Variation in leaf functional traits through the early development of coastal heathland plants

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Cover photo: Plug tray with seedlings of *Digitalis purpurea* in week 8, by Elisabeth Nesheim-Hauge

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ABSTRACT

Seedling recruitment provides a mechanism for re-establishment after fire and is thus key in the life cycle of managed heathland plant species. However, the seedling phase is a vulnerable stage of the plant's life cycle, and seedling growth and survival might be more affected by environmental stressors, such as climate, than adult individuals. Global environmental change impacts on seedlings thus can affect community assembly and ecosystem functioning. I study seedling biology in the threatened coastal heathlands of Norway and Europe.

Plant functional traits, including the leaf economics spectrum (LES), are important tools for understanding changes in vegetation with global change, as traits underlie both plant responses to environmental stressors and their roles in ecosystem functioning. Little is known about how traits vary within and especially between species through the ontogeny in coastal heathlands. To fill this knowledge gap, I tested how functional traits vary over the seedling phase by measuring functional traits of 10 herbaceous species common in coastal heathlands through 16 weeks of growth, in addition to measurements of cotyledons and adult traits. Groups central in the coastal heathland ecology were chosen; forbs and graminoids, early- and late-successional species, and species with a persistent or transient seed bank. Traits related to productivity and growth were measured; leaf thickness, specific leaf area (SLA), leaf dry matter content (LDMC), and relative growth rate (RGR).

The results show that resource acquisitive traits dominate in the early life-history stage of coastal heathland plants and develop toward being conservative. Trait values are more constrained for seedlings than for adults, and interspecific ranking remain constant for species. Trait values are different and change in different directions through time for growth forms and successional strategies. This is not found for seed bank status. My findings suggest that leaf trait differentiation appears early in a plant's life, but adult traits can still not predict the seedling traits, and hence seedling vulnerabilities to environmental stressors. This study can contribute to understanding how the future climate might affect seedling recruitment, and hence biodiversity and ecosystem functioning of coastal heathlands.

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1. INTRODUCTION

The coastal heathlands of northwest Europe are semi-natural landscapes of considerable cultural and natural value (EC Habitat Directive 92/43/EEC; Hovstad, 2018). Vegetation in these heathlands has been extensively managed with burning and grazing to serve as all-year pasture for sheep (Webb, 1998), a land-use regime that has been practiced virtually unchanged the past 4000 years (Gimingham, 1987; Webb, 1998; Prøsch-Danielsen & Simonsen, 2000). A spatially heterogeneous fire regime, where burning is done in patches, ensures availability of fresh, nutritious heather in the different successional stages; pioneer, building and mature (Gimingham, 1972). Combined with grazing and underlying environmental heterogeneity in the form of moisture gradients, burning results in a heterogenous patchwork vegetation (Vandvik *et al.*, 2005). The patches have both varying composition of species (Vandvik *et al.*, 2005) and plants in difference life-history stages. This heterogenous vegetation type functions as habitat for a number of threatened species, including both vascular and non-vascular plant species, insects and birds, where some are predominantly found in coastal heathlands (Nybø, 2010). For instance, the strongly threatened (EN) European eagle owl (*Bubo bubo*) (Henriksen & Hilmo, 2015) often nests in or near heathlands (Nybø, 2010). Coastal heathlands, and the species within them, are now being threatened due to land-use change and, in the north especially, cessation of management practices (EC Habitat Directive 92/43/EEC; de Graaf *et al.*, 2009; Hovstad, 2018). Additionally, coastal heathlands are expected to be severely affected by future extreme weather events due to climate change (Albert *et al.*, 2011), especially combined with land use changes (Peñuelas & Boada, 2003; Fagundez, 2013). Overall, climate is predicted to become warmer and more variable with higher frequency and intensity of drought periods (IPCC, 2007). In a temporal, humid climate like the coastal heathlands, it is expected that the plants will be less adapted to these kinds of stressors (Peñuelas *et al.*, 2007; Vicente-Serrano *et al.*, 2013).

Burning practices are key in maintaining the composition and successional dynamics of the coastal heathland vegetation (Gimingham, 1972; Lee *et al.*, 2013). The successional sequence after fire drives a shift in vegetation composition, reflected in a shift in dominance from nutrient-demanding graminoids and forbs early in the succession to dwarf-shrubs in later stages (Kvamme *et al.*, 2004; Vandvik *et al.*, 2005; Måren & Vandvik, 2009). Additionally, ruderal species are usually the first to emerge and dominate after fire and are replaced by competitive and stress-tolerant species later in the succession (Grime, 1977; Pywell *et al.*, 2003; Caccianiga *et al.*, 2006). The post-fire dynamics thus create unique successional community dynamics in the coastal heathland. Moreover, vegetation dynamics is affected by the availability of seeds of different species for recruitment. In particular, the soil seed bank is an important source for post-fire regeneration in the coastal heathlands (Thompson & Grime, 1979; Meulebrouck *et al.*, 2007; Måren & Vandvik, 2009), where persistent seed banks act as a backup and assurance that the species can persist and reappear in the standing vegetation after fire. Species' regeneration strategies are thus key to their regeneration dynamics after fire, as some species have a transient seed bank, lasting only from the seed dispersal through the regeneration phase, but with little carryover across years. In contrast, other species have persistent seed banks that last over several years (Thompson & Grime, 1979), resulting in a substantial build-up of seeds and thus many seeds in the seed bank, potentially lasting until after the next fire (Thompson & Grime, 1979; Eriksson & Eriksson, 1997; Funes *et al.*, 1999). Successional processes and recruitment from the seed bank are key in maintaining coastal heathland vegetation composition (Måren & Vandvik, 2009). Therefore, it is important to understand the basics of how plants with different ecological strategies have adapted to the heathland fire regimes.

Recruitment from seed is a key life-history transition in the life cycle of managed heathland plant species, as seedling recruitment provides a mechanism for re-establishment and population expansion after fire (Thompson & Grime 1979; Måren & Vandvik, 2009). The seedling stage of the recruitment is a vulnerable phase in the plant's life cycle (Zammit & Westoby, 1987; Fay & Schultz, 2009), and consequently displays the highest mortality of all life-history stages, with the exception of the seed stage (Stebbins, 1971; Fenner, 1987; Eriksson & Ehrlén, 2008). Abiotic and biotic stressors like drought, anthropogenic disturbances, herbivory, and competition affects growth and survival for seedlings (Newell *et al.*, 1981; Fenner, 1987; Hanley *et al.*, 1995; Lloret *et al.*, 2004; Peñuelas *et al.*, 2007; Chacón & Cavieres, 2008). Studies have shown that herbivory and drought display the highest mortality in seedlings (Moles & Westoby, 2004; Vicente-Serrano *et al.*, 2013), which are both relevant environmental stressors in the heathland system. Even though burned patches in the heathland can provide high light availability with increased nutrients and soil pH from the addition of ash (Zackrisson *et al.*, 1996; Neéman *et al.*, 1999; Bargmann *et al.*, 2014), the open post-fire habitat can create an extra stressful existence for the seedlings. Additional stress can come from drought due to the lack of surrounding vegetation that would otherwise hold moisture. Lloret *et al.* (2004) found that both the emergence and the survival of seedlings decreased with induced drought treatments in a Mediterranean shrubland. Furthermore, the grazing livestock prefer newly burned areas with fresh, nutritious vegetation (Rowe-Rowe, 1982; Eby *et al.*, 2014), thus the grazing pressure increases in the early stage of post-fire succession resulting in higher mortality in early seedlings. Consequently, recently burned heathlands can offer both unique opportunities as well as severe challenges for seedlings. Studying seedling adaptations can therefore be key in predicting their survival, and by that future vegetation composition (Lloret *et al.*, 2004; Fay & Schultz, 2009).

Coastal heathland plant species have adapted to the varying biotic and abiotic conditions as a consequence of the unique management practice. Trait-based ecology is based on the assertion that adaptations to such factors can be reflected in plant's functional traits (hereafter traits). The leaf economics spectrum (LES) describes species responses to the environment as a set of traits on a continuous scale from a resource acquisitive to a resource conservative strategy (Wright *et al.*, 2004). Some underlying traits are specific leaf area (SLA), leaf dry-matter content (LDMC), and leaf thickness; leaf traits that reflect the plant's investment in productivity vs. toughness and resistance to environmental stressors. The relative growth rate (RGR) is considered a key trait in predicting species survival and ecological strategies in different environments (Funk *et al.*, 2017). However, measuring RGR requires destructive harvest (Pérez-Harguindeguy *et al.*, 2013) and is therefore not often measured (Funk *et al.*, 2017).

The vast majority of trait studies are short term studies of adult individuals (Niinemets, 2005), however few have studied the seedling stage or change in traits through the ontogeny. The vast majority of these studies have examined how traits change by measuring a few different life stages at a single occasion under field conditions (e.g. Niinemets, 2004, 2005; Ishida *et al.*, 2005; Jullien *et al.*, 2009; Palow *et al.*, 2012). These studies show that traits generally develop from resource acquisitive towards resource conservative through time for herbaceous (McConnaughay & Coleman, 1999; Niinemets, 2004; Jullien *et al.*, 2009) and woody (Palow *et al.*, 2012; Day *et al.*, 2014; Damián *et al.*, 2017) species. In these types of studies, the effects of environmental variation (plasticity), effects of life history (e.g. annual, perennial) and habitat filtering (survival of specific traits at different locations) can significantly affect and bias results (Cornwell *et al.*, 2006). In contrast, experimental studies with controlled conditions and measurements through continuous time control these effects

(Niinemets, 2005; Mason *et al.*, 2013). To the best of my knowledge, Mason *et al.* (2013) is the only study that has used this approach. They investigated variation in the LES through the life cycle of three diverse species of *Helianthus.* Their results show that traits like photosynthetic rate and leaf mass per area vary significantly over the plants' life span, and the resource strategy change from acquisitive to conservative. The highest rate of change in trait values was found between the juvenile and the pre-reproductive stage. Thereafter, the direction of trait values might shift several times through the ontogeny, especially after the flowering stage (Jullien *et al.*, 2009). Although there are several studies of different plant life-history stages, few include large amounts of species from the same vegetation type or have collected continuous data in controlled conditions exclusively focusing on detailed seedling data.

Trait variance between species have been much studied for environmental factors (e.g. Kattge *et al.*, 2011; Fraser *et al.*, 2016; Takahashi & Tanaka, 2016; Stark *et al.*, 2017), however, to the best of my knowledge, no studies have assessed the change in trait variance through the ontogeny for a community. If plants in later stages of their life cycle are strongly affected by competition, so that species with similar traits outcompete each other, variance of traits in that habitat increases (Takahashi & Tanaka, 2016). However, if the community is severely affected by environmental filtering, it will have a lower variation in traits (Grime & Curtis, 1976; Grubb, 1977; Fraaije *et al.*, 2015). This might be particularly relevant in earlier life-history stages, and especially in open habitats, where plants are expected to experience little competition between seedlings (Moles & Westoby, 2004). Thus, the range of trait values found in an assembly of adult plants is expected to reflect a larger range of trait values than for seedlings. In addition to interspecific variance, change in relative ranking of species mean trait values through time is an interesting aspect which is not often included in ontogeny studies. Although, studies show that interspecific ranking remain constant through time and, with some caution (Cornelissen *et al.*, 2003), space for woody species (Kitajima & Poorter, 2010), herbaceous species (Thompson *et al.*, 1997), and a combination of these (Poorter & De Jong, 1999; Garnier *et al.*, 2001). If interspecific ranking of trait values changes from seedling to adult, the composition of species trait values is different in these two life stages. Hence, studying ranking is key in understanding if adult traits for species can predict seedling traits or not.

