Effect of sowing time on field emergence and growth of South African grassland species

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This study investigated seedling emergence in field sowings in terms of rate, and maximum seedling emergence, for twenty one species of forb, grass and geophyte species associated with montane South African grassland communities. Species were sown in early and late spring to compare the effect of sowing date on emergence characteristics and subsequent growth. RGR and mean individual standing biomass were calculated for a 150 day post sowing growth window. Species showed highly significant differences in the time taken to achieve 50% emergence, and species rankings on this basis changed according to the date of sowing. There were large differences in RGR between species that were also reflected in mean standing biomass per individual. The data provide a basis for a preliminary, comparative ecological characterization of these species and an insight into how these species establish and potentially avoid competitive elimination in mixed sowings in restoration ecology or in landscape architecture, in the first growing season. The study also provides some indication on how emergence and growth of individual species might affect recruitment and survival in their habitats.

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1. Introduction

Little is known of the comparative field emergence characteristics of germinating seedlings of the forbs and geophytes associated with the montane grasslands of Eastern South Africa. To date, most germination studies on these species, for example, Ascough et al. (2007), have taken place in laboratories, creating difficulties in extrapolation to the field. Ahmad and Hitchmough (2007) found that field emergence, was for example, significantly lower than in vitro emergence in every species tested. Field emergence data is valuable for a variety of reasons; it can, for example, shed light on establishment phenomena in extant seminatural vegetation (Grime et al., 2007), and how this might be affected by stress and disturbance (Schaffers, 2002). In restoration ecology, it can greatly improve decision making on the amount of seed required to achieve a target population of a given species when designing seed mixes. By potentially providing an indication of the optimal time for sowing, this data assists in devising sowing strategies to obtain maximum value from often limited seed resources, as well as indicating which species are, in the short term, likely to be most competitive in sowing mixes. Assessment of likely competitive dominance is critical to maintaining initial diversity in sown herbaceous plant communities by reducing extirpation of shade intolerant, slow growing, but long lived species by faster, shorter lived species (Shipley and Keddy, 1988; Hitchmough et al., 2008).

Germination and seedling emergence is influenced by many factors, but of particular importance are: seed quality (Alderson, 1987), seed dormancy (Baskin and Baskin, 2001), pre-sowing treatments/requisites (Khan, 2010), water stress (Hegarty, 1978), temperature (Thompson and Grime, 1983), light (Fenner and Thompson, 2005), and predation/pathogens (Kirkpatrick and Bazzaz, 1979; Wilby and Brown, 2001).

The temperature at which species germinate is heavily influenced by the climatic conditions prevailing in the habitat (Grubb, 1977). Cool climate species are often able to germinate at low temperatures (Palazzo and Brar, 1997; Shimono and Kudo, 2005) whilst species from warmer climates require higher temperatures. Many C4 grasses do not germinate until daily mean temperature is > 25 °C (O’Connor and Bredenkamp, 1997). Ascough et al. (2007) found that Watsonia species from winter-rainfall areas germinated optimally at 10–20 °C, whilst summer rainfall species showed optimal germination at 15–25 °C.

Once germination commences, avoidance of severe moisture stress is the critical factor in maximizing emergence, both in the habitat and when sown in restoration ecology or horticultural practice (Keddy and Constabel, 1986; Hitchmough et al., 2003). Fay and Schultz (2009) found that emergence increased with North American prairie forbs when exposed to longer watering intervals, but this appears to be due to an anaerobic germination environment. Noe and Zedler (2000) and Hitchmough et al. (2003) report maximum emergence in

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a wide range of wild occurring species as soil moisture stress decreased. As with temperature, suitable moisture conditions for germination often reflect those experienced in a species habitat (Baskin and Baskin, 1998).

Where soil moisture stress is minimal, temperature is often the critical factor affecting how many seedlings are present at a point in time. The timing of species emergence is important both in natural systems (Meyer and Kitchen, 1994) and in multi-species sowings (Hitchmough et al., 2003). Given equivalent initial growth rates, species that emerge later than other species are more likely to be shaded and outcompeted by earlier establishing species (Grubb, 1977; Quintana et al., 2004). Understanding the effect of temperature on days to emergence is particularly important in sown, multi-species plant communities, when sowing must generally be undertaken on the same day (Turner et al., 2006). Determination of the most appropriate time for sowing is vital if successful vegetation is to be created (Pywell et al., 2003; Jinks et al., 2006).

As above ground competition for light is generally the key factor determining seedling survival in grassland vegetation (Davis et al., 1999), seedling growth rate is important in both the habitat and in sown vegetation (Ten Brink and Bruun, 2011). Determination of the growth rate of different species under comparative conditions helps to predict species relationships in semi-natural vegetation (Grime and Hunt, 1975). Relative growth rate has been extensively used for this purpose with grassland species (Sun and Frelich, 2011).

