APHIS Preliminary Risk Assessment on the Petition for a Determination of Nonregulated Status for Creeping Bentgrass (*Agrostis stolonifera*) Genetically Engineered (Event ASR368) for Tolerance to the Herbicide Glyphosate submitted by Monsanto Company and the Scotts Company.

Introduction

The Animal and Plant Health Inspection Service (APHIS) of the U.S. Department of Agriculture (USDA) in April 2003 received a revised petition from Monsanto Company and the Scotts Company seeking a determination of nonregulated status for a creeping bentgrass (*Agrostis stolonifera* L., synonym *A. palustris* Huds.) designated as ASR368 that is genetically engineered to be tolerant to the herbicide glyphosate (which is marketed for example as Roundup and Touchdown). This petition has been assigned the APHIS number 03-104-01p. In accordance with the Plant Protection Act and agency regulations (7 CFR Part 340.6), we published a notice in the *Federal Register* (Docket number 03-101-1) (web link http://www.aphis.usda.gov/brs/aphisdocs/03_10401p_fr_pc_pet.pdf) to inform the public and to seek comments on whether a plant pest risk would be presented by the deregulation and unconfined release of this grass into the environment.

In that *Federal Register* notice, APHIS is requesting information and comment on certain issues pertaining to potential environmental effects that may result if the petition were to be granted. At a later date, after reviewing comments on the petition and the *Federal Register* notice, in compliance with the National Environmental Policy Act a thorough environmental document will be prepared and announced in the *Federal Register*, and there will then be a second opportunity for public comment. At the present time APHIS is providing this preliminary risk assessment to assist the public in considering the petition.

The companies presented an extensive petition (432 pages) on their creation of the genetically engineered plant (ASR368) from the turf cultivar 'Backspin' and subsequent evaluation of ASR368. The petition (web link http://www.aphis.usda.gov/brs/aphisdocs/03_10401p.pdf) details the laboratory, greenhouse, and agronomic field-testing (under 7 CFR 340) used to evaluate genetic, biological, and agronomic characteristics of this organism.

APHIS, Biotechnology Regulatory Services (BRS) has studied the petition and continues to independently research the biology and ecology of creeping bentgrass. Based on this information a preliminary risk assessment was conducted leading to the major conclusions outlined below.

Conclusions

APHIS believes the following information provides evidence of no major unintended effects from introduction of the genetic material conferring glyphosate tolerance into the genome of creeping bentgrass.

ASR368 contains a single insert of the EPSPS genes.
Techniques used to characterize genetic material, e.g. Southern blot, polymerase chain reactions, and nucleotide sequence analyses, were used to confirm that the transformation event designated ASR368 contains within its nuclear genome a single copy of the engineered genetic construct used to transform the recipient cultivar. This construct contains two copies of the coding region for the CP4-EPSPS protein which is directed to the chloroplast in the cell by inclusion of a chloroplast transit peptide designated CTP2. The CP4-EPSPS protein is an enzyme, 5-enolpyruvyl-shikimate-3-phosphate synthase, derived from *Agrobacterium* sp. strain CP4, that unlike most native plant and microbial EPSPS enzymes, is naturally tolerant to the glyphosate herbicide. This coding region is the same as that used in several other glyphosate tolerant crops, such as soybean, that have been deregulated. Noncoding regulatory regions were attached to the genes to allow the CP4-EPSPS to be efficiently expressed in the plant. See petition pages 79-107, and 117 -119.

The EPSPS genes inserted into ASR368 are inherited as a single Mendelian locus.
Segregation analysis of the progeny from paired reciprocal crosses of hemizygous glyphosate-tolerant plants with nontransgenic plants indicates that the glyphosate-tolerance trait is inherited as a single locus following a Mendelian one-locus model. It is inherited in a stable manner through several plant populations. See pages 113-116.

ASR368 is not significantly different from its parental line or null comparators except for its tolerance to glyphosate.
Agronomic trials were conducted over a three year period in 9 different states covering a range of climate zones of turfgrass adaptation. These trials included experiments to better understand the relative plant pest or weed potential of ASR368 by evaluating such characteristics as vegetative and seed establishment, relative growth rates and survival in several environments under competitive and noncompetitive conditions, flowering period, pollen biology, fecundity (duration of seed set and components of seed yield), and measurement of morphological structures, both vegetative and reproductive. APHIS believes that the provided data show ASR368 is essentially equivalent to its nontransgenic null comparators for morphological traits (see pages 232-242), and essentially equivalent to its nontransgenic null comparators for several agronomic traits (see pages 126-220). Compositional analysis conducted on leaf samples from four different locations (see pages 120-123) also showed that ASR368 is essentially equivalent to its nontransgenic null comparators.

ASR368 does not differ in pest and pathogen susceptibility or resistance from its parent.
Confined agronomic field trials conducted between 1999 through 2002 were also carried out to observe pest and disease susceptibility. APHIS believes the provided data show that the ASR368 plant is phenotypically equivalent to its nontransgenic null comparator

plants in susceptibility to pests and pathogens. See pages 243-247. In addition, DNA sequences derived from plant pests used in the genetic construct do not cause plant disease.

In addition to the information Monsanto provided in the petition concerning the bentgrass family, and the origin, production, uses, biological characteristics, life history, and weediness of creeping bentgrass (see Section II, pp 31-76 of the petition), APHIS/BRS has carried out a general analysis of creeping bentgrass and other species of bentgrass (*Agrostis*) and rabbit's-foot grass (*Polypogon*) that occur in the United States. This analysis helps provide the biological context for understanding risks or biosafety in considering release of the glyphosate tolerant ASR368 creeping bentgrass. This analysis ("Perspective on Creeping Bentgrass, *Agrostis stolonifera*") is found after the following conclusions highlighted below.

Creeping bentgrass (*Agrostis stolonifera*) is a widespread perennial that establishes without cultivation in various habitats. See BRS analysis paragraphs 3.1, 4.1 and 6.1.

Creeping bentgrass can form hybrids with at least 13* U.S. naturalized or native species of *Agrostis* (bentgrass) and *Polypogon* (rabbit's-foot grass);
Hybrids occur naturally with 11 of these species: 8 *Agrostis* and 3 *Polypogon*, and most can be fertile. In experiments, creeping bentgrass crossed with 2 more species, which could also hybridize naturally. None of these species are threatened and endangered and none are on the Federal noxious weed list. However, A. stolonifera and at least four of the *Agrostis* species with which it can hybridize (i.e. *A. gigantea, A. castellana, A. capillaris*, and *A. canina*) have been occasionally reported as undesirable plants in certain situations. Crosses between *A. stolonifera* and *A. capillaris* (colonial bentgrass) and *A. gigantea* (redtop) occur with the most frequency. Over 20 additional species of *Agrostis* inhabit the U.S for which APHIS/BRS has no information regarding their sexual compatibility with *A. stolonifera*. Even if these species are not sexually compatible with *A. stolonifera*, the possibility remains that gene flow from *A. stolonifera* may occur indirectly in those that are sexually compatible with the 13 species capable of hybridizing with *stolonifera*. Even if hybrids are sterile, they might be vigorous and spread vegetatively. See summary in Table 1, paragraphs 1.5, 1.6, 6.6, and 7.3, and for details Table 2. *(Based on a review of additional documents since the submission of the FR notice, APHIS has revised its estimate of the number of species sexually compatible with *A. stolonifera* from 12 to 13).

There is the possibility that glyphosate-tolerant creeping bentgrass and/or glyphosate-tolerant relatives (hybrids) would establish in various urbanized to rural and natural areas. See BRS analysis paragraphs 5.3, 5.4 and 6.2-6.4.

Based on the issues noted above, APHIS is soliciting input to the questions posed in the FR notice.

Perspective on Creeping Bentgrass, *Agrostis stolonifera*

USDA/APHIS/BRS (B. MacBryde, ver. 12/29/2003)

Contents

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

1.1. The genus *Agrostis* (bentgrasses) is in the tribe Aveneae (including Agrostideae), which also contains oats (*Avena*) (*cf.* Mabberley 1998; Watson & Dallwitz 1992, 1998, 1999; Clayton & Renvoize 1986; Phillips & Chen 2003; Jacobs 2001). In the United States 31-34 species of *Agrostis* are native or naturalized, with 17-19 of them also in Canada (Table 1). There are 25-28 native species of *Agrostis* in the USA, and 7-9 established introductions, mainly from Eurasia (7-8 of these species are entirely introduced, 1-2 mostly so). Some field grasses were called *Agrostis* by Theophrastus (370-*c.* 285 BC), director of Aristotle's garden in Athens (Greene 1909). The overall taxonomy of *Agrostis* is unsettled and difficult; there is no comprehensive worldwide or definitive U.S. taxonomic treatment (*e.g.* Philipson 1937; Björkman 1960; Widén 1971; Tutin 1980; Romero García *et al.* 1988b; Koyama 1987; Rúgolo de Agrasar & Molina 1992, 1997a; Edgar & Connor 2000; and Hitchcock & Chase 1951; Carlbom 1967; Simpson 1967; Harvey 1993, 1999; Kartesz 2003). Consequently, the number of species stated above reflects different taxonomic judgements (Table 1). The genus might include over 200 species, occurring primarily and probably originating evolutionarily in the Northern Hemisphere (in Europe), with some species native in the Southern Hemisphere or temperate to cold-temperate areas on tropical mountains. *Agrostis* is in the convenient grouping called cool-season grasses, with a C_3 photosynthetic pathway (*cf.* Campbell *et al.* 1999; Goverde *et al.* 2002).

