Environmental control of dormancy in *Lolium rigidum* Gaud. seeds

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Summary This paper summarises information gathered during research into dormancy of annual ryegrass (*Lolium rigidum* Gaud.) seeds performed in Western Australia over the last five years. Research has taken us a step closer towards understanding (i) the influence that the environment during seed development has on dormancy status at maturity, and the effect of the long-term climate experienced by previous generations of plants and (ii) how the environment controls dormancy release during after-ripening of annual ryegrass seeds.
Keywords After-ripening, annual ryegrass, dormancy, germination, emergence, *Lolium*, seed.

INTRODUCTION

In annual ryegrass (*Lolium rigidum* Gaud.), the major weed across the cropping region of southern Australia, seed dormancy is well timed to ensure maximal emergence at the start of the annual growing season. In the Mediterranean-type climate that prevails across much of the region, seed development occurs during spring months followed by seed fall in early summer. The seeds then experience up to five months of hot weather on or near the soil surface during the summer drought. Germination in response to sporadic rainfall events that occur over summer is likely to be fatal, so dormancy ensures seed survival through to the more dependable rainfall of autumn and winter.

Accurate prediction of the extent and timing of weed emergence can provide important information to assist weed management. If predictive models for emergence are to be improved, seed dormancy status must be incorporated (Forcella *et al*. 2000, Grundy 2003). Therefore, recent research has focused on the role of the environment during both seed development and subsequent after-ripening on dormancy status of annual ryegrass seeds. This paper describes the effect of environmental parameters on dormancy release through after-ripening. An alternative dormancy release mechanism involving changes in sensitivity to light during moist burial is described in Steadman (2004) and Steadman *et al.* (2004a).

VARIATION BETWEEN POPULATIONS

At seed maturity, the proportion of dormant seeds can be highly variable between populations. Germination percent, measured soon after harvest maturity under optimal laboratory conditions ranged from 5 to 75% across 16 Western Australian populations (Steadman *et al*. 2003a, Steadman *et al*. 2004b). Seeds slowly lose dormancy during the subsequent months, and gradually a greater proportion of the population becomes able to germinate under the conditions of the germination test (Figure 1). By the time that the next growing season begins at least 50% of seeds will be able to germinate, resulting in a large flush of emergence. Further cohorts of the population subsequently lose dormancy and emerge during the winter, but a fraction of the seeds remain ungerminable and viable (Figure 1, Steadman *et al.* 2003a, Steadman *et al.* 2004b).

The factors governing the proportion of the population capable of germinating at the start of the growing season are:

1) the initial proportion of germinable seeds (Gi);
2) the dormancy release rate (DRR);
3) the maximum fraction of seeds losing dormancy (Gmax); and

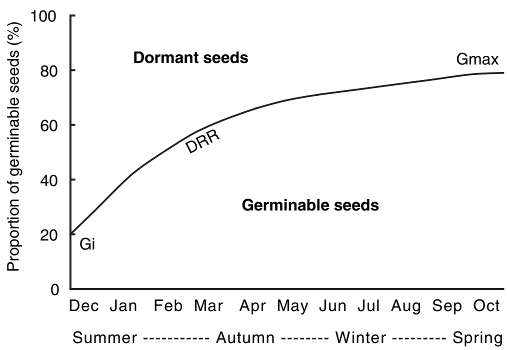

Figure 1. Diagram of typical change in dormancy status of the seed population during the year following development. The initial proportion of dormant seeds (Gi), dormancy release rate (DRR) and maximum fraction of seeds losing dormancy (Gmax) are indicated.

4) environmental conditions at the start of the growing season (water supply, temperature, light).

ROLE OF MATURATION ENVIRONMENT

Temperature during the period of seed development and maturation plays a major role in determining dormancy characteristics of the resulting seeds (Steadman *et al*. 2004b). By comparing climate parameters and dormancy characteristics of seeds collected from 12 different populations across the Western Australian wheat belt, average September temperature was found to be highly positively correlated with both Gi and Gmax. Additionally, subjecting laboratory-grown ryegrass plants to warm temperatures during seed development produced fewer, smaller seeds that had higher Gi and Gmax than seeds that developed at cool temperatures. Thus, two different approaches determined that higher temperatures during seed development correlated with greater germinability (less dormancy) when measured at harvest and following five months of after-ripening (Steadman *et al*. 2004b). These effects of temperature on seed production and dormancy in ryegrass are similar to those previously observed in other grass species (Wiesner and Grabe 1972, Boyce *et al*. 1976, Peters 1982b).