Even though many heathland studies have measured LES traits for adult plants, it is less well known how and to what extent seedling traits vary through time and how traits are different for groups that have ecological importance in the coastal heathland. In general, it is known that species with the same growth form, functional type, or biome can have similar trait values (Hunt & Cornelissen, 1997; Wright *et al.*, 2004; Kattge *et al.*, 2011) and can be expected to respond to climate change in a similar way. For instance, the early-successional species are resource acquisitive ruderals, thus vulnerable to environmental stressors, whereas late-successional species are more conservative, thus more tolerant (Prach *et al.*, 1997; Garnier *et al.*, 2004; Falster & Westoby, 2005). Ruderals also have small seeds (Turnbull *et al.*, 2012) and are therefore persistent in the seed bank, making it more likely that they will survive through time (Thompson & Grime, 1979; Bossuyt & Hermy, 2003). Studies of trait differentiation between grasses and herbaceous forbs, typically found in the early-successional phase, show that graminoids are slightly more conservative than forbs (Kattge *et al.*, 2011), although a large overlap is found for the two growth forms (Huovinen-Hufschmid & Korner, 1998; Wright *et al.*, 2005). Studying differences in traits for different groups that play a large role in the ecology of coastal heathlands can aid in the understanding of how tolerant these groups are to changes in the climate.

As vulnerable seedlings emerge from the seed bank in newly burned patches, they are provided with additional energy from seeds and cotyledons. Seedling and trait studies often includes measurements of seed traits due to their impact on seedling traits and survival (Ganade & Westoby, 1999; Geritz *et al.*, 1999), however few studies include trait measurements of cotyledons. As it is known that cotyledons contribute with additional photosynthesis (Kitajima, 2006), several studies have been conducted for cotyledon photosynthetic capacity. For instance, it is found that photosynthetic rate was higher in cotyledons than for true leaves for tropical tree species (Kitajima, 1992). Some studies have focused on SLA and found that small seeded species had high SLA for cotyledons (Wright & Westoby, 1999 and references therein). Wright and Westoby (1999) also found that cotyledon and true leaf SLA had a strong positive relationship, and that plant RGR has a negative relationship with cotyledon mass ratio, corresponding with traits for true leaves. Field experiments have shown that removal of cotyledons decrease seedling survival in neotropical trees (Kitajima, 2006) and in legume species (Hu *et al.*, 2017). Studies show that seed reserves have a great effect on the recruitment, growth and survival of seedlings, as initial seed mass of the plant is related to germination success, RGR, and cotyledon and whole seedling size (Reich *et al.*, 1998; Ganade & Westoby, 1999; Westoby *et al.*, 2002). Larger seeds provide the seedlings with a larger pool of initial resources (Westoby *et al.*, 2002), produce larger seedlings (Jurado & Westoby, 1992). Larger seedlings are more likely to survive early establishment phases (Geritz *et al.*, 1999), are stronger competitors (Leishman *et al.*, 2000; Westoby *et al.*, 2002), and can have higher seedling survival during extreme events (Leishman & Westoby, 1994; Díaz *et al.*, 2016). It is widely known that seed size and cotyledons are key components of seedling growth and survival. Therefore, including trait measurements of seeds and cotyledons in studies of seedlings in habitats with high disturbance or stress could aid in the understanding of how they contribute to seedling survival in these habitats.

In this study I investigate how plant functional traits develop through the earliest stages of plants from a coastal heathland at Lygra, in western Norway. I focus on traits related to the LES (leaf thickness, SLA, LDMC), in addition to RGR, and I investigate how these traits vary over 16 weeks of their early life, and their connection to adult traits. Additionally, I measure the same LES traits for cotyledons collected from the seedlings in the first week. I further assess the variation of seedling traits between species and between growth forms (graminoids and forbs), successional strategy (early- and late-successional species), and seed bank status (persistent and transient). This information will aid in the understanding of coastal heathland successional ecology, and its response to change in climate. I examine which traits are available in the heathland herbaceous seedling and adult plant community. This may help predicting how the community will handle future changes and if adults can represent seedling responses.

I ask a main question; in which ways are seedlings in the coastal heathland different from adults in terms of traits, and can adult traits predict seedling traits? Based on the literature reviewed above, I hypothesise that (1) resource acquisitive traits are dominating at the early stages of coastal heathland plants’ life cycle, whereas conservative traits dominate at the later stages (Figure 1.1a), (2) seedlings will have more constrained traits than adult plants, thus that there will be an increase in between-species trait variance through time (Figure 1.1b), and (3) seedling traits for species in the same ecological group will express the same trait values and develop in a common direction. In particular, I expect graminoids to have more conservative traits than forbs, early-successional species to have more resource acquisitive traits than late-successional species, and species with a persistent seed bank to have more resource acquisitive traits than species with a transient seed bank. An interesting aspect that I will explore for the change in between-species variance, is if the relative ranking of species trait values changes from seedling to adult (Figure 1.1c). Additional plant measurements enabled me to research the species RGR, seed mass, and cotyledon traits. This will aid in the understanding of the individual's investments in traits and structures closely related to seedling survival.

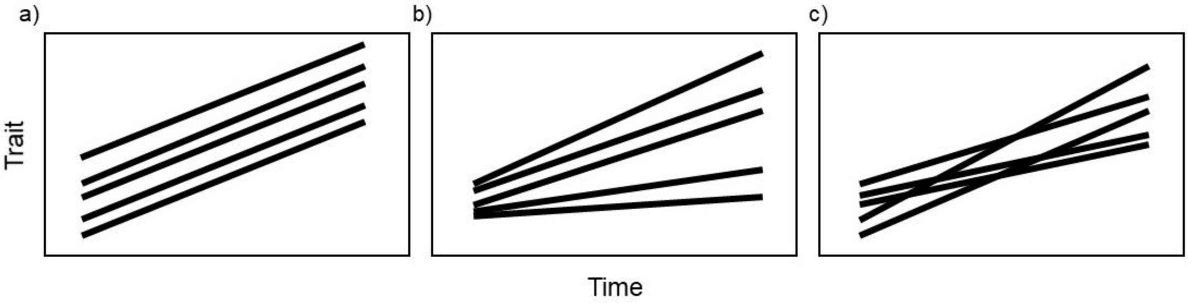


Figure 1.1 *Illustrations of potential types of change; a) increase in trait mean values without any change in interspecific variance or ranking, b) increase in trait mean values as well as an increase in difference between trait mean values (interspecific variance), c) increase in trait mean values as well as a change in ranking of species trait means (interspecific ranking).*

2. MATERIALS AND METHODS

2.1 Study area and species

Seeds and adult individuals were collected from the coastal heathlands of the Lygra island, Lindås (60°420N, 5°50E) (Figure 2.1). The island is located in a fjord approximately 20 km inland from the west coast of Norway and the highest point is 54 m.a.s.l. The climate is oceanic with a mean June temperature of 12 °C and mean January temperature of 2 °C, mean annual precipitation of 1600 mm per year (Måren & Vandvik, 2009), and a relatively long growing season of about 220 days (above 5 °C) (Måren & Vandvik, 2009).

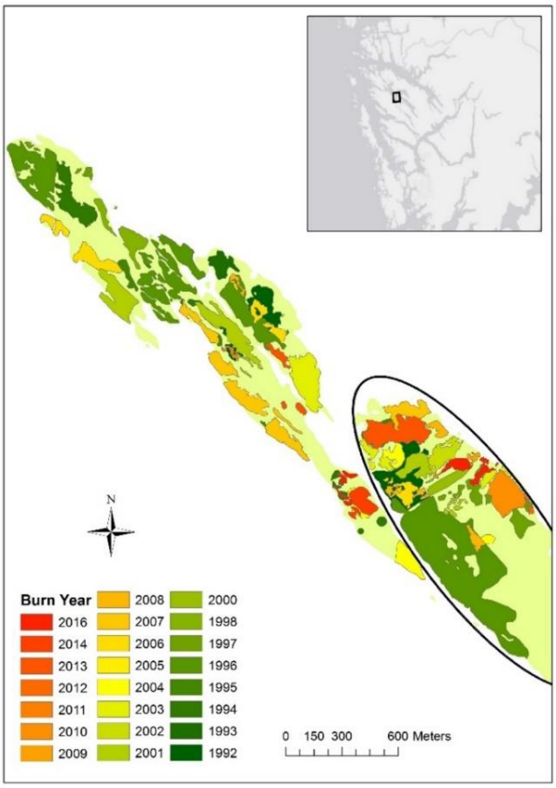


Figure 2.1 *Map of the study area Lygra (east) in western Norway. Colours represent the burn mosaic resulting from prescribed burns at different years. Species were randomly collected within the circled area. Colours red towards green indicate change in stages from pioneer to mature. Modified from ©The Heathland Centre.*

The large variation in soil moisture due to the rugged mesoscale topography with small ridges, slopes, poorly drained depressions, and associated variation in soil depth is a major driver of habitat heterogeneity within the area (Måren & Vandvik, 2009). Dominant vegetation types are *Calluna* heath, mires, Salix shrubs and mixed grass heaths. The most dominant graminoids are *Avenella flexuosa*, *Agrostis capillaris, A. canina* and *Carex pilulifera*, and the most dominant forbs are *Calluna vulgaris, Erica tetralix, Vaccinium vitis-idea, V. myrtillus, Potentilla erecta* (Måren & Vandvik, 2009; unpublished data, Siri Vatsø Haugum).

The coastal heathland at Lygra is currently managed by the local farmers in collaboration with the Heathland Centre at Lygra, aiming to mimic the traditional land-use regime that was in place until ca 1950. This collaboration started in the early 1990s, with a restoration phase to remove trees and reinstall the traditional grazing and fire regimes after the area had gradually fallen out of use and grazing and burning declined during the 1960s – 1980s. The seed bank at Lygra has shown to be a refuge for many common heathland species, creating a vegetation after burning similar to the one before burning (Måren & Vandvik, 2009), this is therefore an important part of the coastal heathland succession.

Species chosen for this study (Table 2.1) were selected from common species in the coastal heathland at Lygra, starting from a list of the most abundant species cumulatively making up 80% of the vegetation cover (unpublished data, Siri Vatsø Haugum, Table A.1). The study was limited to herbaceous plants because (i) the major dwarf-shrub in the system, *Calluna vulgaris*, had too small leaves to enable measurements of seedling leaf traits (ii) woody species generally have lower growth rates than herbaceous plants, which may compromise validity of the comparisons and was also logistically challenging due to time limitations. Further, species with a high probability of germination (Måren & Vandvik, 2009; Royal Botanic Gardens Kew, 2017) were chosen to ensure that resources were not wasted in species with low germinability. Finally, a few species reflecting plant strategies that were not present in the common plant list but are still frequent and characteristic in heathlands were added; *Cirsium vulgare* (large-leaved forb, protected against grazing with spines), *Digitalis purpurea* (large-leaved forb, chemically protected against grazing), and *Sedum anglicum* (succulent-leaved forb). This resulted in a candidate list of 21 species (Table A.1). Mature seeds of these species were collected in the heathlands at Lygra and sown, grown and measured in the greenhouse (see below). In the end, 10 species emerged with enough individuals to provide a sufficient amount of data for analysis (Table 2.1).

All the species in this study are herbaceous perennials, thus have similar life history and timing of life stages. All species have leaflike photosynthetic cotyledons (PEF: phanero-cotylar-epigeal-foliaceous) which means that they are above-ground cotyledons emerging out of the seed coat and expanding towards functional photosynthetic leaves (Garwood, 1996). In this study, I define the young plants (up to 18 weeks old) as seedlings following Gatsuk *et al.* (1980) who indicates that herbaceous perennials can be seedlings up to 1 year before they are classified as juveniles. The factor herbaceous perennials, the definition of seedlings, as well as the relatively short period of measurements that includes only one life stage, explains the choice of measuring traits through time, and not stage, as would be recommended for measurements through the ontogeny (Pérez-Harguindeguy *et al.*, 2013).

