



# 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

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## Introduction

*Calluna vulgaris* (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, European Commission 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). Favourable microclimatic conditions, such as sufficient water supply and humidity are critical for successful seedling establishment (Gimingham 1972; Henning et al. 2017; Ibe et al. 2020). 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 but insufficiently understood yet: (1) management; (2) climate, e.g. vitality-reducing droughts, and (3) nitrogen deposition (e.g. Meyer-Grünefeld 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).

## Methods

### Study areas and sampling

We examined a total of 445 *Calluna* plants in 352 plots of 25 m<sup>2</sup>, randomly placed by QGIS coordinate generation in 19 study areas across the North German lowlands (for location and details see Online Resource 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 (Online Resource 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.

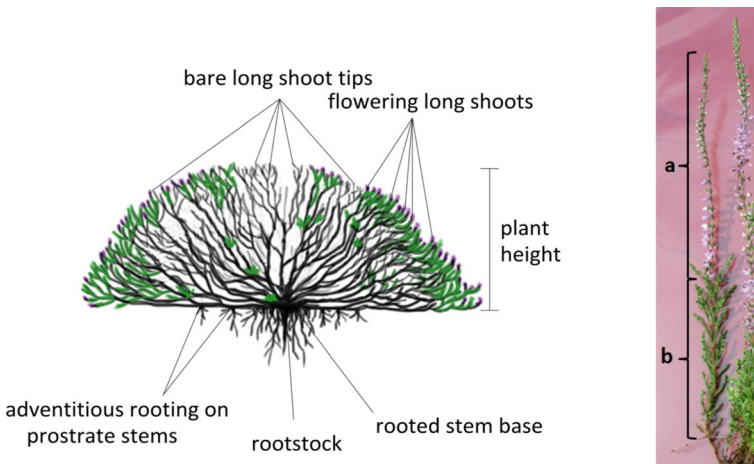
For age determination, growth ring samples were taken from the rootstock just below the soil surface (analysed to reveal the plant age) and in stems at heights of 10–15 cm (stem age). The stem pieces of 3–6 cm length were examined by counting the growth rings on a fresh-cut diameter surface using a binocular 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 2 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.

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 (Online Resource 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 1).

**Table 1** *Calluna* vitality attributes

Vitality attribute	Description	Unit	Numbers of plants examined in data <sub>root</sub> /data <sub>stem</sub>
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. 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. 1: a + b)	cm	218/445
Plant height	Maximum plant height	cm	207/415



**Fig. 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)

**Table 2** Proportion of explained inertia of  $RDA_{\text{root}}$  and  $RDA_{\text{stem}}$  on the vitality parameters presented in Table 1

	Growth rings	Plant life history (primary/secondary)	Con- strained terms	Grazing + Manage- ment + Nitrogen deposi- tion	Unexplained
$RDA_{\text{root}}$	0.13***	0.02 <sup>n.s.</sup>	0.15	0.06	0.79
$RDA_{\text{stem}}$	0.23***	0.03*	0.26	0.06	0.69

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)

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, Online Resource 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 5 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 (Online Resource 2: Fig. 7, Fig. 8).

Airborne nitrogen rates were extracted from the interactive map service to airborne nitrogen deposition in Germany (UBA 2019; Online Resource 1: Table 2), ranging from 10 to 23 kg/ha\*<sub>y</sub>. Oceanicity was calculated using the algorithm of Godske (1944), see Online Resource 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 Online Resource 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<sub>root</sub> ( $n=206$ ) 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<sub>all</sub>). Then, we set up three RDA with different groups of predictors: (1) RDA<sub>env</sub> included only severe management, grazing and nitrogen deposition as predictors to identify their effects without considering any age-related effects; (2) RDA<sub>root</sub> and RDA<sub>stem</sub> 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<sub>area</sub>, 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 et al. 2008), with each vitality parameter as a dependent variable and growth ring counts of rootstock (data<sub>root</sub>) and of stems (data<sub>stem</sub>) 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 (Online Resource 2: Figs. 2 and 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/>).

## 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 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 (Online Resource 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 (Online Resource 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 (Online Resource 2: Figs. 1, 3, and 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 2).  $RDA_{stem}$  revealed a significant influence of life history and branch age on *Calluna* vitality ( $p \leq 0.01$ , Table 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: partial  $R^2$  for lh—life history; Fig. 3).

