White Paper: Perspective on Creeping Bentgrass, *Agrostis stolonifera* L. [1]

USDA/APHIS/BRS (B. MacBryde, ver. 12/12/2005)

Contents

1. Overview of the Genus *Agrostis* and its Species

1.1. Some field grasses were called *Agrostis* by Theophrastus (*ca*. 371-287 BC), director of Aristotle's garden in Athens (Greene 1909). Bentgrasses (*Agrostis*) are in the convenient grouping called cool-season grasses, with a C_3 photosynthetic pathway (*cf*. Campbell *et al*. 1999; Goverde *et al*. 2002). Within the family Poaceae (Gramineae), the genus *Agrostis* is in the tribe Poeae (including Aveneae and Agrostideae), which also contains oats (*Avena*), and in the subtribe Agrostidinae (Soreng *et al*. 2003; *cf*. Clayton & Renvoize 1986; Watson & Dallwitz 1992, 1998, 1999; Mabberley 1998). The genus might include 150-200 species, occurring primarily and probably originating evolutionarily in the Northern Hemisphere in western Eurasia (the European region), with some species having evolved in the Southern Hemisphere and temperate to cold-temperate areas of tropical mountains. The generic limits of *Agrostis* are not obvious (*e.g*. Phillips & Chen 2003), and sometimes *Podagrostis* (Björkman 1960), *Bromidium* (Rúgolo de Agrasar 1982) and *Lachnagrostis* (Edgar 1995; Jacobs 2001) are considered distinct (Soreng *et al*. 2003).

1.2. In the United States, 35 species of *Agrostis* in the broad sense (*sensu lato*) are native or naturalized, with 17-19 of them also in Canada (see Table 1). There are 26-29 native species of *Agrostis* in the USA, and 7-9 established introductions, mainly from Eurasia (7 or 8 of these species are entirely introduced, 1 or 2 mostly so). If the genus is instead considered in the narrow sense (*sensu stricto*) (Soreng & Peterson 2003), two of the native species would be placed in *Podagrostis* and one each of the introduced species in *Bromidium* and *Lachnagrostis* (Table 1). The overall taxonomy within the genus *Agrostis* is unsettled and difficult. There is no comprehensive worldwide or definitive U.S. taxonomic treatment (*cf*. Hitchcock & Chase 1951; Carlbom 1967; Simpson 1967; Harvey 1993, 2004; Kartesz 2004), but there are some thorough floristic treatments and a few definitive regional taxonomic studies (*e.g*. Philipson 1937; Björkman 1960; Widén 1971; Romero García *et al*. 1988b; Tutin 1980; Rajbhandari 1985, 1987; Koyama 1987; Edgar & Connor 2000; Rúgolo de Agrasar & Molina 1992, 1997a). Consequently, the number of North American species stated above is a distillation reflecting different judgements.

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[1] Much of the information in this review is obtainable only by continually noting the references as they are cited and reading the titles.

1.3. Cytological study of chromosomes (karyology) along with experimental hybridization have provided central taxonomic insights, as polyploidy (multiplication of the basic chromosome set) plays a significant role in the evolution of the genus and within some species (*e.g.* Sokolovskaya 1938; Davies 1953; Jones 1953, 1956a-1956c; Björkman 1951, 1954, 1960; Carlbom 1969; Vovk 1970; Widén 1971; Sokolovskaya & Probatova 1974; Tateoka 1975; Tateoka & Michikawa 1987; Rumball & Forde 1977; Romero García & Blanca 1988; Romero García *et al*. 1988a; Frey 1997; Tomić & Šurlan-Momirović 1999; Tomić *et al*. 2003; Bonos *et al*. 2002; Vergara & Bughrara 2003). Substantial taxonomic insight has also come from study of floret anatomy and histology (*e.g.* Björkman 1960; Romero García *et al*. 1988b). The species tend to be accepted as distinct once they are understood (*i.e.* not stay controversial taxonomically); the general stability includes all five of the species of main agronomic interest (Tables 1 & 2) (Beard & Beard 2005; Aldous & Chivers 2002):

- creeping bentgrass, *Agrostis stolonifera* (Warnke 2003);
- colonial bentgrass, *Agrostis capillaris* (Ruemmele 2003);
- velvet bentgrass, *Agrostis canina* (Brilman 2003; Brilman & Meyer 2000);
- dryland bentgrass, *Agrostis castellana* (Brede & Sellmann 2003); and
- redtop, *Agrostis gigantea* (Brede & Sellmann 2003; Balasko *et al*. 1995).

1.4. Nevertheless, making use of the subtle biological distinctions for identification of the species as whole plants (in flower or not), or as seeds, frequently requires acumen and expertise (*e.g.* Widén 1971; Tutin 1980; Steiner & Lupold 1978; Steiner 1982; Romero García *et al*. 1988b; Chicouène 1989; Sell & Murrell 1996; Copping 1974; Cope 1991; Adams 1996; Batson 1998a; Behrendt & Hanf 1979; Nittler & Kenny 1969; and Hillman 1918, 1930; Musil 1942, 1963; van der Burg *et al*. 1979), which can be facilitated by lab analysis (*e.g.* Yamamoto & Duich 1994; Clark *et al*. 1989; Freeman & Yoder 1994; Ohmura *et al*. 1997; Hollman *et al*. 2005; Scheef *et al*. 2003; Ridgway *et al*. 2003; Bonos *et al*. 2002). Routinely, diverse studies either lack full identification, reporting just *Agrostis* sp. or the plural *Agrostis* spp. (*e.g.* Mountford & Peterken 2003); or they have misidentification (from tradition, assumption or error), either of the species of interest (*e.g.* Scott & Hallam 2002) or by not realizing the population has more than one species.

1.5. For example, there is a need in USA for increased awareness to better distinguish *A. capillaris* and *A. stolonifera* from *A. castellana*, which was rather recently found dominant in southeastern Australia by Batson 1996, 1998a (*cf*. Romero García *et al*. 1988b; Paunero 1947, 1953; Brede & Sellmann 2003; Ruemmele 2000a, 2003; Brilman 2001a; Brede 2000; Edgar & Connor 2000; Edgar & Forde 1991; Funk 1998; Sell & Murrell 1996; Cope 1991; Hubbard 1984; Tutin 1980; Steiner & Lupold 1978; Shildrick 1976, 1980; Scholz 1962, 1965; Griffin 1965; Madison 1961; USDA 1948, 1961; Musil 1942; Bartels 1943; Schoth 1930, 1939; Levy & Saxby 1931; Hillman 1930; Henry 1928). Similarly, there is a need to better distinguish *A. canina* and *A. vinealis*, brown bentgrass (Widén 1971; *cf*. Brilman 2003; Warnke 2003; Wipff & Rose Fricker 2001; Funk 1998; Vester 1999; Fryčková 1996; Sell & Murrell 1996; Cope 1991; Hubbard 1984; Tutin 1980; *cf*. Kurchenko 1979a). Thus what may be regarded as variability of a species in natural or managed populations can be more than one species' intermingled behaviors. Fortunately *Agrostis stolonifera* is a distinct and relatively familiar species, particularly in the scope of turf species and golf courses (*cf*. Casler & Duncan 2003; Ruemmele 2000b).

1.6. *Agrostis* is additionally complex in naturally forming F_1 (first-generation) hybrids, which are generally low in fertility or sterile but sometimes vegetatively vigorous, and occur perhaps not infrequently between various species. Such hybrids varyingly include all five of the main agronomic species (*cf.* Brede & Sellmann 2003; Warnke 2003), as well as *Agrostis idahoensis*, Idaho bentgrass (of agronomic interest – Brede & Sellmann 2003; Brede 2004), *A. vinealis*, and several other germane species (see Tables 1 & 2, and Davies 1953; Jones 1956a-1956c; Camus 1958; Björkman 1960; Widén 1971; Bradshaw 1975a, 1975b; Sell & Murrell 1996; Lambinon *et al*. 2004; Paunero 1947; Romero García *et al*. 1988b; Edgar & Forde 1991; Edgar & Connor 2000; Batson 1998a; Wipff & Rose-Fricker 2000, 2001; Wipff & Fricker 2001; Belanger *et al*. 2003c, 2003b; Christoffer 2003). There are a few clear examples of F_2 hybrids (*i.e.* the second generation, F_1 hybrids crossed with each other) (Bradshaw 1975a; Sell & Murrell 1996), and of backcrosses of F_1 hybrids to a parental species (Forde 1991; Edgar & Connor 2000; Batson 1998a; Belanger *et al*. 2003b). In some areas where the *Agrostis* species are native or naturalized, the hybrids are recognized as sometimes being a significant component of vegetation (Widén 1971; Bradshaw 1975a; Sell & Murrell 1996; Edgar & Connor 2000). This composition can occur even with sterile plants because of their vegetative reproduction.

