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1 **Title: How resilient is *Calluna vulgaris* to drought during germination and its seedling**
2 **stage?**

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14 **Keywords:** *Calluna vulgaris*, Coastal heathlands, drought experiment, functional traits,
15 germination rate, plastic, population, seedling growth, succession,

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17 **Running head:** *Calluna* germination resilience to drought

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19 **Funding information:** This project is financially supported by the Norwegian Research
20 Council, under the Landpress project and the Recite project.

21

22 The authors declare no conflict of interest.

23

24 **Author contributions:**

25 VV and LGV designed the field experiment and project on which this research is based.

26 KB, RG, SVH, LGV, and VV designed the seed germination study and experiment.

27 KB wrote the first draft of the introduction and methods for the first submission, with
28 comments and input from RG, SVH, LGV, and VV.

29 KB will be responsible for running the experiment.

30 KB will do the data analysis.

31 KB will write the draft of the final paper, RG, SVH, LGV, and VV will contribute with scientific
32 discussions, comments and approval of the final draft.

33

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40 **Abstract:**

41 The coastal heathlands of North-west Europe are valuable cultural landscapes, created and
 42 maintained over millennia by a land-use regime involving burning and grazing. These
 43 heathlands are now critically threatened throughout their range by land-use change and,
 44 increasingly, climatic changes. The climatic change impacts are complex, as the coastal
 45 heathland regions are experiencing increased temperature and precipitation, but also
 46 increased frequency and severity of extreme events, such as drought. Previous studies reveal
 47 that established heathland vegetation, including *Calluna*, are vulnerable to drought, but also
 48 that these vulnerabilities vary throughout the range, and with successional stage after fire.
 49 Recruitment from seed is an important regeneration strategy for *Calluna* heathland
 50 vegetation after burning, and our study is the first to assess how the seed germination and
 51 early seedling growth of *Calluna* respond to drought. We will do this in a lab germination
 52 experiment, where we will expose *Calluna* seeds to five different drought treatments, from -
 53 0.25 MPa to -1.7 MPa, and measure germination, and record germination percentage,
 54 germination rates, and seedling growth, below-ground allocation, and functional traits
 55 (Specific Leaf Area, Specific Root Length). To allow assessment of variation in drought
 56 responses due to geographic origin, successional stage, and the maternal plants' drought
 57 exposure, we will conduct this experiment on seeds from 540 *Calluna* plants sampled from
 58 across three drought treatments (control, 50%, and 90% coverage), in three successional
 59 stages after fire (pioneer, building, mature), in two regions (60N, 65N), using a factorial
 60 design.

61

62 **Introduction:**

63 Human-induced climate change has caused the global temperature to rise 1 C over the last
 64 century a trend that will continue unless drastic reductions in carbon emissions are made
 65 (IPCC 2019). The rise in global temperature has caused changes in the atmosphere, altering
 66 weather systems and precipitation patterns, which is resulting in an increase in more
 67 extreme weather events, such as drought (Mann et al., 2017; Stott, 2016). In oceanic boreal
 68 regions, such as in Norway, climate change is projected to lead to an overall increase in
 69 precipitation; but also, due to changes in frequency and distribution of precipitation, an
 70 increase in the frequency and severity of drought events (Skaland et al., 2019).

71 These extreme weather events are expected to add more ecological stress to already
 72 vulnerable ecosystems (Gonzalez et al. 2010). Until about a decade ago, the most commonly
 73 observed response to global warming in the Arctic was increased shrub growth, known as
 74 'arctic greening' (IPCC 2014). In recent years, however, a new phenomenon, known as 'arctic

browning', is becoming increasingly prevalent through the arctic and boreal zones globally (Phoenix and Bjerke 2016; Treharne et al. 2019; Bjerke et al. 2017; Wang and Friedl 2019). This refers to wide-spread die-back of evergreen dwarf-shrub heath vegetation, and while the underlying causality is not fully resolved, the phenomenon has emerged as the frequency of extreme weather events has increased (Phoenix and Bjerke 2016). The arctic browning has thus been linked to increased environmental stress due to episodes of low precipitation during winter months, reducing snow coverage, exposing the evergreen vegetation to frost and drought (Bjerke et al. 2014; Bjerke et al. 2017). Such drought-driven winter browning has also been observed at subarctic latitudes, especially in the anthropogenic coastal heathlands (Phoenix and Bjerke 2016).