Species were divided into growth forms (graminoids or forbs), successional strategy (early or late), and seed bank status (persistent or transient) (see Table 2.1). The groups assemble species with wide ecological strategies which relates to the characteristic vegetation types and dynamics in a managed coastal heathland. Species were categorized as graminoid or forb using Lid and Lid (2005) (Table 2.1).

Species were categorized as early- or late-successional according to Fremstad (1998), where species responding positively to fire (early-successional species) are listed (data from percentage species cover after fire). Species not listed were placed in the group of species that do not respond to fire (late-successional species) (see Table 2.1 for full classification).

Species were categorized as having persistent or transient seed bank based on frequency of seeds per species in the seed bank, as persistent seed banks are expected to have a larger frequency of seeds throughout the year, and transient seed banks a low frequency (Thompson & Grime, 1979). Frequency measurements from earlier studies of species occurrence in the soil seed bank of Lygra were used (Måren & Vandvik, 2009). Here, a discontinuity was found between the size of seed banks for species in this study, as few species fell between 10% and 40% in species occurrence frequency in the seed bank. Thus, species with a frequency below 10% were considered to have a transient seed bank and species with a frequency higher than 40% were considered having a persistent seed bank. *Cirsium vulgare* was not found in the study of Måren and Vandvik (2009) and is thus expected to have a transient seed bank (see Table 2.1 for full classification).

Table 2.1 *Overview of the 10 species studied including taxonomic properties (species and family) and growth form (graminoids, forbs), successional strategy (early, late) (Fremstad, 1998; Måren & Vandvik, 2009), and seed bank status (persistent, transient) (Måren & Vandvik, 2009) at Lygra. Species names, taxonomic and growth form information are collected from Lid and Lid (2014) and mean 1000 seed weight is collected from Royal Botanic Gardens Kew (2017).*

Species	Family	Succession	Growth form	Seed bank	Seed weight (g)
Avenella flexuosa	Poaceae	Early	Graminoid	Transient	0.50
Anthoxanthum odoratum	Poaceae	Early	Graminoid	Persistent	0.56
Campanula rotundifolia	Campanulaceae	Late	Forb	Transient	0.06
Cirsium vulgare	Asteraceae	Late	Forb	Transient	2.90
Danthonia decumbens	Poaceae	Early	Graminoid	Transient	1.60
Digitalis purpurea	Plantaginaceae	Late	Forb	Transient	1.10
Juncus squarrosus	Juncaceae	Late	Graminoid	Persistent	0.10
Lotus corniculatus	Fabaceae	Early	Forb	Transient	1.00
Luzula multiflora	Juncaceae	Late	Graminoid	Persistent	1.24
Sedum anglicum	Crassulaceae	Late	Forb	Transient	0.04

2.2 Field sampling

Sampling of adult individuals

Adult plants from ten common coastal heathland species, and in addition *C. vulgare, D. purpurea,* and *S. anglicum*, (Table 2.1) were collected between July and September 2017. Ten individuals were collected per species. To ensure that plants were not from the same individual (genet), they were collected at least 5 m apart. Plants were collected at multiple sites in the heathland, making sure to cover different moisture gradients and successional stages (Figure 2.1). This was done to minimize potential confounding effects of environmental factors and different age, that could not be accounted for in the seedling traits study (see below). Ten individuals were collected per species and put in a bag with moist cotton. Thereafter the plants were either brought to the lab for leaf measurements or stored in 4°C and measured within two days.

Seed sampling

In order to examine seedling growth, ten individuals in a late fruit stage were collected from all ten species between August and September 2017. To ensure that plants were not from the same individual (genet), they were collected at least 5 m apart. Whole plants were collected at multiple sites in the heathland, making sure to cover different moisture gradients and successional stages, and put in paper bags. In the lab, mature seeds were removed from the plants following a seed collecting manual for wild species (ENSCONET, 2009). Seeds were expected to be mature when they easily detached from the plant, and when having the colour of a mature seed for that exact species. A total of 200 seeds, 150 for sowing and 50 for backup, were collected. Seeds from each species were stored dry and in a non-glossy paper envelope at room conditions until sowing.

2.3 Greenhouse growth and trait measurements

Greenhouse growth

Collected seeds were sown and grown in plug trays in a greenhouse at The Arboretum and Botanical Garden at Milde, Bergen, under growing conditions set to parallel the field conditions at Lygra during the growing season (12°C, 12h days, ample watering as needed). The greenhouse study lasted from the seed sowing in October 2017 until all plants were harvested in May 2018. Pots were filled with seeding soil containing a mixture of light (70%)

and dark (20%) *Sphagnum* peat, and sand (10%). Available nitrogen, phosphorous, and potassium was 90, 45, and 100 mg/L respectively. Three or more seeds were spread on top of the soil and covered by a small amount of soil sprinkled on top. Pots were marked with numbers 1 to 50 (Figure 2.2). Additionally, 16 pots were prepared as backup individuals, in cases of failed germination or seedlings showing growth abnormalities. These extra pots were marked B1 to B16. The Royal Botanic Gardens Kew (2017) provide information about species in need of vernalisation and vernalisation conditions. *Danthonia decumbens* needs vernalisation before germination. The Royal Botanic Gardens Kew (2017) does not provide any information about germination preparation for *L. multiflora*, hence this species was also selected for a vernalisation period as a precautionary measure. These two species were therefore stored moist, dark, and cold (4°C) for 8 weeks before germinated in the greenhouse. The time of germination was registered for each individual seed. Any additional individuals emerging within each pot were carefully removed by hand after 4 weeks (or when necessary). Remaining individuals were re-potted in p-soil (and 10 x 10 cm PVC pots where needed) after 8 weeks, for optimal growth conditions. P-soil contains a mixture of light (70%) and dark (20%) *Sphagnum* peat, sand (10%), with nitrogen, phosphorous, and potassium of 950, 40, and 220 mg/L, respectively.

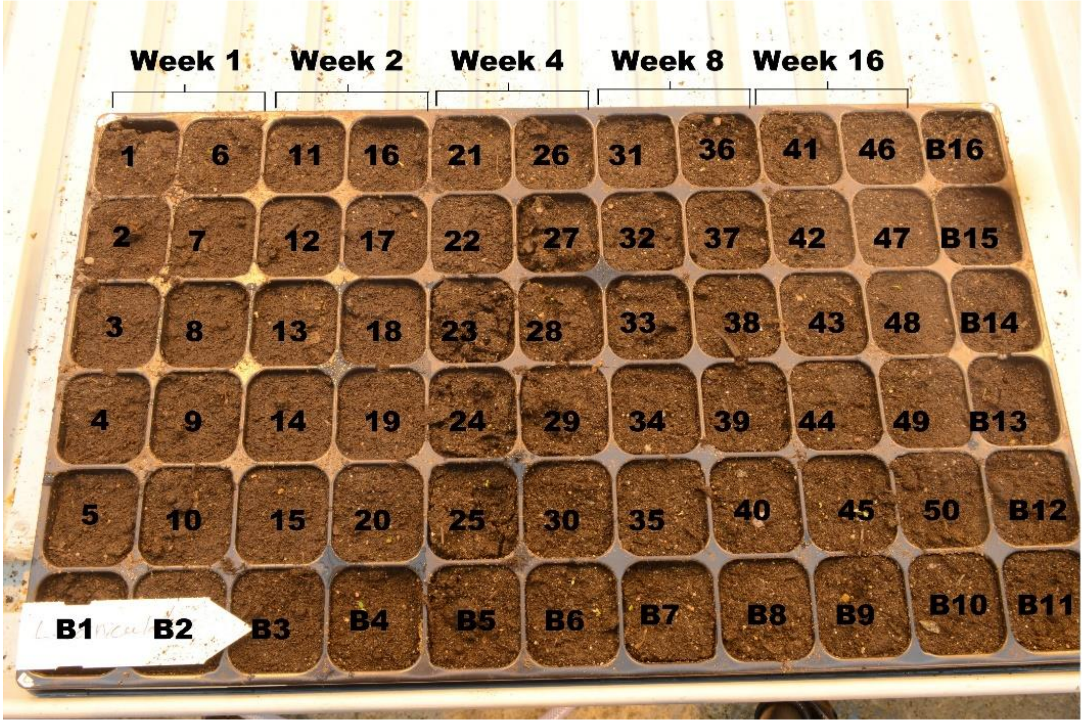


Figure 2.2 *Plug tray with seeding soil. Each pot in the plug tray was numbered from 1 to 50, and backups were marked B1-B16. Ten individuals per species were harvested in week 1, 2, 4, 8, and 16. If a pot was lacking an individual, backups were used.*

Ten seedlings per species were harvested in week 1, 2, 4, 8, and 16, where week 1 started two weeks after germination so that true leaves would have time to emerge and extend. Whole plants (including cotyledons in week 1) were harvested by pulling the plant from the soil by hand and put in bags with moist cotton. Within 12 hours plants were either brought to the lab for measurements or stored in 4°C and measured within two days, as recommended by Perez-Harguindeguy *et al.* (2013).

Leaf trait measurements and calculations

In order to calculate functional traits for adults, seedlings and cotyledons, leaf wet and dry mass, leaf area, and leaf thickness were measured for all sampled plants following the protocol of Pérez-Harguindeguy *et al.* (2013). Measurements were conducted for one healthy, fully erect true leaf per individual. True leaves for forbs were picked with the whole petiole and blade, no stipule, and instantly measured. Graminoid leaves were cut off above the ligule. Above-ground biomass of plants from individuals from the first and last week were used to calculate RGR (Liu *et al.*, 2015). Additionally, for all forbs samples in week 1, one of the cotyledons were measured, using the same methods as for true leaves (see above). Seed mass info was collected from Royal Botanic Gardens Kew (2017).

Wet mass was measured using a scale (Sartorius BP221S, resolution of 0.0001 g +/- 0.0001 g.) to weigh each leaf. Leaves were rinsed, and excess water was removed before weighing. Leaf thickness was then measured using a digital micrometer (Micromar 40 EWR, resolution of 0.001 mm +/- 0.0002). Thickness was measured on three (when possible) different spots on the leaf, avoiding the midrib, for accurate mean thickness. Leaves were scanned (CanoScan LiDE 120) and leaf area was calculated using ImageJ (Abràmoff *et al.*, 2004). Leaves were then put in a drying oven (Termaks TS 5410) at 65-70 °C for at least 72 hours and were thereafter weighed to get the dry weight (using the same scale to minimise errors). To find RGR, dry weight of the leaf that was removed from the individual in week 1 and week 16, was later added into the dry weight of above-ground biomass for that individual.

From these measurements, the following leaf functional traits were calculated:

Specific Leaf Area (SLA)

$$= \frac{One - sided\ leaf\ area\ (cm^2)}{Leaf\ dry\ mass\ (mg)} \ = cm^2\ mg^{-1} \tag{1}$$

Although some studies use leaf mass per area (LMA), I have chosen to use SLA because many of the studies I compare results with use this measurement. As LMA is simply the inverse of SLA (LMD = 1/SLA), I use this transformation when comparing with studies using LMA.