1.7. A summary on the pertinent hybridizations is in Figure 1 and Table 1. In Table 2 are basic details (not all-encompassing) on these species in the USA and their crossing (which is inherently complicated but not atypical in grasses and some other wild plants), along with additional information as follows:

- Notable botanical synonyms (thus subordinate, not just alternative names);
- Common names (*cf.* Monteith 1930; USGA 1932);
- Ranges (where native, and along with the Table 1 information, where naturalized);
- Ploidy (a polyploid has 3 or more sets of chromosomes; frequent levels are **bolded**) (*cf.* Levy & Feldman 2002; Gaut 2002; Soltis *et al*. 2003):
  $\boldsymbol{n = x = 7}$, the basic set of chromosomes in a male or female gamete, **haploid**
  $\boldsymbol{2n = 2x = 14}$, the paired parental sets of chromosomes usual in body cells, **diploid**
  $2n = 3x = 21$, three sets of chromosomes usual in the plant's body cells, triploid
  $\boldsymbol{2n = 4x = 28}$, four sets of chromosomes usual in plant's somatic cells**, tetraploid**:
    allotetraploid (amphidiploid) = 2 unlike paired sets, AABB (*e.g.* hybrid's sets doubled)
    autotetraploid = 4 sets alike, AAAA (*e.g.* within sp., crossing plants' sets doubled)
    segmental allotetraploids = ~ alike, ± halfway, ~ unalike: *e.g.* AAĀĀ, AAÃÃ, AAẬẬ
  $2n = 5x = 35$, five sets of chromosomes usual in plant's somatic cells, pentaploid
  $\boldsymbol{2n = 6x = 42}$, six sets of chromosomes usual in plant's somatic cells, **hexaploid**
  $2n = 7x = 49$, seven sets of chromosomes usual in plant's somatic cells, heptaploid
  $2n = 8x = 56$, eight sets of chromosomes usual in plant's somatic cells, octoploid
  aneuploidy = inexact multiple of chromosomes in all body cells, *e.g.* $2n - 1$, $2n + 2$
  aneusomaty = chromosome number varies ± as in aneuploidy within one plant's body cells
- Genomic configuration (*i.e.*, subgenomes, ancestral chromosome sets, *e.g.* AABBCC);
- *Agrostis stolonifera* hybrids with three species of the genus *Polypogon*, rabbitsfoot-grass or beardgrass (*e.g.* Conley 1993; Barkworth 2004; Giraldo-Cañas 2004).

2. Distribution and Conservation of *Agrostis* Species

2.1. Many species of *Agrostis* are natively widespread in temperate areas, whereas other indigenous species or taxa (*i.e.* subspecies or botanical varieties) are regional, local or rare (WCMC 1998). Using the Natural Heritage Network's assessment criteria (Master *et al*. 2000), several *Agrostis* in the United States are variously rare (Table 1). There is an endemic species in Hawaii, several endemic taxa in California and/or Oregon, an endemic species in Wyoming (Yellowstone National Park), and a rare species in Wyoming, California and Russia (Kamchatka Peninsula) (CNPS 2001, 2005; ONHIC 2004; Tercek *et al*. 2003; Tercek & Whitbeck 2004; Tercek 2005).

2.2. None of these rare *Agrostis* are now listed as endangered or threatened under Federal law; under State law, in California *A. blasdalei* var. *marinensis* (Marin bentgrass) was listed in 1978 as rare, but in 1998 no plants could be found at its single known site, and it is considered a synonym under the species by Harvey (1993, 2004), CNPS (2001, 2005) and Kartesz (2004) rather than being a distinct biological entity. Creeping bentgrass (*A. stolonifera*) probably occurs in meadow or wetland habitats of some threatened or endangered species of animals and plants listed under Federal law, although confirmation may be needed on the identification of this grass in their habitats (*e.g.*, for the threatened western orchid Ute ladies-tresses, *Spiranthes diluvialis*).

3. The Species Creeping Bentgrass, *Agrostis stolonifera*

3.1. *Agrostis stolonifera* L. is a robust, fast-growing perennial which is biologically and ecologically very variable, phenotypically plastic (adjusting locally) and evolutionarily adaptive, with vegetative spread and reproduction by stolons (horizontal aboveground stems or runners), wind-pollinated flowers, and tiny (0.07 mg) seeds (*i.e.* caryopses) dispersed by wind, water and animals (Sell & Murrell 1996; Romero García *et al*. 1988b; Grime *et al*. 1988; Kik *et al*. 1990a, 1990b, 1991; Grime & Hunt 1975; Kurchenko 1975; Eriksson 1989; Shipley *et al*. 1989; Davies & Singh 1983; Misra & Tyler 2000b; Aston & Bradshaw 1966; Jónsdóttir 1991b; Ahmad & Wainwright 1976; Wu 1976, 1981; Kik 1989; Badiani *et al*. 1998; Kaligarič 2001; Teyssonneyre *et al*. 2002; Bradshaw & Hardwick 1989; *cf*. Donohue 2003; Grime & Mackey 2002). Generally the species is an allotetraploid (Jones 1956b, 1956c; Warnke *et al*. 1998; Chakraborty *et al*. 2005), but it also has cytotypes of higher ploidy and other such chromosomal complexity (aneuploidy, aneusomaty, and accessory or B-chromosomes), at least within its native range in the Old World — see Table 2 and Kik *et al*. (1992, 1993). Correlations usually are not taxonomically consistent within its very broad natural range, but sometimes the main ecological and/or genetic tendencies in a region are featured either as informal groups or formally as botanical varieties (*e.g.* Philipson 1937; Paunero 1947; Jansen 1951; Widén 1971; Romero García *et al*. 1988b; Sell & Murrell 1996).

3.2. For example in Great Britain and Ireland, Sell & Murrell (1996) point out that the varieties in their region are ecological, but nonetheless recognize taxonomically *Agrostis stolonifera* (**1**) var. *marina*, forming a close turf in salt marshes and areas within tidal spray — stolons few and usually short, culms (stalks) becoming erect, panicles (flower clusters or inflorescences) often rather lax, usually not lobed; (**2**) var. *calcicola*, forming a close turf on chalk downs — stolons either many and short or absent and plants tufted, culms erect or basally bent, panicles narrow and meager; (**3**) var. *maritima* (synonym *A. stolonifera* var. *compacta*), mainly coastal, in loose sand, isolated plants — stolons many and widely creeping, culms usually much inclined, panicles usually dense and lobed; (**4**) var. *palustris*, in wet places in the lowlands — stolons long, often many, with no indication of tufting, culms tall and usually few, panicles usually dense and lobed; and (**5**) var. *stolonifera*, in a wide variety of grasslands and waste places, isolated plants — usually with stolons many and widely creeping, culms becoming erect, panicles long and usually narrowly pyramidal. In four contrasting populations in Netherlands habitats, Kik *et al*. (1990b; *cf*. Jansen & Wachter 1940) found different relationships of habitat and stolon number per plant: (1) in a salt marsh, plants had many short thin stolons; (2) in a sand dune, plants had a few long thin stolons; and (3) in an inland meadow, plants had a few long thick stolons. A polder population (on estuary land obtained over a decade earlier by holding back the sea) had all three biotypes, which were genetically distinct.

3.3. The related species *Agrostis capillaris* L. (synonym *A. tenuis* Sibth.) has similarly been observed to be quite variable and fine-tuned to a range of habitats (*e.g.* Bradshaw 1959a, 1959d, 1960; Chadwick & Salt 1969; Tasker & Chadwick 1978; Acheroy & Lefèbvre 1983; Funtova & Malyshev 2001; Leyer 2005; Roxburgh *et al*. 1994; Helgadóttir & Snaydon 1985, 1986; Rothanzl 2002; Dostál *et al*. 2005; and López *et al*. 1997; Balocchi & López 2001; Wilson & Rapson 1995).