1.2. 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; Rumball & Forde 1977; Romero García & Blanca 1988; Romero García *et al.* 1988a; Frey 1997; Tomić & Surlan Monirović 1999; 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 stability includes all five of the species of main agronomic interest (Tables 1 & 2):

- 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).

1.3. Nevertheless, making use of the subtle biological distinctions for identification of the species (as whole plants in flower or not, or seeds) frequently requires acumen or expertise, which can be facilitated by lab analysis (*e.g.* Widén 1971; Tutin 1980; Romero García *et al*. 1988b; Chicouene 1989; Sell & Murrell 1996; Batson 1998b; Cope 1991; Behrendt & Hanf 1979; Nittler & Kenny 1969; Steiner & Lupold 1978; Steiner 1982; Adams 1996; Hillman 1918, 1930; Musil 1942, 1963; van der Burg *et al*. 1979; and Yamamoto & Duich 1994; Clark *et al*. 1989; Freeman & Yoder 1994; Ohmura *et al*. 1997; Scheef *et al*. 2003; Ridgway *et al*. 2003; Bonos *et al*. 2002). Routinely, diverse studies (1) lack identification, reporting just *Agrostis* sp. or the plural *Agrostis* spp. (*e.g.* Mountford & Peterken 2003); or (2) have misidentification (by tradition, assumption or error), either (2a) of the single species of interest or (2b) in confounding more than one species by not realizing the population is mixed.

1.4. For example, there is a need in USA for increased awareness to better distinguish *A. capillaris* and *A. castellana* (the latter found dominant in southeastern Australia by Batson 1996, 1998b; *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; Hubbard 1984; Tutin 1980; Steiner & Lupold 1978; Shildrick 1976; Scholz 1962, 1965; Griffin 1965; Madison 1961; USDA 1948, 1961; Musil 1942; Bartels 1943; Schoth 1930, 1939; Levy & Saxby 1931; Hillman 1930; Henry 1928); and as well to better distinguish *A. canina* and *A. vinealis*, brown bentgrass (Widén 1971; *cf*. Brilman 2003; Warnke 2003; Wipff & Fricker 2001; Funk 1998; Vester 1999; Sell & Murrell 1996; Hubbard 1984; Tutin 1980). Thus what may be regarded as the variability of a species in natural or variously managed populations can be 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).

1.5. *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), and *A. vinealis* and several other germane species (see Tables 1 & 2, and Stuckey & Banfield 1946; Davies 1953; Jones 1956a-1956c; Camus 1958; Björkman 1960; Widén 1971; Bradshaw 1975a, 1975b; Sell & Murrell 1996; Romero García *et al*. 1988b; Edgar & Forde 1991; Edgar & Connor 2000; Batson 1998b; Wipff & Rose-Fricker 2000, 2001; Wipff & Fricker 2001; Belanger *et al*. 2003a, 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 1998b; 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), which can happen even for sterile plants because of their vegetative reproduction.

1.6. A summary on hybridization is in Table 1. In Table 2 are some details (but not all-encompassing) on species in the USA and crossing (which is inherently complicated but not atypical in grasses and some other wild plants), and certain additional information:

- Notable botanical synonyms (thus subordinate, not simply alternative names);
- Common names (*cf.* Monteith 1930; USGA 1932);
- Ranges (where native, and along with the Table 1 data, 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):
  - n = x = 7, the basic set of chromosomes (in male or female gamete), haploid
  - **2n = 2x = 14**, paired parental sets of chromosomes usual in the body cells, **diploid**
  - 2n = 3x = 21, three sets of chromosomes usual in the plant's body cells, triploid
  - **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, AAÁÁ (*e.g.* within sp., crossing plants' sets doubled)
    - segmental allotetraploids = ~ alike, ± halfway, ~ unalike: *e.g.* ĀĀÁÁ, ÃÃÂÂ, Ã̄Ã̄ÅÅ
  - 2n = 5x = 35, five sets of chromosomes usual in plant's somatic cells, pentaploid
  - **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.*, the included paired parental/ancestral chromosome sets);
- *Agrostis stolonifera* hybrids with three species of *Polypogon*, rabbit's-foot grass (*e.g.* Conley 1993).

2. Distribution and Conservation of *Agrostis* Species

2.1. Many species of *Agrostis* are natively widespread in temperate areas, whereas other species or taxa (*i.e.* subspecies or botanical varieties) are regional, local or rare (WCMC 1998; Tercek *et al*. 2003). In the United States, one indigenous species in Hawaii, several taxa in California and/or Oregon, and one species in Wyoming (endemic to Yellowstone National Park) are variously rare (Table 1; CNPS 2001; WCMC 1998); none are now listed as endangered or threatened under Federal or State law. 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 (*e.g.*, the threatened western orchid Ute ladies-tresses, *Spiranthes diluvialis*), although confirmation might be needed on the identification of this grass in their habitats.

3. The Species Creeping Bentgrass, *Agrostis stolonifera* L.

3.1. *Agrostis stolonifera* is a robust fast-growing perennial which is biologically and ecologically very variable, phenotypically plastic (adjusting locally) and 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; Kurchenko 1975; Wu 1976; Kik *et al*. 1990a, 1990b, 1991; Grime & Hunt 1975; Eriksson 1989; Shipley *et al*. 1989; Davies & Singh 1983; Misra & Tyler 2000b; Aston & Bradshaw 1966; Jónsdóttir 1991b; Ahmad & Wainwright 1976; Wu 1981; Kik 1989; Teyssonneyre *et al*. 2002; Bradshaw & Hardwick 1989; *cf*. Donohue 2003). In general the species is an allotetraploid (Jones 1956b, 1956c; Warnke *et al*. 1998), but it also has cytotypes of higher ploidy and other 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). Taxonomic correlations usually are not consistent within its broad 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.

4. Creeping Bentgrass Distribution and Utilization

4.1. Creeping bentgrass has become naturalized in temperate to cold-temperate regions throughout the world (*cf*. Tompkins *et al*. 2000), for example New Zealand, Tasmania and southern Australia, South Africa, South America (including Tierra del Fuego, Patagonia and the Andes) and North America, including 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), and is ambiguous (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 1999). 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, probably arriving well before the 1750s (*cf*. Sauer 1942, 1976; Richardson 1818; Odland 1930; Monteith 1930), and likely 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 a popular pasture grass here, it has been suggested for reseeding on some western grasslands (*e.g.* USDA Forest Service 1940; Davis 1952; Fransen & Chaney 2002). The species is naturalized in all states and recorded (mapped present) in the majority of counties, except the warmer southern portions of states in the Southeast (Kartesz 2003; *cf*. USGA 1922a; Moncrief 1964; Ferguson 1964; 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 will enter into force after adherence by 40 countries; currently there are 33 parties, including 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. This 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 161 member nations) held the last IU negotiations over 7 years, and the FAO Conference (184 members) adopted the resultant IT-PGRFA in 11/2001 (USA and Japan abstaining). 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*. PGGR 2003).

4.3. The IT-PGRFA listing could intend creeping bentgrass even though not considering it a major grass forage. With some differences in the use (circumscription) of *Agrostis* names (section 5.8), the listing of *A. stolonifera* needs to be checked, confirming 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 Middle Europe with genetic resources of value because of their utilization for fodder (*e.g.* Balasko *et al*. 1995; Tomić *et al*. 1999, 2003; Chorlton *et al*. 1997, 2000; Dumortier *et al*. 1996; Kratochwil *et al*. 2002; Hill *et al*. 1992; Bañuelos & Obeso 2000; Pieper & Burlison 1930; de Coninck & Bay 1816; Richardson 1818; Haggar 1976; Frame 1990), with both of the latter species of additional value for revegetation ("recultivation") and soil stabilization and improvement (*cf*. Smith & Bradshaw 1979), and all but *A. gigantea* of "ornamental" value (*i.e.* as lawn grasses or turf). An overview on the latter 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 seed trade in bentgrass (± 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 also from an increasing production in New Zealand (USGA 1922b, 1922c, 1925b, 1930b; Hillman 1921, 1930; Henry 1928; *cf.* Suckling & Forde 1978; Levy 1924). Moreover seed was gathered from free-living (naturalized) U.S. populations in coastal New England from about 1900, and chiefly 1924-1934 in the coastal region of Oregon but also Washington and northwestern California, as well as farther inland in western Oregon and perhaps Washington, and from coastal Massachusetts (Hillman 1921, 1930; Henry 1928; USGA 1925a, 1931; Schoth 1930, 1939; Hyslop 1930; Carrier 1921; Odland 1930; Monteith 1930). Additional seed was imported mostly from crop production in southeastern (maritime) Canada, as well as Alberta (Clark 1922; Tregillus 1926; LeLacheur 1930; Henry 1928; Hillman 1930).