Leaf Dry Matter Content (LDMC)

$$= \frac{Dry\ leaf\ mass\ (mg)}{Fresh\ leaf\ mass\ (g)} = mg\ g - 1 \tag{2}$$

Relative growth rate (RGR)

$$= \frac{\left(\overline{\ln w_2} - \overline{\ln w_1}\right)}{(t_2 - t_1)} \tag{3}$$

where W_2 is the final above-ground plant biomass, W_1 is the initial above-ground plant biomass, and t_2-t_1 is the time interval in days, reflecting the gain of dry mass through time. Increased variance in individual dry mass per week, time between harvests, and sample size, lead to a larger variance in the ln transformed plant weights in the last harvest compared to the first. This leads to biased RGR estimates of the species. Hoffmann and Poorter (2002) produced the formula presented in equation (3) to avoid bias in calculated RGR values. Using this formula is relevant in my study due to the long time between harvests.

Leaf thickness is associated with both SLA and LDMC where thick leaves show the trade-off between higher leaf physical strength (toughness) and lower photosynthetic rate (Pérez-Harguindeguy *et al.*, 2013). Additionally, SLA is often strongly correlated to the RGR of the plant (Funk *et al.*, 2017).

2.4 Statistical analysis

Before conducting statistical analyses, the data were prepared. For most species, at least 50 seedlings emerged and survived, however *C. rotundifolia, C. vulgare*, *D. decumbens*, and *S. anglicum* had only 49 measurable individuals, and *L. corniculatus* had 46 individuals. After measurements were conducted, individuals with missing values were removed. Nine individuals were removed due to no registered leaf area which prevents the calculation of SLA, four were further removed because of missing dry and/or wet mass which hinders the calculation of SLA and LDMC, and two due to missing leaf thickness values. Two adult individuals were removed, one due to missing leaf area and one due to missing dry mass. This left a total of 477 seedling individuals and 98 adult individuals to analyse.

Model checking was done visually using residual plots. Leaf thickness was square root transformed and SLA was log transformed to achieve normality and homoscedasticity of the residuals. Separate linear or linear mixed effects models were produced for each trait (SLA / LDMC / leaf thickness). Maximum likelihood was used in all linear mixed effects models.

To test for change in trait values through time from week 1 to week 16, a linear mixed effects model was used. Trait was used as response variable, week as fixed effect, and species as a random effect. To test the difference between seedling (week 16) and adult, I used the same model as above with life-history stage as a fixed effect instead of week. Life-history stage was a categorical variable with two levels, due to unknown age of adult individuals.

Differences between groups (graminoid/forb, early-/late-successional, persistent/transient seed bank) and the interaction between group and time (week 1-16) was examined with separate models for growth forms, successional stages, and seed bank status. The same linear mixed effect model as above was used, including an interaction between week and group with species nested in group as a random effect.

A linear mixed effects model was conducted to examine the relationship between seedling traits in week 1 and adult traits. Seedling trait value was set as response variable, adult trait value as fixed effect, and species as random effect. This model was also used to compare the ranking of species trait means of seedlings and adults. A linear mixed effects model was also used to examine the relationship between seedling true leaf traits and cotyledon traits in week 1. True leaf trait values were set as response variable, cotyledon trait values as fixed effect, and species as random effect. A linear regression model was used to examine the relationship between RGR and SLA (week 1 to 16), and between RGR and seed mass. Seed mass or SLA was set as response variable, and RGR values as fixed effect. All analyses were done using the R statistical computing platform (version 3.3.1) using the nlme package (Pinheiro *et al.*, 2009).

3. RESULTS

3.1 Variation in traits through the ontogeny

Seedlings showed characteristic trait values compared to adults for all traits measured (Figure 3.1, Table 3.1). First-week seedling leaves were thin, with high SLA, and low LDMC. All functional traits had a significant slope for change through time in the seedling stage. Leaf thickness and LDMC increased (i.e. thicker leaves with higher tissue density through time), whereas SLA decreased (i.e. decreasing ratio of leaf area to dry mass through time) (Table A.2). The change from week 16 to the adult stage continued in the same direction as in the seedling stage, and the differences between week 16 and the adult stage was also significant for all traits (Table A.3).

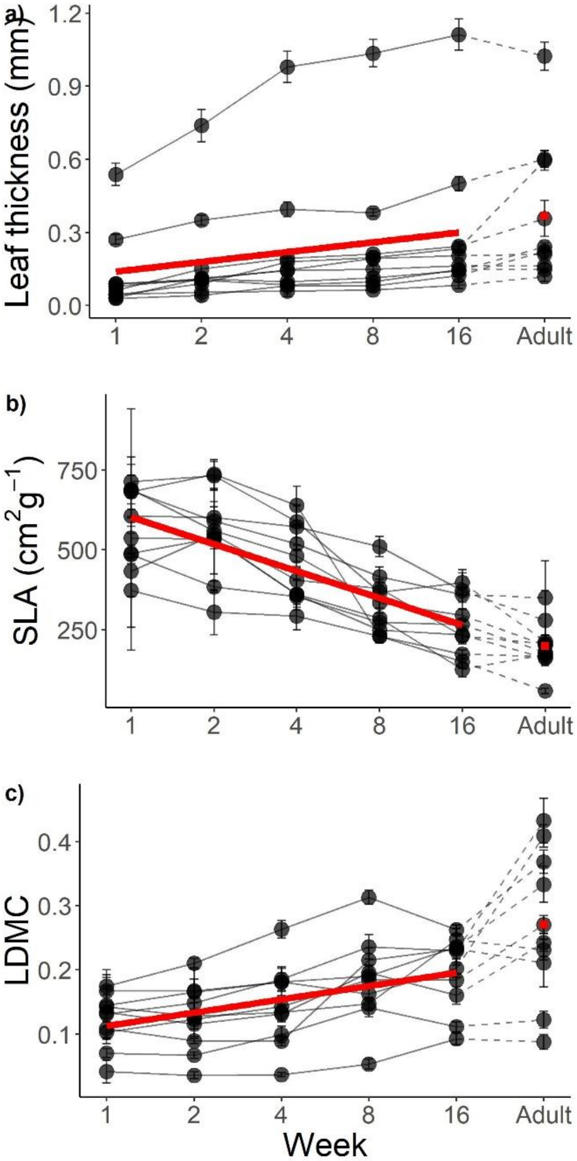


Figure 3.1 *Change in functional trait values for 10 common coastal heathland species during the ontogeny. The plots show mean values for each of the study species' a) leaf thickness, b) specific leaf area (SLA), and c) leaf dry-matter content (LDMC) for seedling and adult leaves for seedling plants. Solid, black lines represent development in mean values through the ontogeny of each species between week 1 and 16 for seedlings grown in a greenhouse. Dashed lines connect mean values from seedling to adult plant, the latter was collected in the field. Red lines represent the linear mixed effects model for seedlings from week 1 to 16, and the red point represents the mean value for adults. Each point represents the mean of 10 individuals and the whiskers show 1.96 standard error for each value (n = 477).*

Table 3.1 *Output from linear mixed effects models testing change in functional trait values through time. The table includes the term that seedlings were tested against, the slope between the fixed effects (estimate), and the t-values and p-values for the slopes. Traits (leaf thickness, specific leaf area (SLA), leaf dry-matter content (LDMC)), and week were fixed effects, and species was a random effect, n = 477. Bold values are significant.*

Trait	Term	Estimate	t-value	p-value
Leaf thickness	week	0.01	7.98	**<0.001**
SLA	week	-21.3	-7.62	**<0.001**
LDMC	week	0.01	7.30	**<0.001**

The range of species mean trait values generally increased from seedling to adults; for leaf thickness it increased by 78 % (from 0.51 mm for seedling to 0.91 mm for adults), and for LDMC increased by 162% (from 0.13 g/g for seedlings to 0.34 g/g for adults). For SLA the range of species means decreased by 19% (from 358 cm^2/g for seedlings to 291 cm^2/g for adults). When testing for homoscedasticity for leaf thickness (df = 188, F = 0.64, P = 0.43), LDMC (df= 188, F= 0.17, P= 0.68), and SLA (df = 188, F = 0.11, P = 0.74), no significant values were found, indicating a significant change in variance between species trait values from week 1 to the adult stage. Leaf thickness and LDMC had higher interspecific variance in the adult stage than the seedling stage. However, SLA had higher interspecific variance in the seedling stage than the adult stage. Additionally, intraspecific variance in SLA was higher in the seedling stage.

For leaf thickness and LDMC, the ranking of species in terms of trait values remained unchanged through the ontogeny (Figure 3.2a). In contrast, a nonsignificant relationship between seedling and adult SLA traits indicated that the species' adult SLA might not be indicative of the species' seedling SLA.

There was a significant relationship between cotyledons and true leaves (Figure 3.2b, Table 3.2). Although, there was no significant relationship between SLA of cotyledons and seedling true leaves. Cotyledon leaves were generally thicker and had lower LDMC than seedling true leaves from the same individual (Figure 3.2b). Cotyledon SLA was strikingly high compared to seedling true leaf SLA (difference in mean true leaf and cotyledon SLA: 961 cm^2/g).

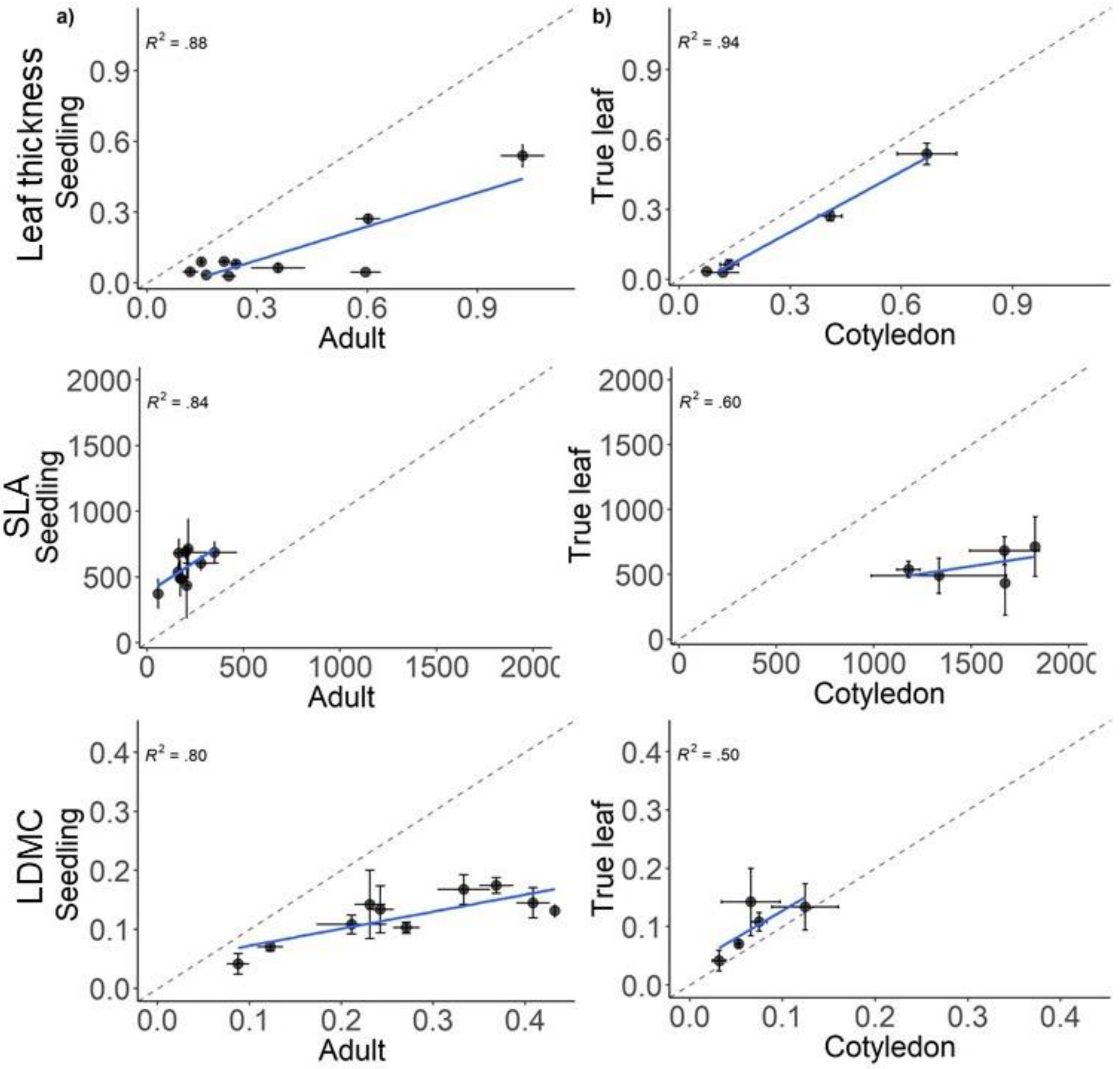


__Figure 3.2__ Comparison of functional trait values for 10 common coastal heathland species between seedlings (week 1) and adult stage (field sampling), and cotyledons and seedlings (sampled in week 1). The plots show a) relationship between seedling leaves and adult leaves, n = 90, b) relationship between cotyledons and true seedling leaves of seedlings, n = 42, for leaf thickness, specific leaf area (SLA), and leaf dry-matter content (LDMC) for all species. Blue lines represent the regression lines for the relationships. Dashed lines represent the 1:1 relationship. The points represent the mean of 10 individuals and the whiskers show 1.96 standard errors for each value.