4. Creeping Bentgrass Distribution and Utilization

4.1. Creeping bentgrass has become naturalized in temperate to cold-temperate regions throughout the world (*cf*. Woodward *et al*. 1986; White & Smithberg 1980; Tompkins *et al*. 2000, 2004), for example in New Zealand, southern Australia including Tasmania, South Africa, South America including Tierra del Fuego, Patagonia and the Andes, North America, and on remote islands such as Hawaii, the Juan Fernández Islands, the Falkland Islands, Gough Island and Tristan da Cunha. *Agrostis stolonifera* is native in Eurasia principally (also Iceland and North Africa), but has an ambiguous status (perhaps native locally) in northern USA and/or in Canada at some salt marshes and freshwater lakes (Hitchcock & Chase 1951; Voss 1972; Dore & McNeill 1980; Harvey 2004). However four close relatives, the other main agronomic species (Tables 1 & 2), are clearly native only in Eurasia or Europe (*e.g.* Widén 1971; Romero García *et al*. 1988a; Warnke *et al*. 1998; Vergara & Bughrara 2003). In the USA, creeping bentgrass is definitely mostly if not entirely naturalized, and probably arrived well before the 1750s (*cf*. Sauer 1942, 1976; Richardson 1818; Odland 1930; Monteith 1930), introduced with seed or hay as forage for cattle, sheep and horses (as in other regions, *e.g.* Argentina – Rúgolo de Agrasar & Molina 1992). Once popular for pasture in the USA, the species has been suggested for reseeding on some western grasslands (*e.g.* USDA Forest Service 1940; Davis 1952; Fransen & Chaney 2002). It is now naturalized in all the states and recorded (*i.e.* mapped present) in the majority of counties, except in the warmer southern portions of states in the Southeast (Kartesz 2004; *cf*. USGA 1922a; Ward 1969; Moncrief 1964; Ferguson 1964; Schmidt & Blaser 1967; Xu & Huang 2001; Huang & Liu 2003; Pote & Huang 2003).

4.2. Under grass forages, *Agrostis stolonifera* and *A. tenuis* (*i.e. A. capillaris* in accord with Tutin in *Flora Europaea* 1980; Widén 1971; Table 2) are included in Annex I ("List of Crops Covered under the Multilateral System") of the International Treaty on Plant Genetic Resources for Food and Agriculture (IT-PGRFA), which was established

November 3, 2001. It entered into force June 29, 2004; parties include the European Community and Canada. Access to certain genetic resources of the listed crops will be regulated multilaterally, as will sharing of benefits, including transfer of technology and payment of an equitable portion of commercial benefits from use of these genetic resources. The treaty derived from the similar International Undertaking on Plant Genetic Resources (IU) (begun in 1983 and last agreed to in 7/2001). FAO's Commission on Genetic Resources for Food and Agriculture (with the United States among its 167 member nations) held the last IU negotiations over 7 years, and the resultant IT-PGRFA was adopted by the FAO Conference (184 members) in 11/2001 (Japan and USA abstaining; USA signed in 11/2002). The Convention on Biological Diversity welcomed the "International Seed Treaty" (IT-PGRFA), anticipating it will be a key international agreement dealing with issues concerning plant genetic resources for food and agriculture (*cf.* Fowler 2004; PGGR 2003).

4.3. The IT-PGRFA could intend the inclusion of creeping bentgrass even though not considering it a major grass forage. With some differences in use (circumscription) of *Agrostis* names (section 5.9), the history of the *A. stolonifera* listing warrants checking for confirmation of the species intended by reviewing how the name was brought into consideration. Hammer & Spahillari (1999) recognize all five main agronomic species (*A. canina*, *A. capillaris*, *A. castellana*, *A. gigantea*, *A. stolonifera*) as minor crops of Central Europe with genetic resources of value because of their utilization for fodder (*e.g.* Balasko *et al*. 1995; DeFrance & Burger 1966; Tomić *et al*. 1999, 2003; Chorlton *et al*. 1997, 2000; Karlsen 1988; Laser & Opitz von Boberfeld 2004; Dumortier *et al*. 1996; Kratochwil *et al*. 2002; Hill *et al*. 1992; López *et al*. 1999; Flores *et al*. 2000; Faville *et al*. 1995; Bañuelos & Obeso 2000; Pieper & Burlison 1930; de Coninck & Bay 1816; Richardson 1818; Haggar 1976; Frame 1990; Sheldrick *et al*. 1990), with both of the latter species of additional value for revegetation ("recultivation") and soil stabilization and improvement (*cf.* Smith & Bradshaw 1979; Wainscott 1961), and with all but *A. gigantea* of "ornamental" value (*i.e.* as lawn grasses or turf). An overview on this species (redtop) with its turf history is given by Brede & Sellmann (2003).

5. Creeping Bentgrass – Establishing a Major Turfgrass

5.1. In the 1890s seeds of a few *Agrostis* species, sometimes including small amounts of *A. stolonifera*, were gathered in mixtures from semi-wild pasture populations in central Europe (present-day Austria and Hungary) and likely first imported to establish golf courses (Duich 1985; Warnke 2003). A large bentgrass seed trade (with ± 6,000,000 seeds per pound) continued for several decades, especially from a range of semi-wild locales across Germany (Edler 1930) (annual imports 388,500 lbs to 294,000 lbs from 1927-1930 – USGA 1930b), and from an increasing production in New Zealand (USGA 1922b, 1922c, 1925b, 1930b; Hillman 1921, 1930; Henry 1928; *cf.* Levy 1924; Suckling & Forde 1978; and Nikolov 1975; Balocchi *et al*. 1998; López *et al*. 1999). Moreover seed was gathered from free-living (naturalized) U.S. populations in coastal New England from about 1900, and chiefly 1924-1934 in the low coastal region of Oregon but also Washington and northwestern California, as well as farther inland in western Oregon and perhaps Washington (Hillman 1921, 1930; Henry 1928; USGA 1925a, 1931; Monteith 1930; Carrier 1921; Odland 1930; Schoth 1930, 1939; Hyslop 1930). Additional seed was imported mostly from crop production in southeastern (maritime) Canada, as well as inland in Alberta (Clark 1922; Tregillus 1926; Malte 1928; LeLacheur 1930; Henry 1928; Hillman 1930).

5.2. The many shipments of "South German mixed bent" seed were variously comprised of mostly *Agrostis capillaris* with some *A. canina*, about 10% or less *A. gigantea*, and sometimes a trace of *A. stolonifera* (Hillman 1921, 1930; Henry 1928; USGA 1922c, 1930b; Piper & Oakley 1922b; Oakley 1923; Monteith 1930). Considering the relatively wild sources of seed from populations in Europe (*cf*. Hultén & Fries 1986), perhaps *A. vinealis* was also included (*cf*. Sell & Murrell 1996; Scholz 2000; Vester 1999; Ridgway *et al*. 2003). Hillman (1930) reported that a distinct bentgrass seed which was being termed "hybrid seed" was coming from Germany under the names "creeping bent" and "German bent", in "recent years…practically all the seed of some lots", and that the real nature of these plants was under study.

5.3. The bentgrass seed imported from New Zealand (*e.g.* 162,600 lbs in 1929 and an impressive 508,900 lbs or 254 tons in 1930) was eventually found to be not solely *Agrostis capillaris* (*cf*. Suckling & Forde 1978; Rapson & Wilson 1992a, 1992b; Karataglis 1980b, 1986), but to include *A. castellana* (which earlier had been considered just a local ecological variation), and to additionally include its hybrids with *A. capillaris* (Rumball & Forde 1977; Edgar & Forde 1991; Batson 1998a; Steiner & Lupold 1978; Henry 1928) — which have been called *A.* ×*fouilladeana* (rather than *A.* ×*fouilladei* P. Fourn. [1934], *nomen nudum* – see Lambinon *et al*. 2004). Similarly, the inland bentgrass of western Oregon and Washington is increasingly being recognized not as a dryland or upland (*i.e.* non-coastal) variation of *A. capillaris* (marketed as 'Highland' bentgrass), but as a landrace of the species *A. castellana* (Henry 1928; Hillman 1930; Schoth 1930, 1939; USDA 1948, 1961; Madison 1961; Griffin 1965; Funk 998; Brede 2000; Brilman 2001a; Ruemmele 2000a, 2003; Brede & Sellmann 2003; *cf*. Vergara & Bughrara 2003).

