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PERSPECTIVE
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Changing Seasonality of *Lolium rigidum* (Annual Ryegrass) in Southeastern Australia

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Lolium rigidum (annual ryegrass) is the most costly winter weed in Australia and has recently been observed growing in summer. The occurrence of *L. rigidum* in winter is well documented, but there is no research on populations of this weed that germinate and grow in summer. Herein, we discuss how the potential cause of this seasonal expansion may be related to a change in dormancy duration. Dormancy can affect germination patterns but the growth and reproduction of a plant species depend on other factors, such as temperature and photoperiod. Therefore, dormancy alone cannot be the sole variable responsible for the presence of *L. rigidum* in summer crops, as typical summer temperature conditions are not favorable for the growth of this weed. Additional changes to the growth and development of summer populations may allow for the adaptation and infestation of *L. rigidum* in summer conditions.

Keywords: annual ryegrass, winter annual, summer, weed, dormancy, germination, plant growth

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INTRODUCTION

Lolium rigidum Gaud. (annual ryegrass) is a winter annual (obligate) weed found in Australian wheat and canola cropping fields. Recently, *L. rigidum* has also been found to occur in summer in the southeastern region of Australia (Thompson and Chauhan, 2019; Thompson et al., 2021; GRDC, 2021). Annual weeds, as their name implies, complete one life cycle annually. The typical life cycle for *L. rigidum* is to germinate in autumn, grow during winter, and set seed in spring. The seeds remain dormant in the soil until the following autumn, when the cycle begins again. Now, for some populations of *L. rigidum*, this lifecycle has shifted later into the year.

Summer *L. rigidum* is not yet a widespread problem in Australia as reports seem limited to irrigated cropping systems of southern New South Wales. While the rate and significance of spread are unknown, limited distribution at present allows for the pre-emptive study of these adaptive populations of *L. rigidum*. The presence of summer germinating *L. rigidum* warrants careful investigation to determine whether it is driven more by adaptive changes in seed dormancy, by changes in agronomic practices, or global warming. We discuss the questions and avenues of investigation that should be addressed in order to better understand the emerging threat.

Lolium rigidum is the most costly winter weed in Australia, requiring high inputs of herbicides and causing significant reductions in crop yield. It causes a revenue loss of >AU$ 93 million per annum to the Australian grain growers (Llewellyn et al., 2016) and this loss is likely to increase significantly if the summer form of *L. rigidum* becomes widespread. Increased reliance on herbicides with the same mode of action has also led to the rise in the occurrence of herbicide-resistant populations. The expansion of *L. rigidum* into summer cropping systems (e.g., cotton; **Figure 1**) could exacerbate the incidence of herbicide resistance, further complicating management options for the species year-round. It presents the potential for devastating effects on Australian agriculture, mainly if seasonally adapted populations can increase their geographic spread.

Due to its significant economic impact, there is widespread existing information on the germination and growth characteristics of *L. rigidum* as a winter cropping weed. This article positions current knowledge against what potential distinctions may be present in newly emerging summer populations. In this article, we put forth possible explanations for how *L. rigidum* has spread across seasons and discuss what future work is required to better understand this phenomenon.

SEED DORMANCY AND GERMINATION

As a winter annual weed species, *L. rigidum* typically germinates in late autumn, allowing its main period of growth to occur during winter. The weed's dormancy occurs during the summer months when rainfall is typically too low in Australia to sustain further growth after germination. Dormancy is regarded as the lack of germination of viable seed, despite experiencing favorable conditions (Bewley, 1997; Finch-Savage and Leubner-Metzger, 2006). This can be affected by temperature, moisture, light, soil salinity, pH, and seed burial depth. Seeds of *L. rigidum* have been shown to germinate in sodium chloride concentrations of up to 160 mM, although at a low percentage (Chauhan et al., 2006; Rahman and Asaduzzaman, 2019).

FIGURE 1 | *Lolium rigidum* plants with seed heads in a cotton crop.

The germination process occurs in three water uptake phases, enabled when seeds proceed from the second to third phase after having lost their dormancy (Bewley et al., 2012). Dormancy is relieved by the dry storage of seeds, a process known as after-ripening. The extent of after-ripening can affect whether the seed can proceed to phase III of water uptake when exposed to moisture. Additionally, the rate at which after-ripening can decrease dormancy is affected by environmental conditions, such as temperature and humidity (Sharif-Zadeh and Murdoch, 2001).

For *L. rigidum*, both light exposure and temperature can affect release from dormancy. As a winter annual, it would be expected that secondary seed dormancy would decline as soil temperature increased so that seedling emergence would coincide with falling autumn temperatures (Footitt et al., 2020). As climate warming occurs, seeds may well mature at warmer temperatures known to reduce primary dormancy (Chen et al., 2021). If seeds are set at a lower dormancy level, this may result in out-of-cycle seedling emergence in an irrigated crop. The reduction of soil temperature by irrigation may create the signal for germination in this winter annual. It may not be universal, but in the Arabidopsis ecotype CVi, an obligate winter annual, seedling emergence only occurs when the soil temperature is falling (Footitt et al., 2020). Alternatively, if soil temperature increases due to global warming, secondary dormancy will be lost more quickly, resulting in increased light sensitivity. Previous studies have shown conclusively the impact of increasing temperature in the dark on reducing dormancy in *L. rigidum* (Steadman et al., 2004). While exposure to higher temperatures reduces dormancy (Steadman et al., 2003), dormancy prediction in *L. rigidum* based on climatic variables has been inconsistent (Owen et al., 2011a), as individual genetics likely play a role in determining release. Gaining a better understanding of dormancy may be crucial for understanding the ability of some populations of *L. rigidum* to germinate in summer conditions.