Table 3.2 *Output from linear mixed effects models examining the relationship between seedling traits in week 1 and adult traits, n = 90 (model 1), and seedling traits in week 1 and cotyledon traits, n = 42 (model 2) for leaf thickness, specific leaf area (SLA), and leaf dry-matter content (LDMC). The table includes the term which seedling was tested against, the slope between the fixed effects (estimate), and the t-values and p-values for the slopes. In model 1, seedling trait value was set as response variable, adult trait value as fixed effect, and species as random effect. In model 2, true leaf trait values were set as response variable, cotyledon trait values as fixed effect, and species as random effect. Bold values are significant.*

Trait	Term	Estimate	t-value	p-value
Leaf thickness	Adult	0.16	2.53	**0.014**
SLA	Adult	0.06	0.51	0.611
LDMC	Adult	0.18	2.92	**0.005**
Leaf thickness	Cotyledon	0.25	1.80	**0.080**
SLA	Cotyledon	0.04	0.88	0.387
LDMC	Cotyledon	0.57	2.99	**0.005**

3.2 Trait differentiation in growth forms, successional stages, and seed bank status

Forbs and graminoids differed significantly in LDMC and SLA in the seedling stage (Figure 3.3a, Table A.6). Graminoids had higher LDMC, and a significant interaction with time indicates that forbs decreased in SLA faster than graminoids through time. The two growth forms did not differ significantly in leaf thickness. Early- and late-successional species differed significantly in all traits (Figure 3.3b, Table A.6). Early-successional species had higher LDMC than late-successional species. Significant interaction terms indicated that late-successional species increased in leaf thickness and decreased in SLA faster than early-successional species through the ontogeny. Seed bank status did not affect any of the traits or through time (Figure 3.3c, Table A.6).

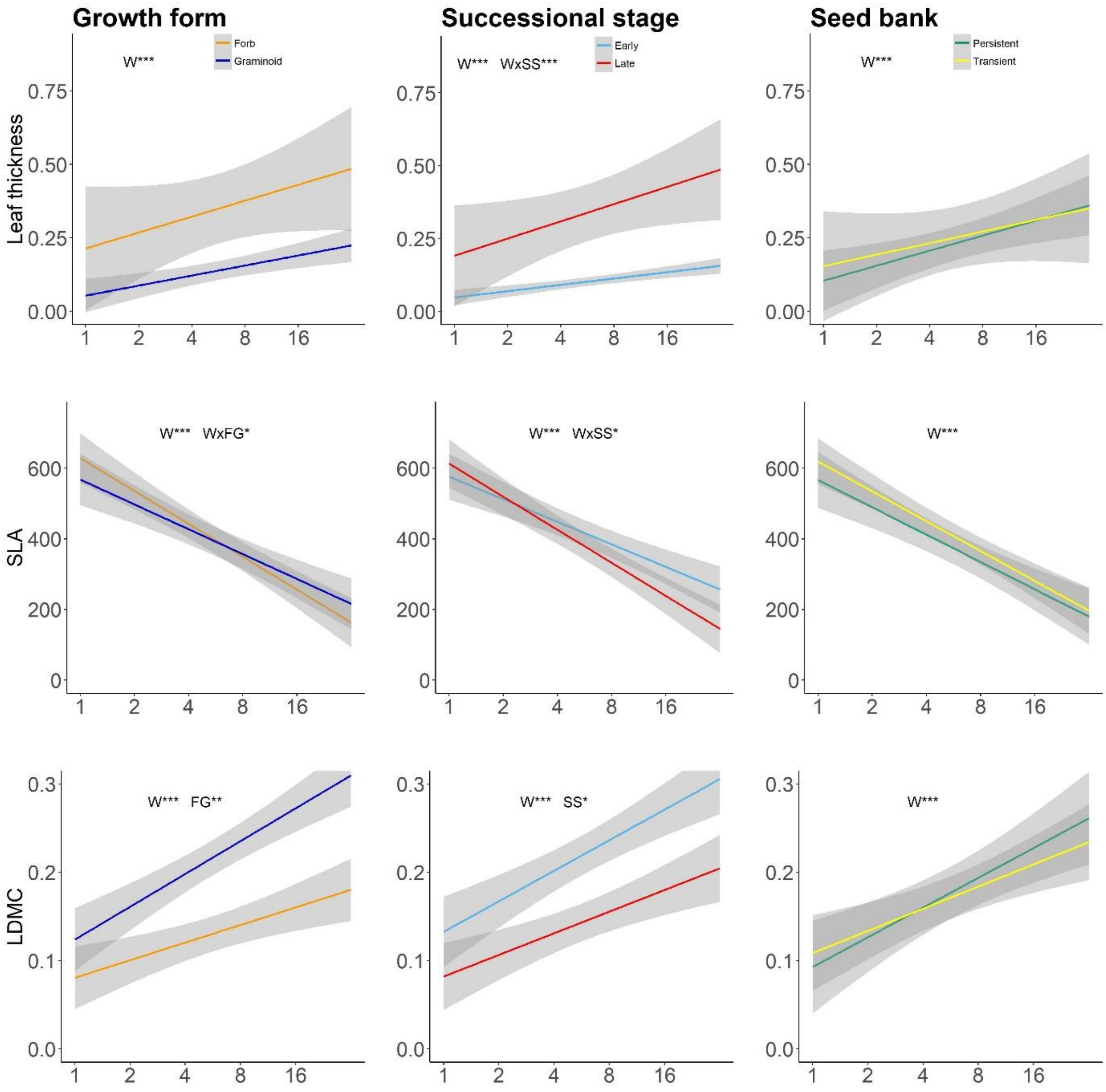


Figure 3.3 Change in functional trait values for 10 common heathland species classified by ecological groups during the ontogeny. The plots show specific leaf thickness, leaf area (SLA), and leaf dry-matter content (LDMC) trait-values for species divided into a) growth forms (GF); 5 species forbs(orange)/5 species graminoids(blue), c) successional stage (SS); 4 species early- (red)/ 6 species late- (blue) successional, d) seed bank status; 3 species persistent(green)/ 7 species transient(yellow) over time from week 1 to week 16, n = 477. Solid lines represent change in mean values for each group over the 16 weeks. The confidence intervals show 1.96 standard errors.

3.3 Relative growth rate in the early stage

Relative growth rate differed between species, ranging from 0.032 $gg^{-1}d^{-1}$ (i.e. slower growth) to 0.064 $gg^{-1}d^{-1}$ (i.e. faster growth) (Figure 3.3). Graminoids (0.057, SE: +/-0.0028) had higher mean RGR than forbs (0.051, SE: +/-0.0065). The range in RGR-values was larger for forbs (0.032 $gg^{-1}d^{-1}$ to 0.063 $gg^{-1}d^{-1}$) than for graminoids (0.049 $gg^{-1}d^{-1}$ to 0.064 $gg^{-1}d^{-1}$). Early-successional plant species (0.053, SE: +/-0.0055) had lower mean RGR than late-successional species (0.055, SE: +/-0.0050). The range in RGR-values was similar for early-successional species (0.038 $gg^{-1}d^{-1}$ to 0.064 $gg^{-1}d^{-1)}$ and for late-successional species (0.032 $gg^{-1}d^{-1}$ to 0.063 $gg^{-1}d^{-1}$). Species with a persistent seed bank (0.056, SE: +/-0.0036) had higher mean RGR than species with a transient seed bank (0.53, SE: +/-0.0050). The range in RGR-values was smaller for species with a persistent (0.049 $gg^{-1}d^{-1}$ to 0.061 $gg^{-1}d^{-1}$) than for species with a transient (0.032 $gg^{-1}d^{-1}$ to 0.064 $gg^{-1}d^{-1}$) seed bank.

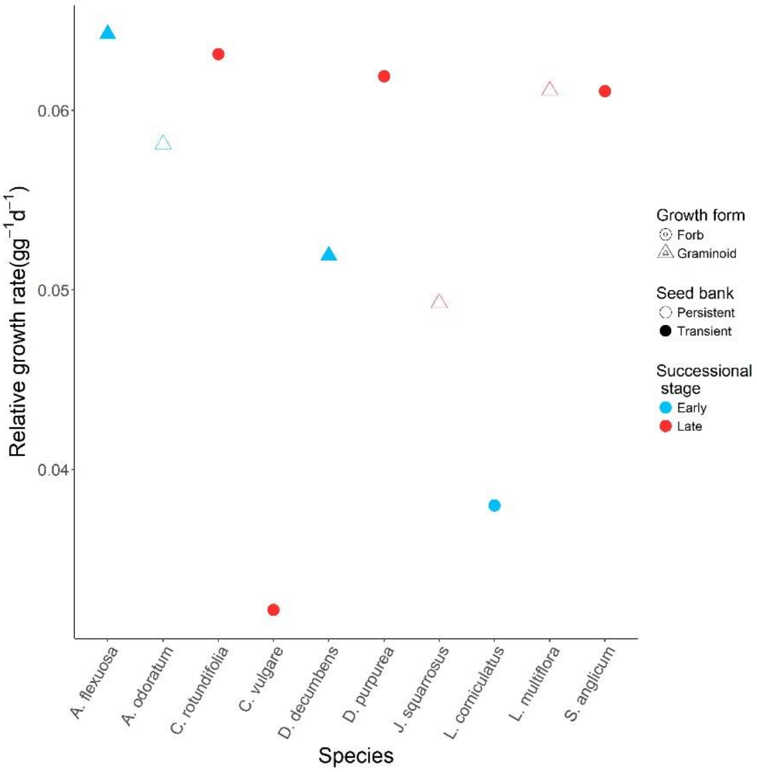


Figure 3.4 *RGR calculated from dried above-ground biomass for 10 common heathland species in week 1 and 16, n= 10. The plots show RGR-values for all species, divided into growth forms; forb(circle)/graminoid(triangle), successional stage; early- (blue)/late- (red), and seed bank status; transient (fill), persistent (no fill).*

RGR had a moderate positive relationship with SLA, although not significant (Figure 3.5a, Table 3.3). The change in RGR with seed mass was negative, and the relationship was strong and significant (Figure 3.5b, Table 3.3).