5.4. The bentgrass seed from the imports and North America was widely distributed and sown on developing golf courses, and as well for municipal parks, playgrounds and fine lawns, with the intention that the most appropriate of the bentgrasses for a site would come through (*cf*. Wilson & Rapson 1995; Rapson & Wilson 1988; Lesica & Allendorf 1999). With golf's rapid geographic expansion, on most of the new courses *Agrostis stolonifera* emerged over the years to be dominant in the turf in many regions, except in the cool Northeast where *A. canina* sometimes out-competed the other bentgrasses (Monteith 1930; USGA 1922c, 1930a; Piper & Oakley 1922b, 1922a; Oakley 1923; *cf*. Skogley 1973; Hurley 1973; Brilman & Meyer 2000; Ruemmele 2000b; Rose-Fricker *et al*. 2004; Hollman *et al*. 2005). Thus creeping bent's characteristics became familiar. Experience for turf was also gained with *A. capillaris* (called Rhode Island bent, later colonial bent), which was introduced to New England early for pasture — it is mentioned in 1747 (Odland 1930) and likely was present a century earlier (*cf*. Cronon 1983; Sauer 1942). Production to respond to the emerging desire (1900-1905) for sports turf and lawns began by gathering seed from naturalized stands in Rhode Island and southern Connecticut, and subsequently Massachusetts. Imports from Germany and New Zealand as well as southeastern Canada later shifted the Rhode Island production to growing *A. canina* and *A. stolonifera* (Odland 1930; Hillman 1930). *Agrostis gigantea* was also common in New England, and care needed to avoid gathering it, but there was deliberate adulteration too in this seed trade (Carrier 1921; Tregillus 1926; Hillman 1930). Stuckey & Banfield (1946) reported finding *Agrostis* in Rhode Island with unusual morphology and aneuploidy (*cf*. Anderson 1948); these plants are now considered hybrids of

A. capillaris and *A. gigantea* (Björkman 1954; Widén 1971; Bradshaw 1975a; Edgar & Forde 1991; *cf.* Sell & Murrell 1996), which are called *A.* ×*bjoerkmanii*.

5.5. So over several decades, creeping bentgrass transitioned from being considered a growth form or obscure minor kind of wild bent sometimes showing up in the "South German mixed bent" seed in small quantities, to a highly desirable foreign species in short supply (Piper & Oakley 1921, 1922a; Monteith 1930). Through U.S. production efforts (Monteith 1941), including encouraging propagation by stolons rather than seeds, *Agrostis stolonifera* became the most successful and popular grass for putting greens (Taylor 1957; Radko 1968), and now is grown extensively and managed intensively for greens as well as tees and fairways — and that is the chief focus in continuing to improve it agronomically (*e.g.* Hurley & Murphy 1996; Morris 2003; Warnke 2003). The species is additionally investigated as a forage (Balasko *et al.* 1995; Tomić *et al.* 1999, 2003), and of interest for restoring some mine sites involving heavy metals (Smith & Bradshaw 1979) and for water treatment (Löser *et al.* 1999; Tyrrel *et al.* 2002; Mazer *et al.* 2001). Sell & Murrell (1996) state that *A. stolonifera* var. *marina* has been used in the formation of lawns. There is still exploration for germplasm (genetic resources) of *A. stolonifera* for turf from populations in its native range (*e.g.* Romani *et al.* 2002; Xie *et al.* 2003).

5.6. Ordinarily the modern turf cultivar (*e.g.* Robinson *et al.* 1991; Brauen *et al.* 1993; Hurley *et al.* 1994; Engelke *et al.* 1995) is seeded, and is a clustering of *A. stolonifera* genotypes bred and selected for a set of distinctive traits (*e.g.* Holt & Payne 1952; Lush 1990; Engelke 1993; Cattani *et al.* 1996; Cattani 1999; Cattani & Struik 2001; Sweeney *et al.* 2001; Murphy *et al.* 2003; DaCosta & Huang 2003; Croce *et al.* 1999; Rogers 1992; Huff & Landschoot 2000; Stier 2003; and Wilkinson & Beard 1972; Warnke *et al.* 1997; Golembiewski *et al.* 1997a, 1997b; Caceres *et al.* 2000; Casler *et al.* 2003; Kubik *et al.* 2003), rather than being a single genetic line distributed by vegetative propagation as in earlier decades (*e.g.* Metcalf 1922; USGA 1924c, 1924b, 1924a, 1930a; Piper & Oakley 1921, 1924; Carrier 1923, 1924; Oakley 1924; Radko 1968; Bengeyfield 1968; *cf.* Abramashvili 1978).

5.7. From its 1923 beginnings in the Pacific Northwest Coast region (Schoth 1930, 1939; Hyslop 1930; USGA 1930b; Monteith 1941; Ferguson 1948; Pojar & MacKinnon 1994; Franklin & Dyrness 1973), the production of seed of bentgrasses for turf for the USA and internationally has become a modern industry concentrated in western Oregon in the Willamette Valley (125 mi × 25-30 mi) between the coast and Cascade Range of mountains. About 6,000 acres are in production, mostly for creeping bentgrass (North & Odland 1935; Cattani *et al.* 2004; *cf.* Wright 1980; Jonassen 1980; Rumball & Robinson 1982; Chastain & Young 1998). Background on this region is in several accounts (Bowen 1978; Johannessen *et al.* 1971; Habeck 1961; Nelson 1919; Mueller-Warrant *et al.* 2003; Clark & Wilson 2001).

5.8. The U.S. turfgrass industry frequently equates creeping bentgrass with *Agrostis palustris* or sometimes *A. stolonifera* var. *palustris*, but this usage does not agree with the detailed botanical concepts of Hubbard (1984) or Sell & Murrell (1996) where the plants are native, and are also utilized. This U.S. habit or convention may reflect the influence of the manual by Hitchcock & Chase (1951, and reprint in 1971) (Chase being the sole reviser of Hitchcock 1935; *cf.* Hitchcock 1905, Piper 1918), instead of recognizing newer taxonomic benchmarks such as *Flora Europaea* (1980 for the grass family, Poaceae or Gramineae, with *Agrostis* by Tutin) and *The Jepson Manual* (1993, *Agrostis* by Harvey).

Moreover, with the originating introductions of creeping bentgrass seeds for years from various European locales and countries and the broad U.S. seed distribution (dispersal), and subsequent adaptation, selection and breeding efforts, the germplasm in USA is a richly heterogeneous mixture quite unlike the native ecological race (ecotype) in Europe that Sell & Murrell (1996) characterize under *A. stolonifera* var. *palustris* (*cf.* Rozema & Blom 1977; Davies & Singh 1983; Winkler *et al.* 2003; Panter & May 1997; Aston & Bradshaw 1966; Olff *et al.* 1993; Ahmad & Wainwright 1976; McNeilly *et al.* 1987; Misra & Tyler 2000b, 2000a; Kik 1987; Kik *et al.* 1990a, 1990b, 1992). Another legacy problem lingering in the USA and Canada is an overly broad scope in use of the name *A. stolonifera* (or *A. alba*) (*e.g.* Malte 1928; Gleason 1952; Gleason & Cronquist 1963; Steyermark 1963; Munz 1968; Cronquist *et al.* 1977; Stubbendieck *et al.* 1982; but *cf.* Welsh *et al.* 1993), occasionally even using the name *A. stolonifera* var. *stolonifera* (rather than *A. stolonifera* var. *major*) for the plants usually called redtop and now well accepted as *A. gigantea* (*e.g.* in Europe, Tutin 1980; Sell & Murrell 1996; and in North America, Fassett 1951; Voss 1972; Bailey *et al.* 1976; McNeill & Dore 1976; Dore & McNeill 1980; Pohl 1978; Gleason & Cronquist 1991; Harvey 1993, 2001; Yatskievych 1999).