Coastal heathlands dominated by evergreen dwarf-shrubs are a characteristic and valuable cultural landscape found throughout the oceanic regions of Europe, with a history dating back more than 5000 years (Kaland, P.E. 1986; Birks et al. 1988; European Commission 2008; IPBES 2018). Coastal heathlands are currently red-listed throughout their range due to abandonment of traditional low-intensity land-use (Lindgaard & Henriksen 2011; Hovstad et al. 2018; IPBES 2018; Wilson et al. 2019) and are now further threatened by climate change. Several studies have aimed to quantify ecosystem responses to drought in coastal heathlands (Britton et al. 2001; Haugum et al. 2021; Log et al. 2017), and these studies demonstrate that browning leads to a reduction in primary production and reproduction, more generally, of the evergreen dwarf-shrub *Calluna vulgaris* (L.) Hull (hereafter referred to as *Calluna*) (Phoenix and Bjerke 2016). In a traditionally managed coastal heathland system, prescribed burning is used to create a fine-scale mosaic pattern of heathlands in different successional stages after fire, pioneer, building and mature (de Hullu and Gimingham 1984; Kaland 1986). This successional mosaic pattern improves year-round pasture quality and access for livestock (mostly sheep, but also goats, horses, cattle), while also increasing biodiversity (Velle et al. 2014). Recent research suggests that heathland management may also lower the risk of large-scale drought damage (Haugum et al. 2021), due to major differences in physiology between age classes of the keystone species *Calluna*. Specifically, mature *Calluna* is more negatively affected by drought (Haugum et al. 2021), and large area abandonment are leaving heathlands more vulnerable to drought damage and thus large-scale browning.

106 *Calluna* revegetate after fire both vegetatively and by seed germination (Mallik and
 107 Gimingham 1985; Mallik, Hobbs, and Legg 1984). It has been found that mature *Calluna*
 108 plants, in the mature successional stage and beyond, has a lower probability of producing of
 109 root sprouts after fire (Berdowski and Siepel 1988; Meyer-Grünefeldt et al. 2015; Miller and
 110 Miles 1970; Hobbs and Gimingham 1984). While all successional stages have abundant seed
 111 production (Mallik, Hobbs, and Legg 1984), these results suggest that mature *Calluna* are
 112 more reliant on seed germination for recruitment, whereas *Calluna* in the pioneer and
 113 building stages use root sprouting as their main form for regeneration. With the increase in
 114 drought events, there has also been observed differences in drought responses between
 115 successional stages. Both very young (Meyer-Grünefeldt et al. 2015; Meyer-Grünefeldt et al.
 116 2016) and mature (Haugum et al. 2021) *Calluna* plants have been shown to exhibit a
 117 relatively low resistance to drought compared to building-stage plants. Yet there is no
 118 research on how this reduced plant fitness under drought may affect the plant's investment
 119 in seeds. The research outlined above suggests contradicting predictions. On one hand, the
 120 mature plants' higher dependence on seeds could predict a higher investment in seeds and
 121 seed quality with plant age. On the other hand, the mature plants' lower resistance to
 122 drought could be hypothesised to lead to reduced seed quality in drought-impacted plants.
 123 Henceforth it could be hypothesized that mature successional stages might have crossed a
 124 threshold, now yielding less viable seeds.

125 *Calluna* is a wide-spread species that exhibits local adaptations to both climate and
 126 traditional land-use management (Vandvik et al. 2014, Spindelböck 2013), and different lines
 127 of evidence indicate possible geographic variation in drought responses. First, populations of
 128 *Calluna* throughout the southern European heathlands do respond differently to drought
 129 (Ibe et al. 2020; Meyer-Grünefeldt et al. 2016). More southern populations exhibit a greater
 130 tolerance to drought, while Atlantic populations are more sensitive (Ibe et al. 2020). This
 131 tells us there is variation among populations of *Calluna* in drought responses in the southern
 132 part of the european gradient, but whether there are differences in responses between
 133 atlantic and the edge of the northern end of the *Calluna* gradient is unstudied. Second, there
 134 is broad-scale geographic patterns in the phylogenetic structure of *Calluna*, with Northern
 135 and Southern populations in Norway being of different descent (Durka et al., unpublished).
 136 Third, populations along the south-north climatic gradient in Norway have been shown to