The amount of summer rainfall in areas of Australia where *L. rigidum* is a widespread problem is not typically sufficient to support the development of the weed through to maturity. As such, dormancy in *L. rigidum* allows the seed to avoid this fate during intermittent rainfall events throughout an otherwise dry summer to germinate in more favorable conditions the following autumn. The incidence of summer germinating *L. rigidum* in Australia suggests that some populations are breaking dormancy earlier than is typical for this species. As the occurrence of summer *L. rigidum* is not widespread, it suggests that any potential reduction in dormancy could be due to either a change in the maternal environment where the seed matures or after-ripens or a change in the genetics of the population adapting to the summer climate of that region. However, whether a reduction in dormancy is the cause of the ability to germinate in summer has not yet been determined, and there is a need to research on this aspect. As dormancy is a trait that is controlled in part by genetics, adaptation to summer conditions *via* changes in the genes related to seed dormancy is possible. Dormancy-related genes are regulated by the environment (Finch-Savage and Footitt, 2017). Furthermore, it could be that any change in dormancy-related genes may be a result of selection pressures put on populations of weeds by the application of herbicides (Owen et al., 2011b). This study suggested the coexistence of dormancy and herbicide resistance due to an adaptation to decades of intense cropping. It proposed that the status of herbicide resistance might have a role as a predictive tool in modeling dormancy in *L. rigidum* at a large spatial scale. Altering the duration of dormancy so that the plant may germinate outside of the typical spraying window will give the plant a greater chance of success than germinating at a time when herbicides are applied, provided that conditions after germination are suitable for development. Environmental factors may also control the regulation of dormancy-related genes. As such, seeds that have developed a shorter period of dormancy in response to the environment of one location may not lose dormancy at the same rate in a location with different conditions. Summer seed germination could also be related to the natural variation in dormancy duration of *L. rigidum* populations from areas of different average summer rainfall levels. Seeds from populations adapted to regions with consistently dry summers that spread to areas with wetter summers may germinate due to an adaptation to a different regional climate. Populations from regions that experience very low rainfall may not have the same barriers to prevent losing dormancy as populations with more frequent rainfall. Exposure to a new location where rainfall is more frequent may prompt germination.

Once dormancy is broken, the environmental conditions must still be favorable for the seeds to germinate in summer. *Lolium rigidum* can germinate in a range of temperatures that can be as high as 35°C (Gramshaw, 1976; Thompson et al., 2021). Though summer temperatures in Australia can exceed this temperature, it demonstrates that temperature may not be a highly restricting factor for preventing the germination of *L. rigidum* in summer. The fact that *L. rigidum* has been reported to grow in summer already provides sufficient evidence that some individual populations can germinate in summer temperatures (Thompson & Chauhan, 2019; GRDC, 2021). Therefore, given that sufficient moisture is present, either through high rainfall or irrigation, germination of non-dormant seeds is likely to occur. However, once the plant has germinated, it must survive through the following summer conditions to pose a problem to farmers and reproduce.

GROWTH AND DEVELOPMENT

Impact of *L. rigidum* on cropping systems depends on the level of infestation and survivability of the weed in that environment. Sparse populations will pose less of a threat to the crop, but even dense populations will not cause issues if the plants cannot survive past the seedling stage. Therefore, it is important to understand what conditions must be met in order for *L. rigidum* to survive during summer and how the growth of summer populations compares to populations growing during winter.

Lolium rigidum is a high-tillering species and this large production of biomass may allow it to compete with crops throughout its development. When present in wheat, *L. rigidum* competes for nitrogen, resulting in lower biomass for the crop throughout its development (Palta and Peltzer, 2001). Increased density of *L. rigidum* also results in crop yield loss (Paynter and Hills, 2009). From these results, we must begin to wonder what effect summer growing *L. rigidum* may have on crop yields. There is currently no data available on the tillering ability and growth rate of summer *L. rigidum*. While the above study discusses density, being the number of plants in a given area, a change in biomass of the weed will also affect the growth of the crop, whether this is due to competition for light or soil nutrients.

Plants have an optimum temperature at which their growth is the highest, and beyond this temperature, growth slows down (Hatfield et al., 2011). Until recently, *L. rigidum* has grown only in winter, indicating that its optimal temperature for growth would be well below summer conditions, particularly for early physiological stages. It could mean that summer populations will grow slower, produce less biomass than their winter counterparts, and give crops more opportunity for competition.

