, as we found regeneration ability being clearly age-related and strongly declining after 10–15 years, confirming Miller and Miles (1970) as well as Mohamed and Gimingham (1970). Our results suggest that high-vital regeneration capacity is confined to dormant buds near rootstock which produce new leading shoots, whereas with the beginning of layering of PS and PR plants, the central rootstock vanishes, and its role is partly taken over by adventitiously rooting stems. We found no older decumbent stems regenerating through high-vital resprouting, but instead mat-shaped regeneration unable to regrow to mature-plant shape.

As a result we also found no evidence of 'repetitive cycling', i.e., several consecutive resprouting cycles, although further studies appear necessary. Layering plants may persist several decades, a stage interpreted by us as prolonged degeneration phase rather than a full cycle. We did not observe regrowth from seeds produced during layering stages, but such rejuvenation may well occur under suitable conditions. In fact, long-term persistence of heathlands without management, as suggested by Marrs and Diemont (2013), would require this kind of regeneration cycle. Those authors described two scenarios of heathland maintenance without management – one driven by endogenous factors controlling dynamics involving generative and vegetative regeneration in an undisturbed habitat, and one with exogenous control by stressors such as frost or drought causing dieback. Both scenarios require specific site conditions to promote seed production, seed germination and seedling establishment. Although recent studies tried to figure out the determinants, (e.g. Henning et al. 2017), our knowledge on the regeneration potential of heathlands is still sketchy, especially under suboceanic-subcontinental climate conditions. Without management, the existence of long-term open heathland requires sufficient impact by natural disturbance as well as fairly low competitive pressure by late-successional species (Marrs and Diemont 2013). It may be assumed, as a consequence, that long-term successful maintenance of open lowland dry heathlands by natural dynamics rather than by management would depend chiefly on chance.

Conclusions

The primary *Calluna* life cycle as established by Watt (1955) and Gimingham (1972) based on the conditions of Atlantic upland heath was confirmed in our study, with minor deviations and an apparently higher mortality rate of pre-mature plants under subcontinental climate conditions, as in the Northeast German lowlands. Our novel findings concern chiefly the regeneration cycle, including an accelerated vigorous regrowth of *Calluna* after severe disturbance. Only plants of 10-15 years at the time of disturbance are capable of such a full additional cycle, given that the microclimate is favourable (Marrs and Diemont 2013).

We showed that *Calluna* plants that regenerated from stems lying on the ground may form stable degeneration stages persisting up to 25 years but are unable to perform a regeneration cycle including the building and mature phase. Especially in older stands, the history of such patches of degeneration heath may not be detectable anymore and may thus be misinterpreted as building-stage plants, due to their dense foliose habit. Such erroneous assessment may lead to an overestimation of the plants' regeneration capacities and consequently to *Calluna* recovery failure after severe management. In fact, our findings suggest reconsideration of the established criteria used for distinguishing building and degeneration-phase plants or plant patches, which are mainly based on visual attributes such as height and the proportion of bare branches indicating ageing.

As a consequence, for the management of dry lowland heathlands under suboceanic-subcontinental climate conditions, our findings suggest:

1) Severe management should be applied primarily on heath consisting of young plants with high resprouting capacity and subsequently quick vegetation recovery. A delayed *Calluna* recovery may enhance a shift in vegetation composition towards a higher proportion of grasses (Grau-Andrés et al. 2018, Marrs and Diemont 2013). This may be of particular importance under a subcontinental climate, where heather recovery is determined by vegetative regrowth rather than by rejuvenation from seeds, as seedling establishment needs favourable microsites, which are rare under subcontinental conditions (Henning et al. 2017). Additionally, the nutrient-poor heathland habitat in much of Northeast Germany, often dune-like with dry sandy soils limited in water and nutrient supply, favours plants with high resilience to drought, hence vegetative regeneration with extant root system and mycorrhizal fungi unimpaired by severe biomass loss as is the case after high-intensity fire (Green et al. 2013).

2) Plants of different ages react differently to disturbances. Our findings suggest that *Calluna* regeneration after severe disturbance is diverse in terms of survival and regeneration

capacity of plants. In consequence, such disturbances do not necessarily promote even-aged uniform heath, but may well support uneven-aged structures with fast regrowth of young resprouting plants to mature stage, accompanied by some older plants, consisting mainly of decumbent stems, providing shelter for seedlings. At 10–15 years after disturbance, plants that regenerated from younger resprouting and from older plants with decumbent stems begin to degenerate, but by then, young plants from seeds should be established. Hence, the type and severity of the management determines the age structure in subsequent heathland, with mowing and burning enabling the survival of *Calluna* rootstocks and sufficiently promoting regeneration. Grazing additionally contributes positively to species diversity and community structure (Kirkpatrick & de Blust 2013, Henning et al. 2017) by prolonging high-vital phases in the *Calluna* life cycle. Sod-cutting, on the other hand, is less advisable for subcontinental heathlands, as the total removal of aboveground biomass in combination with hampered seedling establishment (Henning et. al. 2017) may lead to recovery failure. Moreover, the need to restore suitable trophic conditions by sod-cutting is less pronounced in the northeast German heathlands where humus accumulation and nutrient input are lower than in the Northwest (Lüttschwager and Ewald 2012).

3) Small-scale management that includes sites being subject to short-term rotation (e.g., 10-15 years) and others allowing longer successional development is beneficial for the heathland ecosystem as a whole. Heathland management focussing only on optimum *Calluna* vitality may disregard species adapted to later successional stages. For long-term stability of heathlands, heather rejuvenation from seeds is needed, requiring further investigations on seed germination and seedling establishment especially in subcontinental heathlands. An urgent question to be solved is whether and to what extent seedling establishment takes place in the period between disturbances, with resprouted plants providing favourable microsite conditions and sufficient shelter for a new *Calluna* generation to establish.

Electronic Supplementary Material

ESM3_1: Study areas. This PDF contains supplementary material to all sites, including information to study area location, management, climate, nitrogen deposition and sampling statistics.

ESM3_2: Initial analysis. This PDF contains a brief graphical overview of initial analysis results concerning dataset-inherent correlations and associations, as well as ecological patterns and dependencies. Additionally, they provide further information on the effects of management, nitrogen deposition and oceanicity on the vitality of *Calluna* plants not addressed in the present article.

ESM3_3: Analysis documentation. The zip-folder contains the html documentation of the statistical analysis performed in R.

Chapter 4:

High nitrogen deposition increases the susceptibility of *Calluna vulgaris* recruitment to drought

Abstract

Dry lowland *Calluna vulgaris* heathlands, once widespread in Northwest Europe but declining since the 19th century, is reliant upon disturbance such as burning, mowing or sod-cutting to remain open. Two factors may compromise the success of post-disturbance heather recruitment; droughts and high airborne nitrogen (N) loads. I asked to what extent young *Calluna* plants suffer from drought, whether there is a difference in drought resistance between seedlings and resprouted plants, and if high N deposition reduces the drought resistance. I sampled 683 young heather plants in 19 North German dry lowland heathland areas and analysed how the annual growth, the frequency of damaged leading long shoots and the severity of damage were influenced by the drought severity, mean temperatures and precipitation during the growing season, using negative binomial mixed-effects models. Results were shown for three scenarios of varying intensity of drought, two nitrogen deposition scenarios, separately for seedlings and resprouted plants.

Droughts reduced young *Calluna* plant growth rate and increased tissue damages. Drought resistance was higher in resprouted plants than in seedlings. High N loads increased growth rates and mortality rates as well as the frequency of tissue damages under drought, but rather in seedlings than in resprouted plants. The interaction effect of high N deposition and drought caused a growth stimulation and consequently unfavourable shoot:root ratios in *Calluna* seedlings, inducing a critical water balance exacerbated by the restricted ability of *Calluna* seedlings to regulate stomata conductivity. In contrast, resprouted plants ceased growth under high N and drought, avoiding critical water losses and damages. The drought tolerance strategy of seedlings may provide competitive advantages under moderate drought conditions, but generally, the results rather support a decrease of competitive power under drought and high N, thus hampering post-disturbance *Calluna* recruitment.

Keywords

Calluna, drought, heathland, nitrogen load, regeneration, vitality

4.1 Introduction

Dry lowland heathlands of the North German Plain, dominated by *Calluna vulgaris*, are declining since more than a century as a result of land use changes and consequential habitat destruction, fragmentation and abandonment. What has remained is often threatened by a lack of appropriate management and in addition, by climate- and pollution-driven degradation (EEA 2019a; EEA 2019b; Fagundez et al. 2013; Olmeda et al. 2020). Hereby, the yet unknown threats of the changing climate, in particular the effects of more frequent and more severe drought during growing season, as well as their interaction with other threats and pressures, such like airborne nitrogen deposition (henceforth N deposition), are not well understood yet.

Calluna vulgaris (L.) Hull (henceforth referred to as *Calluna*) is an evergreen ericoid dwarf shrub and the dominant species of Atlantic dry lowland heathlands in Northwest Europe. Those heathland habitats are distributed in regions with oceanic climate, "lacking temperature extremes, whether high or low, but with abundant and well-distributed rainfall and the maintenance of a generally high humidity" Gimingham (1972: 11). They occur mostly on sandy soils with low water holding capacity where *Calluna* is rooting chiefly in the topsoil. Studies showed that *Calluna* generally has a wide tolerance towards water shortage (e.g. Albert et al. 2012; Bannister 1964a, b; Gordon et al. 1999, Kongstad et al. 2012), a high potential for recovery from former droughts (Backhaus et al. 2014; Gordon et al. 1999; Kongstad et al. 2012; Walter et al. 2016) and a high morpho-physiological plasticity to ecological stressors (Bartoli et al. 2013; Ibe et al. 2020; Petrova et al. 2017). Morphological adaptions to drought include the small ericoid leaves, revolute at margins, with the abaxial side reduced to a narrow groove containing sunken stomata and hairs (Gimingham 1972).

However, in oceanic-suboceanic regions, where *Calluna* populations are adapted to a balanced and even water supply during the growing season (Loidi et al. 2010), climate changes provide new challenges for the species' adaption potential. In most parts, the North German Plain is relatively dry, representing the eastern margin of Atlantic lowland heathland vegetation (c.f. Gimingham 1972; Loidi et al. 2010; Meyer-Grünefeldt et al. 2016). Recent studies found evidence for provenance-specific drought resistance in *Calluna* (Meyer-Grünefeldt et al. 2016, Ibe et al. 2020), suggesting a higher drought resistance in marginal populations, but with reduced precipitation in summer and rising temperatures with heat spells during the growing season, the climatic conditions in the region will exacerbate (Alcamo et al. 2007; IPCC 2021; May et al. 2016; Schönwiese & Janoschitz 2008; Spinoni et al. 2015; Wagner et al. 2013).

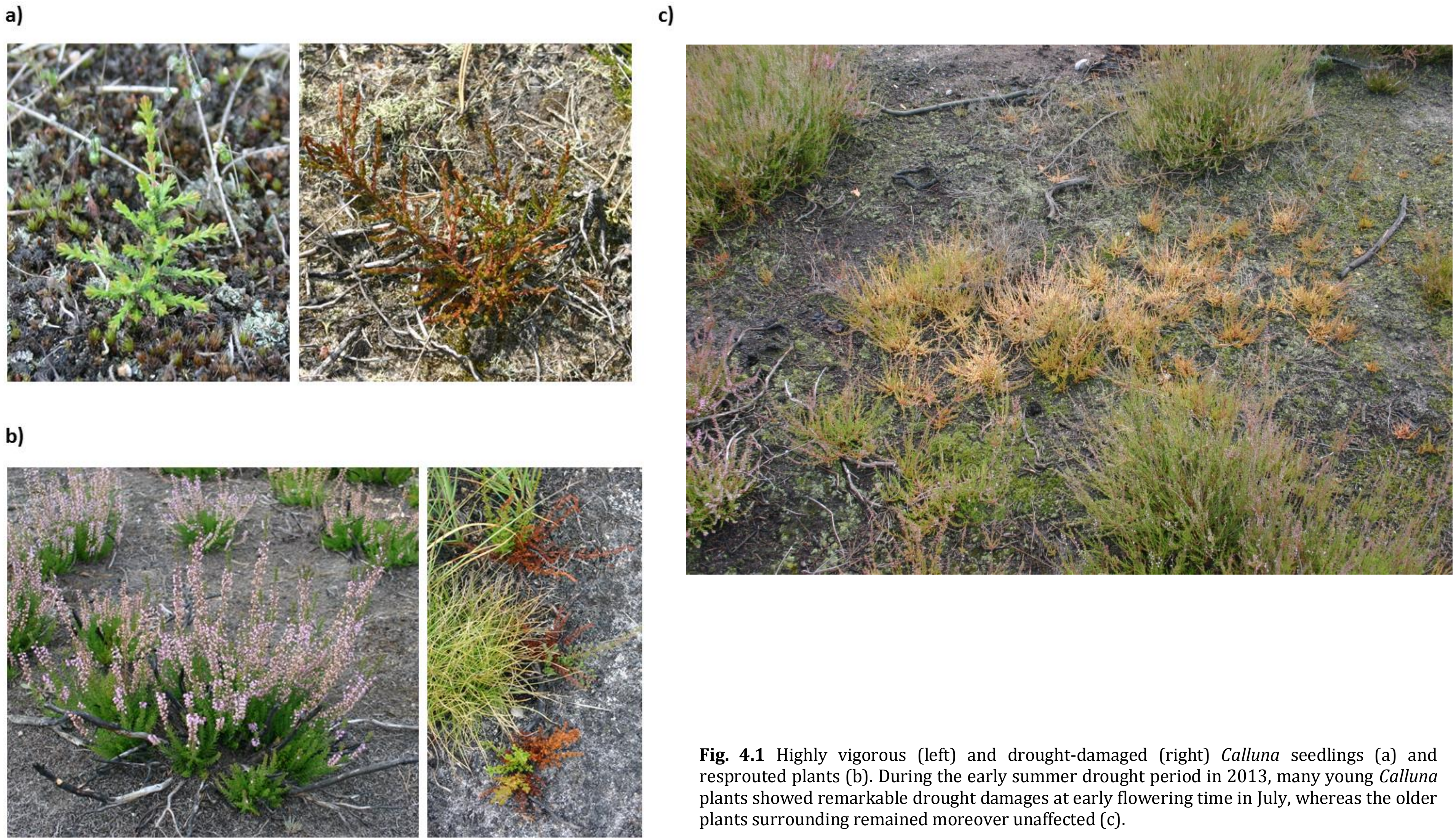


Fig. 4.1 Highly vigorous (left) and drought-damaged (right) *Calluna* seedlings (a) and resprouted plants (b). During the early summer drought period in 2013, many young *Calluna* plants showed remarkable drought damages at early flowering time in July, whereas the older plants surrounding remained moreover unaffected (c).

In Atlantic regions, drought-induced tissue damages occur mainly after cold spells in winter (‘frosting’, ‘winter browning’, Beijerinck 1940), with the sensitivity towards climatic stressors enhanced by drought in the previous growing season (Gordon et al. 1999). Under continental climate, severe tissue damages are moreover induced by droughts during the growing season (Bannister 1964a; Gimingham 1972; Marrs & Diemont 2013; Peñuelas et al. 2004). This became obvious in the North German Plain during the drought years 2013 and 2018, with extensive diebacks of (mostly but not only) young *Calluna* plants (Fig. 4.1).