5.9. Four themes (discovery, research, biological classification, scientific nomenclature) are interwoven in the 250-year historical to current usage of several *Agrostis* names, reflecting improved understanding but lags in communication (*cf.* Spooner *et al.* 2002). (**1**) The natural variation of creeping bentgrasses in Europe led to early recognition of many formal distinctions, such as *Agrostis stolonifera* L. (1753), *A. palustris* Huds. (1762), and *A. stolonifera* var. *compacta* Hartm. (1832). (**2**) The name *Agrostis gigantea* Roth (1788) for redtop was its second name, regarded for a while as superfluous. However, redtop's earlier name of *Agrostis alba* L. (1753) unfortunately was based nomenclaturally (*i.e.* standardized) on a specimen found to be a *Poa nemoralis* L. (wood bluegrass), and so "*Agrostis alba* L." had to become a technical synonym for that species (and thus no longer available for use). (**3**) On a different theme, the determination and classification of biological entities, it was not obvious that the plants called *A. stolonifera* and the plants now called *A. gigantea* represented two species rather than variations of one biological species. If considered to be one (*e.g.* Malte 1928), the species' name had to be the earlier *A. stolonifera*, and the redtop plants were then called *A. stolonifera* var. *major* (Gaudin) Farw. Within this broadly circumscribed single species, all of the more "creeping" bentgrasses would be called *A. stolonifera* var. *stolonifera*, or these plants could still be regarded to have additional inherently distinct populations such as *A. stolonifera* var. *palustris* (Huds.) Farw. or *A. stolonifera* var. *compacta*. (**4**) With increasing familiarity and scientific study, *Agrostis gigantea* has become understood to be a biologically distinct species (as Linnaeus had discerned; Table 2), a hexaploid with rhizomes (underground stems) and panicles that stay open after flowering, whereas *A. stolonifera* is a predominant tetraploid with stolons and panicles that close after flowering. Similarly, *Agrostis castellana* has been recognized to be biologically distinct from *A. capillaris*, and *A. vinealis* distinct from *A. canina*. (**5**) On the other hand, from thorough study of many native European populations of *Agrostis stolonifera* (*sensu stricto*, *i.e.* creeping bentgrass in the narrow sense excluding "var. *major*"), broad ecological amplitude and extensive variability have been found without substantial inherent discontinuites (sections 3.1-3.2) (*e.g.* Kik *et al.* 1990a; Vergara & Bughrara 2003; *cf.* Kurchenko 2002). The usage of common names in North America (Tables 1 & 2) has also become more stable (*cf.* Henry 1928; Monteith 1930; USGA 1932), but can still be variable, and entangled or confused.

5.10. Consequently, when going beyond the extensive information on turf mainly for golf courses, in the North American literature in particular alertness is needed as to the species intended (see Table 2 synonymy). However, the identity of the plants studied frequently cannot be ascertained from the report, and the research is less useful, because several *Agrostis* species occur in the area of study and the plant characteristics were not distinguished nor a taxonomic reference stated (nor the actual originating source clear if plants were supplied). As provisional pragmatic assumptions, *A. alba* tends to mean redtop (*A. gigantea*); *A. stolonifera* to mean creeping bentgrass but sometimes redtop, and occasionally both (*i.e.* the name used broadly or *sensu lato*, sometimes with *A. stolonifera* var. *major* for redtop and *A. stolonifera* var. *palustris* for creeping bentgrass, but possibly *A. stolonifera* var. *stolonifera* used for either); and *A. palustris* is *A. stolonifera* (creeping bentgrass). This confusion makes other literature especially useful in North America for gaining insights on the population dynamics and ecology of the species creeping bentgrass (*A. stolonifera*, synonym *A. palustris*) in natural to variously managed systems.

6. Creeping Bentgrass Habitats, Ecology, and Reproduction

6.1. In Europe where *Agrostis stolonifera* has been taxonomically clear for decades and much more studied in the general environment (although not as much as an amenity turfgrass), the habitats of this common species range from salt marshes and dunes to chalk cliffs, inland marshes, streamsides and ditches, grasslands and pastures, including locales periodically flooded, open woodlands, damp arable land, paths, urban parks and lawns, and rough ground such as roadsides (Sell & Murrell 1996; Hubbard 1984; Jansen & Wachter 1940; Grime *et al*. 1988; Silvertown *et al*. 1999; Rozema & Blom 1977; Eertman *et al*. 2002; Burgess *et al*. 1990; Gipiškis 2000; Panter & May 1997; Gilbert *et al*. 2003; van Eck *et al*. 2004; Kennedy *et al*. 2003; Kohler *et al*. 2000; Hald 2002; Croxton *et al*. 2002; Roovers *et al*. 2004; Cornish 1954; Thompson *et al*. 2004; Ross 1986). Similarly in the USA, the species occurs in coastal habitats (*e.g.* Caldwell & Crow 1992; Wu 1981; USGA 1925a) and has become widely established inland, for example reported in Missouri habitats (Yatskievych 1999) along the margins of ponds and lakes and on streambanks, in moist disturbed areas, various grasslands (including upland prairies), moderately moist (mesic) to rather dry upland forests, on roadsides and railroad embankments, and in sidewalk crevices.

6.2. As well as being grazed by cattle, sheep and horses, creeping bentgrass is grazed by rabbits and hares and migratory wildfowl in Europe such as the wigeon *Anas penelope* and various species of geese (Cadwalladr *et al*. 1972; Owen & Thomas 1979; Loonen & van Eerden 1989; Groot Bruinderink 1989; Chang *et al*. 2005), and it is used for nest building by grebes (Ridley 1930). Throughout the year, at impoverished mine sites it can be the main food of the Eurasian field vole, *Microtus agrestis* (Stoddart 1982; Hunter *et al*. 1987). It is a larval food plant for the widespread small heath butterfly *Coenonympha pamphilus* (Goverde & Erhardt 2003). *Agrostis stolonifera* can host fungal endophytes (*cf*. Clay & Schardl 2002; Faeth 2002; Malinowski & Belesky 2000; Schardl *et al*. 2004), as can *A. capillaris*, *A. castellana*, *A. gigantea* and several native *Agrostis* species (Aldous & Mebalds 1995; Aldous *et al*. 1994; Thrower & Lewis 1973; Bradshaw 1959b; Saikkonen *et al*. 2000; Zabalgogeazcoa *et al*. 2003; White *et al*. 1992; White & Chambless 1991; Zenbayashi *et al*. 1996).

6.3. The numerous tiny seeds of creeping bentgrass are dispersed by the wind and on water (Wolters *et al*. 2005), sometimes to lake islands (Nilsson & Nilsson 1978; Roden 1998), and consumed and sometimes dispersed (still viable) by cattle, sheep, white-tailed deer (*Odocoileus virginianus*), fallow deer (*Dama dama*), and brent geese or brants (*Branta bernicla*) (Welch 1985; Myers *et al*. 2004; Gill & Beardall 2001; Chang *et al*. 2005), and the seeds are also dispersed externally on cattle hair (Couvreur *et al*. 2004). In addition to the seeds, jointed pieces of the stolons (*i.e.* with nodes) can be carried downstream by the water (Mitlacher *et al*. 2002; Widén 1971; Nilsson *et al*. 1994; Andersson *et al*. 2000; Vogt *et al*. 2004; Boedeltje *et al*. 2003; Goodson *et al*. 2003; Levine 2000, 2001, 2003; Wolters & Bakker 2002). Seeds of *A. canina* and *A. capillaris* also are viably dispersed by passing through livestock (Bruun & Fritzbøger 2002; Pakeman *et al*. 2002; Cosyns *et al*. 2005), *A. capillaris* through rabbits (*Oryctolagus cuniculus*) (Cosyns *et al*. 2005), and *A. gigantea* through white-tailed deer (Myers *et al*. 2004). Seeds of *A. capillaris* also are dispersed externally by domesticated and wild ungulates (*via* hair and hooves) (Couvreur *et al*. 2004; Mouissie *et al*. 2005; Heinken & Raudnitschka 2002) and are eaten and apparently dispersed by ants, and the plants sometimes associated with ant-mounds (Rothanzl 2002; Kovář *et al*. 2001; Kovář & Kovářová 1998; Dostál 2005).

6.4. *Agrostis stolonifera* is documented (Grime *et al*. 1988) to have a "competitive-ruderal" ecological strategy in the well-known C-S-R (competition–stress–ruderality) system of plant strategies or functional types (Grime 1977, 1988, 2001), which thus includes weedy characteristics (Booth *et al*. 2003; Baker 1965, 1972, 1974; Keeler 1985, 1989) in relation to competitors and disturbance (*e.g.* Schippers *et al*. 2001; Hill *et al*. 2002; Wilcox 1998; Marshall 1990; Goldsmith 1978; Lenssen *et al*. 2004). The plant's roots (*cf.* Fitts 1925a; Murphy *et al*. 1994; Boeker 1974; Lehman & Engelke 1991; Steer & Harris 2000; Beard & Daniel 1966; Ralston & Daniel 1972; Krans & Johnson 1974; Bowman *et al*. 1998; Christians *et al*. 1981) and shoots (stolons) actively forage in space, exploiting pockets of nutrient enrichment and vegetation gaps (Crick & Grime 1987; Hunt *et al*. 1987; Grime *et al*. 1988; *cf.* Glimskär & Ericsson 1999; Glimskär 2000). Being a clonal perennial organism, the plant can function in a modular way (*e.g.* Jónsdóttir 1991b, 1991a), with the leafy plantlets (rooted tillers) along a stolon able to become somewhat independent (Agha *et al*. 2001; Marshall & Anderson-Taylor 1992). Consequently, severed stolons or dispersed pieces of jointed stolon are more readily able to establish new plants (Boedeltje *et al*. 2003; Widén 1971; *cf.* Fitts 1925b; Carrier 1923, 1924).