5.2. The many shipments of "South German mixed bent" were variously comprised of *Agrostis capillaris* with some *A. canina*, about 10% or less *A. gigantea*, and sometimes *A. stolonifera* in small amounts (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 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 1992; Karataglis 1980a), but to include *A. castellana* (which had earlier been considered just a local ecological variation), and to additionally include its hybrids with *A. capillaris* (Rumball & Forde 1977; Edgar & Forde 1991; Batson 1998b; Henry 1928) — which are sometimes called *A.* × *fouilladei*. Similarly, the inland bentgrass of western Oregon and Washington is recognized increasingly not as a dryland or upland (*i.e.* non-coastal) variation of *A. capillaris* (marketed as 'Highland'), but from the species *A. castellana* (Henry 1928; Hillman 1930; Schoth 1930, 1939; USDA 1948, 1961; Madison 1961; Griffin 1965; Funk 1998; 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 grasses 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.* Hurley 1973; Brilman & Meyer 2000). 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 there a century earlier (*cf.* Cronon 1983; Sauer 1942; Mountford & Peterken 2003). 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 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 sometimes 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 the encouraging of propagation by stolons rather than seeds, *Agrostis stolonifera* became the most successful and popular grass for putting greens (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 agronomically improve it (*e.g.* Hurley & Murphy 1996; Warnke 2003). The species is additionally investigated as a forage (Balasko *et al.* 1995; Tomić *et al.* 1999, 2003), and of interest for restoring suitable mine sites involving heavy metals (Smith & Bradshaw 1979) and for water treatment (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) for turf from populations in the native range of *A. stolonifera* (*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 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.* 1998; 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). From its 1923 beginnings in the Pacific Northwest Coast region (Schoth 1930, 1939; Hyslop 1930; USGA 1930b; Monteith 1941; Ferguson 1948; Franklin & Dyrness 1973), the production of seed of bentgrasses for turf (in the USA and elsewhere) has become a modern industry concentrated in western Oregon in the Willamette Valley (125 mi × 25-30 mi) between the coast and Cascade Mountains. About 6,000 acres are in production, mostly for creeping bentgrass (North & Odland 1935; Wright 1980; *cf.* Jonassen 1980; Rumball & Robinson 1982; Chastain & Young 1998). Background on the region is in several accounts (Bowen 1978; Johannessen *et al.* 1971; Habeck 1961; Nelson 1919; Mueller-Warrant *et al.* 2003; Clark & Wilson 2001).

5.7. The turfgrass industry here 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. convention may in part reflect the continuing influence of the manual by Hitchcock & Chase (1951, and reprint in 1971) (Chase being 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 countries and locales and the broad U.S. seed dispersal (distribution), and subsequent adaptation, selection and breeding efforts, the germplasm here is a rich heterogeneous mixture quite unlike the native ecological race (ecotype) in Europe noted by Sell & Murrell (1996; *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 U.S. 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), even using *A. stolonifera* var. *stolonifera* sometimes (rather than *A. stolonifera* var. *major*) to name the plants usually called redtop and thoroughly accepted now as *A. gigantea* (*e.g.* in Europe, Tutin 1980; Sell & Murrell 1996; and North America, Voss 1972; Bailey *et al.* 1976; McNeill & Dore 1976; Dore & McNeill 1980; Pohl 1978; Gleason & Cronquist 1991; Harvey 1993, 1999; Yatskievych 1999).

5.8. Three themes are interwoven in the 250-year historical to current usage of several *Agrostis* names, reflecting improved scientific understanding but lags in communication. (**1**) The natural variation of creeping bentgrasses stimulated early recognition of many formal distinctions, such as *Agrostis stolonifera* L. (1753) and *A. palustris* Huds. (1762, based on English plants) or *A. stolonifera* var. *palustris* (Huds.) Farw., and *A. stolonifera* var. *compacta* Hartm. (1832) (**2**) The name *Agrostis gigantea* Roth (1788) for redtop was its second name, seemingly superfluous. (**3**) However, its earlier name of *Agrostis alba* L. (1753) became based nomenclaturally (*i.e.* standardized) on a specimen later found to be a *Poa nemoralis* L., and so *A. alba* became the *Poa*'s botanical synonym (thus a name no longer available for use). (**4**) On a different theme (classification of biological entities), it was not clear that the plants called *A. stolonifera* and those called *A. gigantea* represented two species rather than variations of one. If considered one species (*e.g.* Malte 1928), its name had to be the earlier *A. stolonifera*, and redtop was then *A. stolonifera* var. *major* (Gaudin) Farw. (**5**) The creeping bentgrass within that broadly circumscribed species could still be regarded to have distinct variants such as *A. stolonifera* var. *palustris* or *A. stolonifera* var. *compacta*, or to have none and so all creeping bentgrass should be called *A. stolonifera* var. *stolonifera*. (**6**) *Agrostis gigantea* became scientifically understood to be a distinct species (as Linnaeus had discerned), with rhizomes (underground stems) rather than stolons, and a hexaploid (see Table 2). (**7**) From much more study of many native populations of *Agrostis stolonifera* (*sensu stricto*, creeping bentgrass in the narrow sense excluding var. *major*), the variability of the plants has been found extensive, occurring with broad ecological amplitude and without substantial discontinuites (*e.g.* Kik *et al*. 1990a; Vergara & Bughrara 2003). (**8**) Similarly *Agrostis capillaris* has been found quite variable and fine-tuned to a range of habitats (*e.g.* Bradshaw 1959a, 1959d, 1960; Acheroy & Lefèbvre 1983; Funtova & Malyshev 2001; Helgadóttir & Snaydon 1986; Wilson & Rapson 1995; Tasker & Chadwick 1978). (**9**) On the other hand, *A. castellana* has been recognized to be biologically distinct from *A. capillaris*, and *A. vinealis* distinct from *A. canina*. (**10**) The usage of common names (Tables 1 & 2) has become more stable (*cf*. Henry 1928; Monteith 1930; USGA 1932), but can still be variable, confused or entangled.

5.9. Consequently, when going beyond the extensive information on sports 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 frequently cannot be ascertained, 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 the plants were supplied). As provisional pragmatic assumptions, *A. alba* tends to mean redtop (*A. gigantea*); *A. stolonifera* to mean creeping bentgrass or 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 with *A. stolonifera* var. *stolonifera* used for either); and *A. palustris* is *A. stolonifera* (creeping bentgrass). This confusion often makes other literature especially useful for gaining insights on the population dynamics and ecology of creeping bentgrass (*A. stolonifera*, synonym *A. palustris*) here in natural to variously managed systems.

6. Creeping Bentgrass Habitats, Ecology and Reproduction

6.1. In Europe where *Agrostis stolonifera* has been taxonomically clear 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 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; Hald 2002; Croxton *et al*. 2002; Cornish 1954; Ross 1986). Similarly in the USA, the species occurs in coastal habitats (*e.g.* Caldwell

& Crow 1992; Wu 1981) and has become widely established inland (for an example in Missouri habitats – Yatskievych 1999) along the margins of ponds and lakes and on streambanks, in moist disturbed areas, various grasslands (including upland prairies), 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 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), 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), 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; Zenbayashi *et al*. 1996). The numerous tiny seeds of creeping bentgrass are dispersed by the wind and on water, sometimes to lake islands (Nilsson & Nilsson 1978; Roden 1998), and also consumed and sometimes dispersed (still viable) by cattle, sheep and fallow deer (*Dama dama*) (Welch 1985; Gill & Beardall 2001), and jointed pieces of 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; Boedeltje *et al*. 2003; Levine 2000, 2001, 2003; Wolters & Bakker 2002). The seeds of *A. canina* are also viably dispersed by passing through livestock (Bruun & Fritzbøger 2002). Seeds of *A. capillaris* are externally dispersed by wild ungulates (*via* hair and hooves) (Heinken & Raudnitschka 2002) and also dispersed and eaten by ants, and the plants are sometimes associated with ant-mounds (Kovář *et al*. 2001; Kovář & Kovářová 1998).