Calluna heathlands are ecosystems in landscapes associated with pastoral economies. Being “naturally in a continuous state of change” (Chatters 2021), heathlands require disturbance-driven dynamics for their maintenance. Management such as burning, mowing or sod cutting induce heather regeneration, which comprises vegetative regrowth from buds at stem bases and branches (resprouting plants, PR), as well as the establishment of plants germinated from seeds (PS). Young *Calluna* plants are more strongly affected by drought than old ones (Britton et al. 2001; Ibe et al. 2020; Kongstad et al. 2012; Meyer-Grünefeldt et al. 2015), due to their high shoot:root ratio and a limited rooting system (Weiner 2004). Hence, the *Calluna* pioneer stage in the plant’s life-cycle, comprising young plants up to six years, is particularly sensitive to summer droughts (Meyer-Grünefeldt et al. 2015) and substantial damages of *Calluna* regeneration during the early stage may hamper the recovery of heathlands after disturbances, leading to reduced *Calluna* but increased grass cover (Britton et al. 2003; Marrs & Diemont 2013). Up to now, there is no study that examined whether resprouted plants are less susceptible to summer droughts than seedlings, although that is assumable due to a very low shoot:root ratio in the early post-disturbance recovery stage, and the developed Mature-stage rooting system, providing a better water supply.

Apart from the purpose to stimulate heather regeneration, mechanical managements and burning are applied to restore suitable soil conditions to compensate for nutrient and humus accumulation as a result of natural succession processes. Additionally, in the past decades, the need for restoring nutrient balances in the heathland soils, altered by atmospheric N depositions, became important, challenging the heathland management to weigh between the management-type induced trade-offs (Walmsley et al. 2021). High airborne N loads play a major role in dry lowland heathland habitat degradation, the critical loads for dry lowland heathland has been assessed at 10-20 kg/h^{-1}*y^{-1} (Bobbink & Hettelingh 2011). In the study areas, airborne N loads range from 10-23kg*ha^{-1}*yr^{-1} (UBA 2017, PINETI-3 model data for the reference period 2013-2015).

Since the 1980s, as first observations indicated species composition changes possibly related to high airborne N deposition (Heil & Diemont 1983), many studies subjected high N-induced alterations of heathland ecosystem inventory, function and structure (Aerts et al. 1990; Bobbink et al. 1998; Bobbink et al. 2010; Carrol et al. 1999; Diemont et al. 2013; Southon et al. 2012; Stevens et al. 2018; Taboada et al. 2018; Walmsley & Härdtle 2021). Some studies found that high N deposition increased the drought susceptibility and drought damages (e.g. Gordon et al. 1999; Meyer-Grünefeldt et al. 2015).

Both, climate change and air pollution, have been identified to play a major role in future heathland species composition, restoration potentials and for the long-term maintenance of heathland functioning (Gordon et al. 1999; Meyer-Grünefeldt et al. 2015, Carroll et al. 1999; Power et al. 1998; Saebo et al. 2001; Southon et al. 2012). However, the complex interactions are insufficiently understood up to now, in particular concerning the determinants for post-disturbance heathland recovery potentials and the establishment success of young *Calluna* plants under recent and projected climate and N deposition conditions. To gain a better insight, I analysed the responses of seedlings and respouting plants to drought and high N deposition in 19 North-German heathland areas, and asked:

1) How does drought during the growing season affect young *Calluna* plants? I hypothesize a reduction of growth rates and an increase of tissue damages with drought.

2) Is there a difference in drought resistance between seedlings (PS) and resprouted plants (PR)? I hypothesize PR having a higher drought resistance than PS, due to their extant mature-stage rooting system and a beneficial shoot:root ratio.

3) Does high N deposition affect the drought resistance of young *Calluna* plants, and do high N loads alter the PS and PR responses to drought? I hypothesize high N depositions to reduce drought resistance and I generally expect an increase of drought-induced tissue damages in young *Calluna* plants. Thereby, I expect PS more adversely affected than PR, due to their hypothesized generally lower drought resistance.

4.2 Methods

Data sampling

Young *Calluna* plants were collected in August and September 2014 in 19 heathland areas located in the North German Plain (Fig. 2.1, p. 29; Chapter 1.4 for study area details and characteristics). On 259 plots (25m^2), up to 2 randomly selected plants of each growth phase were examined. Wood sections from the root crown, the stem bases and the branches in 10-15cm height were used for growth ring counts. From the total dataset, all plants with up to 3 years of aboveground biomass age were selected.

As a proxy for biomass production, the length of the living leading long shoot yearly increment in mm was noted [LYI]. Tissue damages comprised entirely or partially dead leaves on the axillary short shoots or on the leading long shoots. Damages may be due to unfavourable weather during winter ('winter browning' or 'frosting', Bannister 1964a, b), or by summer drought, insect damage or pathogenic fungi. I focused on summer-drought induced tissue diebacks and therefore distinguished carefully between winter browning (greyish-brownish in colour), damages due to heather beetle *Lochmaea suturalis* (orange-brown, reddish colour), and damages by summer drought (reddish-brown, sometimes dark green-brown), with only the latter used for the present analysis. Plants obviously damaged by insects (e.g. *Lochmaea suturalis,* aphids of *Saturnia pavonia*) were excluded from this study, but *Lochmaea*-induced damage was sometimes hard to distinguish from drought damage. Reddish-purple and violet colouring of tissues is an adaption to high solar radiation and was not accounted as drought damage. Other insect calamities or damages caused by pathogenic fungi could always be detected safely and were not considered.

We distinguished between the extent of a single long shoot damage (PDYI) and the frequency of living but damaged long shoots in a plant, regardless of severity (PDL). For PDYI, I measured the damaged part as a proportion of the total active long shoot length, given as a mean over all living long shoots. For PDL, I estimated the proportion of all active, yet damaged long shoots of the entire plant (Fig. 4.2).

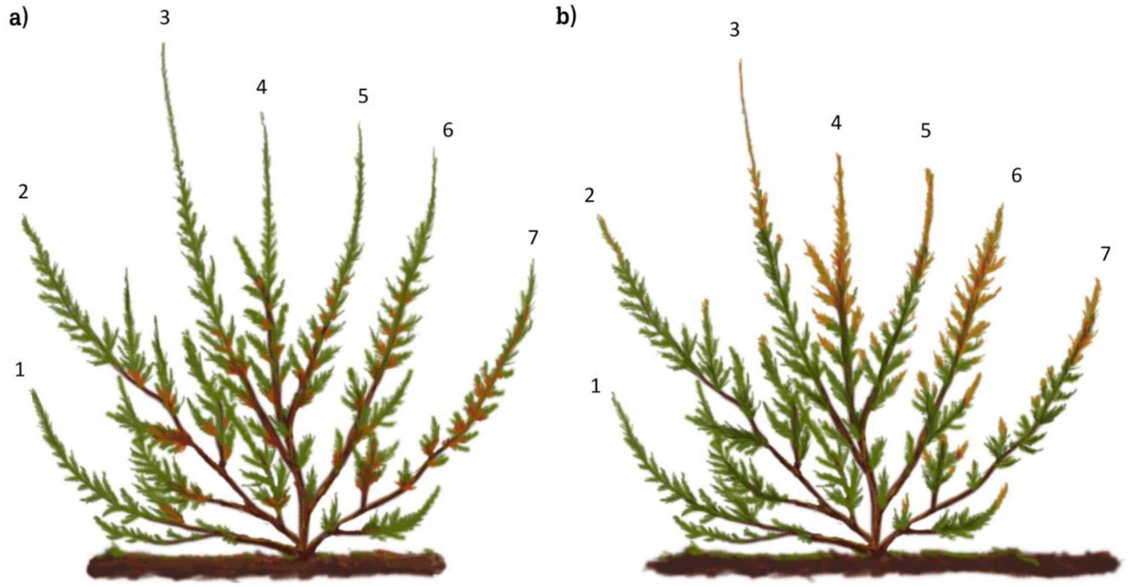


Fig. 4.2 Schematic examples for yearly increment and drought damage data sampling of a 3-year-old *Calluna* plant in August, with a drought in early summer (a) or recently before sampling in late summer (b). The mean annual increment (LYI) of the leading long shoots (1-7) was 15cm, the mean extent of long shoot damage (PDYI) was calculated as the proportion of the mean damaged long shoot part length (3cm) from the mean total annual increment (15cm) = 20% in the left plant (a) and 4cm of 15cm = 26.7% in the right plant (b). The frequency of damaged long shoots was 100% (7/7) in (a) and 6/7 (c. 85%) in (b).

The life history of the *Calluna* plants was assessed from plot history information (e.g. recent burning, mowing or sod cutting), the plant habit and the growth ring counts. I distinguished plants from seeds (PS, n = 476) and one- to three-year-old resprouted plants (PR, n = 207). Most plants were in the first year (total dataset: 83%, PS: 86%, PR: 75%). PR originated predominately from mature plants up to 21 years old, but 95% were younger than 14 years at the date of disturbance. As it turned out that the total plant age had a considerable effect on LYI (ρ = 0.73) and PDL (ρ = 0.59), those effects have been corrected by setting up simple linear models with logarithmized LYI and PDL as the responses and the total plant age as the predictor and then corrected for the age effect by centering the residuals around the predicted model mean. In pretests, I analysed differences of the responses concerning grazing and intense managements by using Kruskal multiple comparisons of means tests, and I detected no differences between the grazing regimes, but significant, marginal differences in all vitality attributes between sites mowed or burnt to those sod cut. These differences turned out to be coupled with the regeneration type, with mowed or burnt sites favouring PR and sod cut sites inducing regeneration with PS. Hence, the potential effects of intensive managements, although not directly included in the final full models are considered by including the life history. All analyses and figures were performed and created with R statistical software (R.project.org, Version 4.1.1).

Climate

The study areas represent a climate gradient from oceanic conditions in the Northwest (>800mm annual precipitation, mean annual temperature up to 10°C, Kotilainen's Index of Oceanicity up to 85) to subcontinental conditions in the East (500-600mm annual precipitation, mean annual temperature 9°C, Kotilainen's Index of Oceanicity lower than 50, Fig. 1.1, p. 14; Table 1.3 p. 16). Observations of mean temperature (T) and precipitation sums (P) over the period 1st of May – 31st of August (hereafter: survey period) were gathered for the years 2011-2020 (DWD 2021). This decade was characterized by a fluctuation between years of severe drought and those of quite wet conditions, with a wide range of rainfall distribution patterns, representing the drought conditions *Calluna* plants are recently faced with in the North German Plain. From those daily observations, I calculated the Standardized Precipitation and Evapotranspiration Index (SPEI), a widely used measure for drought severity (Vicente-Serrano et al. 2010, calculation with R package "SPEI" Beguería & Vicente-Serrano 2017). This index uses the climatic balance (P - Potential evapotranspiration (PET, calculated with the Thornthwaite equation with T)) to identify periods with drought, resulting in a negative SPEI then. SPEI was calculated on a time scale of seven days, implying that the SPEI was calculated as an accumulative effect of a seven-day-period to account for the distribution of drought and non-drought periods.

N deposition

Annual airborne N deposition ranged from $10\text{kg}*\text{ha}^{-1}*\text{yr}^{-1}$ to $23\text{kg}*\text{ha}^{-1}*\text{yr}^{-1}$, roughly corresponding to the macroclimate gradient, increasing in the direction from East Germany to the Northwest (Fig. 1.1, p. 14; Table 1.3, p. 16; UBA 2019, based on the PINETI-3 model for the reference period 2013-2015; Schaap et al. 2018).

GLMM

To analyse effects of the climate, N deposition and life history on the response variables I used negative binomial mixed models, as the tested Poisson-GLMM for LYI was overdispersed, and residual diagnostics indicated rather the usage of the Negative Binomial than the Binomial approaches for PDYI and PDL ('glmmTMB' package: Brooks et al. 2017; residual diagnostics Chambers & Hastie 1992, visual residual diagnostics with package DHARMa: Hartig 2021). All numerical fixed terms were rescaled to values ranging between 0-1 prior to modelling for enhancing comparability between non-equal ranges and variances in the original dataset.

I used a nested random term structure (study area/plot) for accounting spatial auto-correlation and pseudoreplication effects.

For assessing the partial explanatory power of N, life history and their interaction, I conducted partial models containing only the random term (m_{null}), only nitrogen deposition (m_{nitro}), only life history (m_{life}) as well as the interaction of both ($m_{nitro \times life}$) for each response, respectively. Unless otherwise specified, the marginal R^2 values are given in the text for assessing the model explanatory power using the package "performance" (Lüdecke et al. 2021). For the full models I included all fixed terms, with the additive effects of P, N and SPEI in interaction with N and life history (PS/PR): *response variable ~ (SPEI + T + P) * N * life history + (1|study area/plot)*. Model diagnostics included visual residuals diagnostics with package DHARMa (Hartig 2021) and slight deviations from residual uniformity were accepted. An R documentation with all diagnostic plots is provided in ESM4_1.

Based upon the models, I calculated predictions over the CI_{95} range for six scenarios, reflecting three intensities of drought: 1) NoD_2014, representing conditions without severe drought, with the wettest and coldest conditions of the survey year growing season; 2) D_2014 with the driest conditions of the survey year growing season, representing a moderate drought and 3) MaxD_10YEAR with the driest conditions measured in the 2011-2020 time period, representing severe drought, under low ($10kg*ha^{-1}*a^{-1}$) or high N loads ($25kg*ha^{-1}*a^{-1}$), respectively (scenario thresholds: Table 4.1). The prediction dataset was set up from all potential combinations of fixed terms, including the random terms, and due to the large size of over 500.000 recombinations and computational limits, a subset of randomly selected 50.000 samples was used for the further analysis and the plotting of results. From this dataset, the mean differences of LYI, PDYI or PDL between the three scenarios were calculated and tested for significant differences with a non-parametric Kruskal multiple comparison of means test (package pgirmess: Giraudoux 2021). Simple two-group mean comparison significances, e.g. between low and high N-depositions or between the life histories were calculated with the non-parametric Mann Whitney U-test.

Table 4.1 Vitality attributes (responses) and predictors for modelling drought.

Description	Model term	Range 2014 (2011-2020)	Scenario thresholds
LYI: Growth rate, yearly increment	LYI model response	5-370	
PDYI: Proportion of yearly increment with tissue dieback	PDYI model response	0-40	
PDL: Proportion of all living long shoots with tissue dieback	PDL model response	0-100	
P: Precipitation sum: Total precipitation sum fallen in the survey period (1st of May – 31st of August)	Fixed effect	214.8 - 385.7 (40.7 - 480.5)	NoD_2014: 386 D_2014: 215 MaxD_10YEAR: 41
T: Mean air temperature in the survey period (1st of May – 31st of August)	Fixed effect	15.6 - 17.1 (13.6 - 20.2)	NoD_2014: 16 D_2014: 17 MaxD_10YEAR: 20
SPEI: Standardized Evapotranspiration Index in the survey period (1st of May – 31st of August)	Fixed effect	-0.03 - 0.00 (-0.05 - 0.10)	NoD_2014: 0.00 D_2014: -0.03 MaxD_10YEAR: -0.05
N: Airborne N deposition	Fixed effect	10-23$^{kg}/_{ha*y}$	Low N deposition: 10$kg*ha^{-1}*yr^{-1}$ High N deposition: 25 $kg*ha^{-1}*yr^{-1}$
Calluna plant **life history**: regeneration type	Fixed effect		
Study area	Random effect		

4.3 Results

Climate

The ten-year analysis of SPEI, T and P revealed that there are huge fluctuations between the years 2011-2020 (Fig. 4.3). Variation among study areas within a year is highest in P, and quite low in T. Only one study area located near the Danish border had considerably lower annual mean temperatures than the others (SBD, black line Fig. 4.3b).