Species that germinate and emerge rapidly in favorable environments normally have a high relative growth rate (Shipley et al., 1989), Gross (1984), in her study on the effect of seed size and growth form on seedling establishment of monocarpic plants, found that relative growth rates of seedlings were generally inversely related to seed size, with small seeded species having faster relative growth rates than large. Similar trends have been noted by Turnbull et al. (2008). Ultimately establishment success depends on the interplay between characteristics such as emergence time, seedling growth form, and relative growth rate, and these factors are potentially influenced by seed size (Gross, 1984; Rey et al., 2004).

This study explores seed emergence and growth characteristics of species associated with South African montane grasslands in response to different field sowing times. The study was designed to provide understanding on how these factors affect the establishment and initial persistence of South African grassland species sown in experimental climate change adaptation, meadow-like vegetation in UK urban greenspace.

The objectives of the study were:

- To determine the effect of sowing time on seedling emergence rate and maximum percentage emergence
- To determine the effect of sowing time on seedling growth in terms of RGR and mean individual standing biomass across a 150 day post sowing growth period
- To develop a preliminary categorization of the species on the basis of these emergence and growth characteristics

2. Materials and methods

The research involved a petri dish study of radicle and shoot emergence in a growth cabinet at 20/10 °C, and an experiment to investigate emergence and growth characteristics in the field.

Following a review of habitat and distribution characteristics (see Table 1), 21 South African montane grassland species were selected as potentially being appropriate to the climate of the UK. Many of these species are long cultivated in the UK, and seed was obtained from either plants grown on a field station, or purchased from Jelitto Staudensamen, Germany, and Silverhill Seeds, South Africa.

The growth cabinet experiment involved four replicates of each species, with 20 seed per 90 mm petri dish. Seed was sown and wetted with 4 mL of de-ionized water, sealed with parafin wax tape and placed in a growth cabinet at 20/10 °C (16 h light/8 h dark). Dishes were re-randomized at each count and all dishes re-wetted and re-sealed at 7 day intervals. Emergence was scored when the radicle was >2 mm long, and the same procedure applied to shoot emergence in monocots. Shoot emergence in dicots was scored when the cotyledons were free of the testa. The number of days to emergence of 50% of the total number of seedlings that germinated were calculated, using shoot emergence data to allow comparison with field emergence data in the second part of the study.

The field emergence experiment was conducted at Sheffield Botanic Garden for a period of 10 months. A randomized block design was used, with the experimental unit represented by a 150 × 150 mm quadrat sown with one of the 21 species and replicated four times. Seed weight data from the petri dish study was used to estimate the weight of seed to be sown to produce a minimum of 12 seedlings per quadrat. Quadrats were separated from one another by a 50 mm gap. The quadrats were superimposed on a compressed 50 mm layer of coarse sand (size range 0.06–2.0 mm) placed on top of the site soil, a well drained clay loam, pH 5.5–6.0, to bury the soil weed seed bank and maintain weed free conditions throughout the study. Seed was raked into the sand surface and covered with a 5–8 mm layer of horticultural grit to reduce moisture stress. Half of the plots were sown on 16th March 2010 and the other half on 16th May 2010. Where no significant rain (>8 mm) occurred within a 4 day period, plots were irrigated at 2 day intervals to return the sand to field capacity.

2.1. Data collection

The number of seedlings that emerged within each plot was recorded at fortnightly intervals until the end of June (March sown) and the end of August 2010 (May sown). Days to 50% emergence was calculated from count data. Maximum mean percentage emergence of each species was calculated from the mean number of seed sown.

Seedlings were harvested 60 and 150 days after emergence. Harvesting of seedlings sown in March commenced on 1st June 2010, with the second harvest on 1st September 2010. May sown seedlings were harvested on 1st August 2010, and 1st November 2010. Relative growth rate was calculated using the formula of Hunt (2003):

Relative growth rate = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1}

W_1 \quad \text{above ground weight 60 days after emergence}
W_2 \quad \text{above ground weight 150 days after emergence}
t_1 \quad \text{number of days at first harvest}
t_2 \quad \text{number of days at second harvest}

A harvesting procedure was developed to cope with highly variable seedling emergence and different sized seedlings within quadrat seedling cohorts, and to ensure that seedlings were available for the final harvest. The procedure for harvesting at 60 days was as follows:

- ≤3 seedlings, no harvest from that particular quadrat.
- 4 to 7 seedlings, harvest one average sized seedling, if 8–11 seedlings harvest 2 seedlings, a large and a small one.
- > 12–15 seedlings, harvest 3 seedlings (small, medium and large).