6.3. *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, 2001), which thus includes weedy characteristics (*e.g.* Schippers *et al*. 2001; Hill *et al*. 2002; Wilcox 1998; Marshall 1990; Baker 1965, 1972, 1974; Keeler 1985, 1989). 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) 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 functions in a modular way (*e.g.* Jónsdóttir 1991b, 1991a), with the leafy plantlets (rooted tillers) along a stolon able to become nutritionally independent (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).

6.4. The species often reproduces primarily vegetatively, spreading or "creeping" by the stolons, which 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 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 or along a stream. In semi-natural habitats a panicle might have 100-200 flowers, and the plant will have panicles at different stages of maturity. Separate plants of the same genotype (*i.e.* ramets of the same genet, or clones) adjust to their immediate surroundings, so would not necessarily flower synchronously. (*E.g.* Smith 1972; Grime *et al*. 1988; Boedeltje *et al*. 2003; Kik 1987; Kik *et al*. 1990a, 1990b, 1993; Wilson & Thompson 1989; Purves & Law 2002; Pakeman & Marshall 1997; Olff *et al*. 1993; Jónsdóttir 1991a, 1991b.)

6.5. 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). 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 (*cf.* Heide 1994). In field-plot or greenhouse and lab studies (*e.g.* Philipson 1937; Davies 1953; Ponomarev & Rusakova 1968; Fei & Nelson 2003), pollen of creeping bentgrass shed for a few mid-morning hours (exact times differing with locale) or again (perhaps not usually) in early-mid afternoon, and the pollen grains were viable for no more than 3 hours. 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 inconsistent; *A. castellana* might be earlier than *A. stolonifera*; and *A. vinealis* was bimodal with ± pre-dawn and evening shedding (*cf.* Christoffer 2003).

6.6. In experimental field-plot studies on pollen dispersal and potential for hybridization with other species of *Agrostis* and with *Polypogon* (Wipff & Fricker 2001; Belanger *et al*. 2003b; Christoffer 2003), viable pollen of creeping bentgrass traveled up to 958 ft. Using their experimental data (Wipff & Fricker 2001) and accepting a 0.02% level of hybridization (possibly introgression of the gene of interest into the plant population of interest — *cf.* Anderson 1953; Arnold 1997), the pollen was estimated (calculated) to travel up to 4,296 ft. Using independent data from a relatively similar experiment (Belanger *et al*. 2003b), a computer model was developed (Meagher *et al*. 2003) that considered pollen dispersal and variation in fitness of the pollen donor. The model found that pollen dispersal and gene introgression would be limited at some sites and extensive at others, depending on local conditions such as exposure to the wind. All three studies concluded that hybridization can occur in the field between *Agrostis stolonifera* and various other species (Tables 1 & 2). The work thus confirms earlier reports, from experimental hybridization and study of chromosomes (*e.g.* Davies 1953; Jones 1956a-1956c; Björkman 1960; Romero García & Blanca 1988), and fieldwork and taxonomic analysis (*e.g.* Widén 1971; Romero García *et al*. 1988b).

6.7. Of the 10-12 species of *Agrostis* with which it is known that *A. stolonifera* could hybridize here (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*. × *fouilladei*, which can backcross into *A. capillaris*, and for some years all of these were imported unknowingly from New Zealand as *A. capillaris* and widely distributed (section 5.3). *Agrostis capillaris* is also likely to cross with *A. gigantea*, forming *A*. × *bjoerkmanii*, as found in Rhode Island (section 5.4). The hybrids are for the most part sterile or with very low fertility, and could be vegetatively vigorous (see Table 2). Hybridization and introgression have always been aspects of the domestication and improvement of crops and ornamentals (*cf*. Gepts 2002; Anderson 1961). Various new lab techniques facilitate working with hybrid turfgrasses (Brilman 2001b), and efforts are already underway to hybridize *Agrostis* species for traditional reasons such as bringing in disease resistance (*e.g.* Belanger *et al*. 2003c, 2003b).

6.8. Some *Agrostis stolonifera* seeds germinate soon after their dispersal, whereas many persist for a while in the seedbank but germinate or are gone within 1-1½ years, and some seeds can remain viable in the soil for at least 4 years (Jutila b. Erkkilä 1998; Mitlacher *et al*. 2002; Ferris & Simmons 2000; Díaz-Villa *et al*. 2003; Thompson & Grime 1979; Shipley *et al*. 1989, 1991; 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 seedbanks to recruit for example *A. capillaris* (Pakeman *et al*. 1998; Dougall & Dodd 1997; Meerts & Grommesch 2001; *cf*. Edwards & Crawley 1999), *A. gigantea* (Williams 1978) and *A. vinealis* (Bakker *et al*. 1996).

7. Creeping Bentgrass in the Landscape

7.1. The presence of creeping bentgrass in vegetation is quite variable, depending upon habitat or management. The species can be competitive and become a dominant, 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*. 2003) 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.* Elmarsdottir *et al*. 2003; Greipsson & El-Mayas 1999; Wolters & Bakker 2002; Stockey & Hunt 1994; Bullock 2000; Jalloq 1975; Cody *et al*. 2000; Staniforth & Scott 1991; Levine 2000, 2001, 2003). Even though now fairly cosmopolitan, the species is rarely aggressively invasive 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 (Anderson 1953; Arnold 1997) (see Table 2) could be in the vegetation in some areas (*e.g.* Widén 1971; *cf.* Nilsson *et al*. 1994; Sell & Murrell 1996; Fouillade 1911, 1932; Romero García *et al*. 1988b; Edgar and Forde 1991; Edgar and Connor 2000; Stuckey & Banfield 1946). The F_1 hybrids of *Agrostis stolonifera* and *A. capillaris* (see Tables 1 & 2), sometimes called *A.* × *murbeckii*, can out-compete both parents and be plentiful and apparently long-lived in intermediate areas between parental habitats (Forde 1991; Meerts & Lefèbvre 1989; Widén 1971; Bradshaw 1958, 1959c).

7.2. *Agrostis stolonifera* forms hybrids sometimes called × *Agropogon littoralis* (Sell & Murrell 1996; Hubbard 1984; Bradshaw 1975b; Christoffer 2003; Qian & Sun 1998; Weiller *et al*. 1995; Edgar & Connor 2000; Rúgolo de Agrasar & Molina 1997b; Randall 2002) with *Polypogon monspeliensis* (annual rabbit's-foot grass), a Eurasian species naturalized in many countries worldwide which occurs in wet-moist habitats to abandoned arable fields (*e.g.* Conley 1993; Robbins 1940; Tables 1 & 2). Annual rabbit's-foot grass tolerates salinity (Mahmood *et al*. 1996) and can be common in estuaries and suitable inland wetlands (Kuhn & Zedler 1997; Stromberg 1997; Roalson & Allred 1997; El-Din *et al*. 1993; Hussey *et al*. 1997). In South Australia it hosts two organisms associated with the disease floodplain staggers (Bertozzi & McKay 1995; McKay *et al*. 1993; Davis *et al*. 1995); 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; Cadwalladr *et al*. 1972; Eertman *et al*. 2002; Wolters & Bakker 2002; Ungar 1978; McCarty & Dudeck 1993; Rozema & Blom 1977; Tiku & Snaydon 1971; Ahmad & Wainwright 1976, 1977; Ahmad *et al*. 1981; Hodson *et al*. 1985; McNeilly *et al*. 1987; Kik 1989; Wu 1981; Aston & Bradshaw 1966), which is a trait of agronomic interest (*e.g.* Marcum 2001; Kuo *et al*. 1994; *cf.* Wu & Huff 1983). *Polypogon viridis* also forms hybrids with *A. stolonifera*, which are sometimes called × *Agropogon robinsonii* (Table 2). Both *Polypogon* species are in Ciba-Geigy's *Grass Weeds* (Häfliger & Scholz 1981); 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: grassland, aquatic biotopes, perennial crops, rotation crops, and waste places, but it is not considered a major world weed (Holm *et al*. 1997, 1979). The species is also reported as a weed or weedy 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. Here 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 (Table 2), are also considered weeds sometimes or in some areas and can be of particular management concern: *Agrostis gigantea*, *A. castellana*, *A. capillaris* and *A. canina* (*e.g.* Randall 2002; Holm *et al.* 1979; Häfliger & Scholz 1981; Behrendt & Hanf 1979; Grime *et al.* 1988; Hubbard 1984; Barthram *et al.* 2002; Hakansson & Wallgren 1976; Williams 1970, 1973, 1975, 1977, 1978; Skuterud 1984; Courtney 1981; Bylterud 1984; Darbyshire 2003; Roland & Zinck 1998; Matthei *et al.* 1993; Ramírez *et al.* 1992; San Martín *et al.* 2002; Pauchard & Alaback 2004; Edgar & Connor 2000; Walker & Lee 2002; Harris 1974; James & Atkinson 1979; Batson 1998a-1998c; Hill *et al.* 1996; Hussey *et al.* 1997; Boyd 1976; Enomoto 2000).

