

ORIGIN, BIOGEOGRAPHICAL MIGRATIONS AND DIVERSIFICATIONS OF TURFGRASSES

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Executive Summary

Whether a turfgrass species is characterized as native or naturalized to North America has been based on world-wide simplistic observations focused on where the greatest genetic diversity occurred, termed center-of-origin. Research information as to dating and locations of subsequent migration and diversification has been minimal due to a lack of needed research technologies. Intercontinental migration of grasses has been assumed to have been unlikely due to oceanic separation. Recent development of paleobotanical studies using ultrastructural electron microscopic techniques and stable carbon isotope dating instrumentation and research procedures, plus molecular phylogenetic research and cladistic biogeographic analysis of large data sets are clarifying our understanding of migration patterns and dating of multiple secondary centers-of-origin for grasses.

Pre-anthropological intercontinental migration of grasses is now being documented as more significant than previously assumed. Global heating/cooling phases and shifts in sea level appear to have facilitated oceanic island hopping. At varying times, these bridge migrations may have involved the northern Europe to North America route via Greenland, Bering Bridge between Asia and North America, southeast Asia to Australia via New Guinea, South America to North America via Caribbean and later via Panama Bridge, and Africa-Europe via the Gibraltar Straits. Also, the potential for transoceanic migrations is being reconsidered.

Primitive ancestral grasses are now proposed to have appeared during the Late Cretaceous between 65 and 96 mya (million years ago) in Gondwanan Africa. The ancestral Pooideae are estimated to have migrated to the steppes of Laurasian Eurasia during the Eocene ~ 38 to 47 mya. Taxonomic divergence of the base C₃ Pooideae group appears to have been initiated in Europe ~ 26 to 33.5 mya. The base C₄ Pooideae apparently arose in Africa ~ 30 to 33 mya, followed by migration to West Gondwana South America and to East Gondwana India and Australia.

Diversification led to the emergence of an ancient Poeae group known as the fine-leaf fescues (*Festuca*) in central-Europe during the mid-Miocene ~ 13 mya. Subsequent migration occurred via the mountains of central and eastern Asia, across the Bering Land Bridge into North America, southward via the western mountains, over the Panamanian Land Bridge, and across the Andes to Patagonia. This occurred between ~ 3.8 and 10 mya, which is before the anthropological effects of humans. Clearly, the fine-leaf fescues are native to North America, migrating eastward after the ice age glacial melt ~ 1 mya. Similar investigations with other turfgrasses may clarify the migration routing and diversification dating of other turfgrass species. Thus, the current status of turfgrass species in terms of native or anthropological naturalization is presented in this paper and summarized in the following table.

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Summary of native and naturalized categories of 24 turfgrasses found in North America, based on current knowledge.

Native/Naturalized Categories	Grass Genus and Species	Turfgrasses Common Name
Native, based on biogeographical, phenotypic, and phylogenetic studies.	<i>Festuca rubra</i> <i>Festuca trachyphylla</i> <i>Festuca ovina</i>	red fescues hard fescue sheep fescue
Native, based on phenotypic and genetic assessments.*	<i>Axonopus compressus</i> <i>Axonopus fissifolius</i> <i>Bouteloua curtipendula</i> <i>Bouteloua gracilis</i> <i>Buchloe dactyloides</i> <i>Stenotaphrum secundatum</i>	broadleaf carpetgrass common carepetgrass side-oats gramagrass blue gramagrass American buffalograss St. Augustinegrass
Possible native, based on phenotypic assessments and allied species biogeographical, phylogenetic studies.*	<i>Agrostis capillaris</i> <i>Agrostis stolonifera</i> <i>Agrostis canina</i> <i>Poa pratensis</i>	colonial bentgrass creeping bentgrass velvet bentgrass Kentucky bluegrass
Possible naturalized, following anthropological introduction.*	<i>Eremochloa ophiuroides</i> <i>Lolium multiflorum</i> <i>Lolium perenne</i> <i>Paspalum vaginatum</i> <i>Poa trivialis</i> <i>Schedonorus arundinaceus</i> <i>Zoysia japonica</i> <i>Zoysia matrella</i> ssp. <i>matrella</i> <i>Zoysia pacifica</i>	centipedegrass annual ryegrass perennial ryegrass seashore paspalum rough bluegrass tall fescue Japanese zoysiagrass manila zoysiagrass mascarene zoysiagrass
Undocumented, needs research	<i>Cynodon dactylon</i> ssp. <i>dactylon</i> <i>Poa annua</i>	dactylon bermudagrass annual bluegrass

*Needs further biogeographical and phylogenetic research to confirm.

Introduction

Understanding the relatively recent research in grass species evolution and development has dictated revision of how native and naturalized turfgrass species are viewed, especially in North America. The supporting research for this updating is reviewed herein.²

Native Turfgrass Species. Webster's Third New International Dictionary defines native as something indigenous to a particular locality. Indigenous is defined as native and as originating or developing or produced naturally in a particular land or region or environment. The emotive associated terminologies relative to native that have been used include naturalized, alien, exotic and non-native. Criteria for classifying native species that have been utilized or proposed include historical, geographical, economical, behavioral, sociological and/or political considerations. The latter four involve value judgments based on an arbitrary frame time that results in controversy due to the diversity of human preferences and needs (53). Thus, the native aspects of turfgrasses addressed herein will rely on time and geographic dimensions documented by sound, hard science.

There are proponents who consider the plant species present in America when Europeans arrived as the natives that have persisted from time immemorial free from human disturbances. However, recent research indicates there are woodland areas that have developed subsequent to anthropological disturbance during the late-Holocene at least 4,000 years ago (80). These mound-building, early-American populations were active in domesticated crop propagation involving intensive land use by fire to remove forested areas. Such anthropological impacts on plant species disturbance and reinvasion by intermediate succession species have been recently documented for regions in southeastern and in north east central North America (33, 80), and others probably will be found.

One can only speculate as to the grass species that would have been naturally introduced and

persisted in recent times if human disturbance had not occurred. Disturbed environments can have long-term or short-term effects on plant community composition depending on the degree and duration of the disturbance event. Disturbance can be a natural aspect of plant ecosystems as caused by drought, fire, disease, insect, glaciation, heat stress, freeze stress, volcanic smoke, soil deposition, soil salt level, animal pressures, etc. Defining a native plant based on a fixed point in time, such as pre-Holocene, pre-Neolithic, or pre-European colonial, is unrealistic as it assumes no non-human disturbances would have occurred subsequently. It also fails to acknowledge humans as a component of the ecosystem. Historically, the species composition of most plant communities has been a continuous, dynamic process of transitional diversification and recovery. It is likely the natural distribution of plant communities still would be different even if human intervention had not occurred. Similarly, species move geographically in response to environmental changes caused both naturally and by human disturbances. Thus native sites should not be viewed as fixed geographical areas that existed prior to human activity. Also, the premise stated by some individuals that native turfgrasses inherently possess lower cultural requirements, resource inputs, and/or water use rates, plus better human benefits than non-native species is not valid (53).

Application of the native terminology for grasses has varied over the past century, and previously emphasized the effects of tectonic processes that resulted in assumed geographic barriers such as oceanic separation of continents. Some grass taxonomy and flora books include a geographic description that proposes a continent(s) or region(s) where each species is native. In the early 1900s there were North American texts on grass taxonomy that referred to grass species, such as the *Agrostis*, *Festuca* and *Poa*, as natives. Then by the mid-1900s most grass taxonomic, flora and other texts listed such species as native to Eurasia.