The years 2012 and 2017 represent cold and wet conditions during the survey period, with almost only positive SPEI and high P, whereas 2015 and especially 2018 had severe droughts, with high T and low P levels. Although the ten years may not represent general climate changes in the study areas, there is a trend towards higher T (Fig. 4.3b) and lower P (Fig. 4.3c), and a higher fluctuation and amplitude of SPEI (4.3a).

The ranges of SPEI, P and T for the survey year 2014 are given in Table 4.1 and are overall moderate against the background of the ten-year fluctuations (Fig. 4.3). The SPEI ranged from no-drought conditions (SPEI = 0) to moderate drought (SPEI = -0.03). T varied between 16°C and 17°C, and was therefore slightly below the 10-year mean of approx. 17.0°C. The amount of rainfall during the survey period (P) showed the highest variation between study areas, ranging from 215-368mm, but the variation did not correspond to oceanicity effects, as the highest P values were reached in the sites with low and high K (Fig. 4.3c). In contrast, T showed a clear patterning concerning long-term oceanicity and was higher in the more continental areas with a low K than in those with high K.

In the growing season 2014, there were two short drought periods in early summer, one at the end of May and one at the mid of June (Fig. 4.4). From early July to mid-August, a longer drought occurred, with high T in all study regions, but highly variable P. Some areas had heavy rainfall events with more than 30mm*day^{-1}, occurring at the beginning (FH, LT), during (OH, ZW), or at the end of the drought (SBD), and some areas had overall low precipitations during mid and late summer (KS, VH).

The study area with the wettest and coldest conditions was TD, located in Northwest Lower Saxony, showing a balanced SPEI of rd. 0.00, at T = 16°C, and P = 336mm. The two study areas with the driest conditions during the growing season 2014 were in North Brandenburg (RH, VH), with SPEI = -0.03, T = 16.5°C and P = 231mm.

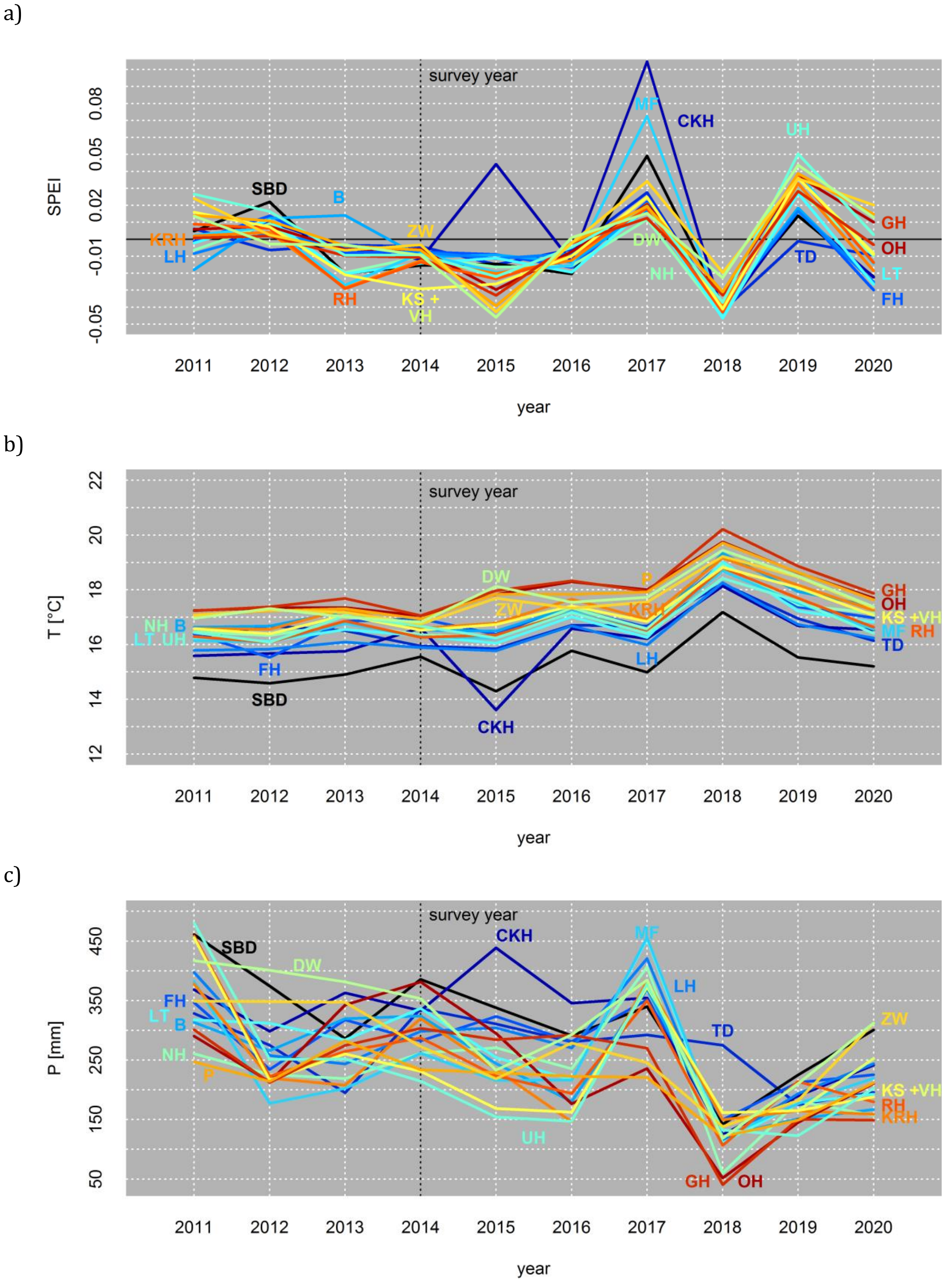
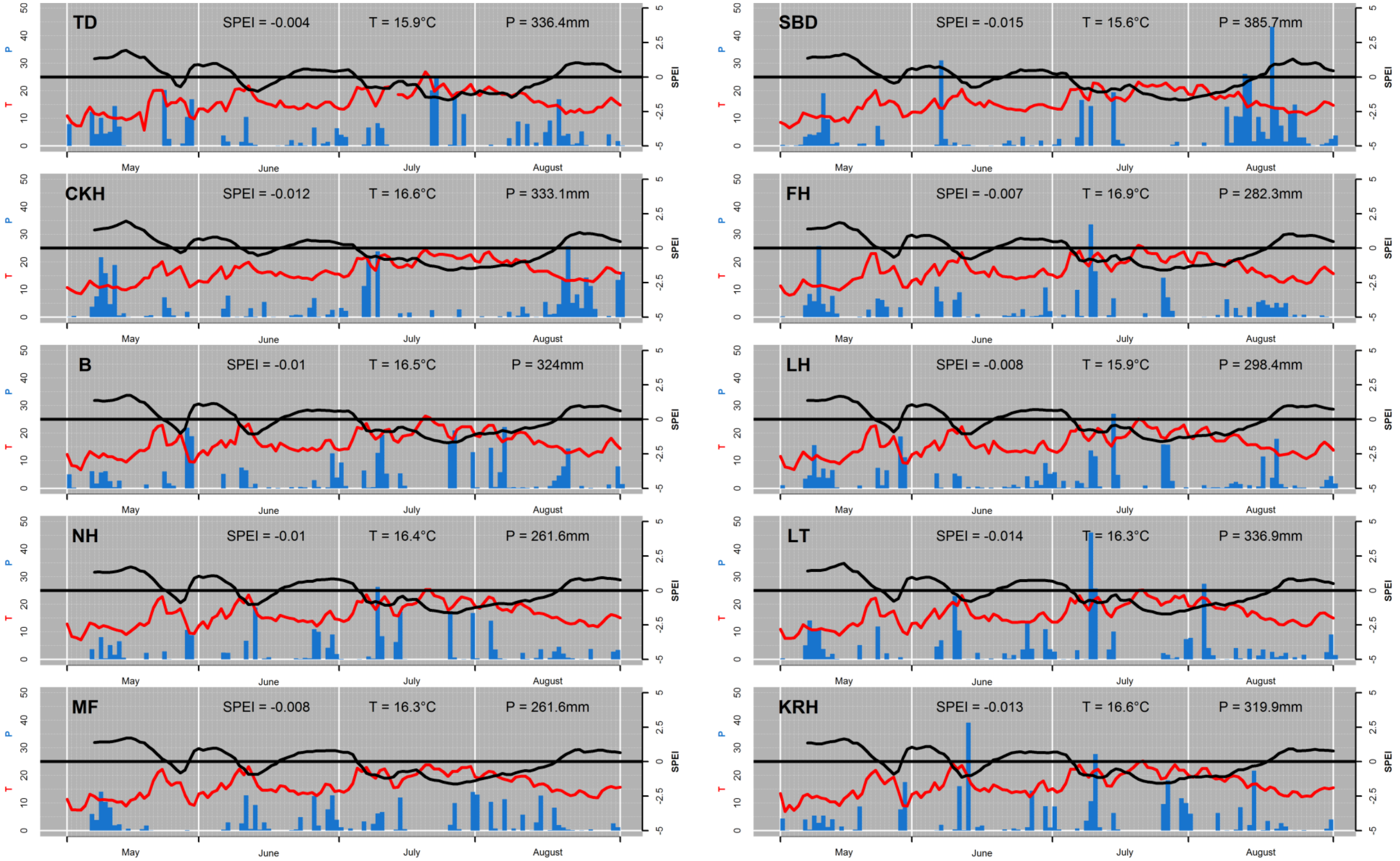


Fig. 4.3 Standardized Precipitation and Evapotranspiration Index (SPEI, a), mean daily air temperature in °C (T, b) and precipitation sum in mm (P, c) during survey period (1st of May - 31st of August) in the 19 study areas. Study area lines are coloured according to their Oceanicity (K, Table 1.3, p. 16), with increasing K from red over orange, yellow, green to blue and black. For full names of study areas see Table 1.3, p. 16 and for location of study areas see Fig. 1.1, p. 14. Study areas KS and VH have nearly identical values, due to their close location and are shown as overlapping lines.


TD
SPEI = -0.004
T = 15.9°C
P = 336.4mm
SBD
SPEI = -0.015
T = 15.6°C
P = 385.7mm
CKH
SPEI = -0.012
T = 16.6°C
P = 333.1mm
FH
SPEI = -0.007
T = 16.9°C
P = 282.3mm
B
SPEI = -0.01
T = 16.5°C
P = 324mm
LH
SPEI = -0.008
T = 15.9°C
P = 298.4mm
NH
SPEI = -0.01
T = 16.4°C
P = 261.6mm
LT
SPEI = -0.014
T = 16.3°C
P = 336.9mm
MF
SPEI = -0.008
T = 16.3°C
P = 261.6mm
KRH
SPEI = -0.013
T = 16.6°C
P = 319.9mm
P
T
SPEI
0
10
20
30
40
50
5
2.5
0
-2.5
-5
May
June
July
August

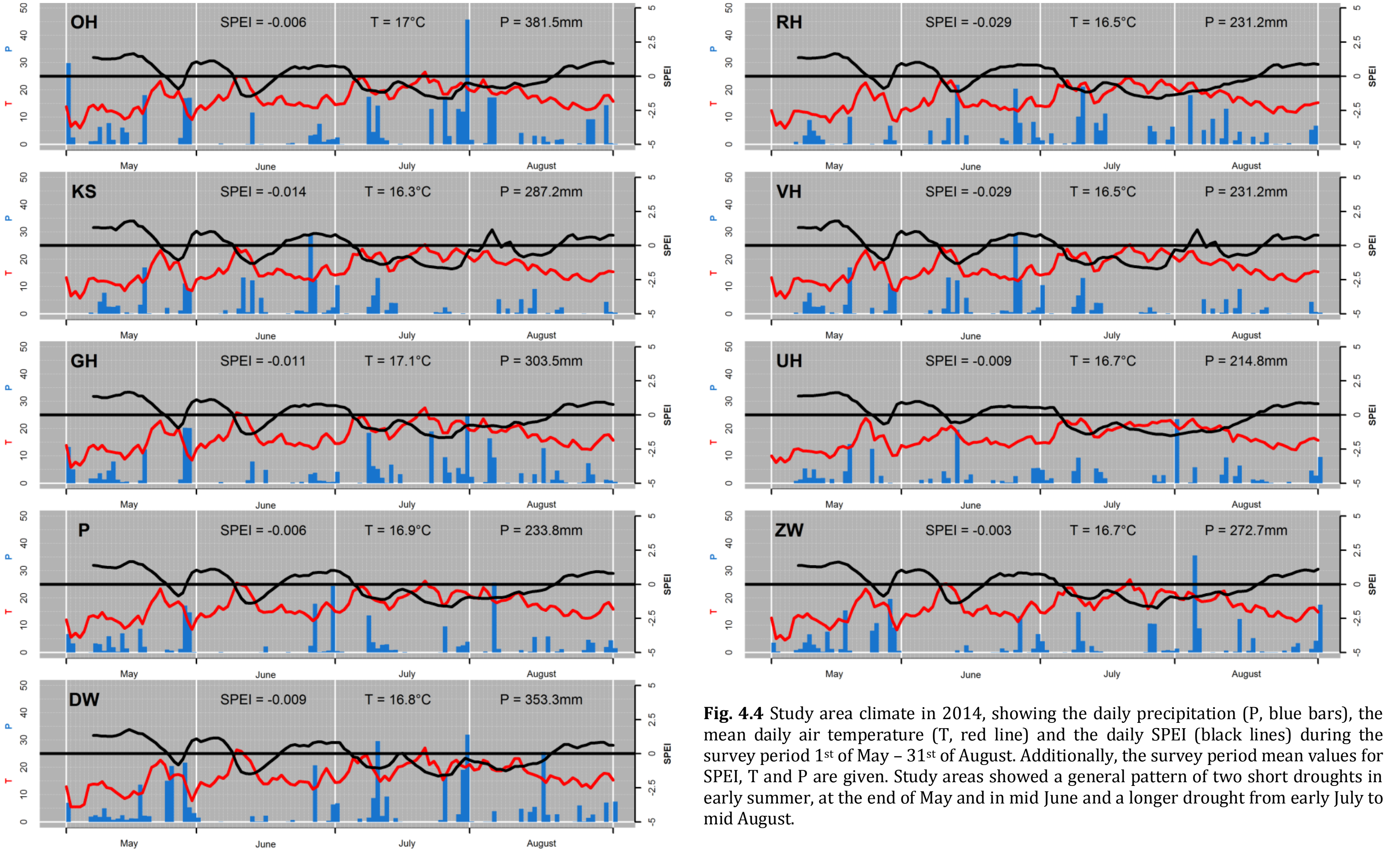


Fig. 4.4 Study area climate in 2014, showing the daily precipitation (P, blue bars), the mean daily air temperature (T, red line) and the daily SPEI (black lines) during the survey period 1st of May – 31st of August. Additionally, the survey period mean values for SPEI, T and P are given. Study areas showed a general pattern of two short droughts in early summer, at the end of May and in mid June and a longer drought from early July to mid August.

