

Seasonal *Poa annua* L. Seedling Emergence Patterns in Maryland

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ABSTRACT

Annual bluegrass (*Poa annua* L.; ABG) can be a major weed problem in golf course turf. Research-based information on the seasonal emergence patterns of ABG is limited. The objectives of this four-year field study were (i) to determine seasonal ABG emergence patterns in Maryland, (ii) to determine peak period(s) of ABG emergence, and (iii) to determine the date and estimated percentage of seedlings emerged when the rate of emergence declines. Annual bluegrass seedlings were found to emerge between August and May in two Maryland golf course roughs. A majority (50–70%) of seedling emergence occurred between late September and mid-October, and peak germination generally was observed in early October. The linear increase in ABG seedling emergence generally ended by early November; however, 24% of all seedlings emerged between November and May. No major ABG emergence cycles were observed during the spring in any year. Mean daily temperatures generally were $\leq 20^{\circ}\text{C}$ during peak ABG emergence periods, and germination was stimulated by precipitation. Since the genetic diversity of ABG is well known, these findings may only be applicable to Maryland and regions with similar environmental conditions.

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Abbreviations: ABG, annual bluegrass; UMGC, University of Maryland Golf Club; WCC, Woodmont Country Club.

ANNUAL BLUEGRASS (*Poa annua* L.; ABG) is a major weed problem of golf course turf in the mid-Atlantic region. Seasonal emergence patterns of ABG can vary greatly by geographic region. According to Vargas and Turgeon (2004), literature concerning ABG seed germination appears inconsistent. Branham (1991) stated that ABG germinated at such high levels in the autumn and spring in Michigan that three applications of preemergence herbicides often were necessary to achieve acceptable control. In Tennessee, ABG was reported to emerge in one extended germination period between mid-to-late November and early January (Callahan and McDonald, 1992). In Maryland, observations suggested that most ABG seedlings emerged between September and December, but some may emerge again in the spring (Dernoeden, 1998). The timing of ABG seedling emergence reported in the Maryland and Tennessee studies was based primarily on results and observations from preemergence herbicide evaluations and not on actual emergence data.

Shem-Tov and Fennimore (2003) evaluated seasonal ABG emergence patterns in a California vegetable field. Data from the three-year study indicated that ABG seedling emergence on average peaked on 5 November and was lowest on 20 June. Additionally, soil samples

Published in *Crop Sci* 47:773–779 (2007).

doi: 10.2135/cropsci2006.03.0191

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collected in spring exhibited little to no ABG emergence (<1%) when incubated under spring or autumn conditions, whereas samples collected in the autumn had emergence levels >95% when incubated under either of the aforementioned conditions (Shem-Tov and Fennimore, 2003). These findings support previous studies indicating that ABG seed undergo after-ripening or dormancy before it can germinate (Standifer and Wilson, 1988b; Tutin, 1957).

No studies have previously been conducted to monitor the seasonal emergence patterns of ABG in turf. Proper timing of preemergence herbicides, based on known emergence patterns, likely would improve herbicide efficacy. Additionally, elucidation of seedling emergence patterns could potentially be used by turfgrass managers to adjust the timing of core aeration and other cultural practices in an effort to either encourage or discourage ABG populations. The objectives of this study were to determine seasonal ABG emergence patterns in Maryland, peak period(s) of ABG emergence, and the date and estimated percentage of seedlings emerged when the rate of germination declines.

MATERIALS AND METHODS

This field study was conducted between 1999 and 2003 at the University of Maryland Golf Club (UMGC) in College Park, MD. Soil was a Sunnyside fine sandy loam (fine, loamy siliceous, mesic Typic Hapludult) with a pH of 4.7 and 50 mg organic matter gr^{-1} of soil. Phosphorus (53 kg P ha^{-1}) and potassium (295 kg K ha^{-1}) levels were low and optimum, respectively. The UMGc study area was not fertilized and received no supplemental irrigation throughout the study. In the final year (2002–2003), ABG seedling emergence also was monitored at Woodmont Country Club (WCC) located in Rockville, MD. Unlike the UMGc site, the WCC site was irrigated between August and October 2002 from incidental water from the automated fairway irrigation system. Soil at WCC was a Manor loam (coarse-loamy, micaceous, mesic Typic Dystrudept) with a pH of 6.5 and 27 mg organic matter gr^{-1} of soil. Phosphorus (126 kg P ha^{-1}) and potassium (332 kg K ha^{-1}) levels were very high. At both locations, turf was mowed to a height of 5 to 6 cm approximately once per week. Daily air temperature and precipitation data were obtained from a USDA weather station located approximately 3 km from the UMGc study site.