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This change in the center-of-origin concept was based on plant exploration that indicated the geographic region thought to possess the greatest morphological diversity. Unfortunately, the true center-of-origination for a species may no longer exist botanically due to severe, extended drought as occurred in Africa or due to ice age glacial presence as in the Northern Hemisphere. Also, the oceanic separation of continents is not proving to be the migration barrier once assumed (48, 85).

The development of molecular phylogenetic techniques during the past two decades, involving DNA sequencing instrumentation and unique phenetic and cladistic analyses via computer programs for large data sets, have drastically changed our understanding of when and where diversifications of grass genera, subgenera, species and subspecies occurred. Thus, an update of the native or naturalized status of the major turfgrass species is addressed herein.

Naturalized Turfgrass Species. The term naturalized turfgrass species is defined herein as a plant that is introduced, becomes established and persists without direct human inputs. The introduction may be unintended or intended. An introduced, heterozygous species may diversify and naturalize as a local ecotype that is well adapted, functionally valuable, and non-invasive. Also, multiple independent origins of similar genotypes have occurred in widely separated but similar environments, as has been documented for *Agrostis capillaris*, *Agrostis stolonifera*, and *Poa annua* (57). The plant community composition is inherently dynamic, with preservation of the status quo on a long-term basis unlikely. It is natural to have both migration/introduction and naturalization of species. Anthropological related naturalization contributes to species diversity of plant communities.

Taxonomy. The grass taxonomy employed herein is that of Barkworth et al. (6, 96, 97). The classification system for grasses is Kingdom - Plantae, Phylum - Magnoliophyta (syn. Division), Class - Liliopsida (syn. Monocotyledonae), Subclass - Commelinidae, Superorder-Poanae, Order - Poales, and Family-Poaceae (syn. Gramineae). Subfamily names end in -oidea, tribes in -eae, and subtribes in -inae.

The traditional grass taxonomic system is based on morphological similarities, especially the inflorescence. A more recent classification system is cladistics, or phylogenetics systematics in which groups or clades are organized based on relative dating of common ancestors with shared diversity of anatomical, physiological, biochemical and morphological features. Basically a clade may encompass all descendant species of an ancestor. Two major grass clades are BEP encompassing the Bambusoideae, Ehrhartoideae, and Pooideae subfamilies and PACCMAD encompassing the Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Micrairoideae, Aristidoideae, and Danthonioideae subfamilies (15, 32, 42, 43, 77).

The BEP clade contains exclusively C_3 grass species, while the PACCMAD clade includes C_4 species, as well as all known C grasses. The latter are mainly distributed within the Chloridoideae, Aristidoideae, and Panicoideae subfamilies. The crown node for the BEP clade is estimated to be ~ 10 million years older than that of the PACCMAD clade (17). Numerous subclades become evident from the cladistic applications (2, 15, 25, 26, 39, 48, 51, 58, 62, 67, 85, 86), resulting in taxonomic classifications that more nearly depict evolution of the grass family. Cladistic classification of the monocotyledons indicates the Joinvilleaceae are a sister group to the Poaceae within the Subclass Commelinidae (35, 51, 86, 89).

Plant Evolution Phases. The geophysical aspects of grass species evolution involve a (a) primitive ancestral center-of-origination, (b) early diversification, (c) migration or dispersal, and (d) species secondary centers-of-origin or diversification in order to adapt and survive changes. These changes include environmental (temperature, water, irradiation, and carbon dioxide), edaphic (soil texture, pH, nutrients, and salts), and biotic (animal grazing, human activities, and pests). There also are continuing intraspecies diversification regions in response to current natural and human environmental disruptions. Accordingly, micro centers-of-diversification occur involving small areas where mutations and hybridization are significant as represented by the presence diploid, triploid, tetraploid, hexaploid, and even octoploid plant species (101).

Previously a sometimes ill-defined center-of-origination had been considered phenotypically to be a region where the greatest diversity of a grass species occurs. More recently, either confirmation or major adjustments in dating and location have been made possible by more sophisticated paleobotany using ultrastructural electron microscopic techniques plus stable carbon isotope dating instrumentation and research procedures. Actually, the secondary species centers-of-origin and/or diversification may be more important than the center-of-origination (48), especially if those ancestors in the center-of-origination became extinct as a result of adverse climatic changes, such as the severe drought that occurred in Africa. Also, key secondary centers-of-diversification for temperate C₃ grasses were formed after subsidence of the last glacial age.

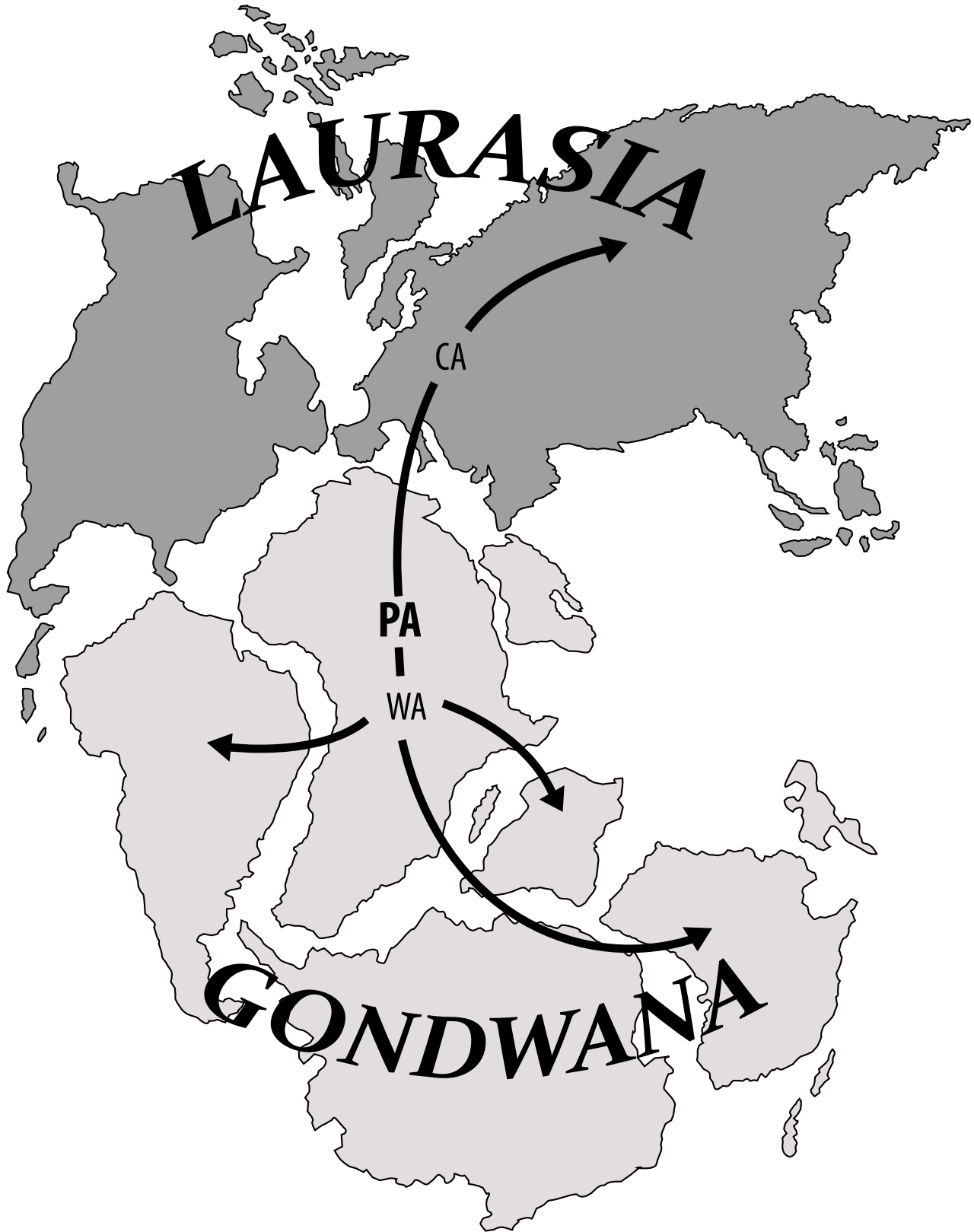
Current data indicate certain morphological diversifications of grasses have occurred at least 23 mya (million years ago) after the origin of a particular character (51). Diversification is a dynamic ongoing process with multiple secondary micro-centers-of-origin. A grass population has the potential for further differentiation that leads to better genetic adaptation to a specific environment by natural selection.