137 differ in regeneration modes and responses, with northern *Calluna* populations having
 138 higher seed germination temperature requirements , and lacking vegetative resprouting,
 139 compared to southern populations which have lower germination temperature
 140 requirements and use both seeds and root sprouting for regeneration (Spindelböck et al.
 141 2013, Nilsen et al. 2005). The lack of vegetative resprouting in the northern populations
 142 might indicate a higher investment in seeds compared to the southern populations, as seeds
 143 are the only mode of recruitment here. At the same time, the southern populations are
 144 adapted to a warmer climate which historically has exposed them to more frequent drought
 145 (Meteorologisk Institutt 2021). These lines of evidence might infer differences in seed
 146 germination responses to drought between Northern and Southern populations, again with
 147 potentially contrasting predictions resulting from the northern populations' higher
 148 dependence on seeds for recruitment, and the southern populations' adaptations to a
 149 warmer climate.

150 Drought might induce a plastic response in the parental generation during seed formation,
 151 that could influence the seed's germination success (Mayer and Poljakoff-Mayber 1982;
 152 Donohue and Schmitt 1998), and with increasing drought, such responses could be expected
 153 for *Calluna*. During drought plants tend to produce larger seeds as a stress response, which
 154 is positively correlated with seedling survival during drought (Vera 1997; Lloret et al. 1999;
 155 Gianoli and González-Teuber 2005). Seed mass is also positively correlated with a higher
 156 root:shoot ratio (Lloret et al., 1999; Gianoli and González-Teuber 2005), which is beneficial
 157 during drought (Karcher et al. 2008; Xu et al. 2015). *Calluna* is more sensitive to drought
 158 during their seedling stage because of their high shoot:root ratio compared to building and
 159 mature stands of *Calluna* (Meyer-Grünefeldt et al. 2015). If *Calluna* has the ability to show a
 160 plastic response to drought, differences in seed size and seedling drought responses could
 161 differ depending on the parental drought exposure.

162 Based on the literature outlined above, we can make a series of partially contrasting
 163 predictions about the responses and tolerances of *Calluna* seed recruitment to drought, and
 164 how these might vary among populations, successional stages, and drought treatments.
 165 First, we predict that northern populations will generally invest more in seeds, as an
 166 adaptation to the lack of vegetative regeneration, increasing seed mass which will result in a
 167 higher germination percentage during drought. However, local adaptations to climate would

predict a wider germination niche and more drought tolerant seedling traits for the Southern population, as it has historically been more exposed to periods of drought. Similarly, mature plants could be expected to invest more in seed production, yet we could predict lower seed mass, lower germination percentage, narrower germination niche and less drought-tolerant seedling traits in seeds from older successional stages under drought, because of the lower resistance to drought damage, leaving older plants with less resources for reproduction. Finally, if *Calluna* has a plastic adaptive response to drought in the parental generation, this could be expressed through greater seed mass, which will result in a higher germination percentage, wider germination niche, and more drought tolerant seedling traits in seeds produced by drought-impacted plants. Specifically, across all comparisons, we expect higher root:shoot ratio as a response to increased drought. We also expect there to be a decrease in specific leaf area (SLA) and increase in specific root length (SRL) with increased drought, as this has been proven to be common responses to low water availability (Liu and Stützel 2004; Metcalfe et al. 2008). In addition, we predict that an increased seed mass will increase germination percentage, germination niche, seedling size, and the plasticity in the root:shoot ratio.

In this study we will investigate the drought responses of *Calluna* seed germination and seedling traits, and test the predictions outlined above about variation in drought responses, by comparing the responses in seeds originating from northern and southern populations, pioneer, building and mature successional stages, and parental ambient vs experimental drought climatic conditions. Using a germination experiment in the laboratory, we are asking the following three questions:

1. Does population, successional stage, and the parental generation's exposure to drought affect *Calluna* seed germination?
2. Do these factors operate through variation in seed mass, and does seed mass infer greater germination success and drought tolerance?
3. Are population, successional stage, and parental generation's exposure to drought effects evident after germination, in seedling traits?

To answer these questions we will be using seeds collected from a drought experiment where coastal *Calluna* heathlands are subjected to ambient conditions and drought

198 treatment by rainout shelters covering 50 and 90 % of the plots. The experiment is
 199 replicated across two regions in Norway (ca. 60N and 65N), reflecting different climates and
 200 also different genetic origins (Durka et al., unpublished), and across three successional
 201 stages after prescribed fire; pioneer, building and mature. The seeds will be germinated
 202 under a five-level drought gradient (including ambient conditions) in a growth chamber,
 203 where seed germination timing and percentage, and specific leaf area (SLA), specific root
 204 length (SRL), and above ground and below ground biomass will be measured on the
 205 seedlings.