7.5. Some species of the genus *Agrostis* are known to 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 *et al.* 1965; Bradshaw & Hardwick 1989). All five agronomic species as well as *A. vinealis* (Farrow *et al.* 1982) and the native *A. scabra* (Archambault & Winterhalder 1995; Koch *et al.* 2000) are among these facultative metallophytes. Arsenic, cadmium, copper, lead, manganese, nickel and zinc are prominent, and the plants on a site are 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 considerable 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 for water-quality improvement by biofiltration (Hares & Ward 1999).

7.6. The repertory of *Agrostis stolonifera* (Duwensee 1993) includes biotypes tolerant to copper (Wu *et al.* 1975; Briggs & Walters 1997), copper and nickel (Jowett 1958), copper and zinc (Wu & Antonovics 1975), and lead and zinc (Gregory & Bradshaw 1965). 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, thus an exclusive habitat where some species are unable to grow but some species have evolved and only occur (*i.e.* endemics) (*e.g.* Baker *et al.* 1993).

7.7. Colonial bentgrass (the zinc-tolerant hybrid's other parent) has been studied most, and there are metal-tolerant cultivars for reclamation available commercially (Bradshaw 1952; Jowett 1964; Gregory & Bradshaw 1965; Jain & Bradshaw 1966; McNeilly 1968; Antonovics 1968; Jones *et al.* 1971; Mathys 1973; Gartside & McNeilly 1974; Walley *et al.* 1974; Simon & Lefèbvre 1977; Simon 1977; Nicholls & McNeilly 1979; Smith & Bradshaw 1979; Karataglis 1980b, 1986; Karataglis *et al.* 1985; Meharg & Macnair 1991; Watkins & Macnair 1991; Boon *et al.* 1998; Meerts & Grommesch 2001; Griffioen & Ernst 1989; Griffioen *et al.* 1994; Malcová *et al.* 2003; Rydlová & Vosátka 2003). *Agrostis capillaris* 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.* 1985; Karataglis 1980d, 1980c; Humphreys & Nicholls 1984; McNeilly & Bradshaw 1968). Most likely separate evolutionary adaptations resulted in the similar metal-tolerance traits of some biotypes (Nicholls & McNeilly 1982; Al-Hiyaly *et al*. 1988, 1990, 1993). The other agronomic species with some of the additional studies are *A. canina* (Gregory & Bradshaw 1965), *A. castellana* (De Koe & Jacques 1993; Schat *et al*. 2002), and *A. gigantea* (Hogan *et al*. 1977a, 1977b; Hogan & Rauser 1979, 1981; Rauser 1984; McLaughlin & Crowder 1988).

7.8. "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 (Pollard *et al*. 2002; Lasat 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 increasing (*e.g.* Macnair 1990, 1993; Macnair *et al*. 2000; Schat *et al*. 2000; Hall 2002).

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 (*e.g.* McCown 2003), and comparing crop domestication, conventional plant breeding, and genetic engineering (*e.g.* Gepts 2002). In addition, 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 release into the environment (*e.g.* Johnson & Riordan 1999; Day & Lee 1997). Examples of experiments to better understand aspects of the biology of these species are the pollen dispersal, viability and fitness studies above (sections 6.5-6.6). The purpose of other experiments (in the greenhouse or a confined field trial) (*e.g.* Lee *et al*. 1997; Gardner *et al*. 2003; 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 articles on the potential benefits perceived from the genetic engineering of turfgrasses are also being published (*e.g.* Harriman & Suttner 2003; Litrenta 2003; Lee *et al*. 1995).

8.2. In *Agrostis*, genetic engineering (on at least an experimental basis in some country) has succeeded and next steps are proceeding with at least four species: especially *Agrostis stolonifera* (Krans *et al*. 1982; Sticklen *et al*. 1996; Xiao & Ha 1997), as well as *A. canina* (Pitcher *et al*. 2000; Pitcher & Zilinskas 2002), *A. capillaris* (Chai *et al*. 2003) and *A. gigantea* (reported as *A. alba*, redtop) (Asano *et al*. 1991; Asano & Unaki 1994). Various lab methods now exist (*e.g.* Rakoczy-Trojanowska 2002) to deliver the gene(s) (DNA) of interest into a plant's genome. At least five methods have succeeded in the transformation of material of *Agrostis* species: (1) microprojectile bombardment or biolistic transformation (Hartman *et al*. 1994; Lee *et al*. 1995); (2) silicon carbide fibers or whiskers (Asano *et al*. 1991; Dalton *et al*. 1998); (3) electroporation (Asano *et al*. 1991; Asano & Unaki 1994; Asano *et al*. 1998; Sugiura *et al*. 1998); (4) polyethylene glycol (Lee *et al*. 1996); and (5) *Agrobacterium tumefaciens* (Pitcher *et al*. 2000; Yu *et al*. 2000; Pitcher & Zilinskas 2002; Chai *et al*. 2003). Traits of interest 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 1977); (2) resistance to particular diseases (Chai *et al*. 2002; Dai *et al*. 2002; Guo *et al*. 2003); and (3) herbicide and disease resistance together. A possible management system using a herbicide that is also known to reduce fungal diseases was successful in reducing them in two species of transgenic herbicide-resistant bentgrasses (Y. Wang *et al*. 2003).

9. References

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Table 1. Summary on *Agrostis* and *Polypogon* in Temperate North America

(see "Perspective on Creeping Bentgrass, *Agrostis stolonifera*" – USDA/APHIS/BRS, B. MacBryde, 12/29/2003)

KEY:

ORIGIN or INTEGRATION IN FLORA, and USE (O/IF, U): Nv = Native, **Nz** = Naturalized, **I** = Introduced, extent of naturalization unknown; **A** = Agronomic.

NATIVE RANK (TNC/NatureServe 2002, ranks in brackets by APHIS/BRS); in native range**: G1** = critically rare, **G2** = rare, **G3** = vulnerable, **G4** = apparently secure, **G5** = widespread, abundant & secure; **T** = a ranking for subsp. or var. (trinomial); **Q** = a question/problem in taxonomy.

WEED CONCERN IN COUNTRY: S = Serious, **P** = Principal, **C** = Common, **X** = Behaves as weed, importance unknown (Holm *et al.* 1979, *A Geographical Atlas of World Weeds*); **H&S:** Häfliger & Scholz 1981, *Grass Weeds 2*; and the following **Others for *Agrostis stolonifera*:** **Serious** weed in Australia pastures and/or crops (*e.g.* Brown & James 1998); **Moderate** invasive threat on California coast in wetlands (Dudley 1998).

HYBRIDS: F1 = F_1 with sterility/fertility not given; **f** = fertile (without details), **s** = sterile, **v** = variable crossing behavior or reports (perhaps sterile and low or higher fertilities); species numbered in alphabetical order, so for example the number **30** = *Agrostis stolonifera*.