This process resulted in a minimum of 3 seedlings for RGR and dry weight analysis for each species at each harvesting time.

2.2. Data analysis

Statistical analysis was undertaken using SPSS Version 16. Data was transformed (log e for weight data, and arcsine square root for percentage data) to improve distributional characteristics and homogeneity.
| Species                      | Family                 | Distribution                        | Habitat                        | Example of community type (from Mucina and Rutherford, 2006) | Altitudinal range in SA (m) | Seed weight (mg) | Origin of population used in study |
|------------------------------|------------------------|-------------------------------------|--------------------------------|---------------------------------------------------------------|-----------------------------|------------------|-----------------------------------|
| Agapanthus campanulatus      | Agapanthaceae          | NE Eastern Cape to Northern KZN     | Grassland and rocky slopes, moist | uKhahlamba Basalt Grassland (Gd7)                             | 700–2700                    | 3.6              | Cultivated                        |
| Agapanthus inapertus         | Agapanthaceae          | Mpumalanga                          | Grassland, moist soil           | Lydenburg Montane Grassland (Gm 18)                         | 500–1800                    | 4.1              | Cultivated                        |
| Aloe ecklonis                | Asphodelaceae          | Widely distributed Eastern South Africa | Grassland and rocky slopes, moist to dry | Drakensberg Foothill Moist Grassland (Gs10)                  | 600–1800                    | 2.0              | Silverhill, unknown               |
| Berkheya purpurea (DC) Mast. | Asteraceae             | Eastern Cape                         | Open grassland and rocky slopes | uKhahlamba Basalt Grassland (Gd7)                           | 1525–3050                    | 3.8              | Silverhill, unknown               |
| Crocosmia masoniorum (L. Bolus) N.E. Br. | Iridaceae          | Engcobo district, Eastern Cape.     | Shaded, wet rock ledges and faces | Drakensberg Foothill Moist Grassland (Gs 10)                 | > 1000                      | 2.7              | Cultivated, Jelitto               |
| Diascia integerrima E. Mey ex Benth. | Scrophulariaceae   | Eastern Cape, KwaZulu-Natal, and Free State | Open grassland and rocky slopes | Southern Drakensberg Highland Grassland (Gd 4)              | 1220–3000                    | 0.1              | Silverhill, unknown               |
| Dierama latifolium N.E. Br.  | Iridaceae              | Eastern Cape to Central KZN         | Grassland, moist                | Drakensberg Foothill Moist Grassland (Gs 10)                 | 600–2100                    | 6.0              | Cultivated, Jelitto               |
| Dierama pulcherrimum (Hook.f.) Baker | Poaceae              | Widespread throughout SA, very common in Eastern Cape-KZN | Grassland, moist | Amathole Montane Grassland (Gd 1)                             | 900–1700                     | 13.7             | Cultivated, Jelitto               |
| Gazania linearis (Thunb.,) Druce var. linearis | Asteraceae          | Widely distributed, Eastern Cape to KZN | Open grassland and rocky slopes | Stormberg Plateau Grassland (Gd 3)                           | 0–3050                      | 1.6              | Cultivated, Jelitto               |
| Gladiolus oppositiflorus Herb. | Iridaceae            | Eastern Cape                         | Open grassland and rocky slopes | Southern Drakensberg Highland Grassland (Gd 4)              | 100–2500                     | 10.0             | Silverhill, unknown               |
| Gladiolus papilio Hook. f.  | Iridaceae              | Eastern Cape Northwards              | Moist grassland, seeps and marshes | uKhahlamba Basalt Grassland (Gd 7)                           | 300–2500                     | 5.1              | Cultivated                        |
| Helichrysum aureum (Houtt.)  | Asteraceae             | Eastern Cape to Mpumalanga          | Open grassland and rocky slopes | uKhahlamba Basalt Grassland (Gs 10)                         | 0–2170                      | 0.2              | Silverhill, unknown               |
| Helichrysum pallidum DC.     | Asteraceae             | Eastern Cape to Mpumalanga          | Moist grassland                 | Northern Drakensberg Highland Grassland (Gd5)               | 50–2700                     | 0.4              | Cultivated                        |
| Hesperantha coccinea (Backh. & Harv.) | Iridaceae          | Eastern Cape to Mpumalanga          | Streambanks and wet grassland   | Drakensberg Foothill Moist Grassland (Gs 10)                 | 250–2745                    | 0.9              | Cultivated                        |
| Kniphofia triangularis       | Asphodelaceae          | Eastern Cape to KZ                  | Grassland, moist to wet.        | Lesotho Highland Basalt Grassland (Gd 8)                    | 1000–2000                    | 2.1              | Cultivated                        |
| Maesa huttonii Baker (Oberm.) | Iridaceae             | Widespread throughout Eastern SA, Eastern Cape northwards | Streambanks and wet grassland | Drakensberg Foothill Moist Grassland (Gs 10)                 | 500–3500                    | 4.0              | Cultivated                        |
| Ornithogalum candidans (Baker) | Hyacinthaceae        | Eastern Cape to Mpumalanga          | Grassland and margins of scrub, moist | Eastern Free State Sandy Grassland (Gm 4)                    | 1280–2150                    | 7.2              | Cultivated, Jelitto               |
| Tritonia drakensbergensis M.P. de Vos | Iridaceae          | Northern Eastern Cape.              | Moist grassland and cliffs      | Lesotho Highland Basalt Grassland (Gd 8)                    | 1100–2300                    | 4.0              | Silverhill, unknown               |
| Watsonia latifolia N.E. Br. ex Oberm. | Iridaceae          | Northern KZN, Swaziland, Mpumalanga | Open grassland and Koppies, moist to dry | Wakkerstroom Montane Grassland (Gm 14)                      | 1000–1500                    | 6.0              | Silverhill, unknown               |
| Watsonia pillansii ex Bolus  | Iridaceae              | Eastern Western Cape to KZN         | Open grassland and rocky slopes | Drakensberg Foothill Moist Grassland (Gs 10)                 | 50–1800                      | 6.1              | Cultivated                        |
| Watsonia pulchra N.E. Br. ex Goldblatt | Iridaceae           | NE KZN to Mpumalanga                | Open grassland and rocky slopes | Lydenburg Montane Grassland (Gm 18)                         | 500–2000                    | 6.0              | Silverhill, unknown               |
of variance for parametric analysis (Zar, 1999). As data was significantly non-normally distributed, and variance far from homogenous (P < 0.05), non-parametric analysis was employed. The Mann–Whitney U-test was used in place of t-test for paired comparisons. Linear regressions and Pearson correlation coefficients were calculated to describe relationships/associations between relative growth rate and seed weight.