Early Plate Tectonics. Grass-dominated ecosystems now cover more than one-third of the earth's

land surface area. This was not always the case. Early evolutionary history of primitive ancestral grasses and their broad migration patterns are thought to have been influenced by shifting positions of land masses (27) and seas that created and even destroyed environments where the ancestral grasses originated or migrated. Plate tectonic theory has been advanced by new geological evidence and contributes to concepts of angiosperm-Poaceae distributions. The supercontinent Pangea formed ~ 500 mya. Its configuration as it existed in the medial Cretaceous prior to continental breakup is shown in Figure 1. Pre-continental separation of Pangea with possible ancestral grass migrations also are shown.

Pangea split into Laurasia, now North America and Eurasia, and into Gondwana, now South America, Africa, Antarctica and Australia, during the late-Mesozoic era ~ 160 mya. A land connection between Gondwanan-Africa and Laurasian-Europe was present in the western Mediterranean region. The early Laurasian land connection between Europe and North America is termed the North Atlantic Land Bridge. Gondwana was characterized by mild temperatures and a huge range of flora and fauna for millions of years. The early West Gondwana formation may have allowed South America to be more directly land accessible to primitive ancestral plant migration from Africa than from Laurasian North America.

Figure 1. Depiction of the probable relative positions of the Laurasian and Gondwanan land masses in the medial Cretaceous ~ 100 mya (adapted from Smith, Briden and Drewry, 1973), and possible broad migration patterns of primitive ancestral grasses (PA), plus later migration of cool-season ancestral grasses (CA) and warm-season ancestral grasses (WA).



Intercontinental Plant Migration. The movement of plant species between continents and directionally across large continental areas is referred to as migration. Transcontinental dispersals have been found to occur earlier and more frequently than was once assumed (48, 85). Wind, birds, animals and/or floating debris may have contributed to such dispersals. Species distributions and multiple centers-of-diversification tend to be influenced by conditions existing since the Pleistocene. Direct intercontinental plant migration of primitive ancestral grasses was possible up to or following specified dating as extensively reviewed by Raven and Axelrod (72) (Table 1). Patterns of potential intermittent ancestral plant migration to North America (72) may have involved a Laurasian direct land route from Europe,

an indirect land route from Asia via the Bering Land Bridge, and a more recently formed land route from South America via the Panamanian Land Bridge (Table 1).

Note that moderate biogeographic plant migration by oceanic island-hopping probably occurred via birds, wind and/or flotation for a significant time following geologic dated continent separation. A narrow gap interspersed with volcanic islands between Africa and South America presumably could have allowed primitive flora migrations up into the Paleocene (58, 72). It has been proposed that tropical grass subfamilies may have continued to migrate until continental separation reached a water gap of 745 miles (1,200 km) during the first half of the Tertiary ~ 50 mya (28, 72).

Table 1. Summary of when possible early intercontinental plant migration patterns for primitive ancestral grasses could have occurred (72).

Event Occurrence	Specific Continental Contact Event	Event Dating (millions of years ago)
Last	Africa and India	~ 100 mya - late-Lower Cretaceous
Last	Africa and South America	~ 90 mya - early-Upper Cretaceous
Last	Africa and Eurasia, prior to Miocene event	~ 63 mya - early-Paleocene
Last	Europe and North America	~ 49 mya - mid-Eocene
Last	South America to Australia via Antarctica	~ 38 mya - mid-Eocene
First	India contacts Asia	~ 45 mya - early-Eocene
First	reestablished between Africa and Eurasia	~ 17 mya - mid-Miocene
First	South America and North America	~ 5.7 mya - late-Miocene

Major island-hopping of animals and grasses is probably represented by southeast Asia - Australia via New Guinea ~ 15 mya, and by South America - North America via an intermittent land connection ~ 10 to 12 mya (72). Migration from Asia-Europe to North America via the Bering Land Bridge has occurred since ~ 55 mya (72). The ancestral Bovidae migrated to North America from Europe-Asia via the Bering Land Bridge (73). There also was a land uprising to form the Gibraltar Strait Bridge between Europe and Africa ~ 5 mya by which Bovidae migrated to Africa. Oceanic island-hopping between South America and North America may have occurred from ~ 45 mya. Mountain-hopping from Europe to Asia to North America to South America may have occurred starting at least 10 mya for *Agrostis*, *Festuca*, and *Poa* (39, 48, 72).

Primitive Ancestral Grasses. Definitive evidence is limited concerning the continental center-of-origination for primitive ancestral grasses. Fossil records for the grass family Poaceae within the angiosperms and their ancestors are very incomplete. Based on paleobotanical evidence, including silicified plant tissues termed phytoliths and stable carbon isotope studies, primitive ancestral grasses appeared rather late in the earth's history at somewhere between 55 and 70 mya (43, 48, 51). It has been proposed and supported by phylogenetic analyses that the Arundinoideae was the ancestor from which the cool-season monophyletic Pooideae arose (28, 52).

Available evidence suggests the primitive ancestors of Poaceae occurred in the tropical forests and fringes of Gondwanan-Africa (17, 28, 58, 86). An extensive review of pollen fossil records by Muller (64) indicates basal Poaceae were present in the Paleocene epoch ~ 55 to 60 mya in central to eastern Africa and east-central South America. Macro-fossil plant remains from a formation in western Tennessee suggest the presence of a common ancestor for the Poaceae under tropical, seasonally dry conditions ~ 55mya (30).

This is a significant finding, relative to native grass species evolution in North America. The crown node of the BEP & PACCMAD clades has been estimated phylogenetically at ~ 57 mya (17). Phytoliths preserved in coprolites from central India revealed five extant Poaceae subclades present during the Upper Cretaceous ~ 65 to 70 mya (70). Molecular phylogenetic and cladistic

biogeographic analyses propose a dating range of Poaceae at Late Cretaceous ~ 65 to 96 mya (16, 17, 26, 35, 58).

Both diversifications and migrations of grasses have been influenced by changing regional environmental, edaphic and biotic influences. Included were changes in tectonic plate processes, ice age glaciation, volcanic activity, tropical dominance, sea level, fire, water availability, favorable temperatures, seasonality, competitive flora and fauna. Note that ice age climatic change during the Pleistocene was particularly disruptive in terms of grass species diversification and migration in the Northern Hemisphere.