Changes in growth rate due to different temperatures during summer may result in *L. rigidum* reaching each development stage at a different rate than its winter counterpart. If summer maximum temperatures are above the optimum temperature of the species, it will likely take longer for summer *L. rigidum* to reach anthesis, develop seeds, and reach maturity than winter *L. rigidum*. Higher temperatures can also lead to lower yields in crops (Hatfield et al., 2011; Hatfield and Prueger, 2015), likely leading to lower seed production in weeds.

On the other hand, part of the adaptation of *L. rigidum* to summer conditions may be an altered optimum growth temperature. So far, we have only discussed how the ability of *L. rigidum* to grow in summer may be due to a change in the dormancy of *L. rigidum*; however, there may also be changes to the further growth of the plant. An increased optimum temperature for growth would allow summer *L. rigidum* to maintain the same growth rate and biomass production that has allowed the weed to compete with crops in winter. Research is needed to determine whether *L. rigidum* growth differs between summer and winter *L. rigidum* populations. Phenology studies on summer biotypes of *L. rigidum* could provide insights into its impact on summer cropping systems. These studies will also provide information on their potential to produce seeds in summer. Summer biotypes producing seeds in the same season may select for lower dormancy.

Another factor that may affect the growth of these weeds during summer is the increase in day length and greater light intensity. Light is a primary driver of photosynthesis, which is responsible for increasing biomass. Increasing day length in plants that would normally grow in short day lengths improves biomass production (Adams and Langton, 2005). In conjunction with this, higher photoperiods cause greater increases in plant growth when combined with increased root-zone temperature (Mozafar et al., 1993). These two conditions that are likely to be met when comparing summer to winter.

To our knowledge, the incidence of *L. rigidum* in summer has been restricted to irrigated fields in southern New South Wales.

The availability of high water levels is crucial for sustaining *L. rigidum* growth into summer. At present, drought tolerance would not play a prominent role in establishing *L. rigidum* in summer, as this would have likely extended the geographic range of incidence beyond irrigated fields. Whether irrigation is the sole determinant of the capability of *L. rigidum* to grow in summer or whether an altered dormancy duration is also at play is currently unclear.

FUTURE DIRECTIONS

Much research needs to understand the germination and growth of *L. rigidum* in summer. As indicated in this article, we do not yet know what distinguishes populations of summer growing *L. rigidum* from winter growing *L. rigidum*. There are large variations among winter populations alone, which increases the importance of gathering data from a large collection of summer populations before any conclusions can be drawn. As summer *L. rigidum* is not currently a widespread occurrence, these conclusions are not close at hand. However, there is still much research to be done with the currently limited populations.

As described in this article, the two major areas of focus are establishing differences in germination, including determining dormancy duration, and differences in the growth and development of the maturing plant. Identifying the dormancy duration of seeds collected from summer-grown plants is a start, but further attention needs to be paid to growing summer plants in winter and determining their dormancy. It will allow us to understand whether these populations are capable of growing in one winter season and emerging in the following summer.

Genetic studies must also be conducted to further understand how dormancy relates to summer and winter growing *L. rigidum*. Identifying genes or genetic regions associated with dormancy can help us understand how summer populations differ from winter populations. Genome-wide association studies could be employed to identify regions of the genome associated with dormancy and find markers we can use to identify seeds capable of germinating in summer. Genetic analysis can also be used to determine the overall genetic diversity between summer and winter populations, which can identify how closely related these populations are.

We must then look to establishing the differences between the developing plants of summer and winter *L. rigidum* to understand why some populations have been able to survive under summer conditions in Australia. It will include monitoring the growth rate of these populations and their biomass production. Additionally, herbicide resistance testing of summer growing populations could aid in establishing whether this adaptation has arisen as a form of herbicide resistance. Lastly, it would be of great importance to growers to determine the impact that summer populations have on summer crops. Information is needed on whether summer conditions stimulate or suppress the biomass of *L. rigidum* and whether this will significantly impact on crop production.

CONCLUDING COMMENTS

Fortunately, *L. rigidum* is still predominately limited to winter conditions. However, we cannot assume that this will always be the case. *L. rigidum* already has a significant impact on the agricultural industry in Australia. Therefore, to ensure it does not become a larger problem by expanding its season of growth, we need to understand its biology better.

An altered state of dormancy is likely to explain why this weed can establish in summer cropping systems. Most *L. rigidum* maintains dormancy throughout the summer months to avoid the unfavorable conditions of that season. Therefore, there is reasonable cause to believe that a decreased duration of dormancy is required for *L. rigidum* germination in summer. This change in dormancy may results from the impact of climate change or the natural genetic variation found in *L. rigidum.* However, it may also result from selection pressure applied *via* herbicide use.

There is no current research to provide any evidence for whether the growth of summer populations is affected by summer conditions. The hotter temperatures may or may not improve growth depending on the optimum temperature for growth for each plant. However, the longer photoperiod may allow for greater growth of plants. Any change in biomass or height of the plant will likely affect the yield of crops that the *L. rigidum* populations compete with.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MT wrote the original manuscript; BC conceptualized the idea and edited the manuscript. All authors contributed to the article and approved the submitted version.

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