In both RDA age models (Table 2) as well as in  $RDA_{env}$ , management during the past 5 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. 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 (Online Resource 2: Figs. 1, 3, and 5). If grazing and/or severe management were included as random terms, they, too, explain parts of the variability (effect sizes: Table 3, Online Resource 2: Figs. 5,



**Table 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<sup>2</sup>, partial R<sup>2</sup> for the included fixed terms and relative explained variance for random terms (total variance = 1)

Model	Partial R <sup>2</sup> for fixed terms				Random terms (relative explained variance, total variance = 1)				
	Response transformation	Fixed terms (random terms)	R <sup>2</sup>	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)	<b>0.18</b>	<b>0.12***</b>	<b>0.10***</b>		<0.01		
Flowers/plant	sqrt	(area)	<b>0.18</b>	<b>1st: 0.14**/2nd: 0.05**</b>			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)	<b>0.58</b>	<b>0.53***</b>	<0.01 <sup>n.s</sup>	lh:RA 0.09***	<0.01		
Relative yearly increment	sqrt	lh (area) (man) (grazing)	<b>0.34</b>	<b>1st: 0.31***/2nd: 0.05***</b>	0.09***		0.05		<0.01
Total yearly increment	sqrt	lh (area) (man) (grazing)	<b>0.12</b>	<b>0.11***</b>	0.04**		<b>0.11</b>		<0.01
Plant height	sqrt	*lh (area)	<b>0.43</b>	<b>1st: 0.39***/2nd: &lt;0.01<sup>n.s</sup></b>	<b>0.11***</b>	lh:RA 1st: 0.09***/2nd: <0.01 <sup>n.s</sup>	<0.01		
b) Growth rings of stems (10–15 cm of plant height)									
Flower density		*lh (area)	<b>0.10</b>	0.07***	0.06***	lh:AAA 0.03***	0.03		
Proportion of flowering long shoots		lh (area)	<b>0.17</b>	<b>1st: 0.05***/2nd: 0.05***</b>	0.08***		0.05		
Flowers/plant	sqrt	lh (area)	<b>0.31</b>	<b>1st: 0.28***/2nd: 0.03***</b>	0.02**		0.03		
Length of inflorescence	sqrt	*lh (area) (man)	<b>0.13</b>	<b>1st: 0.07***/2nd: 0.03***</b>	0.03***	lh:AAA 1st: 0.02***/2nd: <0.01 <sup>n.s</sup>	0.09		0.03

**Table 3** (continued)

Model	Partial R <sup>2</sup> for fixed terms			Random terms (relative explained variance, total variance=1)					
	Response transformation	Fixed terms (random terms)	R <sup>2</sup>	Growth rings	Life history	Interaction terms	Study area	Severe management	Grazing
Proportion bare long shoot tips	sqrt	lh (area) (man)	<b>0.21</b>	<b>0.12***</b>	0.09***		0.03	0.01	
Relative yearly increment	sqrt	(area) (man) (grazing)	<b>0.36</b>	<b>1st: 0.36***</b> <b>2nd: 0.02***</b>			<b>0.11</b>	<0.01	0.04
Total yearly increment	sqrt	*lh (area) (man) (grazing) (area)	0.08	0.03***	0.07***	Lh:AAA 0.02**	<b>0.15</b>	<0.01	<0.01
Plant height	sqrt	(area)	<b>0.53</b>	<b>1st: 0.52***</b> <b>2nd: 0.04***</b>			0.02		

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<sup>2</sup> value of model is for marginal effects, partial R<sup>2</sup> values are given for each of the fixed term. All R<sup>2</sup> values are highlighted in bold when R<sup>2</sup>/partial R<sup>2</sup> > 0.10 and with grey font colour when R<sup>2</sup>/partial R<sup>2</sup> < 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<sup>2</sup> and p-values are given for the linear term (1st order polynomial) as well as the quadratic term (2nd order polynomial)

6, 7, and 8). However, severe management had hardly any explanatory power if included, and grazing had only marginal effects on the relative yearly increment (Tables 2 and 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 (Online Resource 2). Total yearly increment was positively correlated to nitrogen deposition ( $\rho=0.28$  for both  $\text{data}_{\text{root}}$  and  $\text{data}_{\text{stem}}$ ), as well as the relative yearly increment ( $\rho=0.27$  for  $\text{data}_{\text{root}}$ , not evident in  $\text{data}_{\text{stem}}$ ) and the inflorescence length ( $\rho=0.22$  in  $\text{data}_{\text{root}}$ ,  $\rho=0.23$  in  $\text{data}_{\text{stem}}$ ). 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 (Online Resource 2: Figs. 3, and 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 (Online Resource 2: Fig. 2a, d, and g).