3. Results

3.1. Days to 50% laboratory emergence at 20/10 °C

Species varied considerably in terms of days to 50% shoot emergence. Five species reached T50 within 10 days, whilst the slowest germinating species took >30 days (Fig. 1). The fastest emerging species included the asteraceous forbs (Berkheya purpurea, Gazania linearis, and Helichrysum aureum), the forb Diascia integrerrima, the C4 grass (Eragrostis curvula), and the geophyte (Ornithogalum candidans). The slowest to emerge species were all geophytes; Dierama pulcherrimum (49 days), Dierama latifolium (35 days), and Watsonia pulchra (35 days).

3.2. Days to 50% shoot emergence in March and May field sowings

As mean of all species and sowing dates, seed sown in the field took approximately 40–50 days longer to emerge than seed in the laboratory (Fig. 2). The number of days to emergence was longer for seed field sown in March as opposed to May, although not significantly so.

Species varied considerably in the extent to which their emergence in the field was delayed relative to the laboratory. From a March field sowing, the five species whose emergence was most retarded were (in decreasing order of retardation); O. candidans, E. curvula, Gladiolus papilio, Agapanthus campanulatus, H. aureum. These rankings changed with the higher temperatures associated with field sowing in May, with the species most retarded now; G. papilio, Hesperantha coccinea, A. campanulatus, Agapanthus inapertus, H. aureum.

3.3. The effect of sowing season (March vs. May) on speed of seedling emergence in the field

Sowing seeds in May decreased the numbers of days to achieve T50 in eleven species (A. campanulatus, Aloe ecklonis, Berkheya purpurea, Crocosmia masoniorum, D. integrerrima, D. latifolium, E. curvula, Gladiolus oppositiflorus, H. aureum, O. candidans, and Tritonia drakensbergensis) (Table 2).

Seven species (A. inapertus, D. pulcherrimum, G. papilio, H. coccinea, Kniphofia triangularis, Moraea huttonii, W. pulchra) emerged faster when sown in March, although in three species the difference was only a few days.

3.4. Maximum percentage field emergence

Percentage emergence in the field sowings was generally high, and marginally higher (mean of all species) when sown in March (52.18%) than in May (41.38%) (Table 3). Species that showed the greatest reduction in percentage emergence when sown in May, were, in declining order; A. campanulatus, W. pulchra, C. masoniorum, H. coccinea, and M. huttonii. The species that showed the opposite trend, i.e. for emergence to increase when sown in May rather than March (also in declining order) were; G. oppositiflorus, E. curvula, and T. drakensbergensis.