Response overview

Growth rates ranged from 5 to 370mm and were significantly higher in PR than in PS (2.5mm mean difference, $p \leq 0.001$, Fig. 4.5a). Up to 40% of the increment was damaged, independent from life history (PDYI, Fig. 4.5b). The frequency of damaged long shoot per plant ranged from 0% to 100%, with slightly higher values in PR (2.2% mean difference, $p \leq 0.001$, Fig. 4.5c). PDYI and PDL were correlated ($\rho = 0.59$), hence increased tissue damage frequency often, but not necessarily, went ahead with higher damage severity.

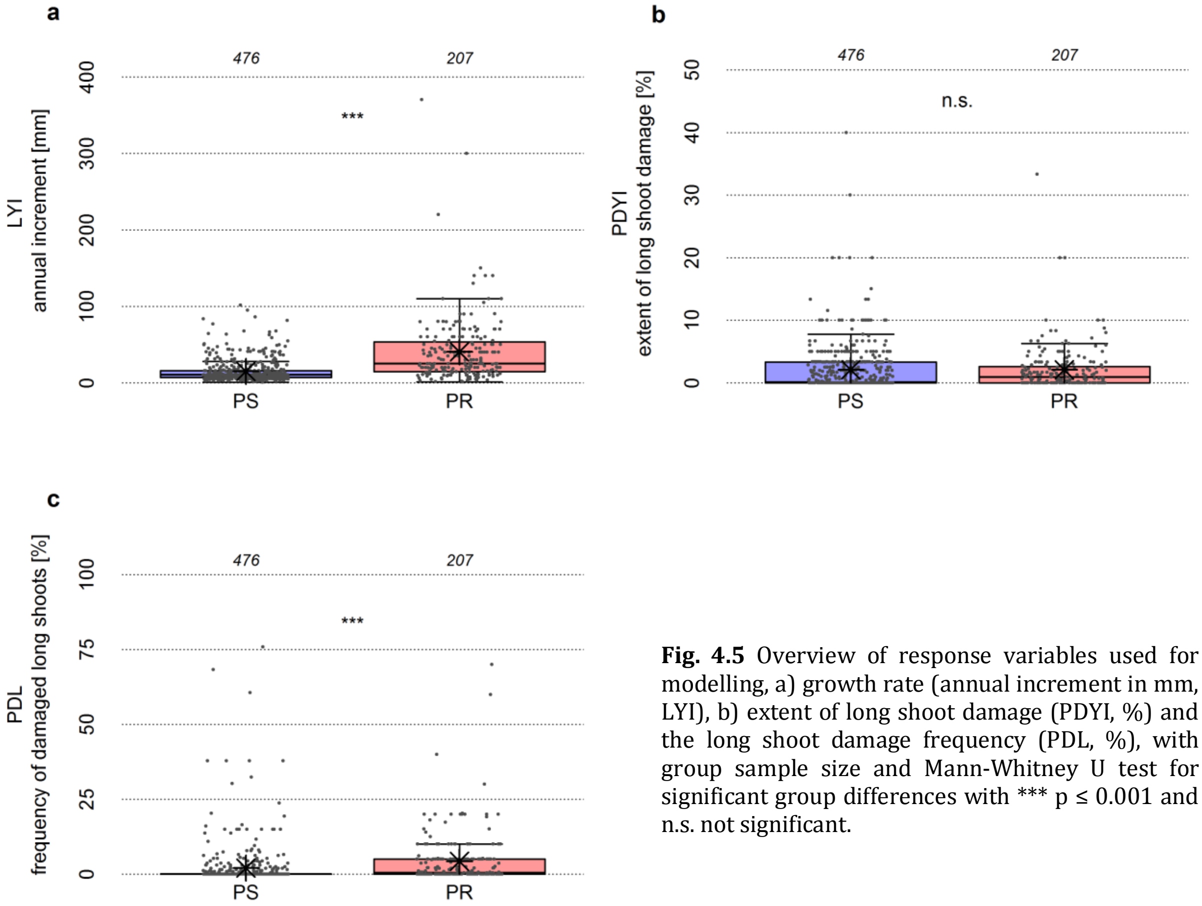


Fig. 4.5 Overview of response variables used for modelling, a) growth rate (annual increment in mm, LYI), b) extent of long shoot damage (PDYI, %) and the long shoot damage frequency (PDL, %), with group sample size and Mann-Whitney U test for significant group differences with *** $p \leq 0.001$ and n.s. not significant.

Effects of drought on young *Calluna* plants

None of the tested climate variables had a single significant effect in one of the models. Generally, LYI was rather affected by life history and N deposition than by climate ($m_{\text{nitro x life}}$ R^2=0.36, full model $R^2 = 0.39$), PDYI responded not considerably to any of the tested fixed term combinations (full model $R^2 = 0.07$), and PDL showed strong interaction effects of life history, N deposition and climate (full model $R^2 = 0.39$, Table 4.2).

LYI was significantly higher in NoD_2014 compared to D_2014 (mean difference 19.4mm, $p \leq 0.001$) and MaxD_10YEAR (14.1mm, $p \leq 0.05$, Fig. 4.6). From the moderate drought (D_2014) to severe drought (MaxD_10YEAR), LYI showed a weak positive mean difference (5.3mm, $p \leq 0.001$), due to some outliers with extraordinary growth rates under MaxD_10YEAR. Unless considering those outliers, the majority of plants had a very low growth rate under the conditions of MaxD_10YEAR.

A LYI of 0 did not occur in the original data, as I only sampled plants alive in 2014, but the model predicted some plants without growth which can be assigned as dead. This mortality rate is 7.7% for NoD_2014, 24.1% for D_2014 and 41.8% in MaxD_10YEAR.

PDL increased significantly from NoD_2014 to D_2014 (11.8%, $p \leq 0.001$) and even more to MaxD_10YEAR (24.1%, $p \leq 0.001$). Under the conditions of MaxD_10YEAR the majority of plants (52%) had all long shoots affected by tissue damages (Fig. 4.6).

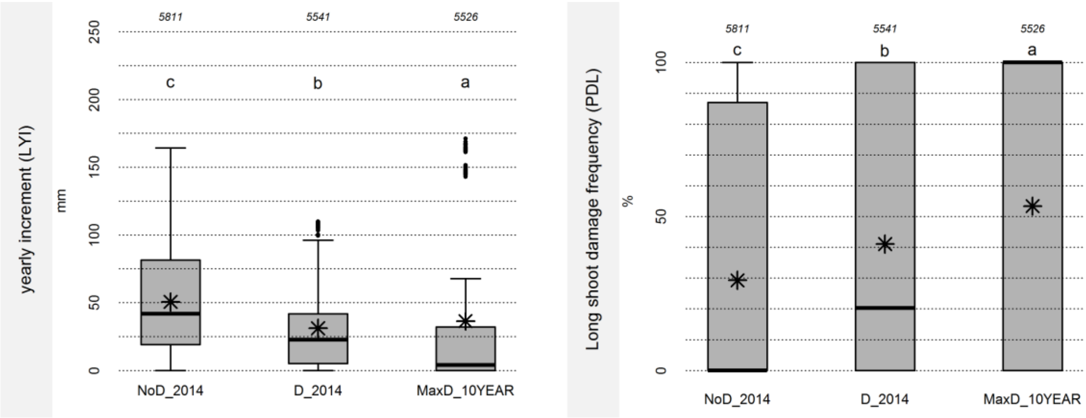


Fig. 4.6 Yearly increment and long shoot damage frequency in the three climate scenarios NoD_2014 representing the coldest and wettest conditions in 2014, with SPEI = 0, T = 16°C and P = 386mm; D_2014 representing the driest conditions in 2014, with SPEI = -0.03, T = 17°C and P = 215mm; MaxD_10YEAR representing the driest conditions in 2011-2020, with SPEI = -0.05, T = 20 and P = 41mm. Stars are indicating means. Significance codes are based on a Kruskal multiple comparisons of means test and indicate significant differences with $p \leq 0.05$. Sample sizes of groups are given above the boxes in italics.

Responses of seedlings (PS) and resprouted plants (PR) to drought

Life history explained considerable parts of LYI variance ($R^2\ m_{life} = 0.31$), although the proportions of variance explained by random terms (study area and plot) were quite high, too (conditional $R^2\ m_{life} = 0.50$, Table 4.2). The additional explanatory power of including climate was relatively low, although the significant interactions of life history with P and with SPEI (both with $p \leq 0.01$) revealed slight differences of growth rates under drought in seedlings and resprouted plants (Fig. 4.7). But those are mainly due to the generally higher growth rates in PR compared to PS in the original data, which were even more pronounced in the models (LYI mm mean differences in original data/m_{life}/$m_{nitro\ x\ life}$/m_{LYI}: 2.5/10.8/7.7/11.2, all with $p \leq 0.001$). The predicted differences between PR and PS decreased with increasing drought (Fig. 4.7), mainly due to the generally lower growth rates under MaxD_10YEAR. The majority of PR (51%) died under the severe drought conditions of MaxD_10YEAR, but the remaining showed a high variation and the potential to reach growth rates similar to those under NoD_2014. PS LYI was similar under MaxD_10YEAR, but with more distinct outliers and a lower mortality rate (34%).

Table 4.2 Explanatory power (R^2) of partial and full models. R^2 values >0.10 were highlighted in bold font.

	LYI			PDYI			PDL		
	R^2	**Cond. R^2**		**R^2**	**Cond. R^2**		**R^2**	**Cond. R^2**	
Random - only model **m_{null}**	<0.01	**0.28**	1)	<0.01	**0.25**	1)	<0.01	**0.19**	
N deposition model **m_{nitro}**	0.03	**0.28**	1)	<0.01	**0.25**	1)	<0.01	**0.21**	
Life history model **m_{life}**	**0.31**	**0.50**	1)	<0.01	**0.25**		**0.13**	**0.45**	1)
Life history and N model **$m_{nitro\ x\ life}$**	**0.36**	**0.50**	1)	<0.01	**0.26**		**0.15**	**0.47**	1)
Full model	**0.39**	**0.52**	1)	0.07	**0.32**	1), 2)	**0.39**	**0.56**	1)

1) residual diagnostics: Residuals vs. Predicted value distribution: slight quantile deviations detected, but acceptable. 2) not used for predictions and plots: explanatory power (R^2) was too low

PDL showed a high study area- and plot-specific variation (m_{null} cond. R^2 = 0.19). The explanatory power improved significantly with including the climate effects in the full model (cond. R^2 $m_{nitro\ x\ life}$ = 0.47, cond. R^2 m_{PDL} = 0.56, Table 4.2). PDL was higher in PR than in PS in the original dataset and also in the partial models m_{life} and $m_{nitro\ x\ life}$ (% mean difference 2.2/12.5/5.2, respectively, all with $p \leq 0.001$), but in the full model, there was a higher PDL in PS than in PR (11.9% more, $p \leq 0.001$, Table 4.3). The reason is that drought significantly increased tissue damages in PS and reduced it in PR (Fig. 4.7). There was a very low PDL in PS under NoD_2014 ($p \leq 0.001$), but it increased for 49.6% in the mean from No_D_2014 to D_2014, and another 18.5% to Max_D_10YEAR, with all long shoots affected in the vast majority of PS (68%). In contrast, in the same scenario, only a third of PR plants (33.3%) had all long shoots affected, the remaining showed a very high variability. Due to the extended prediction range of the climate variables in the scenario MaxD_10YEAR and the higher proportion of PS affected there, PS PDL was now predicted to be higher than that of PR.

There was no effect of life history on PDYI (Table 4.2), but the correlation between PDYI and PDL was higher in PR (ρ=0.67) than in PS (ρ=0.46), resulting in a higher probability for a high-severe suffer with high tissue damage frequency in PR than in PS.

The high variability in predictions showed individual plant-, plot- and area-specific unexplained variance, which was much higher in PR than in PS and higher in PDL than in LYI.

Table 4.3 Scenario differences in predictions, given as mean differences and their significances (non-parametric Mann Whitney U-tests for the simple two-group PR-PS and high N load-low N load comparisons, Kruskal multiple comparison of means for the more complex comparisons). *** p≤0.001

	LYI	**PDL**
Difference PR - PS		
PR - PS	11.2***	-11.9***
PR - PS difference under low N deposition	18.6***	14.6***
PR - PS difference under high N deposition	3.9***	-38.2***
N deposition		
Increase from low to high-load scenario	21.2***	27.3***
PS: increase from low to high N-load scenario	28.5***	53.9***
PR: increase from low to high N-load scenario	13.9***	1.0***
Drought scenario differences		
NoD - D_2014	19.4***	-11.8***
NoD - maxD_10Year	14.1***	-24.1***
D_2014 - maxD_10Year	-5.3***	-12.3***
PS: NoD - D_2014	9.1***	-49.6***
PR: NoD - D_2015	28.9***	24.9***
PS: NoD - maxD_10Year	2.5***	-68.0***
PR: NoD - maxD_10Year	24.9***	20.4***
PS: D_2014 - maxD_10Year	-6.6***	-18.5***
PR: D_2014 - maxD_10Year	-4.1***	-4.5***

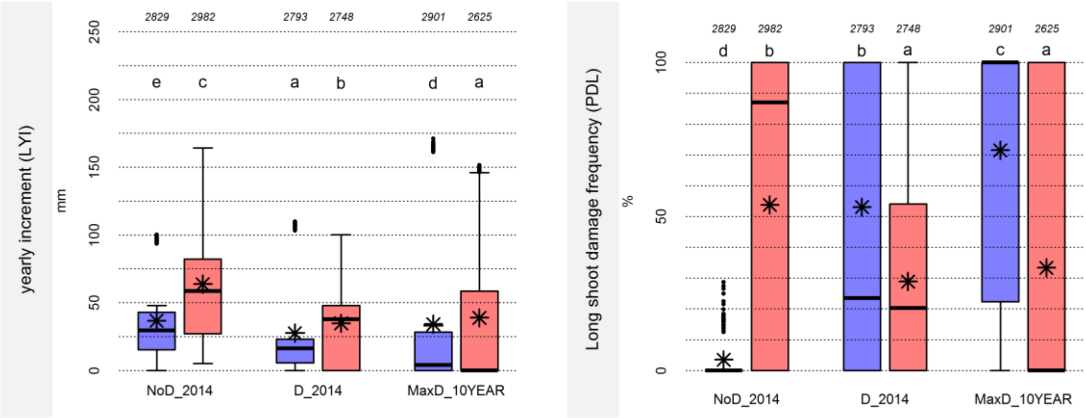


Fig. 4.7 Responses of seedlings (PS, blue) and resprouted plants (PR, red) in the three scenarios: NoD_2014 representing the coldest and wettest conditions in 2014, with SPEI = 0, T = 16°C and P = 386mm; D_2014 representing the driest conditions in 2014, with SPEI = -0.03, T = 17°C and P = 215mm; MaxD_10YEAR representing the driest conditions in 2011-2020, with SPEI = -0.05, T = 20 and P = 41mm. Stars are indicating means. Significance codes are based on a Kruskal multiple comparisons of means test and indicate significant differences with p≤0.05. Sample sizes of groups are given above the boxes in italics.