206 **Methods**

207 Study species (*Calluna vulgaris* (L.) Hull):

208 *Calluna* is a monotypic genus distributed across all of Europe from Scandinavia to Spain and
 209 from the Ural Mountains to the Azores (Tutin et al. 1973). It is an evergreen dwarf-shrub
 210 standing at 10-50 cm tall, but can reach up to 1m in standing height (Lid and Lid 2017). Its
 211 flowering season is from July to September and it has a lot of small purple coloured flowers
 212 (Clapham et al. 1981). Its small seed size allows seeds to be transported by wind (Beijerinck
 213 1940), with a maximum diameter of 0,58mm (SE=0,016mm) (Bullock and Clarke 2000). The
 214 reproduction in *Calluna* is a combination of vegetative resprouting and seedling recruitment
 215 from soil seed storage, with both germination and resprouting strategies varying with
 216 successional age (Berdowski and Siepel 1988; Miller and Miles 1970) and throughout the
 217 species' range (Nilsen 2005; Vandvik et al. 2014; Spindelböck 2013).

218

219 Site description:

220 The study was conducted in two bioclimatic regions, with three heathland successional
 221 stages in each. The northern sites are Buøya representing the pioneer stages, Haverøya the
 222 building stages and Skotsvær the mature stages (Table 1). In the southern region all three
 223 stages and hence sites are found on the same island, Lygra (Table 1). All six sites are
 224 extensively grazed by old Norse sheep or spælsau (Haugum 2020). All sites have an oceanic
 225 climate with vegetation dominated by heather, especially *Calluna*, and a land use history

with fire and grazing. Most sites are nutrient poor wet to dry heath, heathlands, except for Buøya which is a slightly nutrient rich heathland (Halvorsen et al. 2016).

228

Table 1: Ecological and climatic site information. Mean annual precipitation (MAP), mean summer temperature (MST) (June-August) and mean winter temperature (MWT) (December-February) is based on data from 1990 to 2019 (Haugum et al. 2020)

Site name	Successional stage	MAP (mm)	MST (°C)	MWT (°C)	Latitude (Decimal degrees)	Longitude (Decimal degrees)	Burn year
Store Buøya	Pioneer	1254 ± 184	13.4 ± 1.3	0.7±1.6	65.83677	12.224506	2014
Haverøya	Building	1720 ± 461	13.3 ± 1.4	1.5 ± 1.9	64.779	11.2193	2010
Skotsvær	Mature	1254 ± 184	13.4 ± 1.3	0.7 ± 1.6	65.79602	12.22450	Before 1980
Lygra	Pioneer	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	60.70084	5.092566	2013
Lygra	Building	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	60.70084	5.092566	2004
Lygra	Mature	2020 ± 345	13.8 ± 1.5	3.4 ± 1.8	60.70084	5.092566	1996

232

Figure 1

234

Field drought experiment

In the summer of 2016, three blocks of 70-200m² were set out in homogenous vegetation in each of the six sites. In each block we installed three 2x2 meter plots, selected to be dominated by *Calluna* while avoiding larger rocks, bare ground, and animal tracks. To avoid grazing in the experimental plots, each plot was fenced in spring 2017, except for Haverøya which was fenced in spring 2018. Each plot was randomly assigned a treatment, and had rain-out shelters installed following the Drought-Net protocol (Yahdjian & Sala 2002), with three replicates of each drought level: control, 50% and 90% roof coverage. The obtained

243 reductions in rainfall were $32.1 \pm 10.3\%$ for 50% coverage and $43.5 \pm 20.3\%$ for the 90%
 244 coverage (Haugum et al. 2020).

245

246 Collecting seeds in the field:

247 In each plot, 10 individuals of *Calluna* were tagged with a unique identifier and measured for
 248 functional traits annually from 2016 - 2019 (Haugum et al. 2021). The marked *Calluna* were
 249 selected to represent the full range of plant sizes within each plot. For each individual, trait
 250 measurements involved: standing height (mm), three measures of side shoots length (mm)
 251 and three replicates of stem diameter (mm) (Haugum et al. 2021). From each of these
 252 individuals we collected at least 50 seeds. Due to death, grazing disturbance before fences
 253 were up, or a lost tag, extra individuals within the plot were collected as necessary to ensure
 254 ten plants were sampled from each plot. All seed collection was undertaken between
 255 30.09.2019 and 30.10.2019, which is at the end of the flowering season of *Calluna* in Norway
 256 (Bele and Norderhaug 2008). The seeds are dry stored in coffee filters in the lab.