Diversification. Phytogeographical analyses suggest early differentiation of the lineages for tribes of the Poaceae may have started by the end of the Upper Cretaceous (26, 58). The Pooideae probably diversified initially in temperate environments at high latitudes and high altitudes in the tropics (58). From ancestral origination in fringe-forested regions, there appears to have been further evolution to savannas, and then to temperate steppes in the case of the Pooideae. The C₃ cool-season ancestral grasses are estimated to have arisen during the Eocene ~ 44 to 55 mya (30, 95). The Pooideae are estimated to have migrated to the steppes of Eurasia ~ 38 to 47 mya (17). Grass pollen fossils are more abundant during this epoch (64).

The C₄ physiological characteristics of warm-season ancestral grasses evidently appeared as at least 12 distinct events and locations starting in the Oligocene ~ 30 mya and subsequently thru 15 mya (16, 17, 43, 51, 54, 86). The C₄ warm-season ancestral grasses of the Panicoideae and the Chloridoideae are estimated to have originated ~ 26 mya and ~ 29 mya, respectively (17). The emergence of C₄ grasses was associated with a drop in atmospheric carbon dioxide (CO₂) levels (16, 37) and/or seasonally drier climates (28, 56). Macrofossils of Chloridoideae grass leaves from Kansas indicate C₄ Kranz leaf anatomy existed in the Miocene ~ 5 to 7 mya (97). Also, evidence indicates that C₄ grasses expanded in the Americas during the late-Miocene (56).

Early grasses eventually became significant components of plant communities in the dryer savannas, steppes, and prairies. The increasing dominance of grasses was probably aided by periodic

lightning-induced fires that destroyed most tree and shrub competitions, while the grasses survived via basal tillering. Actually the dry grass biomass provided fuel for the fires.

It is postulated that since Gondwana phytogeographically separated into the present major continents, numerous distinct grass diversifications have occurred on four separate continents. The original ancestral grasses have now evolved into a large family of angiosperms with ~ 40 tribes, ~ 800 genera, and ~ 11,000 species (26).

Migration. Grasses had eventually dispersed to all continents ~ 60 million years after their ancestral Gondwanan-Africa origin (17). Phylogenetic studies suggest the first migration within the Pooideae from Eurasia to North America occurred ~ 38 mya via the North Atlantic Land Bridge when there was a global warming trend (17). Subsequently there is evidenced that other BEP taxa migrated from Europe via Asia to North America by the Bering Land Bridge (48).

Modes of seed dispersal away from the parent plant can occur by animals, gravity, wind and water. Certain grass species possess characteristics that allow either internal or external transport by animals. Internal mechanisms can occur via the digestive tract, primarily of large grazing animals (66, 71). The ingestion and internal passage of viable seeds through the digestive systems of animals has been documented for C_3 grasses *Agrostis stolonifera*, *Festuca rubra*, *Festuca elatior*, *Poa annua*, *Poa compressa*, and *Poa pratensis* (34) and for C_4 grasses *Axonopus fissifolius* (19, 65), *Buchloe dactyloides*, *Cynodon dactylon*, and *Paspalum notatum* (19).

Certain chaff-like grass seeds facilitate external transport on the fur coats and hairy hides of mobile animals. Seeds with distinct awns, hairy lemmas, and/or sharp-pointed florets allow penetration in animal hair and resist easy withdrawal (24).

Many grasses adapted for turfgrass purposes have very small, light-weight seeds that can migrate via wind. For example, the approximate number of seeds per pound (0.45 kg) for *Agrostis capillaris* > 5 million, *Cynodon dactylon* > 1.5 million, *Poa pratensis* > 1 million, and fine-leaf *Festuca* > 400,000 (10). Large dust storms from Africa to the Americas may have furthered intercontinental dispersal of certain grass seeds.

The same chaff-like, light-weight seed characteristics also aid migration in flowing water down streams and rivers, especially in association with eroded soil. *Stenotaphrum secundatum* seed has an inflorescence structure that enhances flotation on ocean currents between islands and along coastal shorelines (79).

The presence of a chemical germination inhibitor in the seed is another mechanism by which some species of grass seeds extend the duration for potential migration. *Poa pratensis* is an example with modern cultivars having seed germination delays of 3 to 4 months (10) following maturation. Certain earlier ancestral grasses probably had longer germination inhibition periods due to a higher inhibitor content and/or greater resistance to inhibitor degradation.

Some grass species have what is termed hard seed, in which the seed coat is impermeable to water needed to initiate germination. Typical turfgrass species with hard seeds include *Cynodon dactylon*, *Eremochloa ophiuroides*, and *Zoysia japonica* (10). Germination can be improved by mechanical or acid scarification to open the seed coat barrier. Either the presence of a hard coat or an inhibitor in seed could facilitate distance dispersal of such grass species in the digestive systems of birds and animals, especially herbaceous-grass feeding animals (24).

Grazing Mammals and Turfgrasses. The ancestral species for some turfgrass species evolved in association with herbivorous grazing mammals. Early, now extinct browsing ungulates known as Condylarths evolved while feeding on ancestral C_3 grass terrestrial ecosystems during the early Paleocene ~ 65 mya (8, 42). Subsequently, during the early-Eocene ~ 55 mya, early herbivorous ruminant Artiodactyls arose. The Bovid subfamilies exhibited a rapid diversification ~ 23 mya (63). The Bovidae family, with a distinct tooth structure, arose in the late-Miocene ~ 5 to 9 mya. Evolving in Eurasia were cattle, antelope and bison of the subfamily Bovinae, plus goats, sheep, water buffalo and musk-ox of the subfamily Caprinae (63, 95).

Early grasses persisted as a minor component of a forested plant community for a long time. Eventually, ancient grass-dominated ecosystems developed in certain open regions ~ 5 to 6 mya as a result of significant changes to a drier environment

that caused a decline in tree populations (91). During this time, certain herbivorous mammals also were evolving with mouth parts adapted to grazing more closely, and also with high-crowned teeth and/or constantly-growing teeth needed for grazing on grasses with high phytoliths or silicified fibers (61). Consequently, there was selection toward grass species in certain regions that were structurally adapted to survive severe defoliation (88).

While open-habitat grasses exhibited taxonomic diversification in North America at least 34 mya, phylogenetic studies suggest they did not become ecologically important until formation of the savanna-like Great Plains 23 to 27 mya (90). A major expansion of C_4 grasses occurred during the late Miocene ~ 6 to 8 mya during a major climate change to a dryer environment and lower atmospheric CO_2 levels (23, 37, 56). Intercontinental distribution of both C_3 and C_4 grasses stabilized during the late Miocene ~ 6 mya (61).

Carbon dating of herbivorous mammalian skeletons and attached grass remnants by paleobotanical studies and DNA sequencing confirm a co-migration and even co-evolution among a number of grazing mammals and certain perennial grasses (16, 24). The interrelationship of low-growing grasses and herbivorous mammals continued over an estimated period of ~ 10 to 20 million years (8). The result was a number of grass species having (a) leaves with basal meristems, (b) shoots with short basal internodes, and (c) prostrate, creeping growth habits via lateral stems termed stolons and rhizomes. Evolution of these morphological adaptations in some grasses allowed subsequent use for turfgrass purposes involving frequent, low mowing.

Some centers-of-diversification for temperate grasses are of more recent post-Pleistocene development ~ 2 to 1 mya due to glacial effects from the last ice age. Examples are the North American northeast and midwest regions and the higher altitude meadowlands of Central Europe.