3.5. Effect of time of field sowing on relative growth rate

Species varied greatly in terms of this parameter. Typically the grass and forb species in the study grew more rapidly than geophyte species. The relative growth rates for sowing in March ranged from 0.02 \((×10^{-3})\) \(\text{gg}^{-1}\) \(\text{days}^{-1}\) for A. campanulatus to 19.95 \(\text{gg}^{-1}\) \(\text{days}^{-1}\) for E. curvula. For seed field sown in May, relative growth rate ranged from 0.09 \((×10^{-3})\) \(\text{gg}^{-1}\) \(\text{days}^{-1}\) for Watsonia latifolia to 27.70 \(×10^{-3}\) \(\text{gg}^{-1}\) \(\text{days}^{-1}\) for D. integrerrima (Table 4). G. oppositiflorus was the only species that showed significantly higher (P < 0.05) relative growth rate when sown in March compared to May. Diascia integrerrima and K. triangularis showed significantly higher (P < 0.05) relative growth rate when sown in May. The majority of the species

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**Fig. 1. Days to 50% shoot emergence at 20/10 °C in the laboratory.**

**Fig. 2. Effect of sowing treatment on days to 50% (T50) emergence as mean of all species. Bars labeled with different letters are significantly different at P = 0.001 (Kruskal–Wallis test, pairwise Mann–Whitney U-tests). Error bars represent 1 S.E.M.**
showed no significant difference in growth rate between sowings in March or May (Table 4). There was a tendency for species with small seeds (0.14 mg to 1.55 mg) to have higher relative growth rates than larger seeded species (Fig. 3).

### 3.6. Effect of sowing time on standing biomass

As in the case of relative growth rate, mean standing biomass after 150 days of growth varied greatly between species, by a factor of 212% for March sowings and 2348% for May sowings. A Mann–Whitney U-test found that time of sowing had a significant impact on standing biomass in B. purpurea, D. integerrima, E. curvula, G. oppositiflorus, K. triangularis and W. pulchra (Table 5). The species whose standing biomass significantly increased (P < 0.05) when sown in May included A. ecklonis, B. purpurea, E. curvula, G. linearis, H. aureum, H. coccinea and O. candidans (Table 5). Conversely, D. integerrima, G. oppositiflorus, K. triangularis and W. pulchra, produced significantly more biomass (P < 0.05) when sown in March.

### 4. Discussion

#### 4.1. Seedling emergence in the laboratory as compared to the field

There were large differences in the rate of emergence between species, with dicots and the sole grass species typically emerging faster than geophytic monocots. This is partly due to the fact that radicle emergence is generally more rapid in dicots and grassy monocots than in geophytic monocots, see for example Morgan (1998), and is compounded by the often substantial delay in the latter between radicle and shoot emergence. In dicots radicle and shoot emergence occurs more or less simultaneously. In addition to life form, this study shows distinctive patterns based on taxonomy, with for example, Asteraceae typically being rapid emergers (Morgan, 1998) and the Iridaceae very slow. These patterns also reveal the different ecological strategies (sensu Grime, 2001) of species. Potentially very long lived, and where corm predation is limited, clone forming grassland geophytes exhibit slow seedling emergence but have large seeds that facilitate survival in shaded situations (Leishman et al., 2000). By contrast, the forbs in this study are typically more ephemeral species often of more open habitats, and consequently often have smaller seeds, with rapid emergence and high growth rate.

Emergence/germination in the laboratory (for example, Ascough et al., 2007), as opposed to in the field, is far more widely discussed in the literature. This is because it is more readily standardized and easier to undertake, but potentially provides a misleading estimate of actual emergence behavior in the field (Ahmad and Hitchmough, 2007). This is a significant problem for practitioners involved in restoration ecology or other forms of vegetation establishment via sowing. Germination and emergence rate in non-dormant seed is typically increased by higher temperatures (Holshouser et al., 1996) and given that lab germination is normally undertaken at temperatures approximating to 20/10–25/12 °C, this is higher than spring field soil temperatures associated with temperate environments. Emergence in the field is also delayed by episodes of moisture stress (Evans and Etherington, 1990), whereas laboratory germination avoids these stresses.

Within the species used in this study, the increase in days to 50% emergence in the field was least for the species that have the slowest emergence in the laboratory (D. pulcherrimum, 147.0%; D. latifolium, 206.0%; T. drakensbergensis, 247.0%; and W. pulchra, 260.0%). Species that were very slow to emerge under “optimal” laboratory conditions were similarly slow under field conditions. This suggests that in these