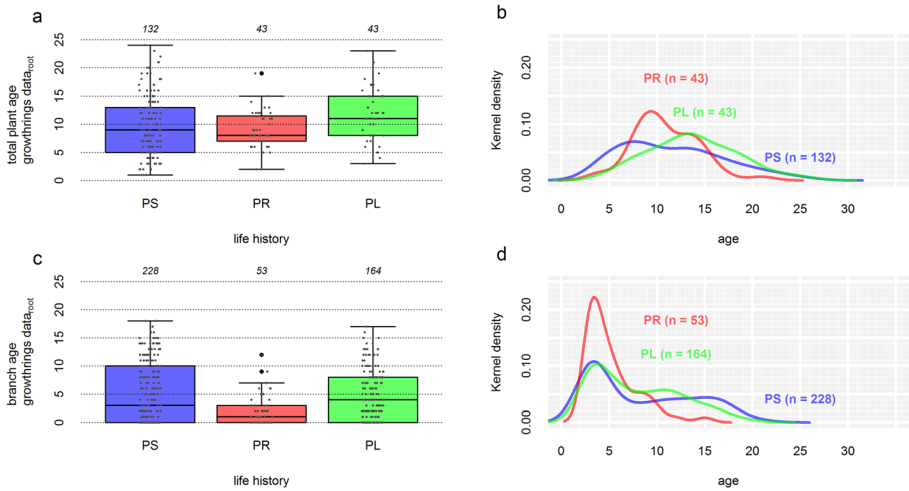
Burning supported vitality in the short-term, with growth rates (length of inflorescences, total and relative yearly increment) significantly higher on burned sites compared to mowed sites or those without any such severe management (Online Resource 2: Figs. 5 and 6). In contrast to mowing, burning effectively 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 (Online Resource 2: Figs. 7 and 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), 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 ( $\text{data}_{\text{root}}$ ) 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. 2a, b). 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. 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).

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



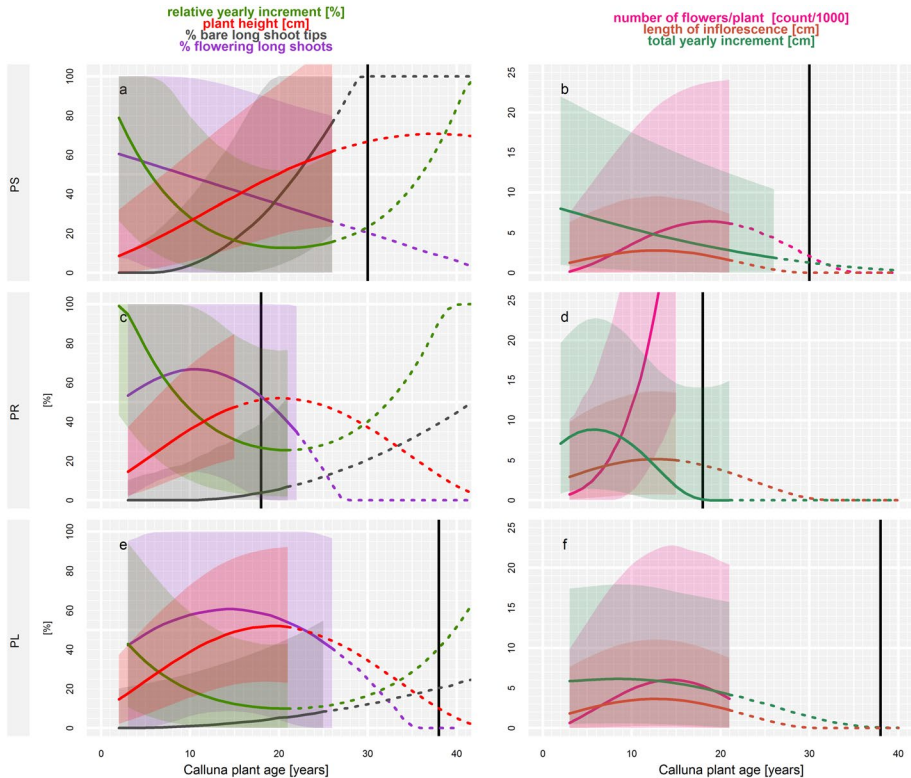
**Fig. 2** Age of the individual plant (a, b) and the stems (c, d), for plants grown from seed (PS), from resprouting (PR) and from layering (PL)

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.