The perennial ABG [*Poa annua* L. f. *reptans* (Hauskn.) T. Koyama] biotype persists under low mowing and routine irrigation and has a prostrate growth habit and dark-green color, and it produces few seedheads (McElroy et al., 2004). It was assumed that a vast majority of the seedlings at the monitoring sites were the annual biotype of [*Poa annua* var. *annua* (L.) Timm], based on its light-green color, upright growth habit, prolific seedhead production, and general decline in summer. Biotypes at the monitoring sites, however, were not identified by DNA analyses or other techniques. Annual bluegrass emergence was monitored at UMGc between 1999 and 2003. On 8 Sept. 1999, four circular areas were sprayed with glyphosate [N-(phosphonomethyl) glycine], and the total number of ABG seedlings emerged initially were counted on 27 September and removed. Annual bluegrass emergence then was assessed by

counting and removing seedlings from inside each fixed circle approximately weekly between 5 Oct. 1999 and 23 May 2000. In 2000, four new circular areas were treated with glyphosate, and ABG seedlings were counted between 11 Sept. 2000 and 23 May 2001. In 2001, ABG emergence was monitored using the above described methods between 14 Aug. and 31 May 2002. In the final year (2002–2003), ABG emergence was monitored in four circular areas at UMGc and WCC between 30 Aug. 2002 and 31 May 2003. In all years, individual circular areas measured between 744 and 1200 cm^2 , and data were adjusted to represent the number or percentage of seedlings emerged 930 $\text{cm}^2 \text{ yr}^{-1}$. Tissue killed with the nonselective herbicide remained as a ground cover during the autumn months, but mostly bare soil was present by spring.

Data from all locations were analyzed using various methods in an effort to meet the three objectives. Seasonal emergence patterns were assessed by plotting seedling emergence data for each year. Corresponding environmental data (temperature and precipitation) obtained 3 km from the UMGc study site also were plotted against the average number of ABG seedlings counted on each rating date. In addition to the actual number of seedlings emerged, percentage ABG emergence and cumulative emergence were determined on each rating date to verify period(s) during which large number of seedlings emerged relative to the total annual number. Linear regression analyses were then performed on the cumulative percentage emergence within each circular area to determine the date on which emergence rate began to decline. Calendar dates were converted to ordinal dates before all regression analyses. The ordinal day on which the next day resulted in a reduction in the R^2 value of the linear regression was determined to be the end of the major emergence flush. The percentage of total ABG seedlings emerged by the end of the linear seedling emergence period also was determined. Where applicable, data were subjected to analysis of variance using the MIXED procedure in SAS (SAS Institute, 2000).

RESULTS

Seasonal Annual Bluegrass Emergence 1999–2000

In 1999, a total of 253 and 62 mm of precipitation were recorded during the months of September and October, respectively (data not shown). The total number of ABG seedlings emerged between 8 and 27 September was 360 seedlings 930 cm^2 (Fig. 1a). It is unknown, however, if the majority of these seedlings emerged near the 27 September rating date or if emergence was dispersed evenly throughout this 2- to 3-wk period. Regardless, seedling emergence declined rapidly, and after 11 October ABG seedlings emerged in low to moderate numbers throughout December. Between January and May 2000, emergence was observed only at very low levels (≤ 6 seedlings 930 cm^2 per rating date).

2000–2001

In 2000, ABG emergence was monitored beginning 18 September. Total precipitation in September was 135 mm.