| Species | March 50% emergence | May 50% emergence |
|---------|---------------------|-------------------|
| Gazania linearis | 15 | 15 |
| Berkheya purpurea | 40 | 21 |
| Eragrostis curvula | 43 | 15 |
| Dióca integerrima | 48 | 27 |
| Ornithogalum candidans | 51 | 27 |
| Hesperantha coccinea | 58 | 89 |
| Helichrysum aureum | 65 | 42 |
| Morea huttonii | 71 | 91 |
| Dierama latifolium | 72 | 51 |
| Dierama pulcherrimum | 72 | 84 |
| Aloe ecklonis | 74 | 42 |
| Tritonia drakensbergensis | 74 | 70 |
| Crocosmia monsiorum | 77 | 68 |
| Kniphofia triangularis | 84 | 98 |
| Agapanthus campanulatus | 91 | 77 |
| Watsonia pulchra | 91 | 94 |
| Agapanthus inapertus | 98 | 102 |
| Gladolus oppositiflorus | 98 | 77 |
| Gladolus papilio | 99 | 102 |

### Table 2

Effect of field sowing in March and May on speed of emergence in relation to laboratory emergence. Species that were >5× slower to emerge than in the lab are shown in bold.

| Species | March 50% emergence | May 50% emergence |
|---------|---------------------|-------------------|
| Gazania linearis | 15 | 15 |
| Berkheya purpurea | 40 | 21 |
| Eragrostis curvula | 43 | 15 |
| Dióca integerrima | 48 | 27 |
| Ornithogalum candidans | 51 | 27 |
| Hesperantha coccinea | 58 | 89 |
| Helichrysum aureum | 65 | 42 |
| Morea huttonii | 71 | 91 |
| Dierama latifolium | 72 | 51 |
| Dierama pulcherrimum | 72 | 84 |
| Aloe ecklonis | 74 | 42 |
| Tritonia drakensbergensis | 74 | 70 |
| Crocosmia monsiorum | 77 | 68 |
| Kniphofia triangularis | 84 | 98 |
| Agapanthus campanulatus | 91 | 77 |
| Watsonia pulchra | 91 | 94 |
| Agapanthus inapertus | 98 | 102 |
| Gladolus oppositiflorus | 98 | 77 |
| Gladolus papilio | 99 | 102 |

### Table 3

Maximum percentage field emergence in response to sowing treatments.

| Species | Maximum emergence (%) |
|---------|------------------------|
| March sown | May sown |
| Agapanthus campanulatus | 32.50 | 12.50 |
| Agapanthus inapertus | 28.75 | 30.00 |
| Aloe ecklonis | 38.75 | 46.25 |
| Berkheya purpurea | 55.00 | 48.75 |
| Crocosmia monsiorum | 35.00 | 16.00 |
| Dióca integerrima | 47.50 | 40.00 |
| Dierama latifolium | 68.00 | 61.00 |
| Dierama pulcherrimum | 68.00 | 42.00 |
| Evagrostis curvula | 58.75 | 71.25 |
| Ornithogalum candidans | 53.75 | 58.75 |
| Gazania linearis | 55.71 | 38.60 |
| Gladolus oppositiflorus | 41.07 | 62.50 |
| Gladolus papilio | 25.80 | 32.50 |
| Helichrysum aureum | 36.50 | 38.50 |
| Helichrysum pullidanum | 1.43 | 1.43 |
| Hesperantha coccinea | 66.25 | 32.50 |
| Kniphophia triangularis | 39.29 | 30.71 |
| Morea huttonii | 61.00 | 31.00 |
| Tritonia drakensbergensis | 61.25 | 70.00 |
| Watsonia latifolia | - | 3.57 |
| Watsonia pulchra | 58.57 | 23.57 |
species the germination processes that lead to emergence are able to take place at relatively low temperatures and are not greatly accelerated by higher temperatures in the laboratory. Most of these species were Iridaceae, for which embryo immaturity at seed shedding has been reported (Baskin and Baskin, 1998), suggesting that germination cannot occur until the embryo has matured post-imbibition, and that this process can take place at relatively low temperatures. In the habitat, these summer rainfall species shed seed in late summer–autumn. Imbibition may take place prior to winter drought allowing seedlings to emerge early in the spring after the first significant rainfall, hence reducing competition with grassy dominants. O’Connor (1995) has described this process for woody species. Species that showed rapid shoot emergence in the lab, took much longer to emerge in the field (O. candicans, 1020.0%; E. curvula, 860.0%; H. aureum, 650.0%; D. integerrima, 600.0%) relative to their performance in the laboratory at 20/10 °C. This suggests that in these species the processes leading to emergence require higher temperatures. In summer rainfall habitats this may allow some of these species to emerge in the autumn prior to winter drought. This appears to be the case with H. aureum in cultivation in Britain (Sayuti, personal observation).