Species / Taxa	Common Names	O/IF,U	U.S. – Canada Distribution	Native Rank	Weed Concern in Country	Hybrids With Other Species / Comments on Taxonomy &/or Range	Hybrids With *A. stolonifera*
1 *Agrostis aequivalvis*	Arctic or Northern Bentgrass	Nv	AK-OR; Canada (BC)	G5?			
2 *Agrostis anadyrensis*	Anadyr Bentgrass	Nv	AK	[G4?]			
3 *Agrostis avenacea*	Pacific Bentgrass	Nz	HI, CA, TX, OH, SC	[G5?]		Syn. of *Lachnagrostis filiformis*, *per* Jacobs 2001; Nv Polynesia, Australia	
4 *Agrostis blasdalei*	Blasdale's or Cliff Bentgrass	Nv	CA endemic	**G2**			
5 *Agrostis canina*	Velvet Bentgrass	Nz, **A**	HI, many N states; Canada	G5	C (Finland, Russia); **in H&S**	Also sF1 with 21 and 34	vF1; rare?
6 *Agrostis capillaris*	Colonial (or Rhode Island) Bentgrass, (Browntop)	Nz, **A**	Most states; Canada	[G5]	P (Chile, NZ, Russia), C, X; **in H&S**	Also vF1 & **vF2** with 7, and with 13, sF1? with 34, and F1 with probably 14	vF1; frequent?
7 *Agrostis castellana*	Dryland (incl. Highland) Bentgrass	(Nz), **A**	WA, OR, AL, many states?; Can.?	[G4G5]	X (Australia, NZ, Portugal)	Confounded with 6, *q.v.* (& Table 2)	vF1; infreq.?
8 *Agrostis clavata*	Clubbed Bentgrass	Nv	AK; Canada (Yukon)	G4G5	C (Japan)		
9a *Agrostis clivicola* var. *clivicola*	Coastal Bluff Bentgrass	Nv	CA endemic	**G3?T3?**		Syn. of 10 *per* Harvey, but not Kartesz	
9b *Agrostis clivicola* var. *punta-reyesensis*	Point Reyes Bentgrass	Nv	CA endemic	[**G3?T1Q**]		Syn. of 10 *per* Harvey, but not Kartesz	
10 *Agrostis densiflora*	Dense-flower Bentgrass	Nv	CA-OR	G3G4		F1? with 12 (Carlbom 1967, p. 88)	
11 *Agrostis elliottiana*	Elliott's Bentgrass	Nv	CA & mainly E US	G5			
12 *Agrostis exarata*	Spike Bentgrass	Nv	W US; Canada	G5	C (Japan)	Also F1? with 10 (Carlbom 1967, p. 88)	sF1 with 30?
13 *Agrostis gigantea*	Redtop, Black Bentgrass	Nz, **A**	Nearly all states; Canada	[G5]	C, X (Australia, Canada, NZ); **in H&S**	Also vF1 & **vF2** with 6 (occasional?), and sF1 with 21 (rare?)	vF1; occasional?
14 *Agrostis hallii*	Hall's Bentgrass	Nv	CA-OR, & WA?	G4G5		fF1 with 25, and F1 with probably 6	
15 *Agrostis hendersonii*	Henderson's Bentgrass	Nv	CA-OR	[**G1?**]		Incl. *A. aristiglumis* (CA endemic) *per* Harvey 1999	
16 *Agrostis hooveri*	Hoover's Bentgrass	Nv	CA endemic	[**G2G3**]			
17 *Agrostis howellii*	Howell's Bentgrass	Nv	OR endemic	**G2**			
18 *Agrostis humilis*	Mountain or Alpine Bentgrass	Nv	W US (AK-CA-NM); Canada	[G5]		Incl. *A. thurberiana* (W US, Can.) *per* Harvey 1999 (but not Harvey 1993)	
19 *Agrostis hyemalis*	Winter Bentgrass	Nv	E US, especially SE; Canada	G5			
20 *Agrostis idahoensis*	Idaho Bentgrass	Nv, (**A**)	W US; Canada	G5			F1
21 *Agrostis mertensii*	Northern or Arctic Bentgrass	Nv	AK-CO & NC; Canada	G5		F1 with 34; sF1 with 5, & 13 (rare?)	F1; rare
22 *Agrostis microphylla*	Small-leaf Bentgrass	Nv	CA-WA & NV; Can. (BC)	G4			
23 *Agrostis nebulosa*	Cloudgrass	I, (Nz)	Nz in OH, perhaps elsewhere	[G3G4]		Nv Iberian Peninsula	
24 *Agrostis oregonensis*	Oregon Redtop or Bentgrass	Nv	W US (CA-WA-WY); Can.	G4			
25 *Agrostis pallens*	Leafy or Dune Bentgrass	Nv	CA-WA & NV; Canada	G4G5		Also fF1 with 14	F1
26 *Agrostis perennans*	Upland Bentgrass	Nv	E US & OR, WA; Canada	G5			
27 *Agrostis rossiae*	Ross' Bentgrass	Nv	WY endemic	**G1**			
28 *Agrostis sandwicensis*	Hawaii Bentgrass	Nv	HI endemic	**G3**			
29 *Agrostis scabra*	Rough Bentgrass	Nv	Most states; Canada	G5			F1
30 *Agrostis stolonifera*	**Creeping, Spreading, Carpet, and Marsh Bentgrass**	**Nz, Nv?, A**	**Nz all states, Nv? Few N states; Canada**	**G5**	**C, X; in H&S; Serious (Austral.), Mod. (CA, OR?)**	**F1 with 13-15 other spp., incl. 10-12 other *Agrostis*: vF1, vF2; common?**	

31 *Agrostis tandilensis*	Kennedy’s Bentgrass	Nz	CA	G3G5		Nv Argentina, S Brazil	
32 *Agrostis trinii*	Trinius’ Bentgrass	Nv	AK	[G5?]		Syn. of 34 *per* Kartesz, but not Koyama	F1
33 *Agrostis variabilis*	Alpine or Mountain Bentgrass	Nv	W US; Canada (BC, AB)	G5			
34 *Agrostis vinealis*	Brown Bentgrass	Nz, Nv	Nz many states?, Nv AK; Can.?	G5?		F1 with 21, sF1? With 6, sF1 with 5	vF1; rare?
Table 1 Subpart: *Polypogon* and Intergeneric Hybrids, × *Agropogon*							
1 *Polypogon fugax*	Hill Rabbit’s-foot Grass	(I?)	HI (old report)	[G?]		Nv Asia Minor	F1
2 *Polypogon monspeliensis*	Annual Rabbit’s-foot Grass	Nz	Most states (incl. HI, AK); Can.	[G5?]			vF1; infreq.?
3 *Polypogon viridis*	Beardless Rabbit’s-foot Grass	Nz	Scattered (16 states, incl. HI)	[G5?]	C (Portugal, Iraq, Egypt), X (NZ)		sF1; rare?

Table 2. Details on *Agrostis* and *Polypogon* in Temperate North America

(see explanation in section 1.6 of "Perspective on Creeping Bentgrass, *Agrostis stolonifera*" – USDA/APHIS/BRS, B. MacBryde, 12/29/2003)