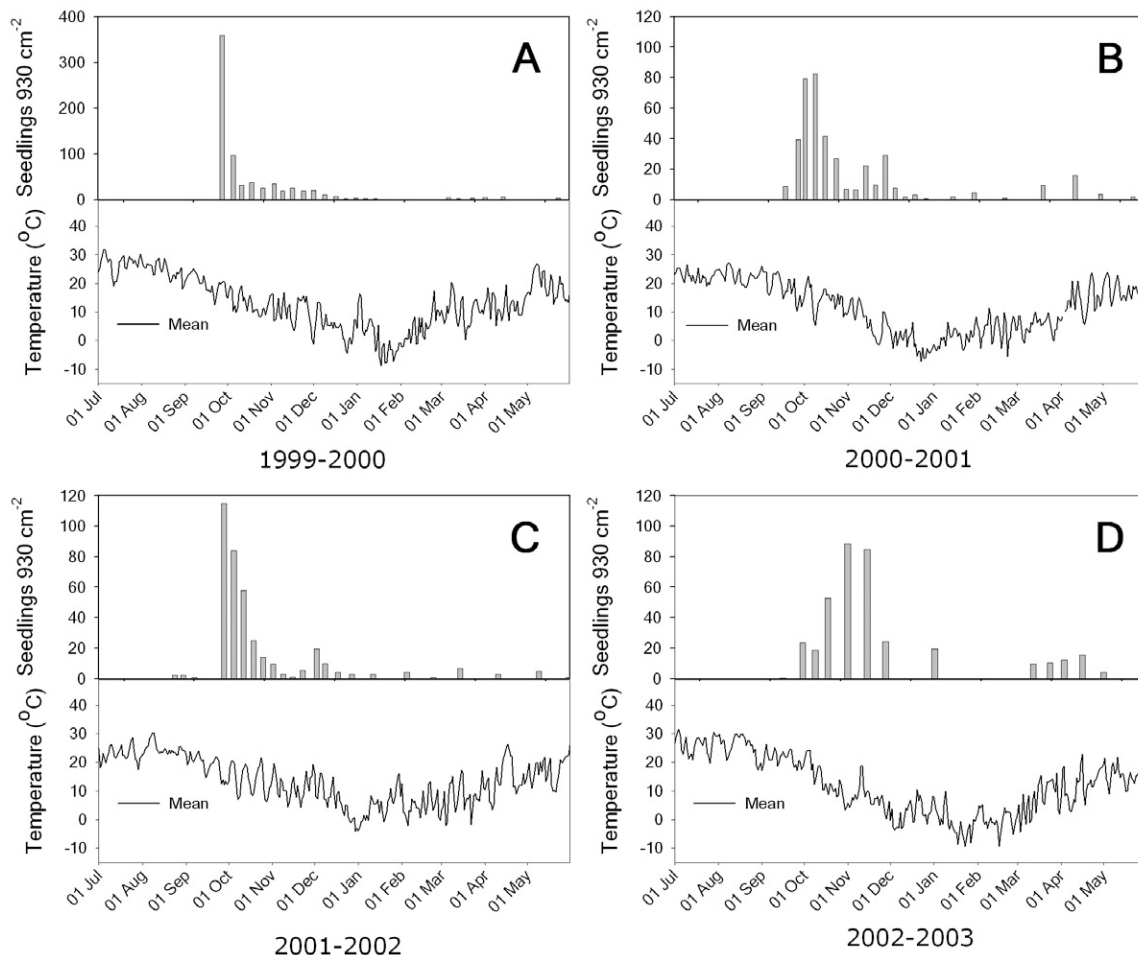


Figure 1. Mean annual bluegrass seedling emergence in a golf course rough, University of Maryland Golf Club, located in College Park, MD (A, 1999–2000; B, 2000–2001; C, 2001–2002; and D, 2002–2003), and the associated mean air temperature.