6.5. The species often reproduces primarily vegetatively, spreading or "creeping" by the stolons (*cf.* Hoeltzener & Maitre 2004), which may become divided (*e.g.* by an animal or machine) and continue growing from the stolon nodes as separate plants, ramets with the same genotype (thus clones). In the intensely managed golf course, the turf is mowed very short often (*cf.* McCartney 2003) and sometimes cut vertically to reduce thatch; consequently flowering is curtailed but fragmentation of plants is likely. In unstable natural habitats such as dunes, more seeds are produced than in grassier habitats such as a meadow. A single panicle may average from 100-200 to as many as 1,480 florets in semi-natural habitats (Prieto-Baena *et al*. 2003), and the plant may have panicles at somewhat different stages of maturity. Separate plants of the same genotype (*i.e.* ramets of the same genet) adjust to their immediate surroundings, so do not necessarily flower simultaneously. For details on these aspects, see Smith 1972; Grime *et al*. 1988; Boedeltje *et al*. 2003; Kik 1987; Kik *et al*. 1990a, 1990b, 1993; Wilson & Thompson

1989; Purves & Law 2002; Lenssen *et al*. 2005; Pakeman & Marshall 1997; Olff *et al*. 1993; Jónsdóttir 1991a, 1991b.

6.6. The flowering period, the seasonal duration (months, weeks or days) of the species bringing forth flowers, varies with the region where the plants occur, for example with a shorter season in the North (*e.g.* Widén 1971; *cf*. Heide 1994; Cooper & Calder 1964). The daily duration (1-4 hrs) of a plant's flowering perhaps differs somewhat among the *Agrostis* species, but also depends on the day's weather. The anthesis period, when the flower begins and ends shedding its pollen during the 24-hr day, is characteristic of the *Agrostis* species and fine-tuned to the local conditions. In field-plot or greenhouse and lab studies (*e.g.* Philipson 1937; Davies 1953; Ponomarev & Rusakova 1968; Fei & Nelson 2003), the pollen of creeping bentgrass shed for a few mid-morning hours (exact times differing with locale) or again (but perhaps not usually) in early-mid afternoon, and the pollen grains were viable for no more than 3 hours. *Agrostis stolonifera* in semi-natural habitats may average 545 pollen grains per anther, thus 1,635 per floret, and up to some 2,420,000 per panicle (Prieto-Baena *et al*. 2003). The species is mainly sexually outcrossing (Davies 1953), with some turf strains perhaps obligately so, but it can also self-pollinate (*e.g.* Belanger *et al*. 2003b; Tomić *et al*. 1999) (a highly selfing turf clone was recently detected – Warnke *et al*. 1998). *Agrostis* species in a locality might be reproductively somewhat isolated temporally by the sequence of their daily anthesis, for example with *A. canina* releasing pollen pre-dawn – dawn, *A. stolonifera* ± mid-morning, and *A. capillaris* variously early- mid- late afternoon. Reports for *A. gigantea* seem to be inconsistent; *A. castellana* might be earlier than *A. stolonifera*; and *A. vinealis* is bimodal with ± pre-dawn and evening shedding (*cf*. Christoffer 2003).

6.7. In experimental field-plot studies on pollen dispersal and potential for fertilization and hybridization with other species of *Agrostis* and with *Polypogon* (Wipff & Fricker 2001; Belanger *et al*. 2003b; Christoffer 2003), viable pollen of creeping bentgrass went as far as 1,161 feet (determined in the resulting progeny using molecular markers). From their data that measured 958 ft, Wipff & Fricker (2001) estimated (by calculation) that the pollen traveled up to 4,296 ft (about 0.8 mile). Based on independent data from a fairly similar experiment (Belanger *et al*. 2003b), pollen dispersal and variation in fitness of the pollen donor were considered in a computer model (Meagher *et al*. 2003). The model found that pollen dispersal and gene introgression (crossing and diffusion into a different population – *cf*. Anderson 1949, 1953; Arnold 1997, 2004) would be limited at some sites and extensive at others, depending on local conditions such as exposure to the wind. In a large-scale experimental study (Watrud *et al*. 2004; Watrud 2005), pollen dispersal and gene flow were found to occur mostly within about 1.25 miles and extend up to 13 miles. All four of the recent studies concluded that hybridization can occur in the field between *A. stolonifera* and some naturalized or native species (Tables 1 & 2). This work using molecular techniques thus confirms and enriches earlier reports, from experimental hybridization and the study of chromosomes (*e.g.* Davies 1953; Jones 1956a-1956c; Björkman 1960; Romero García & Blanca 1988; Forde 1991), and from fieldwork and the taxonomic analysis of plants' morphology (*e.g.* Murbeck 1898; Weber 1920; Malte 1928; Fouillade 1933; Juhl 1952; Bradshaw 1958; Widén 1971; Romero García *et al*. 1988b; Meerts & Lefèbvre 1989).

6.8. Of the 10 (or 11) species of *Agrostis* with which it is known that *A. stolonifera* could directly hybridize in USA (Figure 1, Tables 1 & 2), the most likely crossing is with *A. capillaris*, forming *A.* ×*murbeckii*; and to a lesser extent crossing with *A. gigantea*.

Agrostis capillaris is most likely to cross with *A. castellana*, forming *A.* ×*fouilladeana*, which can backcross into *A. capillaris*, and for some years these species and their hybrids were imported unknowingly from New Zealand all misnamed as "colonial bentgrass" (or "*Agrostis capillaris*") and were widely distributed (section 5.3). The species *A. capillaris* is also likely to cross with *A. gigantea*, forming *A.* ×*bjoerkmanii*, as found in Rhode Island (section 5.4). The various hybrids are for the most part sterile or with very low fertility, but can be vegetatively vigorous (Table 2). Hybridization and introgression have always been aspects of domestication and improvement of crops and ornamentals (*cf.* Gepts 2002; Anderson 1961). Various new lab techniques facilitate working with hybrid turfgrasses (*e.g.* Brilman 2001b; Ovesná *et al.* 2002), and efforts are underway to hybridize *Agrostis* species for traditional reasons such as bringing in disease resistance (*e.g.* Belanger *et al.* 2003a, 2003b, 2004; Li *et al.* 2005).

6.9. *Agrostis stolonifera* seeds can germinate soon after their dispersal or persist for a while in the seed bank then germinate or be gone within 1-1½ years, but with some seeds remaining viable in the soil for at least 4 years (Thompson & Grime 1979; Jutila b. Erkkilä 1998a, 1998b; Mitlacher *et al.* 2002; Ferris & Simmons 2000; Díaz-Villa *et al.* 2003; Shipley *et al.* 1989, 1991; Amiaud *et al.* 2000; Hölzel & Otte 2004; Wolters & Bakker 2002; Brenchley & Warington 1930; Jalloq 1975; Roberts 1981; Hendry *et al.* 1994; Hutchings & Booth 1996; Toole & Koch 1977). There can also be persistent (sometimes quite long-term) seed banks to recruit for example *A. canina* (Matus *et al.* 2003), *A. capillaris* (Smith *et al.* 2002; Pakeman *et al.* 1998; Dougall & Dodd 1997; Meerts & Grommesch 2001; *cf.* Edwards & Crawley 1999; Balocchi *et al.* 1998), *A. castellana* (Traba *et al.* 2004; Rampton & Ching 1966, 1970), *A. gigantea* (Wagner *et al.* 2003; Williams 1978), and *A. vinealis* (Bakker *et al.* 1996; *cf.* Pons 1989).