All vitality parameters—except flower density—showed a response to age (growth rings, Table 3; Figs. 4 and 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. 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.

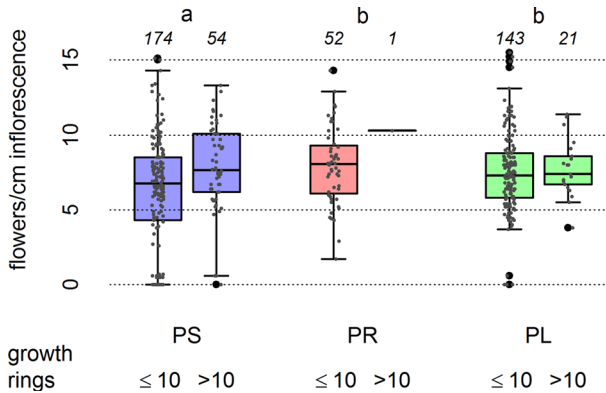
**Fig. 3** *Calluna* plant age at the time of severe disturbance (which commonly prompts resprouting). Calculated as the frequency of the difference between total plant age (measured on rootstock) and stem age of resprouted plants (n = 43)





**Fig. 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). The black vertical line indicates the hypothetical plant death when either bare long shoot tip proportion becomes 100%, or yearly increment is 0 cm

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. 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 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. 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. 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. Figure 2b).



**Fig. 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. (\*\*\*)  $p \leq 0.001$ , \*\*  $p \leq 0.01$ , \*  $p \leq 0.05$ , n.s. = not significant)

**Table 4** Vitality differences between life history categories

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

PS plants grown from seed, PR plants resprouted from stem base, PL plants growing from prostrate stems adventitiously rooting. 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

\*\*\* $p \leq 0.001$ , \*\* $p \leq 0.01$ , \* $p \leq 0.05$ ). Significant differences are highlighted in bold font

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. 4e, f). The inflorescence length and the total number of flowers per plant was significantly lower in PL compared or PR (Table 4).

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. 4, model details: Table 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. 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).

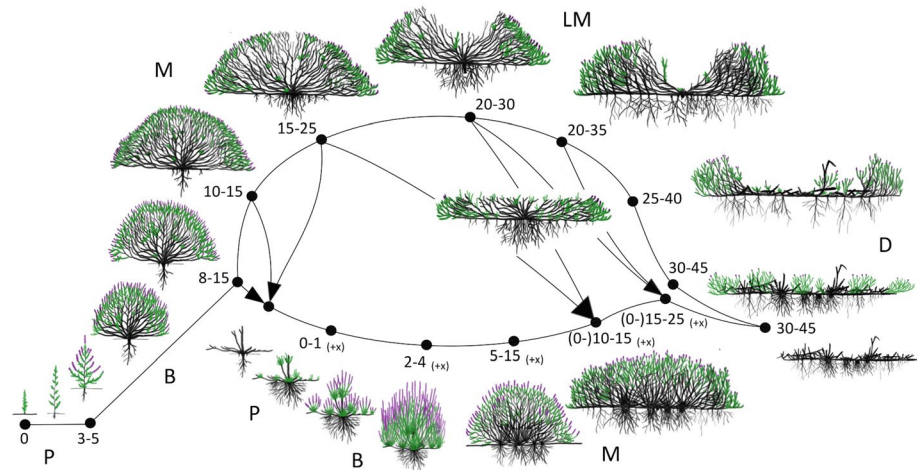
Growth rates were influenced by nitrogen deposition rather than by oceanicity. In our initial analysis, we detected fertilizing effects by nitrogen deposition, in particular increasing total growth rate and longer inflorescences. Additionally, we found symptoms of accelerated ageing and a shorter life 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. 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)





**Fig. 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 50–60 cm. 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

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. 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. 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).

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 is 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 than in PR of the same aboveground biomass age (Fig. 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. 2019, 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 and 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.

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**Data availability** All data analysed during this study are included in this published article [and its supplementary information files]. The authors decided to not share raw data.

**Code availability** Parts of the analysis code is included in the electronic supplementary information files.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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