A total of 9 seedlings 930 cm⁻² had emerged between 11 September (when the area was treated with glyphosate) and 18 September (Fig. 1b). Germination increased in late September, and between 27 September and 9 October, 162 seedlings 930 cm⁻² had emerged. After this peak, ABG seedling emergence decreased until the second week of November. Approximately 3 mm of rainfall were recorded during this period (2 October–7 November), after which time ABG emergence appeared to be stimulated (69 seedlings 930 cm⁻²) by additional precipitation (33 mm) occurring between 9 and 29 November. Similar to the previous year, seedlings continued to emerge in very low numbers (total = 38 seedlings 930 cm⁻²) throughout the winter and spring.

2001–2002

In 2001, ABG emergence was monitored beginning 14 August. Despite adequate rainfall during the month of August (130 mm), only 4 seedlings 930 cm⁻² had emerged by 30 August (Fig. 1c). Low levels of precipitation (5 mm) occurred between 1 and 19 September, and no ABG seedlings were observed during this period. Mean air temperatures at this time were 15 to 24°C.

Toward the end of this three-week period (20 and 21 September), 38 mm of rainfall had occurred. This precipitation appeared to stimulate germination, and a total of 115 seedlings 930 cm⁻² emerged between 21 and 28 September. This peak in ABG emergence was followed by a sharp decrease during October. Similar to autumn 2000, ABG germination was briefly stimulated by additional rainfall events (36 mm) in late November and early December. Low levels of emergence (≤ 7 seedlings 930 cm⁻² per rating date) again were observed throughout the winter and early spring of 2002.

2002–2003

In 2002, ABG seedling emergence was monitored at two locations. Emergence at both sites was monitored beginning on 30 Aug. 2002 and continued until 31 May 2003. Due to almost continuous snow cover, no observations were made at either site between 3 January and 24 March. Very few seedlings emerged between 30 August and 23 September at WCC, despite being irrigated several nights per week (Fig. 2). By late September, however, germination increased rapidly, and 175 (65%) seedlings had emerged by 18 October (Fig. 2). At UMGC, which received only natural rainfall, a

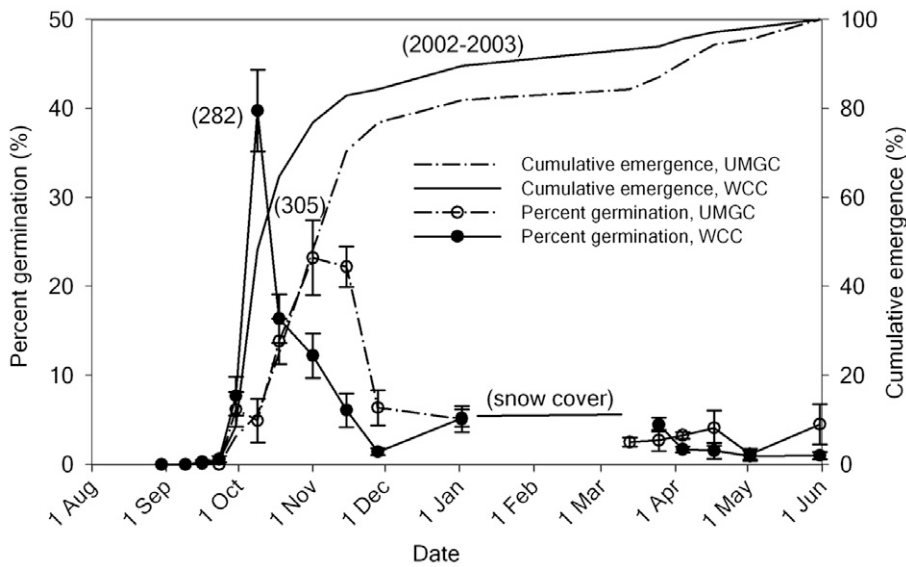


Figure 2. Mean and cumulative percent annual bluegrass emergence in a golf course rough, University of Maryland Golf Club (UMGC), located in College Park, MD, and Woodmont Country Club (WCC), located in Rockville, MD, between 2002 and 2003. Error bars represent the standard error of the means for percent germination within four 930-cm² circular areas (three areas for UMGC) monitored on various dates between August and May.