Some of the species that were particularly slow to germinate in the field, for example, O. candicans, G. papilio, and A. inapertus, are typically lower latitude species in SA and this might in part explain the slow field emergence in Britain. As might be expected, given its C4 pathway, emergence of *Eragrostis* was markedly slower by early sowing, but like *O. candicans* it was not the most retarded species when sown in March, suggesting that temperature requirements for rapid emergence are not particularly high. The mean daily air temperature in Sheffield in March 2010 was 11.2 °C, in May 14.8 °C. Because of higher evaporation, species sown in May were also subject to more rapidly drying soils, even with the same irrigation regime, and the two slowest to emerge species, *G. papilio* and *H. coccinea* are both plants of wet habitats.

Mean maximum percentage emergence for all species sown (42.48%) is a relatively high value for field sowing. Hitchmough et al. (2003) recorded mean maximum emergence of 26% for 25 species of North American and European forbs, and these values appear relatively typical (Ahmad and Hitchmough, 2007; Hitchmough et al., 2008). Mean maximum emergence varies greatly between species, often reflecting seed quality as much as the intrinsic emergence capacity of a genotyp. Because of superior seed cleaning, reduced seed predation (Chambers and MacMahon, 1994), and seed coat fungal infection (Wagner and Mitschunas, 2008), nursery produced seed normally has higher emergence than wild collected. In South African species, pre-dispersal seed predation is potentially very high (Makholela et al., 2003), and likely to have a profound effect on regeneration success, but is relatively little studied.

### 4.2. Relative growth rate and mean individual standing biomass

Relative growth rate has been used as a means of categorizing, particularly for seedlings, the potential of different species to compete for resources (Grime and Hunt, 1975; Grime et al., 2007). Small seeded species typically had higher growth rates (Turnbull et al., 2008) in this study, and tended to be more ephemeral species associated with more open habitats. Long lived, large seeded, clone forming geophyte species associated with productive *Themeda triandra* tussock grasslands, such as *Dierama* (*Mucina* and Rutherford, 2006), have particularly slow seedling growth. Lunt (1997), found that seedling geophyte survival in closed *Themeda* grasslands in Australia depended on the extent of stored carbohydrates in their seeds.

### Table 4

| Species                  | Seed weight (mg) | Relative growth rate sown in March ($\times 10^{-2}$) | Relative growth rate sown in May ($\times 10^{-2}$) |
|--------------------------|------------------|------------------------------------------------------|-----------------------------------------------------|
| *Diascia integerrima*    | 0.14             | 12.72*                                               | 27.70*                                              |
| *Helichrysum aureum*     | 0.24             | 8.04                                                 | 10.87                                               |
| *Eragrostis curvula*     | 0.34             | 19.95                                                | 17.31                                               |
| *Helichrysum pallidum*   | 0.39             | 0.32                                                 |           -                                         |
| *Hesperantha coccinea*   | 0.85             | 0.64                                                 | 0.11                                                |
| *Gazania linearis*       | 1.55             | 12.99                                                | 10.14                                               |
| *Aloe ecklonis*          | 2.00             | 0.27                                                 | 0.33                                                |
| *Kniphofia triangularis* | 2.10             | 1.72*                                                | 0.57*                                               |
| *Appaganthus campanulatus* | 3.63         | 0.02                                                 | 0.11                                                |
| *Berkyeha purpurea*      | 3.80             | 11.36                                                | 8.58                                                |
| *Moreea huttonii*        | 4.00             | 0.29                                                 | 0.23                                                |
| *Tritonia drakensbergensis* | 4.00          | 1.64                                                 | 0.85                                                |
| *Appaganthus inapertus*  | 4.14             | 0.17                                                 | 0.37                                                |
| *Gladiolus papilio*      | 5.05             | 0.82                                                 | 0.41                                                |
| *Crocosmia masoniorum*   | 5.20             | 2.73                                                 | 0.78                                                |
| *Watsonia latifolia*     | 6.00             | –                                                    | 0.09                                                |
| *Watsonia pulchra*       | 6.00             | 0.68                                                 | 0.30                                                |
| *Ornithogalum candidans* | 7.19             | 0.89                                                 | 2.30                                                |
| *Dierama latifolium*     | 9.95             | 1.69                                                 | 1.41                                                |
| *Gladiolus oppositiflorus* | 10.00        | 0.83*†                                               | 0.34*†                                              |
| *Dierama pulcherrimum*   | 13.69            | 2.29                                                 | 1.95                                                |

* Significant differences (P < 0.05) between March and May sown RGR's (Mann-Whitney U-test) are indicated by asterisks.