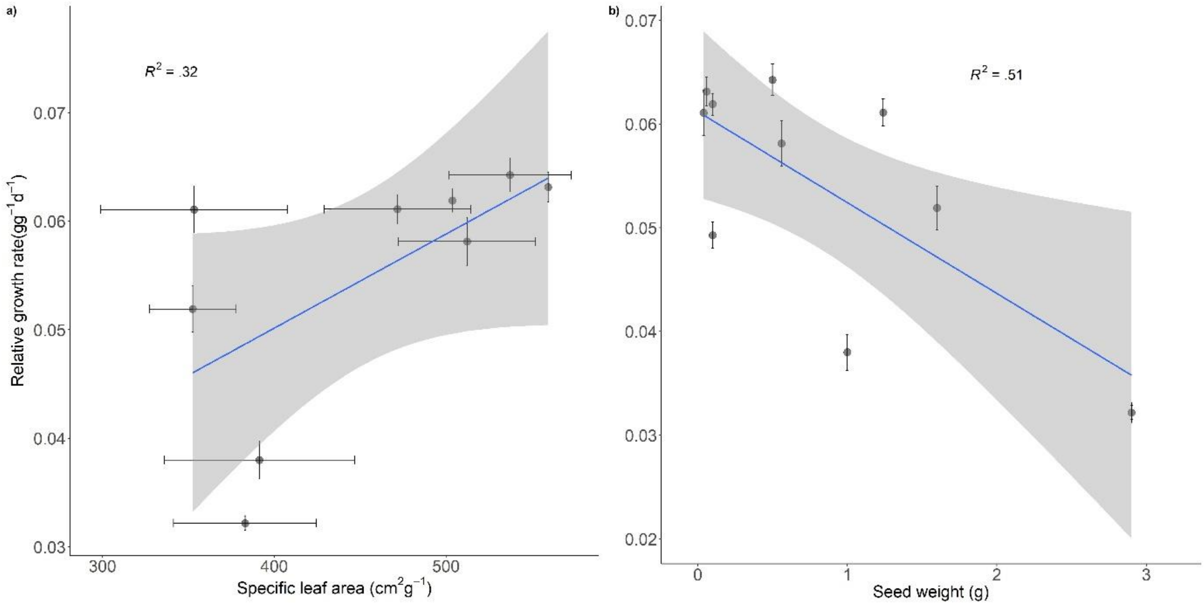


Figure 3.5 *Linear regression showing positive relationship between a) RGR and SLA n =10, and negative relationship between RGR and seed weight, n =10. The blue lines represent the regression line, points represent the relationship between each specie's RGR and mean SLA or mean 1000 seed weight, whiskers show 1.96 standard errors for each value, except seed weight which only had one value (from Royal Botanic Gardens Kew, 2017). Note that the y-axis is plotted on a small scale, and the slope appear steeper than they are (see Table 3.3)*

Table 3.3 *Output from linear regression testing the relationship between relative growth rate (RGR) and specific leaf area (SLA), n = 10, and RGR and seed mass, n = 10. The table includes the terms RGR was tested against, the slope between the fixed effects (estimate), and the t-values and p-values for the slopes. Bold values are significant.*

Trait	Term	Estimate	t-value	p-value
RGR	SLA	0.00	1.96	0.086
RGR	Seed mass	-0.01	-2.90	**0.020**

4. DISCUSSION

In this study I show that resource acquisitive traits dominate in the early life-history stages of coastal heathland plants, whereas conservative traits dominate in the later stages. Seedlings also have more constrained trait values than adults, thus interspecific variance in traits increase with time. The ranking of mean trait values for species remains constant through time. Additionally, trait values depend on the species' growth form and successional strategy, and traits for these groups change in different degrees or directions through time. However, there is no difference between species with persistent and transient seed bank. To the best of my knowledge, this is the first study that empirically assesses the traits of coastal heathland seedlings, and how they develop through the ontogeny and differ by growth forms, successional stage, and seed bank status. My results suggest that seedling traits can provide important insights into the regeneration probability of different plant species, growth forms and successional responses, today and under future climatic stressors. This knowledge may prove particularly useful in predicting future species composition of coastal heathlands.

4.1 Plant functional traits through the ontogeny

Species in the coastal heathland of Lygra show a switch in trait values from resource acquisitive seedlings (thin leaves, high SLA, low LDMC) to resource conservative adults (thicker leaves, lower SLA, higher LDMC), which is in consensus with my first hypothesis. This change in species trait values was significant for all studied traits and is in consent with studies of species in humid alpine meadow (Wu *et al.*, 2013), coastal meadows (Niinemets, 2004), and forest and woody meadow (Niinemets, 2005), as well as the study of Mason *et al.* (2013) conducted with similar methods in a controlled environment. This indicates that herbaceous species in the coastal heathland have similar strategies as species in several other systems, and their behaviour can be compared. The species used in my study represents the most common perennial herbaceous species found at Lygra. However, the dwarf shrubs *Calluna vulgaris* and *Erica tetralix* dominate both the standing vegetation and seed bank at representative of the complete heathland community. Nevertheless, these herbaceous species arguably represent the more vulnerable vascular plants of the heathland, and an important component of the heathland biodiversity. Additionally, focusing on herbaceous perennials enabled me to rule out other large sources of variation in traits, especially growth rate, which vary between woody and herbaceous species, as they vary in life-history strategy (Gatsuk *et* *al.*, 1980). This allowed me to make explicit comparisons between species and ecological groups within the range of taxa studied.

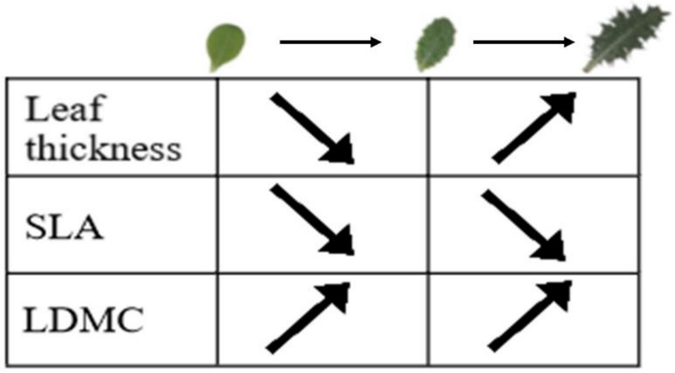
My second hypothesis, that trait differentiation between species should increase through time, was also confirmed for all traits except SLA. I found that species became increasingly different in leaf thickness and LDMC mean values and hence there was an increase in interspecific variance through the ontogeny. This suggests that seedlings have a narrower range of functional traits than adults in the coastal heathlands. The trait driver theory (Enquist *et al.*, 2015) predicts that a rapid change in climate will affect assemblages of plants with different variance in different ways. Communities with lower variance in trait values will be more severely affected than those with higher trait variance, as communities with higher variance have a better ability to change along with different climatic conditions. Environmental filtering has been shown to be especially strong in the plant recruitment stage (Grime & Curtis, 1976; Grubb, 1977; Fraaije *et al.*, 2015). In this stage, species are not as much affected by the limiting similarity as later stages, where species with similar traits may competitively exclude each other, leading to a larger variation of traits in the community (Takahashi & Tanaka, 2016). In the burned patches of coastal heathlands, interspecific competition can be expected to be low, as competition amongst seedlings is found to be low (Moles & Westoby, 2004), and environmental filtering will strongly select towards more similar traits. The life stage of resource acquisitive and functionally similar seedlings will thus be more vulnerable to, and severely affected by extreme climate events like drought. In contrast, adult plants are extra tolerant by being more conservative and variable. The fact that interspecific variance in SLA was higher for seedlings than for adults is due to species having a larger range of SLA values as seedlings compared to adults. However, the change in variance for species SLA means is relatively constant through time. This indicates that the range in photosynthetic activity is higher for seedlings. Including intraspecific and plasticity analyses would aid in the understanding of how species-level and individual trait variation and hence tolerance to environmental change contribute to the whole-community tolerance.

I found that ranking of species in terms of trait values is constant, except for SLA. In particular, relative ranking of species trait means remained constant for leaf thickness and LDMC from the seedling to the adult stages. This is also found in the study of Kitajima and Poorter (2010) where they study ontogenetic traits shifts in woody species. Interestingly, they found that this was true for all the traits measured in their study but lamina area, where ranking of species means changed through time. This may relate to the change in relative ranking found for SLA of species in my study, as SLA is calculated using leaf area. This change implies that the coastal heathland species with the highest SLA relative to other species in the seedling stage, will not necessarily be the species with the highest SLA in the adult stage. Thus, species SLA-values measured in the adult stage would not predict SLA of the seedlings in the coastal heathlands. Another possibility is that the relationship between SLA values for seedlings and adults are not significant because of the large variance in SLA values within species. The lack of change in interspecific relative ranking found for leaf thickness and LDMC indicates that these traits are relatively constant through the change in trait values through the ontogeny. Thus, species with thin leaves and low LDMC, relative to other species, in the seedling stage will also have similarly low values in the adult stage. Even though leaf thickness shows a significant relationship between seedling and adult values, the relationship is based on two species with higher values than the rest of the species. When removing those two points the relationship was no longer significant. The interspecific ranking for leaf thickness and LDMC is stable, and there is a chance that the change in ranking for SLA is due to variation, where repeating the study with more replicates would show a more certain result. Additionally, growing the species in stable conditions in a greenhouse rules out differences in traits found in the field. In the field plants are experiencing competition, less nutritious soil, and periods of water stress and periods of drought stress, whereas in the greenhouse plants are grown in more optimal conditions. For *S. anglicum* (Table A.4) the leaf thickness is lower for adults than for seedlings in week 16. This difference observed in leaf thickness is likely to be an effect of the different conditions between the greenhouse-grown seedlings and the adults collected in the field. The relative ranking of species mean trait values through the ontogeny should be further studied in coastal heathlands, as this can aid in the understanding of how adults can predict seedling community response to environmental change and hence future species composition.

4.2 Functional traits of cotyledon leaves

I found a positive relationship between cotyledons and seedling true leaves for all traits except SLA. Studies have shown that SLA for cotyledon and true leaves show a strong positive relationship (Kitajima, 1992; Wright & Westoby, 1999), as expected due to both having the ability of photosynthesis. This positive relationship for SLA indicates that other leaf traits could also show the same relationship. Additionally, it could be expected that species have cotyledons reflecting the plant's strategy, as the whole seedling is affected by the initial seed mass (Jurado & Westoby, 1992; Leishman *et al.*, 2000; Westoby *et al.*, 2002; Díaz *et al.*, 2016). LDMC showed a strong relationship, although leaf thickness has a weaker relationship, and is based on two species that have higher values than the cluster of the remaining species (as mentioned in last section). The relationship between cotyledons and true leaves was no longer significant after the removal of these two species from the model (exploratory analyses, results not shown). True leaves and cotyledons differ in their relationship between morphology and the function of the leaf, due to cotyledons functioning both as seed reserve storing and photosynthetic organs (Kitajima, 1992). Thus, we cannot necessarily expect cotyledons to behave in the same ways as true leaves. The lack of relationship between cotyledons and seedlings in my study could be due to that cotyledons had a larger leaf area and higher dry mass compared to the true leaves, with a larger difference between these two measurements than true leaves had (Table A.5). The fact that there is no relationship between cotyledons and true leaves, implies that cotyledons have photosynthetic rates that are not in accordance with the strategy of the seedling. However, there is an uncertainty in the results of SLA due to the large variation for species trait values. A further study of the relationship between true leaf traits and cotyledon traits can aid in the understanding of how cotyledons are related to true leaves, and in which manner they affect seedling survival.