small spike in emergence occurred (24 seedlings 930 cm⁻²) in late September following 35 mm of precipitation on 26 and 27 September (Fig. 1d). Additional precipitation did not occur until 16 October. Unlike previous years at UMGC and at WCC in 2002, high levels of emergence appeared only in late October, extending into mid-November. During this period 232 mm of precipitation were recorded, and a total of 226 seedlings 930 cm⁻² had emerged. After this

Table 1. Day of year when the predicted linear increase in annual bluegrass seedling emergence ended and the corresponding percentage of seedlings emerged at two locations, University of Maryland Golf Club (UMGC) and Woodmont Country Club (WCC), 1999–2003.

Year	Day of year	SE _{day} [†]	Emergence %	SE _{emergence} [‡]
UMGC				
1999–2000	313 a [§] (9 Nov. 1999)	± 13	85 a [§]	± 2
2000–2001	296 a (22 Oct. 2000)	± 2	68 b	± 3
2001–2002	292 a (19 Oct. 2001)	± 5	77 ab	± 2
2002–2003	319 a (15 Nov. 2002)	± 0	71 ab	± 8
WCC				
2002–2003	309 a (5 Nov. 2002)	± 4	80 ab	± 2
Mean	305 (1 Nov.)	± 4	76	± 2

[†]SE_{day} = standard error of the mean for the day of year in which a linear increase in annual bluegrass seedling emergence ended within four circular areas (930 cm²) at two locations between 1999 and 2003.

[‡]SE_{emergence} = standard error of the mean for the percentage of emergence that had occurred when the linear increase in annual bluegrass seedling emergence ended.

[§]Means in column followed by different letters are significantly different ($P \leq 0.05$) according to Tukey's least significant difference t test.

later flush of ABG seedling emergence, seedlings continued to emerge at very low levels (total = 89 seedlings 930 cm⁻²) between 29 Nov. 2002 and 31 May 2003, similar to that observed during the previous 3 yr.

Peak Period of Annual Bluegrass Seedling Emergence

Except for the UMGC site in 2002, ABG seedling emergence peaked at all locations between late September (27 September; Day 270) and early October (9 October; Day 283) (Fig. 2 and 3). Percentage emergence during the period of rapid seedling emergence ranged from 31 to 50%. In the final year at UMGC, seedling emergence peaked between 1 and 15 November (Fig. 2). Percentage germination on the aforementioned dates accounted for 45% of the total seedlings emerging in 2002 at UMGC (Fig. 2). On average, peak ABG seed-

ling emergence occurred on 8 October (Day 282) (Fig. 2 and 3). Regardless of year, no major ABG seedling emergence patterns were observed during the spring.

Declining Rate of *Poa annua* Seedling Emergence

Data showed that ABG seedlings continued to emerge at low levels during the winter. Cumulative seedling data were subjected to linear regression analyses to determine the date on which the rate of ABG emergence began to decline. In the first study year, the linear increase in seedling emergence ended on 9 Nov. 1999 (SE = 13 d) and accounted for 85% (SE = 2%) of the total number of seedlings emerged over the monitoring period (Table 1). During the 2000–2001 study year, the linear increase in ABG seedling emergence ceased on 22 October (SE = 2 d), with a total of 68% of the seedlings having emerged. During the next 2 yr, the period of predicted increase in linear emergence ended on 19 October and 15 November for 2001–2002 and 2002–2003, respectively. The WCC site was located 17 km from UMGC, and the linear increase in ABG seedling emergence at WCC ended 10 d earlier, on 5 Nov. 2002. On average, seasonal ABG seedling emergence increased at a linear rate until 1 November (range 19 October–15 November) and accounted for an average of 76% of the total number of seedlings emerged each season. The remaining 24% of the seedlings emerged over a 7-mo period extending from November until May.