257

258 Seed Germination Experiment:

259 The seeds collected above will be used in a germination experiment to assess germination
 260 responses to drought in *Calluna*. Drought conditions will be established using agar infused
 261 with a polyethylene glycol (PEG, molecular weight 8000; 191 Sigma, St Lois, MO, USA)
 262 solution, with five levels of drought, including control, reaching from -0.25 to -1.7MPa
 263 (referred to as levels 1-5 with increasing level of drought). The 50 seeds per Individuals will
 264 be distributed into five petri dishes with ten seeds in each. For individuals with less than 50
 265 seeds, allocation will be prioritised in the following order: extreme drought treatment (level
 266 5, -1.7MPa), control (level 1, 0.25MP) followed by levels 3, 2, and 4. .

267

268 Preparation of petri dishes:

269 The preparation of the dishes will follow the protocol based on Weele *et al.* (2000), with
 270 some alterations, following Gya *et al.* (2020).

271 1% agar will be autoclaved to avoid fungal or bacterial growth during germination, then 20
 272 mL of 1% agar will be added to the 90 mm petri dishes will have To create the drought
 273 gradient, polyethylene glycol (PEG, molecular weight 8000; 191 Sigma, St Lois, MO, USA) will
 274 be added, after the agar is solidified to avoid polymerization of the agar. PEG will be
 275 dissolved in distilled water to reach the target water potentials (Table 2) with 30 mL of PEG
 276 solution added to the 20 mL agar dishes. The dishes will be covered by parafilm and set to
 277 equilibrate for 4 days. Before adding any seeds, any remaining liquid solution in the petri
 278 dishes will be carefully removed.

279 **Table 2:** Treatment level and final water potential.

Treatment (level)	Final water potential for petri dishes (MPa)	Grams of solid PEG added per litre media for overlay solution
Control (1)	-1.25	0
Wet (2)	-0.5	250
Middle value (3)	-0.7	400
Drought (4)	-1.2	550
Extreme Drought (5)	-1.7	700

280

281 Starting the germination experiment:

282 After preparing the petri dishes, ten seeds from each individual (see above for treatment
 283 priorities for individuals with less than 50 seeds available) will be added to each of the five
 284 levels of water potential. Seeds will be placed apart from each other on the agar surface

285 using a tweezer and gloves to avoid any contamination. Afterwards petri dishes will be
 286 covered with parafilm to avoid drying, and placed in a growth chamber (Sanyo Incubator
 287 MIR-553) at 18 degrees Celsius, which is the optimal germination temperature for *Calluna*
 288 (Grimstad 1985), with the light cycle set at 8 hours with light and 16 hours darkness as it is
 289 the optimal germination conditions for *Calluna* seeds from our regions (Måren et al. 2009).

290 The seeds will be monitored once a week until day 20 after onset of the eksperiment, twice a
 291 week as germination rate is expected to increase from this time onwards (Vandvik et al.
 292 2014). Monitoring frequency will return to once a week when the cumulative germination
 293 curves start flattening.

294

295 Trait measurements:

296 The seeds from each individual (10-50 seeds) will be weighed collectively because of the low
 297 seed mass of *Calluna*, and the mean seed mass per individual will be calculated by dividing
 298 the bulked weight by the number of seeds. The seed weight is air dried mass and not oven
 299 dried as the seeds are to be used in the germination trial.

300 Germination traits for analyses will include germination percentage, which will be
 301 germinated seeds as a percentage of viable seeds in a dish, T_{50} (time to 50% germination),
 302 and germination duration (number of days it takes to reach final germination percentage).
 303 To test for viability, all seeds that do not germinate in the non-drought treatment will be
 304 tested using an embryo integrity (squish) test and/or the cut test. We assume that the
 305 proportion of non-viable seeds from the non-drought treatment will be the same for the rest
 306 of the parental individuals' petri dishes as it is randomly assigned seeds from the same
 307 parental plant.

308 To measure seedling growth and allocation, a subsampling will be done with one seedling for
 309 each petri dish measured for the following traits: SLA – Specific Leaf Area; SRL – Specific
 310 Root Length; total biomass; and allocation to below-ground.