### Table 5

| Species                  | Seed weight (mg) | Standing biomass seed sown in March (g) | Standing biomass seed sown in May (g) |
|--------------------------|------------------|----------------------------------------|---------------------------------------|
| *Diascia integerrima*    | 0.14             | 1.309*‡                              | 0.242*‡                               |
| *Helichrysum aureum*     | 0.24             | 0.592                                  | 1.019                                  |
| *Eragrostis curvula*     | 0.34             | 2.973                                  | 9.393*                                 |
| *Helichrysum pallidum*   | 0.39             | 0.014                                  |           -                                         |
| *Hesperantha coccinea*   | 0.85             | 0.050                                  | 0.060                                  |
| *Gazania linearis*       | 1.55             | 1.577                                  | 2.061                                  |
| *Aloe ecklonis*          | 2.00             | 0.015                                  | 0.018                                  |
| *Kniphofia triangularis* | 2.10             | 0.105*‡                              | 0.028*‡                               |
| *Appaganthus campanulatus* | 3.63             | 0.067                                  | 0.031*                                 |
| *Berkyeha purpurea*      | 3.80             | 1.166*‡                               | 2.560*‡                               |
| *Moreea huttonii*        | 4.00             | 0.031                                  | 0.011                                  |
| *Tritonia drakensbergensis* | 4.00          | 0.098                                  | 0.043                                  |
| *Appaganthus inapertus*  | 4.14             | 0.026                                  | 0.017                                  |
| *Gladiolus papilio*      | 5.05             | 0.042                                  | 0.020                                  |
| *Crocosmia masoniorum*   | 5.20             | 0.167                                  | 0.041                                  |
| *Watsonia latifolia*     | 6.00             | –                                      | 0.004                                  |
| *Watsonia pulchra*       | 6.00             | 0.051*‡                              | 0.014*‡                               |
| *Ornithogalum candidans* | 7.19             | 0.073                                  | 0.157                                  |
| *Dierama latifolium*     | 9.95             | 0.102                                  | 0.073                                  |
| *Gladiolus oppositiflorus* | 10.00         | 0.043*‡                              | 0.016*‡                               |
| *Dierama pulcherrimum*   | 13.69            | 0.142                                  | 0.113                                  |

* Significant differences (P = 0.05, Mann-Whitney U-test) are indicated by asterisks.

![Fig. 3. Regression plot of relative growth rate and seed weight of each species across a 150 day growth window.](image-url)
Nearly all species had higher growth rates when sown in May when solar radiation and air temperatures were higher, and RGR's may have been greater still had the study been carried out in South Africa, leading to a different ranking order. Despite the typically montane habitats of the species in this study, those with the most northern distributions (A. inapertus, W. latifolia, and W. pulchra) were likely to have been most poorly fitted to the climate of the experimental site (see Table 6). This is supported by horticultural experience in Britain, where both Watsonia species are slow and difficult to cultivate outdoors. Seedlings of Agapanthus inapertus are also slow. A few species had slower RGR when sown in May, for example H. coccinea, but given that this is a riparian species this probably is due to the greater moisture stress associated with the later sowing time. Despite the trend for higher relative growth rates from the later sowing date, in terms of individual biomass this only differed significantly between the two sowing dates for six species.

RGR tends to be more widely used to characterize species in the ecological literature than standing biomass because it provides a measure of rate of growth, whereas mean standing biomass per plant provides only a summative measure. Both of these parameters are however useful means of indicating the likely outcome of competitive interactions between seedlings, and established plants (Eissenstat and Caldwell, 1987). In this study, relative growth rate was strongly correlated \( (r = +0.75, P < 0.001) \) with mean individual standing biomass.

Under productive conditions, species with high relative growth rates are likely to outcompete shade intolerant species with lower growth rates (Shipley and Keddy, 1988; Hitchmough et al., 2008). In addition to aiding interpretation of the dynamics of semi-natural vegetation, quantification of growth rate can inform sowing rates and other means of determining the initial composition of sown or planted multi-species plant communities in restoration ecology and horticultural practice, with the need for sowing rates to be inversely proportional to the growth rate of component species (Hitchmough, 1987). In this study, relative growth rate was strongly correlated. Fig. 4 shows an ordination of species studied in this paper in terms of these factors, with clusters of species that are less competitive, and initially more competitive. Some of the latter are forbs or grasses.

In conclusion, this study has provided comparative data on seedling emergence and growth in relation to two sowing times. This data is particularly useful when planning sowing of communities of these species either in restoration ecology in the habitat, or when creating nature-like communities of these species in urban greenspace. Categorization of species also provides an initial basis to predict competitive outcomes of interactions between species in naturally occurring and designed vegetation. Many initially very slow growing geophytes (in the absence of high levels of dorm predation) may eventually accrue enough leaf and subterranean corm mass to become competitive dominants, as for example, in the case of some Watsonia, Dierama and Moraees species. This can however only happen if these seedlings survive the initial period of intense competition for light post sowing, with more rapidly emerging and faster growing spontaneous or sown neighboring species.

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