DISCUSSION

Annual bluegrass seedlings were found to emerge between August and May in two golf course roughs in Maryland. Major flushes of ABG seedling emergence, however, only occurred between late September and the first 2 wk of October. During this three- to four-week period, approximately 50 to 70% of the total number of all seedlings had emerged; on average emergence peaked on 2 October (Day 282). Shem-Tov and Fennimore (2003) reported that ABG seedling emergence was greatest between October and November and was lowest from March to July in vegetable fields in the central coast of California. Seasonal emergence varied among years, but the average date by which a linear increase in ABG seedling emergence ended occurred on 1 November. Most ABG seedlings (76%) emerged over a short period of time (late September to early November), while the remaining 24% of seedlings emerged over the remaining 7 mo (1 November to 31 May). Similarly, Shem-Tov and Fennimore (2003) reported that ABG emergence peaked on 5 November and was lowest on 20 June in California. While seedlings emerged at a linear rate between September and late October or early November, ABG emergence generally peaked during the first week of October. Year-to-year differences in seed germination may be due to variations in air and soil temperature during seed formation (Standifer and Wilson, 1988a). In our study, ABG seedlings continued to emerge at very low levels throughout the winter in unfrozen soil and into May. Although seedling emergence was not monitored between June and August, no major ABG seedling emergence patterns were observed between late winter and early spring. Hence, data from the California and Maryland studies suggest that ABG seedling emergence may occur at similar times in the western and eastern USA and that major emergence peaks occur over a relatively narrow period of time.

Mean daily temperatures surrounding peak ABG seedling emergence periods generally were $\leq 20^{\circ}\text{C}$. The direct impact of soil and air temperature, diurnal temperature fluctuations, and photoperiod on ABG seedling emergence, however, remains imperfectly understood. McElroy et al. (2004) found that seedling emergence of southern ABG ecotypes was greater when seeds were incubated at day/night temperatures of 19/10°C compared to higher temperatures (39/29°C). According to Vargas and Turgeon (2004), Bogart (1972) found that ABG seed germinated at similar levels at constant temperatures ranging from 4 to 21°C, but germination was reduced greatly at temperatures above 27°C. It was suggested, however, that soil moisture or temperature alone has little influence on ABG seedling emergence but that ABG caryopses respond more to decreasing photoperiod during late summer and early autumn (Shem-Tov and Fennimore, 2003). This hypothesis, however, is in contrast to the findings of McElroy et al. (2004), who found

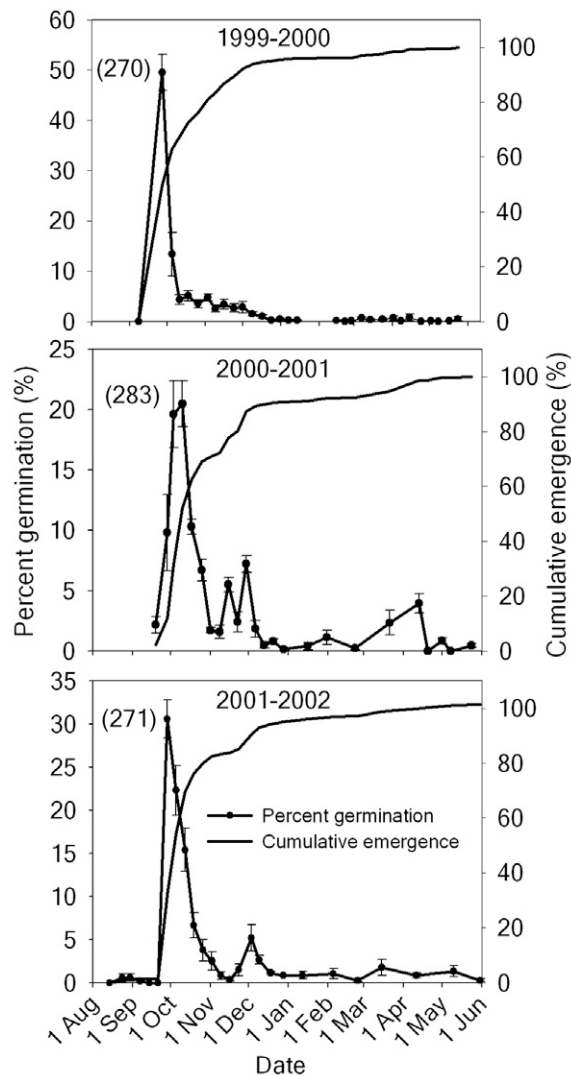


Figure 3. Mean and cumulative percentage annual bluegrass emergence in a golf course rough, University of Maryland Golf Club (UMGC) (1999–2000, 2000–2001, 2001–2002), located in College Park, MD. Error bars represent the standard error of the means for percentage germination within four 930-cm² circular areas monitored on various dates between August and May.