7. Creeping Bentgrass in the Landscape

7.1. *Agrostis stolonifera* presence in vegetation is quite variable, depending upon habitat and management. The species can be competitive and become a dominant (Silvertown *et al.* 1992; Durrett & Levin 1998), for example in moderately grazed pastures (Howe & Snaydon 1986; Bullock *et al.* 1996, 2001; Jutila 1999; Oomes *et al.* 1996; Schulte & Neuteboom 2002; Loucougaray *et al.* 2004; van Oene *et al.* 1999) and various habitats of roadsides (Ross 1986). Or it can occur in early succession and decline over the years or decades, for example on maturing sand dunes or in hay meadows (Pennanen *et al.* 2001; Olff *et al.* 1993; Olff & Bakker 1991). Creeping bentgrass establishes in areas relatively open or bare (seeding into disturbed areas or gaps) and as well in areas somewhat dense and diverse biotically (*e.g.* Fustec *et al.* 2005; Elmarsdottir *et al.* 2003; Greipsson & El-Mayas 1999; Wolters & Bakker 2002; Stockey & Hunt 1994; Klötzli & Grootjans 2001; Bullock 2000; Jalloq 1975; Cody *et al.* 2000; Staniforth & Scott 1991; Levine 2000, 2001, 2003). Even though now cosmopolitan, the species is rarely aggressively invasive (*i.e.* transformative) (Pyšek *et al.* 2004) in natural or semi-natural areas (as on Gough Island and several sub-Antarctic islands – Jones *et al.* 2003; Gremmen *et al.* 1998; Frenot *et al.* 2001). Several different *Agrostis* F_1 hybrids and/or introgressed backcrosses (Tables 1 & 2) can be notable aspects of some vegetation (*e.g.* Widén 1971; *cf.* Nilsson *et al.* 1994; Sell & Murrell 1996; Fouillade 1911, 1933; Lambinon *et al.* 2004; Romero García *et al.* 1988b; Edgar and Forde 1991; Edgar and Connor 2000; Stuckey & Banfield 1946). The F_1 hybrids of *A. stolonifera* and *A. capillaris*, *i.e. A.* ×*murbeckii*, can out-compete both parents and be plentiful and apparently long-lived in intermediate areas between parental habitats (Forde 1991; Ater 1993; Meerts & Lefèbvre 1989; Widén 1971; Bradshaw 1958, 1959c).

7.2. *Agrostis stolonifera* forms hybrids called ×*Agropogon lutosus* (synonym ×*Agropogon littoralis*) (Sell & Murrell 1996; Hubbard 1984; Bradshaw 1975b; Qian & Sun 1998; Weiller *et al*. 1995; Edgar & Connor 2000; Rúgolo de Agrasar & Molina 1997b; Welsh *et al*. 1993; Barkworth 2004; Harvey 2004; Randall 2002; Christoffer 2003) with *Polypogon monspeliensis* (annual rabbitsfoot-grass), which is a mostly European species naturalized in many countries worldwide that occurs in wet-moist habitats to abandoned arable fields (*e.g.* Barkworth 2004; Godfrey & Wooten 1979; Welsh *et al*. 1993; Pojar & MacKinnon 1994; Conley 1993; Harrison *et al*. 2002; Gelbard & Harrison 2003; Robbins 1940) (Tables 1 & 2). Annual rabbitsfoot-grass tolerates salinity (Partridge & Wilson 1987; Mahmood *et al*. 1996) and can be common in estuaries and suitable inland wetlands (Kuhn & Zedler 1997; Callaway & Zedler 1998; Stromberg 1997; Roalson & Allred 1997; Zedler & Kercher 2004; Shaltout & El-Sheikh 1991; Sharaf El-Din *et al*. 1993; Hussey *et al*. 1997). In South Australia, this species (as well as *Agrostis avenacea*) are hosts for organisms associated with the disease floodplain staggers (Davis *et al*. 1995; Bertozzi & McKay 1995; McKay *et al*. 1993); its straw is allelopathic (releasing an inhibiting chemical) (Inderjit & Dakshini 1995). *Agrostis stolonifera* can occur in middle to upper margins of salt marshes, and some ecotypes have considerable salt tolerance (*e.g.* Gray & Scott 1977; Gray 1972; Cadwalladr *et al*. 1972; Eertman *et al*. 2002; Wolters & Bakker 2002; Ungar 1978; Jutila b. Erkkilä 1998a; Pehrsson 1988; Hanslin & Eggen 2005; McCarty & Dudeck 1993; Rozema & Blom 1977; Tiku & Snaydon 1971; Ahmad & Wainwright 1976, 1977; Ahmad *et al*. 1981; Wu 1981; Ashraf *et al*. 1986a, 1986b; Kik 1989; Hodson *et al*. 1985; McNeilly *et al*. 1987; Aston & Bradshaw 1966), which is a trait of agronomic interest (*e.g.* Marcum 2001; Kuo *et al*. 1994; *cf*. Wu & Huff 1983). *Polypogon viridis* (water beardgrass) also forms hybrids with *A. stolonifera*, which are called ×*Agropogon robinsonii* (Table 2). These *Polypogon* species also hybridize with each other (forming *Polypogon* ×*adscendens*). Both *Polypogon* species are in Ciba-Geigy's *Grass Weeds* (Häfliger & Scholz 1981), but neither is considered a major world weed (Holm *et al*. 1997, 1979).

7.3. *Agrostis stolonifera* is included in BASF's *Grass Weeds in World Agriculture* (Behrendt & Hanf 1979) and in Ciba-Geigy's *Grass Weeds* (Häfliger & Scholz 1981) — occurring in all five habitats that they score: grasslands, aquatic biotopes, perennial crops, rotation crops, and waste places, but it is not considered a major world weed (Holm *et al*. 1997, 1979; Weber 2003). The species is also reported as a weed or weedy for example in Japan (Enomoto 2000), Australia (Brown & James 1998; Carr *et al*. 1992; Hussey *et al*. 1997; Rozefelds *et al*. 1999), New Zealand (Reid 1998), Chile (Matthei *et al*. 1993), Germany (Holm *et al*. 1979; Lonchamp 2000), Denmark (Andreasen *et al*. 1996), the U.K. (Hubbard 1984), and Canada (Darbyshire 2003; Eggens 1972). In the United States it is not listed as a Federal noxious weed. Nonetheless in USA the species is sometimes noted as a weed beyond golf turf (*i.e.* the rough) and in lawns, grasslands and wetlands, including riparian areas (*e.g.* Jordan 2001; Williams *et al*. 2000; Dudley 1998; Morrison 2002; Levine 2000, 2001, 2003; Steed & DeWald 2003).

7.4. Other agronomic bentgrasses of European origin and variously naturalized (Table 1), with which creeping bentgrass is able to hybridize (Figure 1, Table 2; *cf*. section 6.8), are also sometimes or in some areas considered weeds and can be of management concern: *Agrostis gigantea*, *A. castellana*, *A. capillaris*, and *A. canina* (*e.g.* Randall 2002;

Holm *et al.* 1979; Weber 2003; Häfliger & Scholz 1981; Behrendt & Hanf 1979; Grime *et al.* 1988; Hubbard 1984; Barthram *et al.* 2002; Håkansson & Wallgren 1976; Williams 1970, 1973a, 1973b, 1975, 1977, 1978; Skuterud 1984; Courtney 1981; Bylterud 1984; Darbyshire 2003; Roland & Zinck 1998; Pojar & MacKinnon 1994; Riege & Del Moral 2004; Biek 2000; Wilson *et al.* 2004; Matthei *et al.* 1993; Ramírez *et al.* 1992; San Martín *et al.* 2002; Pauchard & Alaback 2004; Edgar & Connor 2000; Walker & Lee 2002; Walker 2000; Sessions & Kelly 2000, 2002; Davis & Guy 2001; Rose *et al.* 1995; White 1991; Harris 1974; James & Atkinson 1979; Batson 1998a-1998c; Hill *et al.* 1996; Hussey *et al.* 1997; Godfree *et al.* 2004; Boyd 1976; Enomoto 2000; Tsuyuzaki 1993).

7.5. Of those four species, *Agrostis gigantea* (redtop), *A. capillaris* (colonial bentgrass) and *A. castellana* (dryland bentgrass) are more closely related to *A. stolonifera* (Table 2). Redtop and colonial bentgrass are in general considered more weedy than creeping bentgrass (section 7.4). In the C-S-R system of plant functional types (Grime 1988, 2001), *A. gigantea* also is a competitive-ruderal strategist, whereas *A. capillaris* is a C-S-R generalist (Grime *et al.* 1988).