Although less consistent than that for maturation temperature, a link between lower rainfall during seed development and reduced dormancy was also indicated for annual ryegrass (Steadman *et al*. 2004b). Lower growing season rainfall correlated with a higher Gi when compared across 12 populations. Experimentally droughting plants during seed development did not affect Gi but did produce seeds with a faster DRR (Steadman *et al*. 2004b). The impact of maternal drought on seed dormancy is largely species-dependent (Baskin and Baskin 1998), but drought-stressed plants of other grasses tend to produce seeds with reduced dormancy at harvest (Peters 1982a, Meyer and Allen 1999).

ROLE OF AFTER-RIPENING ENVIRONMENT

Temperature is the major regulator of DRR with warmer temperatures causing faster dormancy release (Steadman *et al.* 2003b), in a response that is fairly typical for winter annuals. The simple relationship between temperature and DRR allows the use of thermal after-ripening time, whereby each seed in a population has a specific thermal requirement for dormancy release. This thermal requirement can be achieved using any combination of temperature and time as long as the temperature is greater than the base temperature (T_b), the temperature below which dormancy release does not occur. Moreover, natural fluctuations in temperature do not alter this relationship, so seeds that experience temperatures fluctuating around an average of 20°C accumulate thermal time at the same rate as seeds that experience 20°C delivered constantly (Steadman *et al.* 2003a,b).

Warmer after-ripening temperatures also appear to be associated with a higher Gmax (Steadman *et al*. 2004b). This will add an additional level of complexity to attempts to model dormancy release.

The ambient relative humidity during the summer can vary considerably on a daily basis. This variation has the potential to cause seed water content to fluctuate. When considering unimbibed seeds, i.e. in the absence of rainfall, water content affects the response to thermal after-ripening time under controlled laboratory conditions, with drier seeds losing dormancy more slowly than wetter seeds (Steadman *et al*. 2003b). However, the magnitude of differences in seed water content under rain-free conditions between seeds after-ripened on the soil surface at the extreme northern and southern ends of the wheat belt does not appear to be enough to modify dormancy release rate (Steadman *et al*. 2003a).

Sporadic rainfall during the summer drought can allow seeds to imbibe to hydration levels that can be sufficient for metabolic processes to occur (Steadman and Plummer unpub.). These hydration events may be akin to seed priming techniques, where a single hydration-dehydration event is used to promote more rapid and uniform germination of low-dormancy seedlots (Taylor *et al.* 1998). In a laboratory experiment using annual ryegrass seeds, a greater proportion lost dormancy during a 12 week period when they received one or more hydration events than seeds that remained dry throughout after-ripening (Gallagher *et al*. 2004). This benefit has also been measured in seeds after-ripened under field conditions (Steadman and Plummer unpub.), and this area certainly deserves further consideration in future research into dormancy.

ROLE OF LONG-TERM ENVIRONMENT

High levels of seed dormancy at dispersal are often associated with habitats with a high probability of summer storms that could trigger premature germination into a lethal environment (Meyer *et al.* 1997). However, in a comparison of seeds from 12 Western Australian populations, annual ryegrass growing in areas that have a higher proportion of rainfall falling early in the year, prior to the start of the growing season, appear to retain fewer seeds in the seedbank for future years (Steadman *et al.* 2004b). Therefore, rather than being considered as risky, summer rainfall may reduce the need for annual ryegrass to conserve seeds for future years, possibly by restocking soil water in advance of the growing season. Indeed, in the Mediterranean climatic regions of Western Australia the presence of stored soil moisture resulting from summer rainfall significantly improves early growth and yield of wheat, particularly in drier regions with heavy soils (Asseng *et al.* 2001). Further research is required to confirm this hypothesis.

INFLUENCE OF GERMINATION ENVIRONMENT

The rate of increase in annual ryegrass seed germination as dormancy release progresses is dependent on the germination test conditions applied. For example, dormancy release is slower when the germination test is performed in darkness than when germination is tested in light/dark (Steadman *et al*. 2003a). This property is species-dependent, as the rate of dormancy release of *Bromus tectorum* L. seeds depends on germination test temperature, but those of *Oryza sativa* and *Elymus elymoides* (Raf.) Swezey are independent of germination test temperature (Roberts 1965, Bauer *et al*. 1998, Meyer *et al*. 2000). This means that including dormancy release in an emergence model for annual ryegrass will be potentially quite complex, and the relationship between dormancy release and germination conditions needs more work before an accurate model can be achieved.