Human Dispersal. Intercontinental human grass dispersals may have occurred even earlier than New World colonial times. Over 600 years ago world voyagers and global explorers may have dumped from their ships at various world-wide locations sweepings containing straw and hay

bedding composed primarily of grasses. Later colonists traveling via boat to the New World, primarily from Europe, brought grasses for agrarian forage and pasture purposes. These introduced grasses had been selected for more than 400 years based on a higher yield or biomass production needed for feeding herbivorous domesticated animals (81). These early colonists preferred the taller-growing, high-yielding, introduced grasses for agrarian purposes. The European forage and pasture grasses were less desirable as turfgrasses, especially in early times of laborious manual mowing. Many European-introduced grass genotypes naturalized in North America through intraspecies diversification and natural selection over a period of 300 to 400 years. These grasses became interspersed with pre-colonial native grass communities, especially in eastern North America. For example, a good germplasm source for turfgrass selection is in old cemeteries that have been mowed regularly, but typically not irrigated or fertilized. Clarification as to the specific genetic sources from which many contemporary turfgrass cultivars were derived will require molecular phylogenetic research.

Modern Diversification. Globally, there are ~ 40 grass species utilized as turfgrasses to varying degrees. Most are heterozygous with inflorescence fertilization by wind-aided cross-pollinated. The result is a wide range in diversity with many grass ecotypes that have specific adaptation potentials to the numerous global variations in the environmental, edaphic and biotic components contributing to the broad array of ecosystems. Furthermore the diversification process for individual grass species is ongoing with new genotypes emerging and some genotypes possibly becoming extinct if poorly adapted to the specific environment in certain ecosystems (81).

To the untrained observer a turfgrass community, such as a lawn, may appear to lack diversity. This is because the basic leaf characteristics are more similar in shape, orientation and color compared to the broad-leaf dicotyledonous species such as trees, shrubs, and flowers. Actually the genetic diversity is substantial in most mature turfgrass lawn communities. It is a key to the capability of grasses to recover and survive as perennials under wide seasonal variations in temperature, water, shade, traffic, and pest stresses.

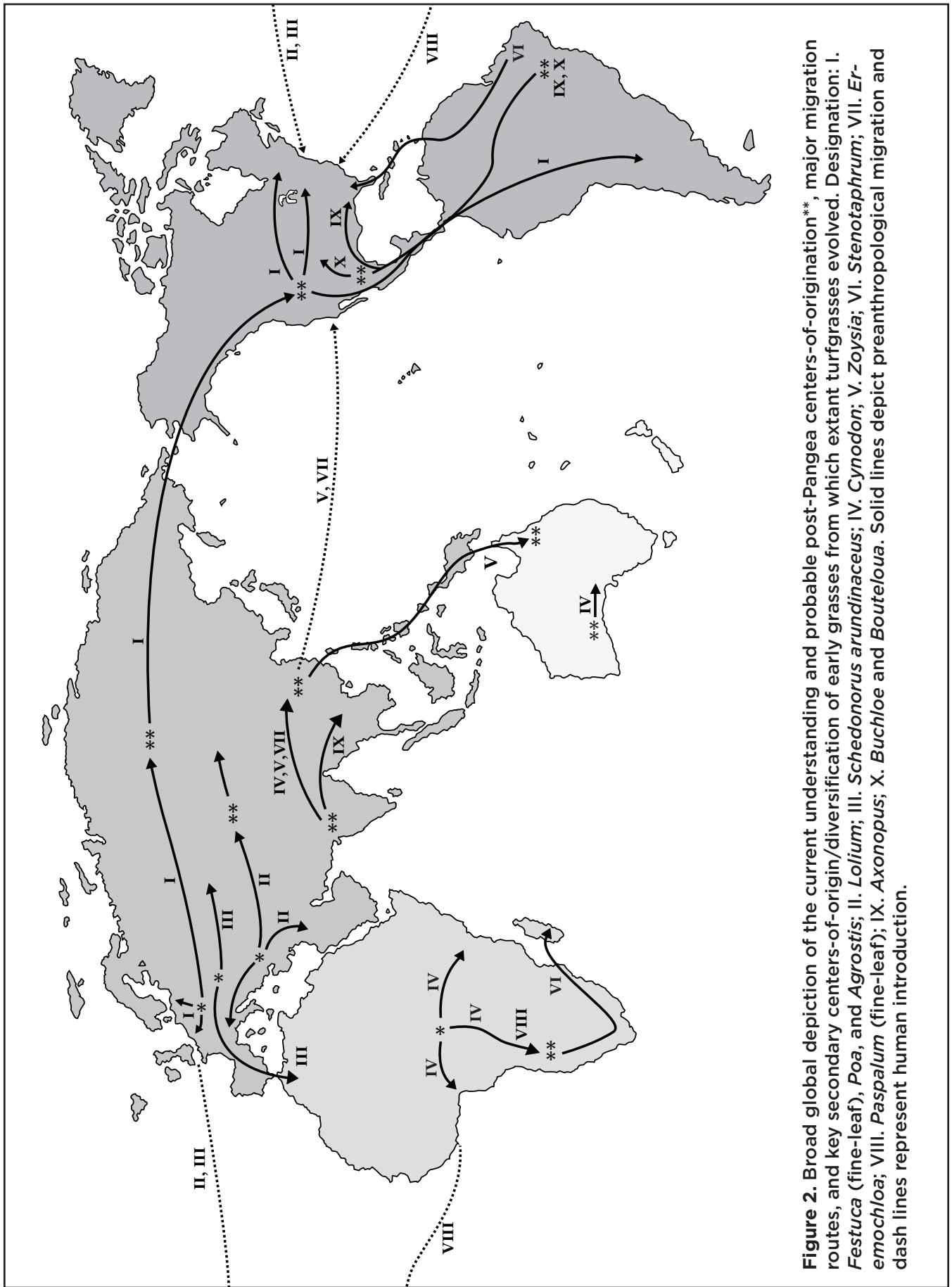


Figure 2. Broad global depiction of the current understanding and probable post-Pangea centers-of-origination**, major migration routes, and key secondary centers-of-origin/diversification of early grasses from which extant turfgrasses evolved. Designation: I. *Festuca* (fine-leaf), *Poa*, and *Agrostis*; II. *Lolium*; III. *Schedonorus arundinaceus*; IV. *Cynodon*; V. *Zoysia*; VI. *Stenotaphrum*; VII. *Eriochloa*; VIII. *Paspalum* (fine-leaf); IX. *Axonopus*; X. *Burchloe* and *Bouteloua*. Solid lines depict preanthropological migration and dash lines represent human introduction.

COOL-SEASON TURFGRASSES

The primitive ancestral center-of-origination for cool-season grasses (Pooideae) is thought to have been from the tropical forest margins of Africa at higher altitudes (28). The unique evolutionary feature possessed by Pooideae was adaptation to cold climates that allowed migration to the temperate steppes of Eurasia (28). Subsequently the Pooideae may have emerged under a tree-shrub dominant, temperate ecosystem with sufficient precipitation for sustained growth and possibly survival during occasional short periods of droughty conditions. Taxonomic divergence of the base Pooideae group appears to have been initiated after a global super-cooling period ~ 26 to 33.5 mya (78). Diversification also was probably characterized by a cool temperate climate, plus reasonably good precipitation and soil fertility. Cool-season grass diversification in Eurasia may have been greater in the mountainous areas where shade from trees was reduced. Plant explorers³ report greater diversity within the *Festuca*, *Poa* and *Agrostis* species in Europe-Asia at altitudes above 3,000 feet (915 m).