7.6. Some species of *Agrostis* have a robust capacity to adapt genetically and establish populations tolerant to heavy metals and metalloids, for example on soil at contaminated mine sites (Bradshaw 1952; Bradshaw *et al.* 1965; Bradshaw & Hardwick 1989). All five of the main agronomic species as well as *A. vinealis* (Farrow *et al.* 1981) and the common native *A. scabra* (Archambault & Winterhalder 1995; Koch *et al.* 2000) are among these facultative metallophytes. Arsenic, cadmium, copper, lead, manganese, nickel and zinc can be prominently involved, and the plants on a site able to tolerate one or more of these ordinarily toxic substances. The zone between tolerant and nontolerant biotypes can be narrow, and without hybrids. Some of the research (*cf.* Bone & Agnes 2001; Levin 2001) has led to classic evolutionary studies used in teaching (*e.g.* Briggs & Walters 1997), and to efforts for mine-site reclamation and ecological restoration (*e.g.* Cotter-Howells & Caporn 1996; Lepp *et al.* 1997; De Koe 1994; *cf.* Lesica & Allendorf 1999) and water-quality improvement by biofiltration (Hares & Ward 1999). *Polypogon monspeliensis* also has good potential for management of wastewater contaminated with selenium or arsenic (Ye *et al.* 2003).

7.7. The repertoire of *Agrostis stolonifera* (Duwensee 1993) includes biotypes tolerant to copper (Wu & Bradshaw 1972; Wu *et al.* 1975; Masarovičová and Holubová 1998; Briggs & Walters 1997), copper and nickel (Jowett 1958), copper and zinc (Wu & Antonovics 1975), and lead and zinc (Gregory & Bradshaw 1965; *cf.* Harkot & Czarnecki 1999). A biotype of its hybrid *Agrostis ×murbeckii* tolerant to zinc has been detected (Gregory & Bradshaw 1965). Creeping bentgrass has also adapted to serpentine (Marrs & Proctor 1976), natural rock outcroppings high in magnesium and low in available calcium and water-holding capacity (Baker *et al.* 1993), thus an exclusive habitat where some species are unable to survive but some species have evolved and only occur (*i.e.* endemics).

7.8. Colonial bentgrass (the zinc-tolerant hybrid's other parent) has been studied most, and there are metal-tolerant cultivars for reclamation available commercially (Jowett 1964; Gregory & Bradshaw 1965; Jain & Bradshaw 1966; McNeilly 1968; Antonovics 1968; Jones *et al.* 1971; Mathys 1973; Gartside & McNeilly 1974; Whalley *et al.* 1974; Simon 1977; Simon & Lefèbvre 1977; Nicholls & McNeilly 1979; Smith & Bradshaw 1979; Karataglis 1980c; Karataglis *et al.* 1985; Symeonidis *et al.* 1985a; Meharg &

Macnair 1991; Watkins & Macnair 1991; De Koe *et al*. 1992; Boon *et al*. 1998; Meerts & Grommesch 2001; Griffioen & Ernst 1989; Griffioen *et al*. 1994; Malcová *et al*. 2003; Rydlová & Vosátka 2003). *Agrostis capillaris* also has biotypes with multiple-metal tolerance, to variously two, three or four metals, and that can have large within-population variability (Hertstein & Jäger 1986; Symeonidis *et al*. 1985b; Karataglis 1982, 1980e, 1980a, 1980d; Humphreys & Nicholls 1984; Turner 1970; McNeilly & Bradshaw 1968). Separate evolutionary adaptations apparently have resulted in the similar metal-tolerance traits of some biotypes (Nicholls & McNeilly 1982; Al-Hiyaly *et al*. 1988, 1990, 1993). The other agronomic species and some metal-tolerance studies include *A. canina* (Gregory & Bradshaw 1965), *A. castellana* (De Koe *et al*. 1992; De Koe & Jaques 1993; Schat *et al*. 2002) and *A. gigantea* (Hogan *et al*. 1977a, 1977b; Hogan & Rauser 1979, 1981; Rauser 1984a, 1984b; McLaughlin & Crowder 1988).

7.9. "What is it about the genome of *Agrostis* species that they can evolve tolerance to almost any metal anywhere…?" (Macnair 1987). These species are considered metal excluders rather than hyperaccumulators (Memon *et al*. 2001; Lasat 2002; Pollard *et al*. 2002). *Agrostis capillaris* for example avoids cadmium, copper, lead, and zinc by precipitating them in the rhizosphere (Dahmani-Muller *et al*. 2000). The genetics and physiology of such metal-tolerant plants are now better delineated and precise understanding is becoming possible (*e.g.* Macnair 1990, 1993; Macnair *et al*. 2000; Schat *et al*. 2000; Hall 2002; Memon *et al*. 2001).

8. Biotechnological Developments in *Agrostis*

8.1. Many publications are providing substantial current overviews on aspects of the improvement of plants for various purposes and genetic engineering. Recent summaries include technological developments over 100 years and prospects (*e.g.* McCown 2003; Chandler 2003), and comparing crop domestication, conventional plant breeding, and genetic engineering (Gepts 2002). There are overviews on genetic engineering for turf and forage grasses (*e.g.* Wang *et al*. 2001; Maqbool *et al*. 2002; Chai & Sticklen 1998; Lee 1996), and on transgenic turfgrasses and risk assessment in considering the release of a particular modified plant into the environment (*e.g.* Johnson & Riordan 1999; Day & Lee 1997). Consequent experiments to better understand aspects of the biology of these species are the pollination and hybrid studies noted above (sections 6.6-6.7). The purpose of other experiments (in the greenhouse or a confined field trial) (*e.g.* Lee *et al*. 1997; Gardner *et al*. 2003, 2004; Fei & Nelson 2004; Hart *et al*. 2005; Wang *et al*. 2003) is to evaluate the transgenic plant's biology for any unexpected effects, or to study the trait put into the plant to see if the result is as desired. Semi-popular and professional trade articles on methods and potential benefits perceived in the genetic engineering of turfgrasses are also available (*e.g.* Lee *et al*. 1995; Sticklen 2001; Harriman & Suttner 2003; Litrenta 2003; Ostmeyer 2004a, 2004b, 2004c; Jones 2005).

8.2. In *Agrostis*, genetic engineering (on an experimental basis in several countries) has succeeded, and next steps are proceeding with at least four species: especially *Agrostis stolonifera* (Krans *et al*. 1982; Blanche *et al*. 1986; Tanpo *et al*. 1992; Terakawa *et al*. 1992; Zhong *et al*. 1991, 1993; Sticklen *et al*. 1996; Xiao & Ha 1997; Basu *et al*. 2003; Luo *et al*. 2004; Fu *et al*. 2005a), as well as *A. canina* (Pitcher *et al*. 2000; Pitcher & Zilinskas 2002), *A. capillaris* (Chai *et al*. 2003, 2004) and *A. gigantea* (Asano & Sugiura 1990; Asano *et al*. 1991; Asano & Ugaki 1994). Various lab methods now exist (*e.g.* van den Eede *et al*. 2004; Rakoczy-Trojanowska 2002) to deliver gene(s) (DNA) of interest into a plant's genome. At least five methods can transform material of *Agrostis* species: (1) microprojectile bombardment or biolistic transformation (Hartman *et al.* 1994; Lee *et al.* 1995; Lee & Day 1998); (2) silicon carbide fibers or whiskers (Asano *et al.* 1991; Dalton *et al.* 1998); (3) electroporation (Asano *et al.* 1991; Asano & Ugaki 1994; Asano *et al.* 1998; Sugiura *et al.* 1998); (4) polyethylene glycol (Lee *et al.* 1996; Lee & Day 1998); and (5) *Agrobacterium tumefaciens* (Pitcher *et al.* 2000; Yu *et al.* 2000; Chai *et al.* 2000; Kim *et al.* 2001; Pitcher & Zilinskas 2002; Chai *et al.* 2003, 2004; Luo *et al.* 2004; Han *et al.* 2005; Hu 2005). The traits of interest (*cf.* Chandler 2003) include (1) resistance/tolerance to particular herbicides (Hartman *et al.* 1994; Lee *et al.* 1995; Asano *et al.* 1997, 1998; Sugiura *et al.* 1998; Chai *et al.* 2003; Z.-Y. Wang *et al.* 2003; *cf.* Fisher & Wright 1980; Heim *et al.* 1993); (2) resistance to particular diseases (Warkentin *et al.* 1998; Chai *et al.* 2002; Dai *et al.* 2002; Guo *et al.* 2003; Fu *et al.* 2005b) or insects (Hu 2005); (3) herbicide and disease resistance together; and (4) stress tolerance (McKersie & Bowley 2001; Aswath *et al.* 2005). A potential management system using a herbicide that also reduces fungal diseases was successful in reducing them in transgenic herbicide-resistant *A. canina* and *A. stolonifera* (Y. Wang *et al.* 2003).

9. References

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