Specific leaf area and LDMC values for species measured in this study indicates an even stronger resource acquisitive strategy for cotyledons than for true leaves (Figure 4.1, Appendix B). This contrasts leaf thickness, which shows a shift where cotyledon and adult plant leaves are thicker than



Leaf thickness	↘	↗
SLA	↘	↘
LDMC	↗	↗

Figure 4.1 *Change in trait values from seedling cotyledons to true leaves (column 1), and from seedling leaves to adult leaves (column 2). The arrows indicate increase or decrease in the trait value.*

seedling leaves. Cotyledons have been shown to decrease in dry mass as water content increases (McAlister & Krober, 1951). This might explain why cotyledons have thick leaves at the same time as high SLA and low LDMC. Kitajima (1992) found that SLA was higher for photosynthesising cotyledons thinner than 1 mm, and the SLA got higher with thinner leaves. In contrast, Izuta *et al.* (1995) found that cotyledons of cucumber plants had lower SLA than true leaves. The high SLA found in my study is due to the large difference between leaf area and dry mass values, as mentioned above. The SLA values were not specified in the studies of Kitajima (1992) and Izuta *et al.* (1995), although I would expect extreme values to have been mentioned. Due to the missing SLA values in their studies, it is problematic making further assumptions. More studies of traits for cotyledons, and their trait values relative to true leaves, would yield information about cotyledon contribution to seedling survival.

4.3 Change in traits through time for species with different growth forms, successional stages, and seed bank status

Coastal heathland species' mean trait values and how traits change through time depends to a large extend whether they are graminoid or forb, and early- or late-successional for most traits. This indicates that differences in several traits for growth forms and species with different successional strategy can be found already in the seedling stage. This is mostly in accordance with my third hypothesis, although not all traits showed the results that were expected. No difference in traits was found for species with different seed bank status.

I found that species with different growth forms and species emerging at different successional stages had significantly different trait means for LDMC. Graminoids and early-successional species had tougher leaves than forbs and late-successional species in the seedling stage. I also found that forbs and late-successional species started out with higher SLA followed by a shift in week 4 and 2, respectively, where graminoids and early-successional species had increasingly higher SLA. There is a lack of studies of traits for growth forms and successional stages in coastal heathland. Although, studies of ruderal species, which can reflect those who are early-successional, and of growth forms from other systems show that early-successional species and forbs are expected to have high SLA compared to late-successional species and graminoids (Poorter & Remkes, 1990; Huovinen-Hufschmid & Korner, 1998; Wright *et al.*, 2005). This also indicates that they have low LDMC and thin leaves (Caccianiga *et al.*, 2006). My results show unexpected leaf thickness and SLA values for growth forms, where, although not significant, forbs have thicker leaves than graminoids, and graminoids also have higher SLA after the 4th week. The switch in SLA for growth forms and for successional stages found in my study could be due to cotyledons starting to wither around that time. This implies that cotyledons have a large effect on true leaf SLA and affect species with different growth forms and successional strategies in different ways. The unexpected thick leaves for forbs might be because of two reasons. Firstly, the succulent leaves of *S. anglicum* increases the mean value, as well as the thick leaves of *C. vulgare* (Table A.4). Secondly, most of the graminoids are also early-successional species (see discussion below), which have thin leaves due to their fast growth relative to late-successional species. The fact that most graminoids are early-successional, and opposite, could also explain why early-successional species have higher LDMC. Even though there is a link between these results, it is harder to figure out if it is the growth forms that are driving the traits of the species in different successional stages, or opposite, due to both showing unexpected values. By comparing results of growth forms and successional stages it is clear that there are some consistent patterns. For example, forbs and late-successional species, and graminoids and early-successional species show similar trends through time. This could be explained by the fact that as many as four species are both forb and late-successional and three species are both graminoids and late-successional (see Table 2.1). This leaves few species with other combinations. The reason there are mixed results might be due to the early-successional species in my study not being typical ruderal species. Additionally, a large and overlapping range of SLA trait means have been found in graminoids and forbs (e.g. Huovinen-Hufschmid & Korner, 1998; Wright *et al.*, 2005), which can lead to difficulties in separating these groups without a high number of species and a large sample size. This might also be true for the species with different successional strategies in my study, as all of them are herbaceous perennials. Thus, trait values of species in my study might be too similar to separate between the chosen groups. The grouping of species into early- and late-successional based on Fremstad (1998) has also later shown to not be in complete agreement with species implied as early-successional in the PCA ordination diagram of Måren and Vandvik (2009). This might be due to Fremstad (1998) referring to Norwegian coastal heathlands in general, and Måren and Vandvik (2009) specifically studied Lygra (and a similar neighbour island). Choosing grouping criteria for the studied species based on results from the same study system would be beneficial for future studies. In addition, including annuals and woody species of the coastal heathland would complement the different groups measured in my study, especially species of different successional stages.

This will improve the results of how these groups contribute in the trait pool in coastal heathlands.

Seed bank status did not seem to influence trait values whereas no difference was found in traits for species with persistent and transient seed banks, contrasting my hypothesis. This might again be due to the species grouping, which was based on seed frequency in the seed bank sampled by Måren and Vandvik (2009). The study of Måren and Vandvik (2009) collected seed bank samples in early May, when both transient and persistent seed banks are available. Using the data from their study, I grouped species based on the knowledge that species with a high frequency of seeds in the seed bank at this stage have a persistent seed bank, and those with low frequency have e transient seed bank (Thompson & Grime, 1979). Although Måren and Vandvik (2009) presented their samples as collected from a persistent seed bank in their study, thus did not divide species into transient or persistent, as in my study. A better way of grouping the species would be to register which species are available in the seed bank sampled before seed dispersal in autumn, when most of the seeds from the prior year's seed dispersal would have germinated. The species left in the seed bank at this point will be species with persistent seeds. In addition, sampling from only deeper soils would exclude the transient seed bank, which could create a better picture of which species are truly persistent in the seed bank.

4.4 Relative growth rate for seedlings

Relative growth rate (RGR) is the rate of increase in dry mass per unit mass through time. This whole-plant trait is key in predicting plant survival and ecological strategies in different environments (Funk *et al.*, 2017).

I found that species in my study had low RGR (range of values) compared to other studies. Values found in these studies collectively had a large range from 0.03 to 0.35 (Poorter, 1989; Poorter & Remkes, 1990; Maranon & Grubb, 1993; Ryser & Wahl, 2001; Turnbull *et al.*, 2012), where most values were above 0.1. The reason for the low RGR values in my study can be explained by plant growth being negatively affected by temperature (Hunt & Lloyd, 1987; Loveys *et al.*, 2002) and low nutrient availability (Ryser & Lambers, 1995; Hunt & Cornelissen, 1997). Especially as plants adapted to a poor habitat have low RGR even when exposed to stable conditions (Ingestad & Kähr, 1985; Poorter, 1989; Wright & Westoby, 1999). Growth temperature for the studies I used for comparison was around 20°C, which yields a higher RGR than the 12°C selected for species in my study. This is in accordance with the study of Hunt and Lloyd (1987) where growth rate of *A. flexuosa* was approximately 0.06 at 12°C, which is the same as for individuals of *A. flexuosa* in my study. My species are adapted to a low nutrient level due to acidic bedrock at Lygra, where low RGR is the response. Thus, it seems like the low RGR-values found for species in coastal heathland are a result of adaption to low temperatures and nutrient poor soils.

Unexpected RGR values were found for species of different growth form and successional strategy. Graminoids had higher RGR than forbs and late-successional species had higher values than early-successional. However, as expected, species with a persistent seed bank had slightly higher RGR than those with a transient seed bank. This is in accordance with the negative relationship between RGR and seed weight, and the fact that small seeds are expected to be persistent in the seed bank (Thompson & Grime, 1979; Bossuyt & Hermy, 2003). These groups have not been much studied, although early successional species are known to have high RGR, as they are ruderals (Poorter & Remkes, 1990; Prach *et al.*, 1997; Pywell *et al.*, 2003). Additionally, Hunt and Cornelissen (1997) found in their study that herbaceous monocots had higher mean RGR than herbaceous dicots, although overlap was found in the RGR values due to high variation in trait values. This overlap might be found for species in my study as well. The difference between RGR mean values for the growth forms, successional strategies and seed bank status was so small, and the variation in RGR was so large, especially for early- and late-successional species, that conclusions cannot be made. However, the unexpected values might also in this context be a consequence of the link between growth forms and successional strategies and that species are not typical ruderal species (both explained above). Including more species of different life-histories would also in this context be an advantage for giving the complete range of traits available in the different groups.

4.5 Community response to climate change and cessation of management practices

Norwegian coastal heathlands have experienced several events of destructive winter drought and increased temperatures the last years (met.no). This will affect vulnerable seedlings occupying the open, exposed, burned patches of soil. It is shown that the strongest response to increased warming on European heathlands is in the stable, wet and cold sites (Berry & Bjorkman, 1980; Loveys *et al.*, 2002; Peñuelas *et al.*, 2007). Even though the coastal heathland climate is mild, an increase in temperature will lead to the species adapted to stable conditions being extra vulnerable (Berry & Bjorkman, 1980). Additionally, a prolonged growing season will increase decomposition of biomass, leading to increased nutrient availability, and altered species composition (Peñuelas *et al.*, 2004). The species in coastal heathlands have adapted to fire, grazing and succession through thousands of years. These species have either ruderal, competitive or stress tolerant strategies. Although, the combination of high disturbance and high stress has “no viable strategy” (Grime, 1977, p. 1170). Climate change adds an additional challenge for managed heathlands, where many species might struggle to persist in the vegetation, especially in their vulnerable seedling stage.

Warming shows a positive effect on abundance of graminoids, especially in cold climates (Elmendorf *et al.*, 2012). Moreover, plants growing in humid climates, like coastal heathlands, have been shown to have low adaptability to storing water, thus they might be extra prone to long periods of drought (Vicente-Serrano *et al.*, 2013). Heathland regeneration relies on germination of the seed bank and seedling survival (Thompson & Grime, 1979; Meulebrouck *et al.*, 2007; Måren & Vandvik, 2009), and with increased periods of drought there are several consequences. Lloret *et al.* (2004) found that the number of established seedlings was lower in drought treatments. Drought also decreased species richness in their study, implying an increased selection pressure toward traits for drought tolerance. The study of Lloret *et al.* (2004) was conducted in a Mediterranean shrubland, however the effect of drought in their study was highest in the seasons which usually has the most rainfall. Thus, drought could show similar, maybe larger, effects in temperate heathlands. As longer periods of drought decrease seedling survival, species with a more persistent seed bank, like early-successional species, will have a higher chance of long-term survival (Bossuyt & Hermy, 2003; Cristofoli *et al.*, 2010). However, survival is higher in slow growing seedlings with conservative traits (Ryser, 1996; Wilson *et al.*, 1999; Poorter & Bongers, 2006). Thus, the high RGR strategy of plants in early post-fire succession might not be favourable in periods of drought. Essentially, the species with more conservative traits will have higher seedling survival in drought periods. My results show that graminoid seedlings have tougher leaves, thus are more tolerant, than forbs. It can therefore be expected that, relative to the species included in my study, future population composition will include more graminoid species. All these elements affecting seedling survival could lead to an alteration in species composition and selection pressure towards higher seed mass and more tolerant and resource conservative seedlings. Thus, an alteration in the future community and trait composition, which might eventually influence ecosystem functioning in the coastal heathlands (Fenner, 1987; Schulze *et al.*, 1996; Prieto *et al.*, 2009; del Cacho *et al.*, 2012).