The cool-season turfgrasses discussed herein are taxonomically classified in the Pooideae, with C_3 physiology (96). Within the Pooideae there are two supertribes, including Poodae, and seven tribes, including Poeae. The Pooideae includes ~ 3,300 species. The Poeae encompass ~ 115 genera and ~ 2,500 species (6), and occur with a high species frequency percentage in the higher latitudes and higher altitudes where summer and winter temperatures are colder (92). The cool-season turfgrasses occur in the temperate climates of both the northern and southern hemisphere and in mountains of the tropics, with an optimum temperature range of 60 to 75°F (16 to 24°C) (10, 11). Migration bridges of certain C_3 cool-season perennial grasses evidently occurred by mountain-hopping. The likely migration route for the freeze tolerant *Agrostis*, *Festuca* and *Poa* species into the South American Andes was via the North American, Asian and European mountains (18, 48). In North America these three genera typically have their largest range of species diversity in the western mountainous regions. Geophysical aspects of extant cool-season turfgrass will be addressed

for the major species utilized in the United States. Included are the fine-leaf fescues, bluegrasses, bentgrasses, ryegrasses and broad-leaf tall fescue.

Fine-Leaf Fescue. The early species center-of-origin for fine-leaf fescues (*Festuca* species) has been reported to be in central-Europe during the mid-Miocene ~ 13 mya based on phenotypic and biogeographical analyses (48). *Festuca* is reported to be an ancient group and a main evolutionary line in diversification of the Poeae Tribe (19). Two main *Festuca* clades are evident from phenetic and phylogenetic analyses, being fine-leaf and broad-leaf, that had split into diverging lineages (29, 31, 93, 94). Within the fine-leaf *Festuca* clade arose the *F. ovina* and *F. rubra* groups (94). The latter is smaller in number of subgroups (69) and is yet to be fully defined due to the paraphyletic nature (2, 6, 10). The *F. ovina* complex is the oldest of the turfgrass-types (31), followed in lineage by *F. trachyphylla* and *F. rubra* ssp. *rubra*. Based on phenetic distance analysis *F. ovina* and *F. trachyphylla* are distinct, but closely related (2).

Fine-leaf fescues probably diversified in cool, continental, open forest regions, possibly in mountainous areas, and are included in the *Festuca* subgenus (1, 2, 6, 7). Diversification of the *Festuca* genus resulted in a major expansion, with ~ 400 known species (6). Their extant occurrence ranges from temperate to alpine to polar regions of both hemispheres (2). Chewing's fescue (*F. rubra* ssp. *commutata*), hard fescue (*F. trachyphylla*), sheep fescue (*F. ovina*), slender-creeping red fescue (*F. rubra* ssp. *littoralis*), and strong-creeping red fescue (*F. rubra* ssp. *rubra*) are the fine-leaf *Festuca* species now used as turfgrasses in the United States (10, 11). These five fine-leaf *Festuca* are seed propagated and largely cross-pollinated. The taxonomic classification of Chewing's fescue as traditionally used is open to question (2). The fine-leaf fescues migrated outward throughout much of Europe, into central and eastern temperate Asia (25), and into Africa. Eventually they moved across the Bering Land Bridge into North America and migrated southward into Central America and over the Panamanian Land Bridge into South America (Figure 2). The basic route in the Americas was

³ Personal communication with William A. Meyer of Rutgers University, New Jersey, USA.

north-to-south via the western mountains of North America to the Andes to Patagonia over a period ~ 3.8 to 10 mya. This migration route has been documented among the *Festuca* species by biogeographical analyses (48). There also were outward migrations into the temperate climatic regions of the continent. These fescues are used as a turfgrass in the cooler portions of the cool climatic regions of the United States, being especially adapted to shaded and low-nitrogen fertility conditions (10, 11).

Most turfgrass-type fine-leaf fescue species (*Festuca*) are native to North America, having persisted for more than three centuries. There are at least 37 *Festuca* species that are native to North America (6, 7), including the red, hard, and sheep fescues now used as turfgrasses.

Bluegrass. The early species center-of-origination for the bluegrasses (*Poa*) based on phenotypic and cladistic analyses (85) is temperate, open Eurasia. The *Poa* genus is classified in the *Poeae* tribe (96), with diversification being expansive to ~ 500 known species. Global distribution studies reveal the *Poa* species have the highest relative specific differentiation in regions of high latitude and high altitude (47). *Poa pratensis* evolved and diversified in geographical regions characterized by a cool continental climate and probably in fringe-open meadow areas interspersed in forests on relatively fertile soils. *Poa trivialis* is thought to have evolved in the cooler, northerly, forest regions of Europe under relatively wet climatic and soil conditions on clayey soils. The diploid *P. trivialis* ssp. *trivialis* has naturalized in North America (6). The bluegrass species are propagated by seed and vegetatively by lateral stems such as rhizomes or stolons.

Poa annua is a ubiquitous, cosmopolitan grass that is very well adapted to anthropological habitats. It is considered an annual weed in some turfgrass ecosystems, especially the bunch-type annual bluegrass (*P. annua* var. *annua*). The stoloniferous perennial creeping bluegrass (*P. annua* var. *reptans*) tends to dominate when under a long-term managed component in certain turfgrass situations (11). *Poa annua* is thought to have arisen from hybridization between *P. infirma* and *P. supina* (6).

A biogeographic migration pattern similar to the fine-leafed fescues through Asia via the Bering

Land Bridge to North America (72) is probable for the bluegrasses (Figure 2), especially as many *Poa* species have similar temperature responses including good to excellent freeze stress tolerance (2, 9). *Poa pratensis* has a circumpolar distribution (85), with a capability to develop numerous ecotypes to thrive in distinctly different habitats (93). More than 60 species of *Poa* are now considered native to North America (6). *Poa* has a high species frequency percentage in regions with a July mid-summer isotherm below 75° F (24°C) (47). Chloroplast-DNA phylogenetics and cladistic analyses for biogeographical events revealed at least six groups of *Poa* species had independently colonized secondary centers-of-diversification in North America, including Kentucky bluegrass and Texas bluegrass. The *Poa* are found extensively in the western mountain ranges of North America (41), and the *P. pratensis* complex has been termed native to the Rocky Mountains (50). The extant Kentucky bluegrasses of eastern United States may be of an integrated ancestry with post-glacial reinvasion from the west or south and European colonist introductions (22).

The *Poa* species utilized in the United States as turfgrasses resulting from diversification/migration include Kentucky bluegrass (*P. pratensis*), rough bluegrass (*P. trivialis*), and Texas bluegrass (*P. arachnifera*) (10, 11). *Poa pratensis* is a facultative apomictic and highly polyploid. Kentucky bluegrass is widely used as a turfgrass in the cool climatic regions of the United States under minimum shade, while rough bluegrass is best adapted in moist to wet, shaded conditions in the cooler portions of the cool-humid climatic region (10, 11).

Texas bluegrass is unique among the turfgrass-type *Poas* in adaptation to warm climates and is native to the southern Great Plains (85). It is best adapted to moist, fertile soils and bottom lands. Available evidence suggests *P. arachnifera* or its ancestor migrated north from South America, as two very close sister species occur there (85). Recently hybrid cultivars of *P. pratensis* x *P. arachnifera* have been developed for turfgrass use.

To conclude, a number of *Poa* species are possible North American natives, including *P. arachnifera* and *P. pratensis*. Biogeographical analyses/molecular phylogenetic research with a range of *Poa* species similar to that for the fine-leaf fescues are needed

for proper documentation, which should include *P. annua* and *P. trivialis*.