that ABG seedlings did not appear to be influenced by day length as seeds germinated in complete darkness, and photoperiod preference was not representative as a means of distinguishing ecotypes.

Annual bluegrass seeds must overcome a series of events for germination to occur. Following flowering in the spring, seed of the annual biotype (*P. annua* var. *annua*) have an absolute dormancy and require an after-ripening period to break dormancy (Standifer and Wilson, 1988b). Standifer and Wilson (1988b) found that ABG seeds of the annual variant develop a conditional dormancy when subjected to varying temperature regimes and that dormancy was broken most rapidly when seed was stored at 35°C. The summer dormancy or after-ripening requirement helps explain the peak in ABG seedling emergence observed in the autumn and suggests that the primary biotype at these

sites was *P. annua* var. *annua*. During late August and early autumn, ABG seedlings emerged during periods in which air and soil temperatures were declining. When temperatures become favorable for germination, soil moisture (precipitation) likely becomes a limiting factor. In our study, an average of 76% of the ABG seedlings had emerged by 1 November, during which time mean daily air temperatures for September and October averaged between 16 and 20°C. Similarly, Shem-Tov and Fennimore (2003) reported that the average soil temperature during the major ABG seedling emergence period in California was 15.6°C. Few seedlings emerged between December and April, when mean air temperatures for this period were 4.5 to 7.7°C.

Annual bluegrass cover in turfgrass stands increases greatly in the spring, which has been attributed to rapid tillering rather than a flush in spring seedling emergence (Dernoeden, 1998). In the northeastern and mid-Atlantic USA, however, significant populations of ABG have been observed to emerge in spring where winter stress has eliminated large areas of turf. Bare soil may be more conducive to promoting ABG seed germination. In this study, necrotic turfgrass tissue remained in the monitored areas during the autumn, but these areas generally were void of tissue by spring. The number of seedlings found emerging between March and May ranged from 16 to 69 seedlings 930 cm⁻² and averaged 35 seedling 930 cm⁻² over 4 yr. These levels could account for the ability of ABG to rapidly colonize bare areas in the spring. This would be especially likely in bare areas that were core aerified or otherwise disturbed, thus redistributing more ABG seed to the surface. Undoubtedly, ABG seedlings would tiller and provide a rapid cover in the absence of competition from a perennial turfgrass. Regardless, relatively small numbers of seedlings emerging during the spring may account for a significant increase in annual bluegrass populations.

Based on these findings, preemergence herbicides should be applied in late August or early September in Maryland to provide their maximum benefit. Soil-disturbing cultural practices should be planned around these timings to either encourage or discourage ABG populations. Peak emergence patterns in the northeastern USA likely would be earlier north of Maryland and later in the southeastern USA. This hypothesis is partially substantiated by Callahan and McDonald (1992), who reported that ABG germinated mostly between mid-to-late November and early January in Tennessee. Previous studies have shown that biotypes of ABG growing on greens, fairways, and roughs have different requirements for germination (Lush, 1989; Wu et al., 1987; Wu and Harivandi, 1993). While ABG seedling emergence was monitored in mostly nonirrigated roughs, it is unknown if similar emergence patterns occur on greens and fairways in Maryland.