Change in climate combined with cessation of management practices will also have severe consequences. Firstly, it is shown that the largest effect of winter drought was on old heathlands with no or little management (suggested in Hovstad *et al.*, 2018, although not documented). Secondly, if management ceases (i.e. burning) there will be a lack of new seedlings of coastal heathland species emerging from the seed bank. Seedlings from larger shrubs and trees like *Juniperus sp.* and *Betula sp.* will take over (Kvamme *et al.*, 2004; Manning *et al.*, 2004), which will be too strong competitors for coastal heathland seedlings. Hence, ceased management will also lead to a change in species composition. Both continuing and ceasing the heathland management can lead to change in species composition and loss of heathland species. Adjusting the management to the plants' responses to climate change could make it possible to maintain the coastal heathlands. Studying plant traits, especially for vulnerable seedlings, in managed heathlands is key in understanding how this system will be affected by climate change.

4.6 Concluding remarks and future research

In this study, I found that seedlings and adults differ in strategy and interspecific trait variance. Thus, traits of the adult life-history stage do not reflect the traits of the seedling stage. Seedling traits are generally resource acquisitive and have a small variance in mean trait values between species, thus seedlings are strong competitors for light but also vulnerable to stressors and change in the environment. Adults tend to be more resource conservative and have a higher range of trait values, thus adults are more tolerant to stress and change in the environment. The relative ranking of species' trait means did in general not change from seedling to adult, making it easier to predict species strategies based on adult traits. Traits for cotyledons have shown to reflect seedling true leaf traits, thus cotyledons reflect seedling strategy. Already as seedlings it is possible to detect difference in several traits for different growth forms and successional strategy, thus different groups have different strategies, and are more stress tolerant or intolerant than others. It is clear that seedlings are in a vulnerable stage in the plant life cycle. As founders of the next generation, this phase is also an important part for understanding the development of the community composition. Therefore, predictions of future community composition, and thus ecosystem functioning, in coastal heathlands could be improved by including seedling traits, and their ecological role, to aid in the understanding of plant establishment under a changing climate.

In this study, I have shown that cotyledons have a strong relationship with leaf thickness and LDMC of true leaves. This raises new questions like: do some species have a more one to one relationship between cotyledons and true leaves than others? For instance, species with the same true leaf LDMC can vary in cotyledon LDMC. If so, are there specific trait values for cotyledons that affect the performance of the seedling more than other? For instance, that higher LDMC for cotyledons compared to true leaf LDMC could induce survival when seedlings are experiencing environmental stress. Experimental studies with induced stress would allow research of such questions.

Another interesting aspect to study further is the variance between trait mean values through the ontogeny. Traits of species in my study increase in variance for leaf thickness and LDMC, and SLA ranking varies from seedling to adult. Further analysis of my data, preferably with an addition of a larger number of species, could reveal if certain strategies have a steeper slope from seedling to adult than others. Studying the difference in slopes and rankings for species with varying strategies might aid in understanding the accuracy of predicting seedling traits from adult. Interspecific variance in trait values was an important factor through the ontogeny of coastal heathland plants. This yields an understanding of how the community could respond to changes in the climate (Enquist *et al.*, 2015). To study adaptability in coastal heathlands in more detail, additional information of how intraspecific variation and plasticity change from seedling to adult would be useful. This would add information about the adaptability in each species and individual for seedlings and adults. If seedlings have high intraspecific variance and/or plasticity, there is a change that they can better adapt to changes than predicted in this study.

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APPENDICES

A. Choice and elimination of species

Table A.1 *The first column shows the 80% most common species of the coastal heathland at Lygra (species). Species were chosen (**x**) based on following criterea: being herbaceousm, having high germinability, and species that emerged with enough individuals to provide sufficient data for the analysis. The last column shows the species that were used in this study.*

Species	Herbaceous	Germinability	Final
Agrostis capillaris	**x**	**x**	**x***
Anemone nemerosa	**x**		
Anthoxanthum odoratum	**x**	**x**	**x**
Avenella flexuosa	**x**	**x**	**x**
Calluna vulgaris			
Campanula rotundifolia	**x**	**x**	**x**
Carex echinata	**x**	**x**	
Carex nigra	**x**		
Carex panicea	**x**	**x**	
Carex pilulifera	**x**	**x**	
Chamaepericlymenum suecicum	**x**	**x**	
Cirsium vulgare	**x**	**x**	**x**
Dactylorhiza maculata	**x**		
Danthonia decumbens	**x**	**x**	**x**
Digitalis purpurea	**x**	**x**	**x**
Erica tetralix			
Eriophorum angustifolium	**x**	**x**	
Eriophorum vaginatum	**x**		
Euphrasia officinalis	**x**		
Festuca vivipara	**x**		
Galium saxatile	**x**	**x**	
Juncus squarrosus	**x**	**x**	**x**
Juniperus communis			
Lotus corniculatus	**x**	**x**	**x**
Luzula multiflora	**x**	**x**	**x**
Luzula pilosa	**x**		
Molinia caerulea	**x**	**x**	
Nardus stricta	**x**		
Narthecium ossifragum	**x**		
Polygala vulgaris	**x**	**x**	
Potentilla erecta	**x**	**x**	
Sedum anglicum	**x**	**x**	**x**
Trichophorum cespitocum	**x**		
Trientalis europea	**x**	**x**	
Vaccinium myrtillus			
Vaccinium uliginosum			
Vaccinium vitis-idea			

**A. caipllaris* was measured, however excluded due to several (8) individuals having unexpectedly high SLA (over 1000 cm^2/g). The reasons for these high values was not further explored due to time limitation.

B. Change in traits through the ontogeny

Table A.2 *Mean values for leaf thickness (mm), specific leaf area (SLA- cm^2/g), and leaf dry-matter content (LDMC) in week 1, n = 92, versus adult, n = 98. Sample size (n) and standard error (SE).*

Stage	Trait	Mean	SE
Seedling	Leaf thickness	0.13	0.016
	SLA	576.90	21.345
	LDMC	0.12	0.005
Adult	Leaf thickness	0.36	0.028
	SLA	199.32	10.788
	LDMC	0.27	0.012

Table A.3 *Output from linear mixed effects models testing change in leaf thickness (mm), specific leaf area (SLA- cm^2/g), and leaf dry-matter content (LDMC) values from week 16 to adult, n = 477. The table includes the slope between the fixed effects (value), standard error (SE), and the t-values and p-values for the slopes and interactions. Traits and week were fixed effects, species was the random effect. Bold values are significant.*

Trait	Value	SE	t-value	p-value
Leaf thickness	0.009	0.003	7.98	**<0.001**
SLA	-21.30	2.400	-7.62	**<0.001**
LDMC	0.005	0.000	7.30	**<0.001**

Table A.4 *Leaf thickness (mm) mean values and standard error (SE) for Sedum anglicum and Cirsium vulgare in week 1, 16 and for adults.*

Species	Week	*n*	Mean	SE
S. anglicum	1	9	0.538	0.0235
S. anglicum	16	10	1.111	0.0329
S. anglicum	Adult	9	1.023	0.0299
C. vulgare	1	10	0.271	0.0103
C. vulgare	16	10	0.501	0.0150
C. vulgare	Adult	10	0.602	0.0172

Table A.5 *Leaf area(cm^2) and dry mass(g) mean values, n = 10, ± standard error for cotyledons and seedlings collected in week 1.*

Taxon	Cotyledons		Seedling	
	Leaf area	Dry mass	Leaf area	Dry mass
C. rotundifolia	0.16 ± 0.020	9.9E-05 ± 1.35E-05	0.04 ± 0.009	6.8E-05 ± 1.16E-05
C. vulgare	3.34 ± 0.140	2.9E-03 ± 0.000133	1.03 ± 0.112	2.0E-03 ± 0.000223
D. purpurea	0.63 ± 0.058	4.0E-04 ± 4.2E-05	0.11 ± 0.022	1.8E-04 ± 3.59E-05
L. corniculatus	0.23 ± 0.021	2.1E-04 ± 6.33E-05	0.07 ± 0.021	1.7E-04 ± 2.08E-05
S. anglicum	0.14 ± 0.019	1.3E-04 ± 2.66E-05	0.03 ± 0.007	6.4E-05 ± 1.63E-05

Campanula rotundifolia cotyledons had the thinnest leaves (0.07 mm, SE: +/- 0.01), highest SLA (1859 cm^2/g, SE: +/- 0.045), and highest tissue density (LDMC) (0.13 g/g, SE: +/- 0.024) of species. In contrast, *S. anglicum* cotyledons had the thickest leaves (0.67 mm, SE: +/- 0.04) and lowest tissue density (LDMC) (0.03 g/g, SE: +/- 0.008). Additionally, the SLA was intermediate (1335 cm^2/g, SE: +/- 0.02). *Cirsium vulgare* cotyledons had thick leaves (0.41 mm, SE: +/- 0.02), the lowest SLA (1179 cm^2/g, SE: +/- 30.5) and low tissue density (LDMC) (0.05 g/g, SE: +/- 0.001).

C. Change in traits for growth forms, successional stages, and seed bank status

Table A.6 *Output from linear mixed effects models testing change in functional trait values through time for growth forms, successional stage, and seed bank status, n = 477. The table includes the slope between the fixed effects (value), standard error (SE), and the t-values and p-values for the slopes and interactions. Traits (leaf thickness (mm), specific leaf area (SLA-cm2/g), leaf dry-matter content (LDMC)), growth form (graminoid/forb), successional strategy (early/late), or seed bank status (persistent/transient), and week were fixed effects. Species nested within growth form, successional stage or seed bank status were random effects. Bold values are significant.*

Trait	Groups	t-test				
		Effect	Value	SE	t-value	p-value
Leaf thickness	Growth form	Intercept	0.247	0.076	5.81	**<0.001**
		Graminoid	-0.167	0.108	-1.46	0.181
		Week	0.013	0.003	7.67	**<0.001**
		Graminoid:Week	-0.007	0.004	-1.75	0.081
	Successional strategy	Intercept	0.250	0.080	3.08	**0.002**
		Late	0.180	0.100	1.76	0.116
		Week	0.010	0.001	4.74	**<0.001**
		Late:Week	0.000	0.002	3.40	**<0.001**
	Seed bank	Intercept	0.143	0.095	3.91	**<0.001**
		Transient	0.034	0.122	-0.05	0.963
		Week	0.008	0.004	5.12	**<0.001**
		Transient:Week	-0.001	0.005	-0.08	0.939
SLA	Growth form	Intercept	599.57	50.04	64.42	**<0.001**
		Graminoid	-66.43	70.71	-1.00	0.346
		Week	-25.71	2.78	-8.01	**<0.001**
		Graminoid:Week	8.79	3.93	2.14	**0.033**
	Successional strategy	Intercept	552.28	58.21	54.2	**<0.001**
		Late	22.78	75.08	0.29	0.778
		Week	-16.36	3.25	-4.19	**<0.001**
		Late:Week	-8.21	4.18	-2.47	**0.014**
	Seed bank	Intercept	529.9	56.4	55.8	**<0.001**
		Transient	60.5	72.8	0.88	0.404
		Week	-19.3	3.7	-4.48	**<0.001**
		Transient:Week	-3.3	4.8	-0.53	0.596
LDMC	Growth form	Intercept	0.085	0.015	5.81	**<0.001**
		Graminoid	0.073	0.021	3.53	**0.008**
		Week	0.006	0.001	5.70	**<0.001**
		Graminoid:Week	-0.001	0.001	-0.64	0.523
	Successional strategy	Intercept	0.157	0.02	7.96	**<0.001**
		Late	-0.059	0.02	-2.33	**0.048**
		Week	0.006	0.001	5.42	**<0.001**
		Late:Week	-0.001	0.001	-0.85	0.397
	Seed bank	Intercept	0.123	0.02	5.04	**<0.001**
		Transient	-0.003	0.03	-0.11	0.915
		Week	0.004	0.001	4.09	**<0.001**
		Transient:Week	0.001	0.001	0.96	0.336