Bentgrass. Based on phenotypic evidence the early diverged species center-of-origination for the bentgrasses (*Agrostis* species) was in south-central Mediterranean Eurasia (84). The *Agrostis* genus is of ancient origin, and has been morphologically classified in the Poaceae, with ~ 200 known species (6, 96, 97) including at least 21 native North American species. The *Agrostis* probably diversified in an environment characterized by fringe-forest zones of partial shade, and minimal moisture stress on poorly-drained, clayey soils. Mountainous regions favored the origination of polyploid forms of *Agrostis* (84), with most adapted to narrow habitats (7). Diversification resulted in three bentgrass turfgrasses as now utilized in the United States, including colonial bentgrass (*A. capillaris*, syn. *A. tenuis*), creeping bentgrass (*A. stolonifera*, syn. *A. palustris*), and velvet bentgrass (*A. canina*) (10, 11).

Low levels of interspecific hybridization may occur between *A. stolonifera* and both *A. capillaris* and *A. castellana*, but are not likely for *A. canina* (13). Allotetraploids *A. capillaris* and *A. stolonifera* have the A_2 subgenome in common (49, 85). Phylogenetic analyses and divergence time estimates indicate these two species diverged from a common ancestor ~ 2.2 mya (76). Cluster analysis shows the primary cultivated species *A. capillaris* and *A. stolonifera* are more similar to each other than the diploid *A. canina* is to either (4). *Agrostis clavata* has been suggested as a progenitor of *A. capillaris* and *A. stolonifera* based on MITE - display marker clustering and ploidy prediction (3). Also genetic marker studies suggest *A. canina* may have contributed to the evolution of *A. stolonifera* as the likely maternal parent (74). Turfgrass-type *Agrostis* species are propagated primarily by seed, being largely cross pollinated. *Agrostis stolonifera* also can be propagated vegetatively by stolons.

A mountainous migration pattern of *Agrostis* species from Europe to North America (72) probably occurred similar to that documented for the fine-leaf fescues (Figure 2). The turfgrass-type *Agrostis* have good to excellent freeze stress tolerance (9, 11). Northern salt marsh and lakeside populations of *A. stolonifera* are considered native to North America (6). The species is well adapted to temporary flooding and wet soil sites, reflecting the

conditions under which creeping bentgrass originated in Eurasia. The extant bentgrass cultivars tolerate close, frequent mowing while sustaining good shoot density (10, 11).

The turfgrass-type *Agrostis* species have been viewed by some as being introduced to the United States due to oceanic separation from the early center-of-origination. By inference from recently available evidence, specifically from the fine-leaf fescue research, the turfgrass-type bentgrasses would be considered possible natives to the United States. Hopefully, needed clarifying biogeographical analyses/molecular phylogenetic investigations will be accomplished.

Ryegrass. The early species center-of-origination for the ryegrasses (*Lolium* species) based on genetic diversity was the open, temperate, southern Eurasian region along the Mediterranean Sea. The *Lolium* genus is classified in the Poaceae (96), with diversification limited to ~ 5 known species that occurred starting ~ 2 mya (6, 48). It has been proposed that the *Lolium* genus and *Schedonorus pratensis* evolved from a common ancestor (74, 79), and split ~ 2.8 mya (48). Extant *Lolium* turfgrass cultivars tend to have limited shade adaptation and their center-of-origin and diversification probably were characterized by open areas.

Propagation is by seed being cross-pollinated, with most mowed turfgrass cultivars being bunch-types. The turfgrass-type species used in the United States include perennial ryegrass (*L. perenne*) and annual ryegrass (*L. multiflorum*) (10, 11). They are interfertile and naturally intergrade (6). The turfgrass-type perennial ryegrasses are utilized in the warmer portion of the cool climatic region of the United States and for winter overseeding of warm-season turfgrasses. They are best adapted to mild winters and cool-moist summers, and to fertile soils (10, 11).

Migration of the *Lolium* was south into northern Africa, especially in mountainous regions, into northern Europe, and also eastward into Asia and India (Figure 2). Transcontinental pre-Holocene migration research is lacking. Lack of freeze stress tolerance (9, 10, 11) may have prevented migration to North America via the Bering Land Bridge.

Thus, based on the available phenotypic evidence the ryegrasses utilized for turfgrass purposes

in the United States are probably naturalized grasses first introduced by human trans-Atlantic movement in the mid-1600s for forage and pasture utilization in domestic animal agriculture. Confirmation is needed via biogeographical analyses/molecular phylogenetic research.

Tall Fescue. The early species center-of-origination for broad-leaf *Schedonorus* was in mild-temperate Eurasia, separating from fine-leaf *Festuca* during the Miocene ~ 15 mya (48, 93). The *Schedonorus* genus is classified in the *Schedonorus* subgenus (96, 07), with the turfgrass-type being allopolyploid tall fescue (*Schedonorus arundinaceus*, syn. *Festuca arundinacea*) (6). Tall fescue probably diversified under summers characterized by higher temperatures and less rainfall. *S. arundinaceus* is younger in lineage than the turfgrass-type fine-leaf *Festuca*, and based on cluster analysis is closely related to *Schedonorus pratensis* (6, 99). Biological clock estimates indicate the Asian-American clade of broad-leaf *Schedonorus* apparently diverged from the fine-leaf *Festuca* clade ~ 12 mya (48). Certain hexaploid turfgrass-type tall fescues, such as Rebel II and Bonanza, are clustered in a subgroup according to cluster analysis (99). Propagation is

by seed being primarily cross-pollinated, with tall fescue behaving as a bunch-type when regularly mowed as a turfgrass.

Migration of *S. arundinaceus* from Europe extended eastward into Asia and south into Africa, especially via the mountainous regions (Figure 2). Potential transcontinental migration to the United States prior to Holocene human activities has not been properly investigated. Northward dispersal in Europe may have been limited due to a lack of freeze stress tolerance (9, 10, 11). Tall fescue is best adapted for turfgrass use in the transitional and warmer-cool climatic regions of the United States under regular mowing at moderately high heights (10, 11).

Based on the limited available information, tall fescue is considered a naturalized species thought to have been first introduced into the United States by transcontinental human activities in the mid-1800's for forage and pasture use in domestic animal production. Biogeographical analyses/molecular phylogenetic research are needed for confirmation.

Table 2. A representation of key events in grass origin and evolution during the latter portion of earth geological history, based on current knowledge.