Nitrogen deposition affecting *Calluna* recruitment under drought

N had no effect on LYI, PDL or PDYI in the partial models m_{nitro} ($R^2 < 0.05$), but revealed a strong interaction effect with life history for LYI ($m_{\text{nitro x life}}$ $R^2 = 0.36$), and weaker for PDL, too ($R^2 = 0.15$, Table 4.2). In the full models, high N depositions showed complex effects.

The most pronounced effect is the 'fertilizing effect' which generally increased LYI for 21.2mm ($p \leq 0.001$) from the low-load ($10kg*ha^{-1}*yr^{-1}$) to the high-load scenario ($25kg*ha^{-1}*yr^{-1}$, Table 4.3). Thereby, this growth boost effect was stronger in PS (+28.5mm, $p \leq 0.001$) than in PR (+13.9mm, $p \leq 0.001$), and may explain the outliers in Fig. 4.7. The high N-load-induced growth boost varied among the drought scenarios. Whereas PS growth stimulation was more pronounced under drought (D_2014 & MaxD_10YEAR), PR showed it only under NoD_2014. Under drought, PR growth was reduced under high N, and for the moderate drought scenario (D_2014), this reduction was significant (high N–low N LYI: -7.5mm, $p \leq 0.001$).

High N loads increased the mortality rate. Under low N, 16% of all PS and 34% of all PR died under the severe drought scenario (MaxD_10YEAR, Fig. 4.8). In contrast, under high N, a third of all PS died in each of the scenarios, independent from drought. In PR, 33% of plants died under MaxD_2014 (+33% in comparison to low-N load), but mortality rate in MaxD_10YEAR was stable compared to the low N-load. In the end, the mortality rate of seedlings and resprouted plants under high N load and drought (MaxD_2014 and MaxD_10YEAR) was similar (33%).

The differences in growth rates between PS and PR were more pronounced under low N deposition (mean difference -18.6mm, $p \leq 0.001$) than under high N load (-3.9mm), due to the generally higher growth rate of PR under low N but an indifferent and highly variable growth rate response in the scenarios under high N for both, PS and PR.

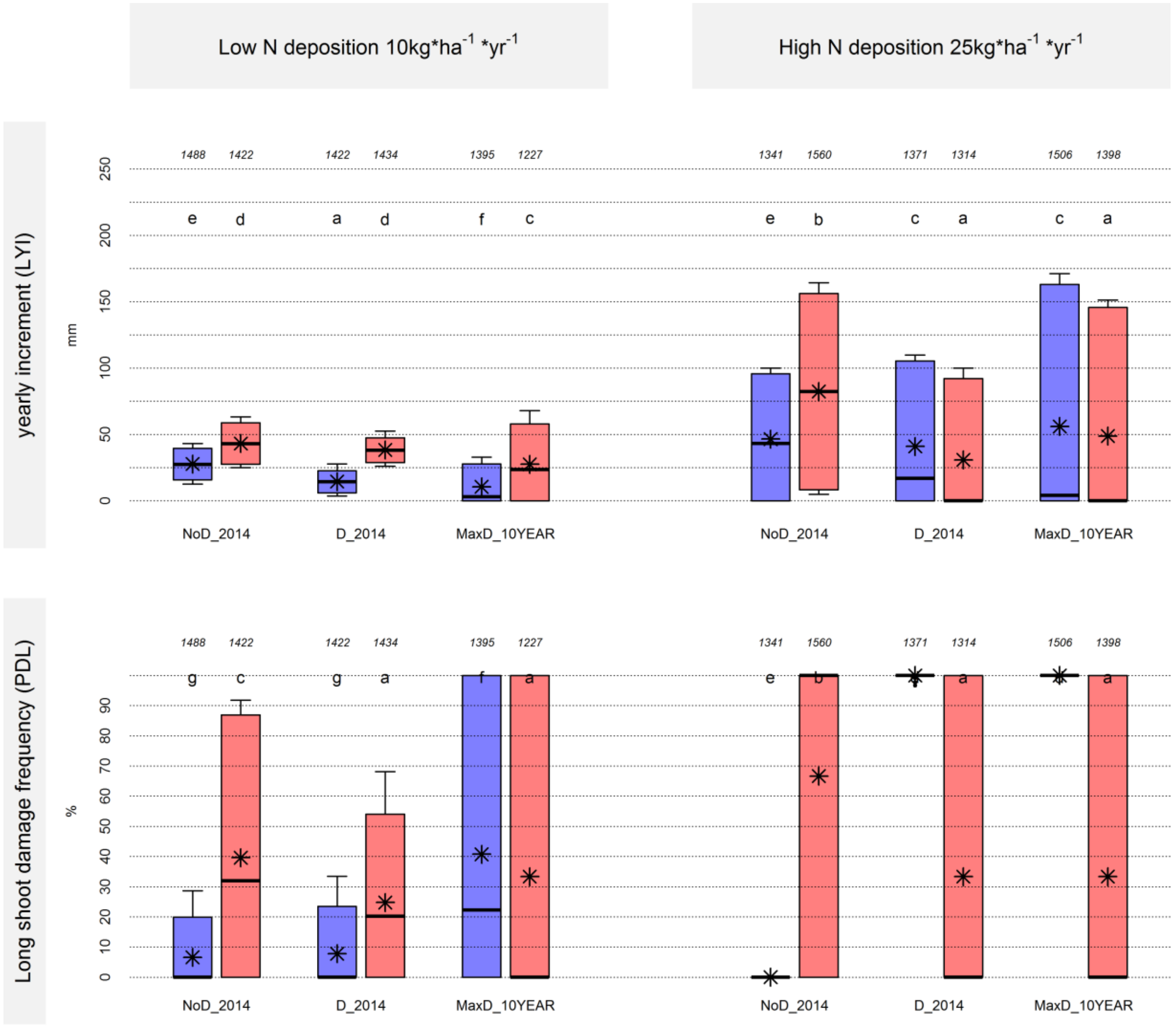


Fig. 4.8 Effects of life history (PS: blue bars, PR: red bars) and low (lefthand) or high (righthand) N deposition on yearly increment and long shoot damage frequency, for the three scenarios: NoD_2014 representing the coldest and wettest conditions in 2014, with SPEI = 0, T = 16°C and P = 386mm; D_2014 representing the driest conditions in 2014, with SPEI = -0.03, T = 17°C and P = 215mm; MaxD_10YEAR representing the driest conditions in 2011-2020, with SPEI = -0.05, T = 20 and P = 41mm. Significance codes are based on a Kruskal multiple comparisons of means test and indicate significant differences with p≤0.05. Sample sizes of groups are given above the boxes in italics.

Under high N, growth rates were highly variable. Although the model revealed that growth rates were significantly reduced from NoD_2014 to MaxD_2014 and MaxD_10YEAR independent from N load (Table 4.3), high N loads increased the variability in LYI towards drought, indicating that interacting effects of high N-induced growth boost and drought-induced growth reduction were determining the individual plant-specific growth. As a consequence, in PS, drought-induced growth reduction could be compensated and even superimposed by high N growth boost. Some few PS even reached the highest growth rates under severe drought conditions and high N. Thereby, LYI showed a slight significant reduction in the mean from No_D2014 to the other both, but there was no difference between MaxD_2014 and MaxD_10YEAR. However, although the mortality rate of PS was stable with 34% in all scenarios, the boxplots suggest an increasing proportion of low growth rates with increasing drought (Fig. 4.8), indicating that the potential for the compensation of drought-induced growth reduction decreases with drought.

In contrast, the high N-induced growth stimulation in PR was restricted to NoD_2014 and only some few plants in the drought scenarios, but was less sufficient for compensating the drought-induced growth reduction.

High N loads increased PDL for 27.3% ($p \leq 0.001$, Table 4.3), but much more in PS than in PR (PS: +53.9%, PR: 1%, both $p \leq 0.001$). There was a scenario- and life-history-specific reaction to drought under the varying N depositions. Under low N, PS showed only marginal tissue damages, not differing between NoD_2014 and MaxD_2014, and significantly less than the damages of PR. Under severe drought (MaxD_10YEAR), the damages are predicted to strongly increase in PS, where those of PR got reduced (Fig. 4.8). With high N, all PS had the maximum PDL under drought (D_2014 & MaxD_10YEAR), whereas PR tissue damages were only high under non-drought conditions (NoD_2014). There, two thirds of all plants had tissue damages on all of their long shoots, but the rate halved under drought (D_2014 and MaxD_10YEAR). Hence, under high N load, tissue damages in PR occurred rather under non-drought conditions.

4.4 Discussion

How does drought during growing season affect young *Calluna* plants?

In the survey year 2014, two moderate droughts in early summer and a more severe drought in mid-late-summer (July to the mid of August) occurred. Due to the duration and the severity, the latter can be held responsible for the drought-induced vitality suffer detected in this study.

Based on the survey year growing season conditions (1st of May to 31st of August), I modelled young *Callun*a plant responses towards three drought scenarios, representing the 1) wettest and coldest conditions during the survey year growing season, 2) moderate drought conditions, with the driest conditions measured in the growing season 2014, and the 3) most severe drought conditions *Calluna* plants were potentially recently faced with in the North German Plain.

The results confirm that droughts during the growing season reduce the growth rate and increase the tissue damage frequency of young *Calluna* plants considerably, supporting the hypothesis and the findings of other studies (Albert et al. 2012; Chavez et al. 2002; Gordon et al. 1999; Southon et al. 2012). Surprisingly, the third vitality attribute, the severity of long shoot damage, could not be explained by life history, N deposition or climatic conditions validly in the models as the explanatory power was too weak.

Contrary to the expectations, some young *Calluna* plants increased their growth rates even under strong drought conditions, a phenomenon already observed in other studies (Bannister 1964a, b; Gobin et al. 2015; Ibe et al. 2020). This is due to the very high tolerance towards water shortage and little or no reaction of stomatal conductivity reduction observed there, suggesting the maintenance of photosynthesis activity (Bannister 1964b; Gobin et al. 2015). Albert et al. 2012 emphasized that *Calluna* withstands enduring water shortages with preserving photosynthesis on a low level, without tissue damages. The results confirm this, and even under the most severe drought conditions I modelled, many plants were able to survive. As a consequence, the establishment of young *Calluna* plants is hampered, but not generally restricted under drought.

The role of regional drought adaption potentials is a factor that contributes to a better understanding of drought resistance and its variability across studies and regions. Provenance-specific drought resistances have been found in several species, e.g. beech (Rose et al. 2009), and is also reported for *Calluna*, with a higher drought resistance in subcontinental plant provenances than in plants from Atlantic heathlands (Ibe et al. 2020; Meyer-Grünefeldt et al. 2016). Plants from subcontinental provenances showed no growth reduction under drought, enabling for a competitive advantage and additionally provided higher sclerenchymatic tissue contents, a morphological adaption for a higher drought resistance (Ibe et al 2020). Such adaptions to regional drought conditions may explain the varying stomatal reaction sensitivity to a specific extent, and may contribute to the explanation of the growth rate variation in the study. On the other hand, the analysis of the ten-year period shows that between-year fluctuation in drought conditions is very high in the North German Plains, and higher than those between the most oceanic and continental site. As a consequence, the probability for droughts is quite high in oceanic sites, too. Whether the adaption potential is determined by individual plant transgenerational effects (Walter et al. 2016) or by ecotype- or provenance-specific adaption potential, is still unclear. Further research is needed, in particular to determine the speed and efficiency of drought adaption mechanisms in *Calluna*.

Differ resprouted and germinated young plants in their resistance to drought?

As *Calluna* regeneration and reproduction potentials are similar throughout the range of the species (Henning et al. 2015; Mohamed & Gimingham 1970; Schellenberg & Bergmeier 2021), the plants' capacity to resprout and to germinate appears to be unrestricted under subcontinental conditions. However, seedling establishment rates are low and successful establishment seems to be limited to years of favourable weather conditions (Britton et al. 2003; Gimingham 1972; Henning et al. 2015; Lorenz et al. 2016; own observations). The study confirmed the hypothesis that seedlings indeed have a lower drought resistance than young resprouted plants.

The key trait for a plant's susceptibility to drought is the shoot-root ratio (Weiner 2004). Due to their limited root range and slower growth, seedlings have a much higher shoot-root ratio than resprouted plants and consequently should have a lower drought resistance (Meyer-Grünefeldt 2015). Indeed, I found both, seedlings and resprouted plants, to decline in growth rate under drought, but in contrast to PR, PS tissue damages increased under drought, with the consequence that half of the seedlings had all long shoots affected by drought-induced tissue damages under severe drought. Due to their mature-stage rooting system and a drought-induced growth cease, PR remained moreover unaffected, even under critical drought conditions. Hence, the critical drought limits are reached earlier in PS than in PR, confirming the hypothesis of a higher drought resistance in resprouted plants.

The growth rate measurement in the present study does not account for recovery processes after droughts. *Calluna* plants profit from favourable post-drought climate conditions and compensate for growth reduction during drought (Kongstad et al. 2012). In the 2014 climate data, droughts are mixed with non-drought periods, and after the early summer droughts, colder and wetter conditions may have induced a high increment. This may partly explain the high variation under drought and weakens the explanatory power of the relationship between growth rate and drought.

Does nitrogen deposition reduce young *Calluna* plants' resistance to drought?

High N loads stimulated growth ('fertilization effect'), resulting in higher aboveground biomass production, like evident in many other studies (e.g. Bähring et al. 2017; Bobbink et al. 1998; Gordon et al. 1999; Taboada et al. 2018; Uren et al. 1997). Drought resistance of young *Calluna* plants was generally reduced under high N, with evidence in increased tissue damages and mortality, confirming findings of e.g. Gordon et al. 1999 or Meyer-Grünefeldt 2015. Under low N deposition, the general *Calluna* drought resistance strategy with a high resistance towards drought stressors renders survival of critical drought possible, even at the cost of severe, though not lethal, damages. The same drought conditions under high N loads caused potentially lethal damage, indicating that high N loads generally decreased the drought resistance of *Calluna* plants.

There was a complex life history-specific interplay between high N-induced growth boost and drought-induced growth reduction. Seedlings potentially profited from N-induced growth boost rather than resprouted plants, compensating for the drought-induced growth rate reduction, but at the cost of critical tissue damages. Whether the biomass was produced during the drought or in the non-drought periods between could not be determined in the study, hence a conclusion to whether seedlings continue growing under drought or are able to regenerate well after drought remains unclear. However, the larger tissue damages indicate that critical drought conditions are reached earlier in seedlings than in resprouted plants.

Although the total mortality rate of seedlings and resprouted plants under high N load and drought was similar, the resprouted plants that survived often had only marginal tissue damages, indicating that more plants have been affected less severe. As a consequence, the hypothesis of seedlings rather affected by high N-induced increased drought susceptibility than resprouting plants could be confirmed.

The physiological mechanisms behind the interaction of high N depositions and drought are only partially identified yet. One explanation is the high N-induced growth stimulation which alters the shoot:root ratio, with negative consequences for the plant water balance (Meyer-Grünefeldt et al. 2015; Weiner 2004). The increased biomass production induces a higher water demand (Bannister 1964b, Garnier & Laurent 1994; Terzi et al. 2013), and as long as root biomass is not increasing as well, the water uptake capacity may be not sufficient under drought conditions. The results presented here suggest that seedlings indeed seem to be limited by this effect. Due to the extant rooting system, resprouted plants do not have such limitation problems.