***Agrostis* Species** (some synonyms), [and Section or Subgenus]; **also Bigeneric Hybrids**	**U.S.; & Nativity (Native Range)**	**Species, Bigeneric Hybrids: Ploidy & Genome Details** (bolded main cytotype)	**Natural Hybrids: Parents of Crosses**	**Natural or Spontaneous Hybrids: Country of Reported Occurrence** ("spontaneous" hybrids are from naturalized parents)	**Experimental Hybrids: Cross in Greenhouse, or by Spontaneous Pollen Flow in Field Test**. (Analysis **K**aryological; **T**ransgenic; or **O**ther)	**Hybrids: Ploidy & Genome, Information About Sexual Reproduction; Comments**. (Not indicating direction of cross, *i.e.* which species was female parent, which the male)
30. ***A. stolonifera*** (*A. alba* of some authors, but not Linnaeus; *A. alba* var. *palustris*, *A. stolonifera* var. *palustris*, *A. palustris*; *A. stolonifera* var. *compacta*) [Sect. *Vilfa*]; **Creeping Bentgrass**	Naturalized only or perhaps native on some northern salt marshes and lakesides (but not in New England). Native Iceland, Eurasia, and North Africa.	**2n = 4x = 28**, $A_2A_2A_3A_3$ (strict allotetraploid – Jones 1956b, 1956c; Warnke *et al.* 1998); also, at least in Europe (Harvey 1999), 2n = 5x = 35, $A_2A_2A_3A_3A_3$ or $A_2A_2A_2A_3A_3$ and 2n = 6x = 42, $A_2A_2A_2A_3A_3A_3$ Also aneuploidy (frequent), B-chromosomes, aneusomaty (Björkman 1954, Kik *et al.* 1993, Frey 1997).	30 × 5; 30 × 6 (***A. × murbeckii***); 30 × 7; 30 × 12 (apparently); 30 × 13; 30 × 21; 30 × 32; 30 × 34; 30 × 1P (intergeneric); 30 × 2P (intergeneric); 30 × 3P (intergeneric).	See under the other parental species. Some hybrids sterile but vegetatively vigorous by stolons and/or rhizomes.	30 × 5 (T + O); 30 × 6 (T + K); 30 × 7 (T); 30 × 13 (T + K); 30 × 20 (T); 30 × 23 failed (T); 30 × 25 (T); 30 × 29 (T); 30 × *A.* sp. (T); 30 × 32 (T + O); 30 × 34 (K); 30 × 1P (T + O); 30 × 2P (T + O); 30 × 3P (T + O).	See *Agrostis stolonifera* hybrids under the other parental species (listed alphabetically). Reproduction of *Agrostis stolonifera* often mainly vegetative, by stolons (*e.g.* Kik *et al.* 1990b, 1992). Sexual reproduction predominately outcrossing (Davies 1953; Belanger *et al.* 2003b), with some cultivars perhaps obligately so (Warnke *et al.* 1998; *cf.* Belanger *et al.* 2003b). Also highly self-fertile clone, and selfing has been utilized (Warnke *et al.* 1998; Tomic *et al.* 1999).
5. ***A. canina*** (*A. canina* var. *fascicularis*; *A. pallida* With., but not DC.) [Sect. *Agrostis*]; **Velvet Bentgrass**	Naturalized. Native Europe into E Asia.	**2n = 2x = 14**, A_1A_1 And aneuploidy, possibly polyploidy (4x, 5x, 6x, 8x); also B-chromosomes (Romero García & Blanca 1988, Frey 1997).	30 × 5; 5 × 6 & 5 × 13 (both unconfirmed, or error – Widén 1971).	**30 × 5:** Fennoscandia, rare (Widén 1971).	30 × 5: Greenhouse (Belanger *et al.* 2003b; had failed – Davies 1953, Björkman 1954); and transgenic field tests; 5 × 21 (Björkman 1954); 5 × 34 (Davies 1953, Björkman 1954).	**30 × 5** (would be 2n = 21 *per* Widén 1971): Needs confirmation – Bradshaw (1975a); transgenic tests: field – Wipff & Fricker 2001, Christoffer 2003, greenhouse – Belanger *et al.* 2003b. **5 × 21:** Certainly sterile (Widén 1971). **5 × 34** (2n = 21)**:** Quite sterile (Widén 1971).
6. ***A. capillaris*** (*A. tenuis*; *A. vulgaris*) [Sect. *Vilfa*]; **Colonial Bentgrass (Rhode Island Bentgrass, Browntop)**	Naturalized. Native Eurosiberia.	**2n = 4x = 28**, $A_1A_1A_2A_2$ (segmental allotetraploid, partly from a 2x *A. canina*-like ancestor – Jones 1956b, 1956c, *cf.* Romero García *et al.* 1988b). Occasional aneuploidy, B-chromosomes (Frey 1997).	30 × 6 (***A. × murbeckii***); 5 × 6 (unconfirmed, or error – Widén 1971); 6 × 7 (***A. × fouilladei***); 6 × 13 (***A. × bjoerkmanii***); 6 × 14 (probable); 6 × 34 (***A. × sanionis***).	**30 × 6:** *e.g.* Fennoscandia (Widén 1971); Germany (Weber 1920); U.K. (Bradshaw 1958, 1975a, *cf.* Smith 1972, Sell & Murrell 1996); Belgium (Meerts & Lefèbvre 1989); France (Fouillade 1932); Spain (Romero García *et al.* 1988b); **Canada** (Malte 1928); **NW U.S.?** (Carlbom 1967); New Zealand (Edgar & Forde 1991, Edgar & Connor 2000). **6 × 7:** U.K. (Sell & Murrell 1996); France (Fouillade 1932); Spain (Romero García *et al.* 1988b); Australia (Batson 1998b); New Zealand (Edgar & Forde 1991, Edgar & Connor 2000). **6 × 13:** U.K. (Sell & Murrell 1996); **NE U.S.** likely (Stuckey & Banfield	30 × 6; 6 × 7 (New Zealand: Edgar & Forde 1991, Rumball & Forde 1977 *per* Batson 1998b); 6 × 13; 6 × 34 (Davies 1953, but probably most were not hybrid crosses *per* Widén 1971).	**30 × 6** (2n = 28, $A_1A_2A_2A_3$)**:** Parents readily crossing, with F_1 vegetatively vigorous and widespread, but with high sterility (Bradshaw 1975a, Sell & Murrell 1996); almost wholly abortive pollen, exceptionally a few seeds observed (Widén 1971); semi-fertile in New Zealand, with pollen fertility 41% (Edgar & Forde 1991); suspected U.S. hybrid in OR (Carlbom 1967, p. 39); transgenic tests: field – Wipff & Fricker 2001, field and greenhouse – Belanger *et al.* 2003a, 2003b. **6 × 7** (some 2n = 35)**:** Partially fertile (Sell & Murrell 1996). Backcrossing into #6 in New Zealand (Edgar & Forde 1991, Edgar & Connor 2000). **6 × 13** (2n = 35, $A_1A_1A_2A_2A_3$)**:** Crossing rather readily, including backcrosses and F_2. F_1 vegetatively vigorous, but "infertile" (pollen fertility 45%, seeds 50%). F_2 and backcrosses

				1946, *per* Björkman 1954, Widén 1971, Bradshaw 1975a, Edgar & Forde 1991). **6 × 14: NW U.S.?** (Pendergrass 2001). **6 × 34:** U.K., Europe, Russia (Widén 1971, Bradshaw 1975a, Sell & Murrell 1996).		aneuploid, low vigor (Bradshaw 1975a). Highly sterile (Sell & Murrell 1996). **6 × 14:** Probable in OR (K.L. Pendergrass [U.S. FWS], via M. Jordan [TNC] 2001 letter to J.L. White [APHIS]). **6 × 34** (2n = 28)**:** Unclear difficulty or ease of crossing in nature and experimentally (readily crossing *per* Harvey 1999); most purported experimental hybrids (Davies 1953, Jones 1956b) likely instead selfs of #34 or #6 (Widén 1971, Bradshaw 1975a). Probably natural hybrids sterile (Sell & Murrell 1996, Widén 1971).
7. ***A. castellana*** [Sect. *Vilfa*]; **Dryland Bentgrass (including Highland Bentgrass)**	Introduced. Native Western Mediterranean.	**2n = 4x = 28**, $A_1A_1A_2A_2$ and 2n = 6x = 42, $A_1A_1A_1A_2A_2A_2$ In Portugal also aneuploidy, B-chromosomes (Frey 1997).	30 × 7; 6 × 7 (***A. × fouilladei***)	**Both:** France (Fouillade 1932); **6 × 7:** U.K. (Sell & Murrell 1996); France (Fouillade 1932); Spain (Romero García *et al.* 1988b); Australia (Batson 1998b); New Zealand (Edgar & Forde 1991, Edgar & Connor 2000).	30 × 7 (varied results in transgenic field tests); 6 × 7 (New Zealand: Edgar & Forde 1991, Rumball & Forde 1977 *per* Batson 1998b).	**30 × 7:** Pollen very irregular (Romero García *et al.* 1988b); transgenic tests: greenhouse and field – Belanger *et al.* 2003a, 2003b, field – Wipff & Fricker 2001, but not Christoffer 2003. **6 × 7** (some 2n = 35)**:** Partially fertile (Sell & Murrell 1996). Backcrossing into #6 in New Zealand (Edgar & Forde 1991, Edgar & Connor 2000).
12. ***A. exarata***; **Spike Redtop, Spike Bentgrass**	**Native** Far E Siberia and W North America: Alaska–Mexico.	**2n** = 4x = 28, **6x = 42**, and 8x = 56 (Harvey 1999, Frey 1997, Taylor & Mulligan 1968).	30 × 12 (apparently).	**W U.S.?** (Carlbom 1967; Welsh *et al.* 1993).		Suspected hybrids in WA and OR, sterile (Carlbom 1967, pp. 109-110, 112).
13. ***A. gigantea*** (*A. stolonifera* var. *major*, *A. stolonifera* var. *gigantea*, *A. alba* var. *gigantea*; or just *A. stolonifera* or *A. alba* for some authors; *A. nigra*) [Sect. *Vilfa*]; **Redtop (Black Bentgrass)**	Naturalized. Native Eurasia (especially Central Asia).	**2n = 6x = 42**, $A_1A_1A_2A_2A_3A_3$ (Jones 1956c; ancestry perhaps by fusion of $A_1A_2A_3$ gametes of an *A. × murbeckii* – Widén 1971). Also B-chromosomes (Frey 1997).	30 × 13; 5 × 13 (unconfirmed, or error – Widén 1971); 6 × 13 (***A. × bjoerkmanii***); 13 × 21	**30 × 13, 6 × 13, & 13 × 21:** Fennoscandia (Widén 1971). **30 × 13:** Sweden (Blom 1961, *per* Widén 1971); U.K. (Davies 1953, Bradshaw 1975a, Sell & Murrell 1996). **6 × 13:** U.K. (Sell & Murrell 1996); **NE U.S.** likely (Stuckey & Banfield 1946, *per* Björkman 1954, Widén 1971, Bradshaw 1975a, Edgar & Forde 1991).	30 × 13; 6 × 13	**30 × 13** (2n = 35, $A_1A_2A_2A_3A_3$)**:** Experimental F_1 cross easy; vegetatively vigorous, but only 25% pollen and seed fertilities (Bradshaw 1975a), or highly or usually sterile (Sell & Murrell 1996, Dore & McNeill 1980, Widén 1971); transgenic tests: field – Wipff & Fricker 2001, greenhouse – Belanger *et al.* 2003b. **6 × 13** (2n = 35, $A_1A_1A_2A_2A_3$)**:** Crossing rather readily, including backcrosses and F_2. F_1 vigorous vegetatively, but "infertile" (pollen fertility 45%, seeds 50%). F_2 and backcrosses aneuploid, low vigor (Bradshaw 1975a). Highly sterile (Sell & Murrell 1996). **13 × 21** (2n = 49)**:** Probably not easily formed in nature; rare, no pollen or seeds (Widén 1971).
14. ***A. hallii***; **Hall's Bentgrass**	**Native** Calif. & Oregon, & also Wash.?	**2n = 6x = 42** (Harvey 1993).	6 × 14 (probable); 14 × 25 (apparently).	**6 × 14: NW U.S.?** (Pendergrass 2001). **14 × 25: NW U.S.?** (Carlbom 1967).		**6 × 14:** Probable in OR (K.L. Pendergrass [U.S. FWS], via M. Jordan [TNC] 2001 letter to J.L. White [APHIS]). **14 × 25:** Probable (and fertile) in OR (Carlbom 1967, pp. 98, 126).
20. ***A. idahoensis***; **Idaho Bentgrass, Idaho Redtop**	**Native** Western North America — Alaska to California and New Mexico.	**2n = 4x = 28**			30 × 20 (transgenic test – Christoffer 2003).	**30 × 20:** Transgenic test: field – Christoffer 2003.