CONCLUSION

Major advances in our understanding of the role of the environment in dormancy status of annual ryegrass have been made in recent years. The relationship between after-ripening temperature and Gmax, the effect of imbibition during summer rainfall on dormancy release, and the relationship between dormancy release and germination test environment need further research before an appropriate predictive model can be developed. Furthermore, the extent to which long-term environment determines inter-population differences in dormancy release characteristics deserves detailed investigation.

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REFERENCES

Asseng, S., Turner, N.C. and Keating, B.A. (2001). Analysis of water- and nitrogen-use efficiency of wheat in a Mediterranean climate. *Plant and Soil* 233, 127-43.

Baskin, C.C. and Baskin, J.M. (1998). 'Seeds, ecology, biogeography, and evolution of dormancy and germination.' (Academic Press, San Diego, USA).

Bauer, M.C., Meyer, S.E. and Allen, P.S. (1998). A simulation model to predict seed dormancy loss in the field for *Bromus tectorum* L. *Journal of Experimental Botany* 49, 1235-44.

Boyce, K.G., Cole, D.F. and Chilcote, D.O. (1976). Effect of temperature and dormancy on germination of tall fescue. *Crop Science* 16, 15-8.

Forcella, F., Benech-Arnold, R.L., Sanchez, R. and Ghersa, C.M. (2000). Modelling seedling emergence. *Field Crops Research* 67, 123-39.

Gallagher, R.S., Steadman, K.J. and Crawford, A.D. (2004). Alleviation of dormancy in annual ryegrass seeds by hydration and after-ripening. *Weed Science* in press.

Grundy, A.C. (2003). Predicting weed emergence: a review of approaches and future challenges. *Weed Research* 43, 1-11.

Meyer, S.E. and Allen, P.S. (1999). Ecological genetics of seed germination regulation in *Bromus tectorum* L. Reaction norms in response to a water stress gradient imposed during seed maturation. *Oecologia* 120, 35-43.

Meyer, S.E., Allen, P.S. and Beckstead, J. (1997). Seed germination regulation in *Bromus tectorum* (Poaceae) and its ecological significance. *Oikos* 78, 475-85.

Meyer, S.E., Debaene-Gill, S.B. and Allen, P.S. (2000). Using hydrothermal time concepts to model seed germination response to temperature, dormancy loss, and priming effects in *Elymus elymoides*. *Seed Science Research* 10, 213-223.

Peters, N.C.B. (1982a). Production and dormancy of wild oat (*Avena fatua*) seed from plants grown under soil water stress. *Annals of Applied Biology* 100, 189-96.

Peters, N.C.B. (1982b). The dormancy of wild oat seed (*Avena fatua* L.) from plants grown under various temperature and soil water conditions. *Weed Research* 22, 205-12.

Roberts, E.H. (1965). Dormancy in rice seed IV. Varietal responses to storage and germination temperatures. *Journal of Experimental Botany* 16, 341-9.

Steadman, K.J. (2004). Dormancy release during hydrated storage in *Lolium rigidum* seeds is dependent on temperature, light quality and hydration status. *Journal of Experimental Botany* 55, 929-37.

Steadman, K.J., Bignell, G.P. and Ellery, A.J. (2003a). Field assessment of thermal after-ripening time for dormancy release prediction in annual ryegrass (*Lolium rigidum*) seeds. *Weed Research* 43, 458-65.

Steadman, K.J., Bignell, G.P. and Michael, P.J. (2004a). Stimulating dormancy release and emergence of annual ryegrass (*Lolium rigidum*) seeds using short-term hydrated storage in darkness. *Australian Journal of Agricultural Research*, in press.

Steadman, K.J., Crawford, A.D. and Gallagher, R.S. (2003b). Dormancy release in *Lolium rigidum* seeds is a function of thermal after-ripening time and water content. *Functional Plant Biology* 30, 345-52.

Steadman, K.J., Ellery, A.J., Chapman, R., Moore, A. and Turner, N.C. (2004b). Maturation temperature and rainfall influence seed dormancy characteristics of annual ryegrass (*Lolium rigidum*). *Australian Journal of Agricultural Research*, in press.

Taylor, A.G., Allen, P.S., Bennet, M.A., Bradford, K.J., Burris, J.S. and Misra, M.K. (1998). Seed enhancements. *Seed Science Research* 8, 245-56.

Wiesner, L.E. and Grabe, D.F. (1972). Effect of temperature preconditioning and cultivar on ryegrass (*Lolium* sp.) seed dormancy. *Crop Science* 12, 760-4.