Additionally, there is evidence that high N loads alter the plant response to drought by affecting the stomatal sensitivity. Gordon et al. 1999 reported that drought under high N deposition caused unsustainably high transpiration rates, what they did not observe if only drought or only N-fertilization was applied in their experiments. Ghashghaie & Saugier (1989) found that *Festuca arundinacea* plants grown under low N deposition had a higher stomatal sensitivity than plants under high N. They concluded that plants under low N had the strategy to rather avoid critical water deficits with an early stomatal closure, whereas those under high N tolerated high water deficits and continued transpiration.

The stomatal sensitivity is controlled by abscisic acid (ABA) contents in leaves and roots (Bresinsky et al. 2008), but there is an insufficient knowledge how N availability affects ABA concentrations and thus affects the stomatal sensitivity. Both, high and low levels of N are reported to increase stomatal sensitivity (Ghashghaie & Saugier 1989; Song et al. 2019; Yang et al. 2012). In a *Populus* species, high N concentrations increased ABA and drought resistance (Song et al. 2019); other studies confirmed a positive effect of high N to mitigate effects of drought (Dulamsuren & Hauck 2021; Yang et al. 2012).

The results presented here show that stomatal sensitivity in *Calluna* seedlings seem to decline under high N and drought, supporting the findings of (Ghashghaie & Saugier 1989), resulting in a poorly restricted photosynthesis activity even under severe drought, with lethal consequences. *Calluna vulgaris* is a competitor/stress tolerator (CS) plant, with a very high tolerance towards water shortage, and its drought resistance strategy is moreover a tolerance strategy, comprising the maintenance of photosynthesis on a quite high level, even under drought, for the cost of a high risk for dying. This strategy seems appropriate in terms of competing with other heathland species, such as *Deschampsia flexuosa* or *Molinia caerulea* (Albert et al. 2012; Britton et al. 2003; Friedrich et al. 2012; Kreyling et al. 2008). The potential to recolonize recently disturbed sites quickly and to tolerate drought stress within that time is a crucial determinant for the successful establishment process and the initiation of early-successional heathland structures. Under high N, this strategy is limited by the disability of young *Calluna* seedlings to prevent for exceeding the physiological drought limit.

The role of the high-N induced growth boost may be beneficial on sites with *Calluna* dominance and no or only little grass cover, but offers risk for high seedling mortality under drought, thus contributing to the increased grass dominance of heathlands under high N loads (Britton et al. 2003; Diemont et al. 2013).

In contrast, resprouted plants ceased growth and suffered less damage under drought and high N loads, thus showed a completely different drought resistance strategy. They avoid water stress rather than tolerate it, by persisting unfavourable drought with preserving the existent biomass, but not increasing it. This confirms findings of Gordon et al. 1999 who found that Building stage *Calluna* height, density and increment was reduced under drought and very high N load ($50^{kg}/_{ha*a}$). Following the finding of Ghashghaie & Saugier (1989) that *Festuca arundinacea* plants limited by N showed the drought stress avoidance strategy and those grown under high N rather tolerated drought stress; this might indicate that N-limitation determines the strategy in *Calluna* plants as well. Seedlings may reach levels of N saturation and limitation by other photosynthesis source materials earlier than resprouted plants, as the latter have more reserves in their roots and stem bases, and additionally have a better supply with their mature rooting system. Hence, as long as N is the limiting nutrient, the tolerance strategy, at the cost of lethal damage, is prevailing. In terms of the limitation by other factors, e.g. carbon starvation due to drought-induced stomatal closure over a longer time (Sevanto et al. 2014), growth ceases or tissue damages occur, like observed for the resprouted plants in this study, but further studies are needed to prove this.

Another reason for the high tissue damages under non-drought conditions may be undetected *Lochmaea* damage. A re-inspection of the dataset revealed that tissue damages were generally higher in areas where *Lochmaea* (heather beetle) infestation was detected, namely in the oceanic German Northwest, with generally higher mean daily precipitation rates, cooler conditions as well as higher N depositions, factors known to promote *Lochmaea* outbreaks (Britton et al. 2001; Melber & Heimbach 1984; Power et al. 1998; Stevens 2018, Taboada et al. 2016; Webb 1986). Larvae and adult *Lochmaea* beetles feed on *Calluna* leaves, as well as on young stems and bark (Gimingham 1972), and although I removed plants with a validated *Lochmaea* damage, I cannot exclude that some tissue damages may be induced by *Lochmaea*. It is unclear whether the dataset may be biased towards generally reduced vigour due to severe past year(s) *Lochmaea* damages, as I have no information whether the resprouted plants may originate from Mature plants severely affected by the beetle, and whether a resprouted plant's vitality is generally affected by past year(s) heather beetle attacks, or the extent of reduced vitality as a result of former droughts.

The higher prediction range under high N loads indicated that other factors' influences on the *Calluna* drought reaction increased with N. Positive and negative plant- or area-specific effects are interacting with climatic and edaphic conditions and cause a more complex situation. As a consequence, individual plant-specific water uptake efficiency and extent of the rooting system determines the plant's performance under drought conditions and high N.

Electronic Supplementary Material

ESM 4.1: Model diagnostics (html-files with Rcodes and outputs)

Chapter 5:

Synthesis

5.1 New insights into North German dry lowland heathland ecology

Heathland plant community ecology and floristic patterning

The present study assessed the commons and differences in species composition and patterns of structural and species diversity across dry lowland heathland habitats in the North German Plains. The results revealed that patterns in species composition and vegetation structures are shaped primarily by the complex interaction of edaphic conditions and site history, but only weakly by climate. As a consequence, the seven plant communities identified in Chapter 2 represent stages of heathland development on two edaphically determined successional pathways: 1) the psammophilous pathway representing succession on poor drift sands in young heathlands, often with an inland dune-like character and 2) the consolidated heathland pathway, representing the typical historical heathlands, on somewhat developed, but still poor sandy soils.

Species inventory was rather determined by edaphic conditions and *Calluna* density than by development stage. Although the study showed that there are development-specific species assemblages, there were only few species showing a strict association with one of the heathland development stages, e.g. *Placynthiella oligotropha* for early lichen-rich stages, or the open sand grassland group for mature stages, as well as *Galium saxatile* for late Mature or Degeneration stands.

The results do not support that lichens of the genus *Cladonia* are generally assigned to be typical for Late Mature and Degeneration stages (e.g. Gimingham 1972), as they occurred from Pioneer up to Late Mature stage, as typical, high frequent species in the lichen-rich psammophilous heathland pathway. The prevailing life form group in early heathland developments stages are the lichens, due to favourable conditions in the dry, exposed and nutrient-poor environment of pioneer drift sands. The persistence of lichens during later succession is determined by the presence of strong competitors, such like *Deschampsia flexuosa* or pleurocarpous mosses (Müller et al. 1993), but also suitable soil conditions. Hence, with persisting soil and interspecific competition conditions, lichen-rich synusia are persistent over one or even more *Calluna* lifetimes. Hence, they are rather characteristic for an edaphically determined heathland pathway than a specific *Calluna* age-related heathland development stage.

Additionally, our results show that many of the vascular species assigned to be typical for heathlands in the matter of nature conservation status assessment (c.f. Chapter 1.3) are moreover distributed over a wide range of heathland development stages, without a specific informative value to the habitat quality. Species like *Hypochaeris radicata, Hieracium pilosella, Agrostis spec., Carex pilulifera, Deschampsia flexuosa* and *Rumex acetosella* did occur in almost all of the communities; hence they provide no further informative character than being a species occurring in heathlands.

The findings of this study revealed that the informative value of species composition concerning habitat quality increased considerably with considering also vegetation structures. Thereby, the formation of either *Calluna* mosaic or dominance type is determined by site history, recent management and edaphic conditions, but is not associated with species diversity or heathland development stage. As a consequence, dominance stands, which are often built from even-aged *Calluna* and are therefore often poor in age structures, are not *per se* poor in species, too. The results presented in Chapter 2 offered that lichen-rich Building and Mature dominance stands may lack in *Calluna* age diversity, but host a large number of threatened lichens, with a high value for the local species pools.

Calluna mosaic heathland communities are not restricted to early-stage or degeneration stages only (c.f. Gimingham 1972, van der Ende 1993), but are usually rich in *Calluna* age structures, and often in life form group diversity, too. Hence, they potentially harbour a high species diversity, unless the gaps between *Calluna* bushes are filled with only one dominant species, such like *Molinia caerulea, Deschampsia flex*uosa or *Hieracium pilosella*.

Heathlands are generally poor in species (Ellenberg & Leuschner 2010) and the results presented here confirm this in terms of vascular plant diversity. On the other hand, the results support that cryptogam diversity is high in the psammophilous heathland pathway.

These findings emphasize the need for maintaining and restoring early-successional stages with the highest potential to harbor not only a high species diversity, but also to host many threatened species, in particular lichens. This is a finding which is not new and is reported several times before (e.g. recently Haugum et al. 2021, Webb et al. 2010), but it highlights again the need for the provision of suitable early-stage habitat conditions, achievable with high-intense (soil) disturbance (e.g. de Graaf et al. 2009; Walmsley & Härdtle 2021).

The present study confirms that especially the low productive stages of *Corynephorus* grassland-heathland mosaics on bare drift sands provide a suitable host for a lot of threatened species (Müller et al. 1993). Such sites are typical for many former military training areas in the German East. Although we found only weak support for a floristic-based distinction of Atlantic and subcontinental heathland plant communities, the extent and the wide distribution of such *Corynephorus* grassland-heathland patches on former military training areas in the suboceanic – subcontinental German East may be not only determined by the site history, but also by climate. Droughts are potentially more severe there (c.f. Chapter 4), in particular under inland dune-like conditions, where the specialists of pioneer grasslands, especially many lichens, favour from the reduced competitive power of many typical Atlantic heathland species, which are only able to reproduce and establish in years of favourable climate. Additionally, many processes, such like raw humus accumulation and podsolization rates are slower under subcontinental conditions, because drought reduces mineralisation rates and leaching processes (Lache 1976; Härdtle et al. 1997). As a consequence, the seral progression of sandy grasslands to heathlands and later to woodlands may be delayed due to marginal conditions for typical Atlantic dry heathland species, with a resulting longer persistence of grassland-heathland mosaics.

Another reason may be the lower N loads in East Germany than in the northwestern part, as high N loads inhibit lichen growth, mainly due to the shift of competitive advantages to more productive species and high N-induced metabolism alterations (Carter et al. 2017; Johansson et al. 2010; Gutiérrez-Larruga et al. 2020; Hauck 2010; Müller 1993; Van Herk et al. 2003). The military training created large sand drift areas with prevailing early successional stage conditions in the past century (Ellwanger & Ssymank 2016), providing favourable conditions for the establishment of diverse and stable populations and species pools for the lichen-rich heathland succession stages present today. They are threatened by succession, unless intense management counteracts.

The *Calluna* life cycle revisited

The results presented in Chapter 3 provide new insights to age-dependant vitality changes during the *Calluna* life cycle. Thereby, the visual attributes such like the flowering intensity or the proportion of dead, bare leading long shoots as well as annual increments are rather determined by the aboveground plant age than by the total plant age, but they are not completely independent from the latter.

Regeneration processes provide the potential for improving the vigour on the short term, but the term ‘rejuvenation’ may be misleading, as it suggests a re-entry in a highly vigorous regeneration life phase again, similar to an undisturbed growth. The results presented in this study clearly show that disturbance indeed increases the vigour, and that a post-disturbance regeneration by resprouting may produce a similar growth habit than undisturbed plants, but the highly vigorous time is limited to a shorter timespan than that of undisturbed plants. Additionally, the capacity to resprout vigorously is restricted to quite young plants up to 15 years, confirming former studies (e.g. Mohamed & Gimingham 1970). Hence, even if there were mechanisms supporting repetitive cycling from vegetative growth, they may not produce highly vigorous plants on the long-term.

The reasons for that are determined in habitual shifts induced by plant ageing and disturbances, more specifically in the reduction of the primary central rooting system to a decentral branch-wise one. This process goes ahead with general shifts in the capacity to regrow to mature plants again. In young plants resprouting, the clusters of shoots emerging are close together and provide the highest post-disturbance vitality. In older plants, resprouting may still take place, but due to the shift from the primary to the adventitious rooting system, the stems emerging from the buds will rather form dense regeneration cushions than distinct bushes. As a consequence, regeneration may proceed up to high total plant ages, but the total vigour reduces.

Resprouting from young plants with an intact primary rooting system induces increased root development from the stem bases and therefore initiates adventitious rooting, with a subsequent death of the primary root. As a consequence, mature plants originating from resprouting seldom provide an intact rootstock any more. Hence, the present study failed in determining total plant life spans on the basis of growth ring counts, but the modelling results suggest a total life span of about 30-45 years, which is in accordance to those reported from British heaths (Gimingham 1972). Compared to the growth phase persistence there, the results from the present study suggest a slight acceleration of the time *Calluna* needed to grow from of a seedling to the mature plant. This is maybe due to general environmental conditions varying between British heathlands in the 1970s, where the *Callun*a life cycle was originally referred to, and the suboceanic - subcontinental German heathlands today, with influences of airborne N depositions and climate change. High N depositions are found to increase the yearly increment (c.f. results in Chapter 3 and 4); hence a faster growth may explain the accelerated growth to Mature and Degeneration stages. Additionally, high N loads increased the vigour in resprouted plants on the short term, as it triggers flowering intensity and biomass production, but could not compensate for the fast decline in vitality after 10-15 years though.

On the other hand, drought and high N inputs reduce the regrowth of resprouting plants (Chapter 4); hence recovery times are determined by summer drought conditions as well. Dieback induced by drought occurs more often under subcontinental climate (Marrs & Diemont 2013), hence the longevity of *Calluna* plants may be reduced as a consequence of frequent severe droughts. The results of the study presented in Chapter 3 support this, but further studies are needed to assess drought-induced demographic changes on the long-term.

However, the analysis provided in this thesis found no evidence that the total life span of *Calluna* in the North German Plain heathlands is generally either reduced by faster growth, drought-induced early dieback or elongated by a vegetative (sub)cycle compared to other regions. Due to the complexity of the field dataset and probable trade-off effects of components influencing the *Calluna* life, further research is needed, specifically long-term studies on *Calluna* plant individuals. Consequently, the answer to the question whether high N loads reduce the highly vigorous life time by accelerated ageing or altered responses to drought remains unclear. Local site managers reported that, e.g. for the Lüneburg Heath (pers. comm. D. Mertens, VNP), but to the best of my knowledge there is no study confirming this scientifically. Additionally, effects of general higher temperatures on the life cycle are not studied yet, but are not unlikely as growth rates and developments are reported to be slower under colder climate (Haugum et al. 2021).

Many studies analysed the (potentially) cyclical dynamics in heathland demographics, but up to now, there is no satisfactory answer to the question whether regeneration processes in heathlands may have a 'repetitive cycle' character or *Callun*a life is of a seral and limited character (Gimingham 1972, 1988; Marrs and Diemont 2013; Wallen 1980).

This study provided no evidence for a cyclical vegetative and generative reproduction as part of the natural long-term dynamics in dry lowland heathlands. The analysis of plant communities and their soil-related pathways of heathland development clearly show that the succession pressure from grasses and trees increases with time, thus reducing the competitive power of *Calluna*. However, very poor inland-dune-like conditions on drift sand areas with a military training history show a delayed succession, where cyclical regeneration and reproduction seems to be feasible for several *Calluna* generations, but not on the long-term.