The genetic diversity of ABG biotypes and ecotypes within and among regions is well known, and our findings may be applicable only to Maryland and regions with similar environmental conditions. The exact timing of and temperatures influencing germination, seedling emergence, tillering, and seedhead production undoubtedly vary due to segregation of ABG ecotypes in response to prevailing regional environmental conditions and management practices (Cline et al., 1993; Johnson and White, 1997a, 1997b; Sweeney and Danneberger, 1995). Therefore, it would be beneficial to further investigate and define the influence of regional environmental conditions on ABG biology. Future investigations would benefit from the development of geostatistical models similar to that developed for crabgrass (Main et al., 2004). Attempts to monitor the emergence patterns of ABG should be determined for each biotype in environmentally diverse regions and under varying cultural management systems (i.e., greens, tees, fairways, and roughs).

References

- Bogart, J.E. 1972. Factors influencing competition of annual bluegrass (*Poa annua* L.) within established turfgrass communities. Master's thesis. Michigan State University, East Lansing, MI.
- Branham, B. 1991. Dealing with *Poa annua*. *Golf Course Manage.* 59:46–60.
- Callahan, L.M., and E.R. McDonald. 1992. Effectiveness of bensulide in controlling two annual bluegrass (*Poa annua*) subspecies. *Weed Technol.* 6:97–103.
- Cline, V.W., D.B. White, and H. Kaerwer. 1993. Observations of population dynamics on selected annual bluegrass-creeping bentgrass golf greens in Minnesota. *Int. Turfgrass Soc. Res. J.* 7:839–844.
- Dernoeden, P.H. 1998. Use of prodiamine as a preemergence herbicide to control annual bluegrass in Kentucky bluegrass. *HortScience* 3:845–846.
- Johnson, P.G., and D.B. White. 1997a. Flowering responses of selected annual bluegrass genotypes under different photoperiod and cold treatments. *Crop Sci.* 37:1543–1547.
- Johnson, P.G., and D.B. White. 1997b. Vernalization requirements among selected genotypes of annual bluegrass (*Poa annua* L.). *Crop Sci.* 37:1538–1542.
- Lush, W.M. 1989. Adaptation and differentiation of golf course populations of annual bluegrass (*Poa annua*). *Weed Sci.* 37:54–59.
- Main, C.L., D.K. Robinson, J.S. McElroy, T.C. Mueller, and J.B. Wilkerson. 2004. A guide to predicting spatial distribution of weed emergence using geographic information systems (GIS). Available at <http://www.plantmanagementnetwork.org/ats/> (verified 1 Feb. 2007). *Appl. Turf. Sci.*, doi:10.1094/ATS-2004-1025-01-DG.
- McElroy, J.S., R.H. Walker, and G.R. Wehtje. 2004. Annual bluegrass (*Poa annua*) populations exhibit variation in germination response to temperature, photoperiod, and fenarimol. *Weed Sci.* 52:47–52.
- SAS Institute. 2000. SAS OnlineDoc: Version 8. SAS Institute, Inc., Cary, NC.
- Shem-Tov, S., and S.A. Fennimore. 2003. Seasonal changes in annual bluegrass (*Poa annua*) germinability and emergence.

Weed Sci. 51:690–695.

Standifer, L.C., and P.W. Wilson. 1988a. Dormancy studies in three populations of *Poa annua* L. seeds. Weed Res. 28:359–363.

Standifer, L.C., and P.W. Wilson. 1988b. A high temperature requirement for after ripening of imbibed dormant *Poa annua* L. seeds. Weed Res. 28:365–371.

Sweeney, P.M., and T.K. Danneberger. 1995. RADP characterization of *Poa annua* L. populations in golf course greens and fairways. Crop Sci. 35:1676–1680.

Tutin, T.G. 1957. A contribution to the experimental taxonomy of *Poa annua* L. Watsonia 4:1–10.

Vargas, J.M., Jr., and A.J. Turgeon. 2004. *Poa annua*: Physiology, culture, and control of annual bluegrass. John Wiley & Sons, Hoboken, NJ.

Wu, L., and A. Harivandi. 1993. Annual bluegrass ecology and management. Golf Course Manage. 61:100–106.

Wu, L., I. Till-Bottraud, and A. Torres. 1987. Genetic differentiation in temperature-enforced seed dormancy among golf course populations of *Poa annua* L. New Phytol. 107:623–631.