21. ***A. mertensii*** (*A. borealis*) [Sect. *Agrostis*]; **Northern or Arctic Bentgrass**	**Native,** somewhat circumpolar, plus mountains.	**2n** = 2x = 14, 3x = 21, 6x = 42 (but 6x is *A. scabra* *per* Harvey 1999), 7x? = 49, and **8x = 56**; also aneuploidy? (Frey 1997).	30 × 21; 13 × 21; 21 × 34	**All three:** Fennoscandia (Widén 1971).	5 × 21 (Björkman 1954); 21 × 34 (Björkman 1954).	**30 × 21** (2n = 42) (Björkman 1954, Widén 1971). **5 × 21:** Certainly sterile (Widén 1971). **13 × 21** (2n = 49)**:** Probably not easily formed in nature; rare, no pollen or seeds (Widén 1971). **21 × 34** (2n = 42) (Widén 1971).
23. ***A. nebulosa*** [Subg. *Zingrostis*]; **Cloudgrass**	Cultivated; occasional escape, in Ohio established (Harvey 1999). Native Iberian Peninsula.	**2n = 2x = 14**			30 × 23 (no transgenic flow found in field test – Christoffer 2003).	No transgenic flow found (Christoffer 2003).
25. ***A. pallens*** (*A. diegoensis*); **Leafy or Dune Bentgrass**	**Native** Western North America: B.C. — Nevada & California.	**2n = 6x = 42**, 8x = 56 (Harvey 1993, 1999, Frey 1997).	14 × 25	**NW U.S.?** (Carlbom 1967).	30 × 25 (transgenic test – Wipff & Fricker 2001, Christoffer 2003).	**30 × 25:** Transgenic test: field – Wipff & Fricker 2001, Christoffer 2003. **14 × 25**: Probable (and fertile) in OR (Carlbom 1967, pp. 98, 126).
29. ***A. scabra*** (*A. hyemalis* or *hiemalis* var. *scabra*); **Rough Bentgrass, Ticklegrass**	**Native** North America and NE Asia.	**2n = 6x = 42**	30 × 29	**W U.S.?** (Welsh *et al.* 1993).	30 × 29 (transgenic test – Christoffer 2003).	**30 × 29:** Transgenic test: field – Christoffer 2003.
***A.* sp.**	Unknown: from eastern Oregon		30 × *A.* sp.		30 × *A.* sp. (transgenic field test – Wipff & Fricker 2001).	Species unidentified (Wipff & Fricker 2001); native or introduced and perhaps naturalized.
32. ***A. trinii*** (*A. vinealis* subsp. *trinii*, *A. coarctata* subsp. *trinii*; *A. flaccida* subsp. *trinii*); **Trinius' Bentgrass**	**Native** E Asia to W Alaska.	**2n** = 2x = 14, **4x = 28** (Frey 1997). Also B-chromosomes (Frey 1997).	30 × 32 (***A. × ussuriensis***)	Far E Russia (Probatova 1984).	30 × 32 (transgenic test – Christoffer 2003).	**30 × 32:** Transgenic test: field – Christoffer 2003. Note: *A. trinii* taxonomy unsettled; a synonym of *A. vinealis* in Kartesz 2003 ms, but variously recognized by Koyama (1987) for Japan and various authors for Russia (*e.g.* Kurchenko & Ianova 1976, Kurchenko 1979c, Tsvelev 1984, Malyschev & Peschkova 1990, and Probatova 1984 *etc.*).
34. ***A. vinealis*** (*A. stricta*; *A. canina* subsp. *montana*; *A. canina* var. *arida*; *A. coarctata*) [Sect. *Agrostis*]; **Brown Bentgrass**	Introduced. **Native** Alaska and Eurasia.	**2n = 4x = 28**, $A_1A_1A_2A_2$ or $A_1A_1A_1A_1$ (somewhat as autotetraploid with 2x *A. canina*-like ancestry, or perhaps from cross of 4x *A. canina* [if such] and *A. capillaris* – Jones 1956b, *cf.* Romero García *et al.* 1988b, but the "*A. canina*" ploidy over 2x may not be *A. canina* – Romero García & Blanca 1988; *cf.* Vergara & Bughrara 2003).	30 × 34; 6 × 34 (***A. × sanionis***); 21 × 34	**All three:** Fennoscandia, with 30 × 34 rare (Widén 1971); both **30 × 34 & 6 × 34:** U.K. (Hubbard 1984, Sell & Murrell 1996).	30 × 34; 5 × 34 (Davies 1953, Björkman 1954); 6 × 34 (Davies 1953, but probably most were not hybrid crosses *per* Widén 1971); 21 × 34 (Björkman 1954).	**30 × 34** (2n = 28)**:** Experimental hybrids completely sterile (Bradshaw 1975a); a few viable seeds (Davies 1953). Björkman (1954) also made a cross of 5x #30 and #34. **5 × 34** (2n = 21)**:** Quite sterile (Widén 1971). **6 × 34** (2n = 28)**:** Unclear difficulty or ease of crossing in nature and experimentally (readily crossing *per* Harvey 1999); most purported experimental hybrids (Davies 1953, Jones 1956b) likely instead selfs of #34 or #6 (Widén 1971, Bradshaw 1975a). Probably natural hybrids sterile (Sell & Murrell 1996, Widén 1971). **21 × 34** (2n = 42) (Widén 1971).

Table 2 Subpart: Intergeneric Hybrids, *Agropogon stolonifera* × *Polypogon* species, × *Agropogon*

Bigeneric Hybrids	Hybrid Range	Hybrid Ploidy	Natural Hybrids	Country of Reported Occurrence	Experimental Hybrids	Hybrids' Sexual Reproduction; Comments
1P. (× *Agropogon*, but since without name use cross)	Not native if in U.S. (HI), but likely not there (*cf.* Herbst & Clayton 1998, also Wipff & Fricker 2001).		**30 × *Polypogon fugax*** [sp. (2n = 42, Björkman 1954) native in Asia Minor, not found in Hawaii since 1916 – Herbst & Clayton 1998]. Unknown if Hybrid Native, Spontaneous (from introduced parents), or Experimental (Björkman 1960, *per* Wipff & Fricker 2001). Transgenic test – Christoffer (2003).			**30 × 1P:** Transgenic test: field – Christoffer 2003.
2P. **× *Agropogon littoralis***; **Coast Agropogon**	Spontaneous, naturalized parent(s). Native Western Eurasia, North Africa.	**2n = 4x = 28** (Tutin 1980, Sell & Murrell 1996).	30 × *Polypogon monspeliensis* [sp. (2n = 28 & 35, Harvey 1993) Europe to SW Asia - Annual rabbitsfoot grass]	U.K., France (Sell & Murrell 1996, Hubbard 1984); Canada (BC), **W & SE U.S.** (Kartesz 2003 ms); Chile (Rúgolo de Agrasar & Molina 1997b); China (Qian & Sun 1998); Australia (Weiller *et al.* 1995- ms); New Zealand (Edgar & Connor 2000).	30 × 2P (transgenic test – Christoffer 2003).	**30 × 2P:** Almost complete pollen and seed sterilities. Vigor varies, perhaps because of hybridization with different ecotypes of #30, which is more vigorous (Bradshaw 1975b). Transgenic test: field – Christoffer 2003.
3P. **× *Agropogon robinsonii***	Spontaneous, naturalized parent(s). Native Western Eurasia?	**2n = 4x = 28**	30 × *Polypogon viridis* (*Agrostis semiverticillata*, *Agrostis viridis*) [sp. (2n = 28, Harvey 1993) Europe to SW Asia - Beardless rabbitsfoot grass]	U.K., rare (Hubbard 1984, Sell & Murrell 1996); **W U.S.?** (Welsh *et al.* 1993).	30 × 3P (transgenic test – Christoffer 2003).	**30 × 3P:** Experimental crossing ease uncertain. Parents highly self-incompatible; hybrid has complete pollen sterility (Bradshaw 1975b, Hubbard 1984). Short-lived perennial (Sell & Murrell 1996). Transgenic test: field – Christoffer 2003.