Repetitive cycling without generative reproduction but with several consecutive resprouting cycles could not be verified in the present study. The first resprouting may regrow to a plant with a habit similar to a plant grown from seed, but it is unlikely that further subsequent resprouts will do so, as the results presented in Chapter 3 show that the disturbance-induced modifications of the root biomass allocations from the primary rooting system to the decentral adventitious one induces a different plant habit after resprouting, building rather flat cushions than hemispherical shapes.

Repetitive cycling on a low productive level with layering plants continuously creeping and rooting, like reported for Swedish and Scottish heathlands (Gimingham 1972, Wallen 1980, Webb 1986), seems to be the most likely type of any natural cyclical regeneration processes in heathlands. Such 'immortal' stand characteristics are reported for heathlands on peat in Northeast Scotland, but also for sand dunes in South Sweden (Wallen 1980), but the study presented in Chapter 3 provides no evidence, neither for the existence nor the absence of such ‘immortal’ layering processes. Layering is a common process in North-German dry lowland heathlands, with the potential to form quite stable-state stands, but the results do not allow for any assessment of persistence times, as the total plant age was no more detectable. However, concluded from observations of successional old heathland stages, with prevailing layering plants, *Calluna* immortality seems unlikely due to the constant reduction of *Calluna* biomass with age of layering plants. Although the layering phase represents the last life phase before plant death, it may provide low-productive, but stable biomass production and flowering, enabling for the provision of heathland ecosystem functions on a minimum level, but potentially stabilizing heathlands suffering from diebacks and low establishment rates (Chapter 3).

Calluna recruitment response to drought and high airborne nitrogen loads

The immediate effects of droughts on *Calluna* comprise tissue damage and dieback, but more complex interactions with plant vitality and long-term effects are not well understood. Droughts can alter *Calluna* biomass allocation (Schuerings et al. 2014), may induce earlier biomass production in the subsequent spring and increase frost susceptibility (Gordon et al. 1999). Droughts can also delay or reduce the flowering period (Jentsch et al. 2009; Nagy et al. 2013). It has been shown that drought affects the *Calluna* root-associated mycobiome, with as yet unknown consequences for the plants’ vitality, soil nutrient processes and heathland productivity (Dahl et al. 2021; Tobermann et al. 2008).

Drought resistance is determined by morphological and physiological traits of plants, as well as their adaptive potential, which is generally assumed to be quite high in *Calluna*, due to its wide distribution and plasticity (e.g. Albert et al. 2012; Backhaus et al. 2014; Bannister 1964a; Bartoli et al. 2013; Gordon et al. 1999, Ibe et al. 2020; Kongstad et al. 2012; Petrova et al. 2017; Walter et al. 2016). In fact, this study provides evidence that even severe drought conditions and high N loads revealed to be seldomly lethal for resprouting plants, resulting in a high potential for a fast and successful recovery after disturbances even under drought conditions. In contrast, droughts under high N lethally affected most of the seedlings.

The physiological background of the interaction between high N loads and drought sensitivity is still insufficiently understood. There is evidence that drought resistance is altered under high N loads by affecting the stomatal sensitivity. A study on *Festuca arundinacea* (Ghashghaie & Saugier 1989) revealed that plants under N-limitation reacted earlier with stomata closure under drought conditions than those under high N supply, a finding supported by the results presented in this study. The *Calluna* seedlings showed a drought-induced growth reduction under low N deposition, but not under high N loads. Stomatal regulation was probably hardly existent under high N, resulting in severe tissue damage and a high mortality rate. In contrast, the resprouted plants generally reduced growth, but had only marginal damage, indicating that they were less affected by the high N-induced stomatal sensitivity alteration. I assume N limitation to be responsible for that, because the load for N saturation in seedlings should be lower than that for resprouted plants, as the latter profit from a higher nutrient reservoir in their biomass compensating for the limitation of other nutrients. As a consequence, seedlings under N saturation have a high-risk strategy to tolerate drought, with maintaining photosynthesis and biomass production, thus potentially increasing their competitive power under moderate drought. In contrast, resprouted plants show a strategy of avoiding even moderate drought stress by a growth cease, probably induced by stomatal closure. As a conclusion, N depositions of 25kg*ha^{-1}*yr^{-1} do not induce N saturation in Mature *Calluna* plants (Walmsley & Härdtle 2021) and may increase drought resistance in resprouting plants under moderate drought, but for the cost of reduced growth and hence reduced competitive power, thus favouring plants dealing better with drought under high N loads during the post-disturbance re-establishment phase, such like *Deschampsia flexuosa* or *Molinia caerulea* (Albert et al. 2012; Britton et al. 2003, Diemont et al. 2013; Friedrich et al. 2011). This confirms former findings that re-establishment after drought-induced *Calluna* dieback altered the heathland species composition, and *Calluna* was substituted by fast-growing and more drought-tolerant grasses dominating, especially under high N deposition levels (Albert et al. 2012; Britton et al. 2003; Kreyling et al. 2008; University Hasselt 2021). It is yet unknown whether these changes will be temporary, providing shelter for the next *Calluna* generation (Marrs & Diemont 2013), or signalize a persistent loss of typical *Calluna* heathland under the conditions of frequent severe drought and high N loads. Further research is needed to assess potential accumulative effects of reduced vitality as a consequence of frequent droughts and the recovery potential for *Calluna* in years with more favourable climate.

Plants with a high adaption potential and a wide tolerance to water shortage provide a certain climate change resilience (Bannister 1964a, Richter et al. 2012). Gordon et al. (1999) and Kongstad et al. (2012) claimed such an adaptation effect after repeated drought, indicating that drought resistance is adjustable. The high adaption potential and morphological plasticity of *Calluna* may be the reason for its wide distribution, with provenance-specific adaptions to the drought conditions in subcontinental marginal populations, but the complex interactions of N depositions, drought and provenances are still poorly understood. A recent study showed that *Calluna* from subcontinental and suboceanic provenances showed different reactions to elevated VPD, indicating higher drought resistance in plants from subcontinental regions (Ibe et al. 2020), whereas other studies found no or only little effects (Meyer-Grünefeldt 2015; Meyer-Grünefeld, 2016). However, even if there was higher drought resistance in seedlings of subcontinental ecotypes, this effect is overlaid by effects of high N- induced higher drought susceptibility (Meyer-Grünefeldt et al. 2016). Further research is needed to understand the adaption potential of *Calluna* under changing climate and whether this natural potential is altered by high N depositions.

5.2 Implications for future dry lowland heathland management

The role of management for the provision of high nature conservation value heathland

The conductance and combination of several managements to ensure the habitat diversity and functionality is a great challenge in recent heathland management (Olmeda et al. 2020, Walmsley et al. 2021). The strategies need to be assessed in the context of the complex trade-offs related to different management targets, for example biodiversity protection, climate change adaptation, compensation of airborne nitrogen inputs, or the protection of landscape multifunctionality (Ibe et al. 2020; Walmsley 2021). The results presented in this thesis show that heathlands are faced with a complex situation of inter- and counteracting factors, thus it is vital to understand heathland habitat dynamics in their complexity in a changing environment. That emphasizes the need for a more detailed look on specific responses of *Calluna* to the known stressors, and how they may contribute to the overall decline in heathland habitat quality. Therefore, this study provides a specific view on the interaction of factors influencing *Calluna* vitality under field conditions to improve the understanding how they recently influence heathlands and may determine future heathland dynamics and structures. This knowledge is necessary to include the consequences of heathland management in the further planning and conduction of nature conservation measures.

Therefore, the results presented in this thesis provide some new insights into the complex determinants for heathland species composition and vegetation structures, thus helpful in understanding the heathland dynamics in North German lowlands differing across regions, characterized by different site histories, edaphic and climatic conditions, recent managements and N deposition rates, all affecting the *Calluna* demographics and vitality.

This study showed that the main determinants for heathland vegetation of high nature conservation value are 1) the provision of suitable soil conditions, favouring early-successional stages and structures as well as 2) low N depositions to increase the competitive power of *Calluna* and other low-productive, but high-value heathland species, such like threatened lichens. This study showed that species assemblages of high nature conservation value need components from structural and edaphic conditions, local species pools and favourable competition conditions, thus a suitable management has to provide the most beneficial services to achieve this. Thereby, management can only prepare the starting conditions for the seral succession, followed by initial developments that already determine the heathland successional pathways. Post-disturbance regeneration species composition depends chiefly on the soil conditions and the species pool present in adjacent sites, hence the site-specific potential for high species diversity is always determined by the surrounding habitats, a finding which highlights the need for habitat connection and the necessity to preserve local species pools (Piessens et al. 2004, 2005).

Heathland formation character is the predominant structural trait in dry lowland heathlands, as it determines either a *Calluna*-only dominance or a mosaic of dwarf shrubs and other life form groups. Heathland plant communities of a mosaic character provide a high diversity, but are prone to grass invasion (Britton et al. 2003). The conversion of heathlands to grasslands, dominated by *Deschampsia flexuosa, Molinia caerulea* or others, is among the main reasons for heathland habitat decline (e.g. Olmeda et al. 2020). *Deschampsia flexuosa* acts as the strongest competitor under suboceanic- subcontinental conditions with drought and high N and on sites with raw humus accumulation (Heil & Diemont, Britton et al. 2003), whereas under more oceanic conditions and P-limitation, it is moreover *Molinia caerulea* (Friedrich et al. 2012). Thereby, the interaction- and counteracting effects of co-occuring *Calluna* and the grasses showed that already small shifts in competitive advantages induced a conversion of heathland into grasslands (Aerts et al. 1990; Britton et al. 2003), indicating that minor changes may be sufficient to hamper *Calluna* recruitment during early successional stages and to favour grasses instead. The results presented in this study provide evidence that high N loads and drought decrease the competitive power of *Calluna* and consequently confirm that the risk of grass dominances increases then.

Whether heathland formation is a heathland mosaic or a dense dominance stand of *Calluna*, is determined by several factors, beginning with the management or disturbance type, the initial post-disturbance soil conditions, and the early post-disturbance development of the vegetation. This study showed that climatic conditions and nitrogen deposition potentially alter this early post-disturbance regeneration (Chapter 4).

Managements that induce vegetative regrowth, e.g. mowing and burning, often build dominance stands, unless they have been very open before. This is due to the dense resprout from stem bases, with the regenerating plants having a higher cover when reaching the pre-disturbance growth phase again (Fig. 3.6, p. 71).

Regeneration which is predominately from seed provides a higher probability to form mosaic stands. With a sufficient supply from the seed bank, the absence of strong competitors and moderate climate conditions (i.p. no drought), seedling-dominated regenerations sites may become dominance stands, too, especially on sites with a high fire frequency (e.g. shooting lanes on military training area Bergen, Lower Saxony, own observations).

Regeneration from seed on bare drift sands is slower than on consolidated sands, due to the better supply of water and the presence of ericoid mycorrhiza in the latter, especially when the site was previously already colonised by *Calluna* (Green et al. 2013; own observations). Bare drift sands are usually colonised by pioneer grassland species first to stabilize the mobile sands, with a subsequent slow invasion of *Calluna,* forming open grassland-heathland patches. Those successional stages with a small-scale mosaic patch structure provide the highest potential to harbour a rich pool of threatened species and a very high structural diversity, but need expensive, intensive management for the provision of suitable initial development conditions, and low N deposition rates.

Managing *Calluna* demographics under changing climate and high N depositions

To ensure suitable soil conditions and early-stage habitat conditions, intensive managements, such like mowing, burning or sod-cutting are essential, but need a careful weighing between the provision of landscape structure aspects, such like the removal of trees and providing bare drift sand landscapes, and the provision of edaphic conditions enabling heathland vegetation to succeed in the re-establishment phase. For managing heathlands successfully, a fundamental knowledge to *Calluna* ageing as well as regeneration and establishment potentials is needed. Assessments to these potentials are derived from the *Calluna* life cycle, with using visual attributes that are informative about the plant age to determine plant and regeneration age. This thesis contributes to a specified determination of age-related changes in *Calluna* habit and vigour, in particular the differences between plants grown directly from seed or regenerated after biomass disturbance (Chapter 3). Hence, with this improved knowledge, it is easier to determine and interpret *Calluna* age structures in the field, and to estimate regeneration potentials. The findings of the present study sharpen the view on the distinction of plants grown from seed or regenerated from resprouting, and this allows for explaining and predicting the persistence of highly vigorous phases. The observations and results presented in Chapter 4 explain the rapid decline of stands regenerating predominately from resprouting, which we found not predominately determined in higher N depositions, but rather the general vitality decline of resprouted plants, due to plant age – related morphological changes. However, the assessment on the role of high N deposition affecting the *Calluna* life cycle needs further research, as the results presented here suggest a general acceleration of early life stages, independent from the individual plant life history, probably induced by a faster growth.

Calluna demographics seem to be only marginally influenced by climate; subcontinental marginal population dynamics are not fundamentally different to those in the main Atlantic lowland heathland areal. But the results presented here suggest that although *Calluna* showed a high resistance towards drought, severe droughts have the potential to reduce seedling establishment rates and cause considerable damage on mature plants as well, especially under high N deposition rates. *Calluna* has a high potential to recover completely after biomass disturbance, hence also drought-induced growth reductions or diebacks can be compensated by higher growth rates under favourable post-drought conditions. Especially resprouted plants may ensure a fast post-disturbance *Calluna* regeneration and re-establishment then (Kongstad et al. 2012). But to the best of my knowledge, little is known whether frequent severe droughts rather affect *Calluna* vigour and regeneration potentials negatively on the long-term, or whether adaption may compensate for that.

In our study region, the subcontinental sites are simultaneously those with the lowest N depositions (10-12kg*ha^{-1}*yr^{-1}) hence the additional high N deposition-induced drought resistance reduction is not present there, but in study areas with higher N loads, already moderate droughts may hamper post-disturbance *Calluna* establishment considerably. As a consequence, the reduction of *Callun*a's competitive power favours grass dominances and habitat degradation.

Although needed to create suitable soil and nutrient conditions (de Graaf et al. 2009), vigorous heather regeneration (Chapter 3) and typical habitat structures (Olmeda et al. 2020; Webb 1998), mechanical management has to be applied with caution in respect to the drought susceptibility of post-disturbance *Calluna* establishment and to N loads (Britton et al. 2001). Seedlings need stable conditions of high air humidity and sufficient, moreover even precipitation (Britton et al. 2003, Gimingham 1972). A nursing shelter, provided by older plants, is favourable (Henning et al. 2015). High-intense practices, such as sod cutting, create exposed ground with *Calluna* plants only sparsely germinating in the first 1-3 years (own observations). In contrast, practices such like burning or mowing favour young resprouting plants, showing a fast and vigorous recovery after disturbance. This thesis provides evidence for a high potential of plants emerging from resprouting to persist even critical drought periods with reduced growth but without severe damage. In consequence, a post-disturbance site with plants both grown from resprouting and from seed provides a fast and drought-resistant *Calluna* establishment by resprouting plants first, and later favours seedlings to survive droughts by the provision of nursing effects.