311 The chosen individuals will be harvested 1 week after recorded emergence, and separated
 312 into above ground and below ground sections at the point where the individual emerges

313 from is going into the agar. The above-ground parts will be divided into leaves and stems,
 314 and all parts will then be scanned. After scanning all seedling parts will be placed in coffee
 315 filters tagged with the seedling ID in a drying oven at 60 degrees for 48 hours (Díaz et al.
 316 2016). After drying the above and belowground biomass will be weighed. SLA is found using
 317 the scanned area of the upside of the leaf divided by its dry mass and SRL is found using the
 318 length of the root divided by the dry mass (Díaz et al. 2016). To calculate the total leaf/above
 319 ground area, the “LeafArea” package in R will be used (Katabuchi 2019). The below-ground
 320 allocation (BG) will be calculated as the ratio between below-ground and total biomass.

321

322 Statistical analysis:

323 To investigate the drought effect on germination of *Calluna* we will use linear-mixed effect
 324 models performed in R (R Core Team 2019) using the lme4 package (Bates et al. 2020) and
 325 lmerTest (Kuznetsova et al. 2020). A binomial distribution will be assumed for the
 326 germination percentage, which will be analysed using a logit link function. A Poisson
 327 distribution will be assumed for count data, including days to germination, T_{50} and time to
 328 max germination where we will use a log link function. Traits (SLA, SRL, seed mass, biomass
 329 and root:shoot) will likely be normally distributed, either with or without a log
 330 transformation. Here we will assume a Gaussian distribution.

331 To test how population, successional stage, parental drought treatment relate to
 332 germination success under different drought conditions we will fit linear mixed effect
 333 models. For each response variable, seed mass, germination percentage, T_{50} (time to 50%
 334 germinated), maximum germination, SLA, SRL, above and below ground biomass and
 335 root:shoot, we will construct one global model to evaluate the treatment effects. In these
 336 models, the fixed effects will include field drought treatment, population, successional stage
 337 and lab drought treatment, and all interactions. Petri dish, blocks and sites and random
 338 effects in the models. The specific predictions below will then be tested by inspecting
 339 specific effects or interactions in the full model (e.g., P1 predicts a significant population
 340 effect for germination percentage, whereas P2 predicts a significant population*lab drought
 341 interaction). We will use post-hoc tests to further explore significant interactions between
 342 predictor variables, according to the specific predictions below.

343 Questions and their predictions will be investigated as follows:

344

- 345 1. Does population, successional stage and the parental generation's exposure to
346 drought affect the germination strategy?

347 For question one we specifically predict: P1) The Northern population will have a higher
348 germination percentage. P2) The Southern population will have a broader germination
349 niche. P3) Mature successional stages will have a lower germination percentage and smaller
350 germination niche when interacting with field drought treatment and lab drought treatment.
351 P4) Drought exposed parental generation will have an increased germination percentage and
352 germination niche. To test the effect of the lab drought treatment on germination
353 percentage and niche for population, successional stage, and drought exposed parents, we
354 will model the linear effect of the lab drought treatment interacting with population,
355 successional stage, and field drought treatment on a given germination metric (germination
356 percentage, T_{50} (time to 50% germinated), maximal germination).

357

- 358 2. Do these factors affect seed mass, and does larger seed mass affect germination
359 success and root:shoot ratio?

360 For question two we predict: P5) The Northern population will have a higher seed mass. P6)
361 The mature successional stage will have lower seed mass. P7) Drought exposed parental
362 generation will have greater seed mass. P8) A larger seed mass across all factors will increase
363 germination percentage and increase root:shoot ratio. For P8 we will add seed mass as a
364 predictor variable for germination percentage and root:shoot ratio.

365

- 366 3. Are population, successional stage and parental generation's exposure to drought
367 effects evident after germination, in seedling traits?

368 For the last question: P9) The Southern population will have a higher root:shoot ratio, lower
369 SLA and higher SRL in response to drought. P10) Mature successional stages will have lower
370 root:shoot ratio, higher SLA and lower SRL. P11) Drought exposed parental generation will

371 have a higher root:shoot ratio, lower SLA and higher SRL. P12) Across all factors there will be
 372 an increase in root:shoot and SRL, and decrease in SLA, as a response to drought.

373

374 Data availability

375 Data will be available at the Open Science Framework, and the script for data management
 376 and analysis will be made available at GitHub.

377

378

379 Ref:

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