Practical approaches to compensate the climate-change related enhanced susceptibility of post-disturbance *Calluna* recruitment may be

1) Heathlands with higher heterogeneity provide a higher resilience towards ecological stressors and climate change (Haugum et al. 2021). Hence, maximising the spatial heterogeneity of disturbed and undisturbed sites on a small scale for minimizing the effects of drought-induced failing *Calluna* establishment and subsequent grass dominances.
2) On sites selected for shallow sod-cutting, mowing or burning: Enabling highly vigorous resprouting by the provision of a sufficient amount of Mature plants with the capacity to do so (<15 years, vigorous) for a save and fast re-establishment even under drought conditions. A few years later, they provide a nursing shelter for seedlings to reduce drought susceptibility during the early post-disturbance stage.
3) Minimize the need for high-intense soil disturbance by retarding successional and *Calluna* ageing processes. To compensate for rapid degeneration after disturbances, grazing is the most efficient method to keep *Calluna* in a highly vigorous lifetime, especially after burning or mowing (e.g. Kirkpatrick & de Blust 2013; Gimingham 1975, Olmeda et al. 2020). However, grazing alone is insufficient to induce sufficient aboveground biomass disturbance and to provide suitable soil conditions on the long-term (Brunk et al. 2004). Additionally, it may alter *Calluna* growth on the long-term as it promotes dense mats with short internodes (Gimingham 1974, 1994; own observations).

In the end, the results presented in this thesis suggest that site-specific management schemes should be developed that respect different local species pools, heathland successional pathways, regeneration potentials, as well as the whole framework of edaphic and climatic conditions.

Implications for the future nature conservation status assessment and monitoring

Two of the key actions in the EU Habitat Action Plan are the improvement of knowledge about the habitat and its importance for biodiversity as well as improving the mapping instructions (Olmeda et al. 2020). This thesis contributes to these two aims by providing a fundamental revision of heathland plant community ecology and their dynamics, an improved validity of vitality-based heath conservation status assessments and thus strengthens the biological-ecological knowledge required for informed advice on heathland management. Defining criteria for mapping instructions needs suitable references, but they can only be defined on a national or even regional scale (Olmeda et al. 2020). The present study provides an analysis of a wide range of dry heathlands varying along gradients of climate, diversity and structures, and may act as an overview to the North German Plain lowland heathland ecology. Hence, it can be used for improving and specifying the criteria for heathland habitat quality assessments, based on the quality range given from the North German Plain heathlands. Therefore I suggest:

1) To revise the HT 2310 and HT 4030 definitions, mapping instructions and assessment schemes. The results presented in this study revealed that the distinction of the HT 4030 and 2310 in the North German Plains could be based on the recent floristic composition, heath stand structure and soil conditions, culminated in a psammophilous heathland pathway (HT 2310) and a Consolidated sand pathway (HT 4030). The restriction of the HT 2310 occurrences on ‘dunes’ only, with varying definitions and without a further unique specification over the EU member states disregards the ecological constraints shaping this habitat type, which is moreover determined by poor loose drift sands, but not necessarily to dunes of a specific dimension. The ecological conditions of initial soil development on loose sands and the mosaic structure with close contacts to acidic pioneer grasslands are the determinants for the HT 2310, and therefore the related reference criteria should focus on floristic and structural aspects, but not on geological substrate only. Therefore, the lists for the ‘typical species’ inventory should be revised to strengthen the floristically based distinction between the HT 2310 and HT 4030. Valuable species should represent the close contact to the pioneer grasslands and should include early-successional mosses and lichens.

2) To specify and clarify the heathland age structure assessment. First, it has to be emphasized that the prevailing *Calluna* growth phase is not necessarily congruent to the heathland successional stage. Several management cycles with a removal of aboveground biomass, but no removal of raw humus or upper mineral soil horizon will keep the aboveground *Calluna* biomass in an early development stage, but edaphic conditions comply with an advanced soil development. As a consequence, the competition conditions for *Calluna* differ between real early stage soil conditions and

those of advanced conditions, critically determining the re-establishment processes. As a consequence, the heathland succession stage should be assessed independently from the *Calluna* age. Heathland succession stage is determined by the sand type (loose/consolidated), raw humus, the humus content in the topsoil, as well as tree cover or the presence of typical early or late-successional species (e.g. lichens and acrocarpous mosses for early stages, pleurocarpous mosses for late stages). The *Calluna* age structures should not only be assessed in the cover of the four growth phases, but also by an appraisal of the life history composition of the stand. Signs of any vitality damage, either by insect calamities, drought, or other biomass disturbances should be noted, as well as an approximate age of the aboveground biomass, for each of the growth phases. Layering processes should be carefully distinguished from resprouting processes with a better prospect for highly vigorous regrowth, thereby, the habitual diagnostic should base on the extent of adventitious rooting and the shape of the plant patches.

3) As N deposition is an important factor for habitat degradation, it should be included in the monitoring assessment scheme (like in England, Olmeda et al 2020), and also should be considered in the management planning and conduction.

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Appendix

Table A-1 Assessment criteria for the estimation of nature conservation status potential of communities found in the present study. Basing on the criteria defined in the mapping instructions for the federal states of Lower Saxony (NLWKN 2012) and Brandenburg (LfU 2014a & 2014b). 1) not considered in community-scale estimate of nature conservation status assessment due to insufficient data. 2) not considered separately. 3) list of heathland-typical plant species differs between federal states; a pooled list of all mentioned specimen in the above mentioned mapping instructions was used for community potential assessment.

		A favourable			**B unfavourable - inadequate**			**C unfavourable - bad**		
criteria/ subcriteria	**habitat type**	**Lower Saxony**	**Brandenburg**	**criteria for community potential**	**Lower Saxony**	**Brandenburg**	**criteria for community potential**	**Lower Saxony**	**Brandenburg**	**criteria for community potential**
habitat-typical structures										
Calluna age structures	**4030/2310**	all growth stages present	- all growth phases present, Degeneration < 50 % OR - Pioneer/Building phase > 75 % and Degeneration < 25%	- all growth phases present on 25 m^2, Degeneration < 50 % OR - Pioneer/Building phase > 75 % and Degeneration < 25%	not all growth stages present	- three growth stages present OR - Degeneration 50 - 75 %	not all growth stages present at 25 m^2	low structural diversity, Degeneration dominant	Degeneration > 75 %	Degeneration > 75 % at 25 m^2
typical relief	**4030/2310**	present	2)	1)	overall present	2)	1)	only partially	2)	1)
proportion of open sand [%]	**4030**	5 - 10	> 10	> 5 / 25 m^2	< 5	5 - 10	1 - 5 / 25 m^2	no	< 5	0 / 25 m^2
	2310	5 -25	> 10	> 5 / 25 m^2	< 5	5 - 10	1 - 5 / 25 m^2	no	< 5	0 / 25 m^2
habitat-typical species composition										
heathland-typical species	**4030/2310** 3)	≥ 6 typical vascular plant species, upgrade option when high diversity of cryptogams (without specification)	Among Calluna, at least 8 typical vascular plant species, if less: > 25 cryptogam species	mean occurence of ≥ 5 typical vascular plant species/4m^2, optional ≥ 5 cryptogam species/4m^2	3 - 5 typical vascular plant species, upgrade option when high diversity of cryptogams (without specification)	Among Calluna, 2-5 typical vascular plants, if less: < 15 cryptogam species	mean occurence of 2-4 typical vascular plant species/4m^2 in the community, optional 2-4 cryptogam species/4m^2	1 - 2 typical vascular plant species, upgrade option when high diversity of cryptogams (without specification)	Among Calluna at least 1 typical vascular plant species	Among Calluna, 1 typical vascular plant species, low cryptogam diversity, too
Threats										
tree invasion	**4030/2310**	< 10 % tree cover	< 10 % tree cover	< 10 % tree cover/ 100 m radius	10 - 25 (35) % tree cover	10 - 30 % tree cover	10 - 30 % tree cover/ 100 m radius	> 25(35) % tree cover	30 -75 % tree cover	> 25 % / 100 m radius
destruction of habitat-typical structures 1)	**4030/2310**	no	< 5 %	1)	small-scale	5 - 10 %	1)	intensive	>10 %	1)
Cover of heathland-destructive grasses such like Deschmapsia flexuosa	**4030/2310**	< 30 %	< 10 %	< 10 % / 4 m^2	30 - 50 %	10 - 30 %	10 - 30 % / 4 m^2	> 50 - 90 %	30 - 75 %	> 30 % / 4 m^2
ruderals, nitrophytes, neophytes	**4030/2310**	< 1 % cover	no	< 1 % cover / 4 m^2	< 10 % cover	> 5 % cover	> 5 % cover / 4 m^2	> 10 % cover	> 10 % cover	> 10 % / 4 m^2
afforestation 1)	**4030/2310**	2)	no	1)	2)	≤ 5 tree groups	1)	2)	> 5 tree groups	1)

Table A-2 Weather stations used in the present study for calculating long-term climate conditions (DWD 2015), ten-year-trends (DWD 2019) as well as survey period conditions 2014 (DWD 2019). In some areas, stations differ due to data availability issues:

	Weather stations
1 - Tinner Dose	Lingen
2 - Cuxhavener Küstenheiden	Cuxhaven
3 - Suederluegumer Binnenduenen	Leck
4 - Fischbeker Heide	Hamburg-Neuwiedenthal
5 - NATO trainig area Bergen-Hohne	Celle-Wietzenbruch
6 - Lüneburger Heide	Soltau
7 - Nemitzer Heide	Lüchow
8 - Leussower Heide	Boizenburg (Elbe)
9 - Marienfliess	Marnitz
10 - Kyritz-Ruppiner Heide	Neuruppin
11 - Oranienbaumer Heide	Wittenberg1), Jessnitz2)
13a - Kleine Schorfheide	Zehdenick
13b - Vietmannsdorfer Heide	Zehdenick
14 - Glücksburger Heide	Wittenberg
15 - Bundeswehr training area Jägerbrück	Ückermünde
16 - Prösa	Doberlug-Kirchhain
17 - Zschornoer Wald	Döbern1), Bad Muskau2)
18 - Daubaner Wald	Kubschütz

1) data used only for years 1980-2020, 2) data used only for 2011-2020 and survey period conditions 2014.

Electronic Supplementary Material
Folders and files on included CD

Chapter 1

ESM1_1: Field protocols

Chapter 2

Article pdf and electronic supplementary material to the article

Schellenberg J, Bergmeier E (2020) Heathland plant species composition and vegetation structures reflect soil-related paths of development and site history. Applied Vegetation Science 23: 386–405. https://doi.org/10.1111/avsc.12489

ESM2_1: Additional information to study sites and community distribution. (identical to Appendix S1 in original article)

ESM2_2: Floristic and phytosociological remarks. Text and Synoptic Tables. (identical to Appendix S2 in original article)

ESM2_3: Additional results. Figures for *Calluna* growth phase composition, site history, climate, edaphic conditions, grazing regimes and intense managements in heathland plant communities. (identical to Appendix S3 in original article)

ESM2_4: Nature conservation status additional information. Tables of rare species and nature conservation status assessment criteria applied. (identical to Appendix S4 in original article)

ESM2_5: R source codes and original data Tables. (identical to Appendix S5 in original article)

Chapter 3

Article pdf and electronic supplementary material to the article

Schellenberg J, Bergmeier, E (2021) The *Calluna* life cycle concept revisited: implications for heathland management. Biodiv Cons https://doi.org/10.1007/s10531-021-02325-1

ESM3_1: Study areas. This PDF contains supplementary material to all sites, including information to study area location, management, climate, nitrogen deposition and sampling statistics. (identical to OR 1 in original article)

ESM3_2: Initial analysis. This PDF contains a brief graphical overview of initial analysis results concerning dataset-inherent correlations and associations, as well as ecological patterns and dependencies. Additionally, they provide further information on the effects of management, nitrogen deposition and oceanicity on the vitality of *Calluna* plants not addressed in the present article. (identical to OR 2 in original article)

ESM3_3: Analysis documentation. The zip-folder contains the html documentation of the statistical analysis performed in R. (identical to OR 3 in original article)

Chapter 4

ESM4_1: Model diagnostics (html-files with Rcodes and outputs)

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Academic Curriculum Vitae

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Education

2009–2022	PhD studies, Department Vegetation & Phytodiversity Analysis, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen. Thesis title: Vitality of heather (*Calluna vulgaris*) along gradients of climate, structure and diversity in dry lowland heathland habitats of Northern Germany.
2012–2015	Doctoral scholarship Deutsche Bundesstiftung Umwelt (DBU) in the scholarship program „Scientific research on DBU natural heritage sites“ (translated). Thesis title: Vitality of heather (*Calluna vulgaris*) along gradients of climate, structure and diversity in dry lowland heathland habitats of Northern Germany. Department Vegetation & Phytodiversity Analysis, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen.
2005–2009	Advanced studies in Biology, Georg – August – University of Göttingen. Examinations: Botany, Nature conservation and Soil Science. Diploma thesis (translated): Vegetation dynamics of pioneer Corynephorus grasslands and *Calluna* heaths on a former military training area in Northeast Brandenburg, Germany.
2002–2005	Basic studies in Biology, Christian – Albrechts – University of Kiel.
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Work experience

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2019-2020	Lecturer “statistical methods for plant ecologists”, Conception and implementation of workshops, specific counselling for BSc and MSc students.
2016-2017	Freelance work: Project “Free ranging Red deer grazing as a management tool in heathland ecosystems” (translated). Development, implementation and evaluation of a questionnaire survey. Sifting David, Erfurt.
2010 – 2012	Employee as Head of coordination, conception and implementation of the Natura2000 heathland habitat mapping and monitoring, FFH area „Colbitz-Letzlinger Heide“. GISCON Braunschweig geo.engineering GmbH.
2010	Freelance work: Report about the effects of heathland management in selected areas of the nature „Kleine Schorfheide“, Brandenburg, Germany.
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Öder V, Petritan AM, **Schellenberg J**, Bergmeier E, Walentowski H (2021) Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. For Ecol Man 487. https://doi.org/10.1016/j.foreco.2021.118977

Fried O, Westphal C, **Schellenberg J**, Grescho V, Kühn I, Van Sinh N, Settele J, Bergmeier E (2021) Vascular plant species diversity in Southeast Asian rice ecosystems is determined by climate and soil conditions as well as the proximity of non-paddy habitats. Agric Ecosys Environ 314: https://doi.org/10.1016/j.agee.2021.107346

2020 **Schellenberg J**, Bergmeier E (2020) Heathland plant species composition and vegetation structures reflect soil-related paths of development and site history. Appl Veg Sci 23: 386–405. https://doi.org/10.1111/avsc.12489

2019 Pätsch R, Bruchmann I, **Schellenberg J**, Meisert A, Bergmeier E (2019) Elytrigia repens co-occurs with glycophytes rather than characteristic halophytes in low-growing salt meadows on the sou-thern Baltic Sea coast. Biologia 74: 385–394. https://doi.org/10.2478/s11756-019-00195-1

2014 **Schellenberg, J** & Bergmeier E (2014). Atlantische und subkontinentale Heiden in Norddeutschland. Nat Landsch 89(3): 110-117.

Other publications:

2017 **Schellenberg J** (2017) Vitalität der Besenheide (*Calluna vulgaris*) in trockenen Zwergstrauchheiden entlang von Klima-, Struktur- und Diversitätsgradienten im norddeutschen Tiefland. In: DBU, Schaefer, Schlegel-Starmann (eds.) Ergebnisse aus dem Stipendienschwerpunkt „Forschung auf DBU-Naturerbeflächen – Ökologische Dynamik zwischen Offenland und Wald. Available online: (https://www.dbu.de/OPAC/ep/Ergebnisse-Stipendienschwerpunkt.pdf

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