Epoch	Cumulative Time* (millions of years)	Approximate Duration (millions of years)	Major Plant/Grass Events	Related Events
Lower/Early Cretaceous	99.6 - 145.5	45.9	<ul style="list-style-type: none"> ▶ extinction of many species of African flora 	<ul style="list-style-type: none"> ▶ South America isolated from Africa ▶ India, Antarctica, and Australia separate from Africa ▶ climate mild to tropical
Upper/Late Cretaceous	65.5 - 99.6	34.1	<ul style="list-style-type: none"> ▶ evolution of nongrass flowering plants ▶ reports of grass pollen fossils 	
Paleocene	55.8 - 65.5	9.7	<ul style="list-style-type: none"> ▶ definitive reports of grass pollen fossils ▶ flowering plants become more successful ▶ extant plants appear 	<ul style="list-style-type: none"> ▶ North America-Greenland isolated from Europe ▶ seas retreat and climate tropical ▶ rapid spread of mammals ▶ early herbivorous mammals ▶ India contacts Asia
Eocene	33.9 - 55.8	21.9	<ul style="list-style-type: none"> ▶ primitive C₃ cool-season grasses arise - Poaceae ▶ increasing evidence of grass pollen fossils and macrofossils 	<ul style="list-style-type: none"> ▶ warm climate and seas flood the land ▶ Australia separates from Antarctica ▶ Alps and Rocky mountains form ▶ modern mammals emerge
Oligocene	23.0 - 33.9	18.9	<ul style="list-style-type: none"> ▶ abundant grass pollen fossils ▶ diversification of C₃ grass species ▶ trees and grasses cover much of land ▶ migration of C₃ grasses to Africa ▶ primitive C₄ warm-season grasses evolve 	<ul style="list-style-type: none"> ▶ climate cools and becomes dryer ▶ widespread forests ▶ atmospheric CO₂ levels lowered ▶ increased fire frequency
Miocene	5.3 - 23.0	17.7	<ul style="list-style-type: none"> ▶ fine-leaved fescues emerge in Europe - Festuca ▶ grasses become ubiquitous globally ▶ large temperate grasslands form globally 	<ul style="list-style-type: none"> ▶ sea level falls, Himalayas and Andes rise ▶ Bovidae evolve in Europe and Asia ▶ golden age of mammals, with most diversity
Pliocene	2.6 - 5.3	2.7	<ul style="list-style-type: none"> ▶ expansion of grasslands and grasses emerge on US Great Plains ▶ savannas replace many forests in Africa 	<ul style="list-style-type: none"> ▶ climate cools and becomes dryer ▶ continents in present position ▶ Bovidae invade Africa
Pleistocene	0.01 - 2.6	2.59	<ul style="list-style-type: none"> ▶ shift in grass species of US Great Plains 	<ul style="list-style-type: none"> ▶ Panamanian Land Bridge forms ▶ last ice age covers northern lands and sea level falls ▶ humans evolve & develop hunting skills ▶ withdrawal of the ice sheets/glaciers of ice age
Holocene (ongoing)	0 - 0.01	0.01	<ul style="list-style-type: none"> ▶ present flora and fauna ▶ turfgrass use developed in last 800 years ▶ natural diversification/selection of cultivars in mowed turfgrass areas 	<ul style="list-style-type: none"> ▶ climate warms and sea level rises ▶ development of agriculture by humans ▶ rise of human civilization

*The geologic time scale is from The Geological Society of America (2009).

WARM-SEASON TURFGRASSES

The primitive ancestral center-of-origination for the warm-season grasses is thought to have been Gondwanan-Africa (28, 72), with West Gondwana migration to South American and East Gondwanan migration to India and to Australia via Antarctica. Key synapomorphies include Kranz leaf anatomy and chloridoid bicellular microhairs on the leaf epidermis (55). The C_4 photosynthetic pathway characteristic of warm-season grasses evolved in Africa from C_3 ancestral grasses at a later time in the earth's history, and involved multiple biochemical and histological C_4 events (16, 17, 32, 51, 82). The first evidence of C_4 photosynthesis in the Chloridoideae occurred ~ 33 to 30 mya (15, 17).

Fossil records indicate the ancestral species of warm-season Poaceae originated in West Gondwana, now Africa, mainly in savanna ecosystems (72). Phylogenetic analyses suggest the monophyletic Panicoideae and Chloridoideae are derived from the ancestral polyphyletic Arundinoideae (32, 52). The PACCMAD clade exhibited phylogenetic diversifications during the mid-Miocene through late-Quaternary (16). Phylogenetic molecular studies reveal the Chloridoideae may date as early as the late-Oligocene ~ 31 mya (16, 17), but major global migration may not have occurred until the Pliocene (67). Species of C_4 turfgrass-types tend to have multiple secondary centers-of-origination in geographical regions closer to the equator under warm climatic conditions. Twenty-four shifts in phylogenetic diversification rates have been identified among the C_4 grass lineages, with 19 during the Miocene and 5 during the Pliocene (16).

Most warm-season turfgrasses are taxonomically classified within either the Chloridoideae or Panicoideae (96). The Chloridoideae has eight tribes including Cynodonteae and Zoysieae, while the Panicoideae encompasses two tribes including the Paniceae. Extant warm-season turfgrasses occur mostly in the warm, tropical and subtropical climates, with an optimum temperature range of 80 to 95°F (27 to 75°C). Most are prone to chill stress in the 52 to 58°F (11 to 15°C) range, with resultant low temperature discoloration and winter dormancy (10, 11, 12). Extant Chloridoideae typically are adapted to survive at mean temperatures for the coldest months above 50° F (10° C) (64).

Locations and dating for species centers-of-origination and geophysical migrations are increasingly based on phenotypic, molecular phylogenetic, and allied cladistic assessments. Fossil types of evidence are limited as fossilization was restricted in dry savanna climates where warm-season grasses diversified. Geophysical characteristics of extant warm-season turfgrasses are addressed for the major species utilized in the United States, including bermudagrass, zoysiagrass, St Augustinegrass, centipedegrass, seashore paspalum, carpetgrass, American buffalograss, and gramagrass.

Bermudagrass. The primary center-of-origination for the bermudagrasses (*Cynodon* species) is in open, southeastern Africa (38). Subsequently early diversification was associated with grazing pressure from large herds of herbivorous African, hoofed mammals. Based on biostematic and phylogenetic molecular research, the *Cynodon* species secondary centers-of-origin/diversification include South Africa, India, Afghanistan, China, and Australia (45).

The ubiquitous, cosmopolitan *C. dactylon* is now found throughout the warm-temperate, subtropical, and tropical climatic regions of the world (45). The *Cynodon* genus is classified in the Cynodonteae and Chloridinae, with limited diversification of ~ 9 known species and 10 varieties (6, 46, 67, 96). Cluster analysis of DNA amplification products has confirmed this earlier taxonomic classification. Evidently the genetic diversity of *C. dactylon* var. *dactylon* was generated internally (45). It thrives under soil disturbance on sunny sites. Low-growing *Cynodon* species used as turfgrasses in the United States include dactylon bermudagrass (*C. dactylon* var. *dactylon*), a sterile hybrid bermudagrass (*C. dactylon* x *C. transvaalensis*), and a natural sterile triploid hybrid (*Cynodon* x *magennisii*) (10, 11). Molecular phylogenetic analysis has identified cluster groups broadly based on relative leaf width (20).

The presumed geophysical migration of the ancestral grass was via the East Gondwana land connection. Subsequent pre-Holocene migration was outward around Africa, and into southern Europe, Asia, and Australia (Figure 2). Propagation is vegetatively by stolons and rhizomes, and

by seed for *C. dactylon* being cross-pollinated. The climate under which bermudagrass species evolved was subtropical with typically dry summers that resulted in a deep extensive root system, low evapotranspiration rate, extensive lateral stem development, and superior drought resistance. The modern *Cynodon* turfgrass cultivars have retained these water-conserving characteristics, but most lack shade adaptation (10, 11).

Unintended trans-Atlantic human movement of *C. dactylon* via ships of the Spanish conquistadors probably occurred in the 1600's to both North and South America (100), followed by further dispersal/naturalization and intraspecies diversification in the warm climatic regions. The *dactylon* bermudagrass (*C. dactylon* var. *dactylon*) introduced into the United States was readily dispersed, and became naturalized. The questions are when, by what means, and if extant native *C. dactylon* were already present in the United States as a result of earlier natural migration from Africa, possibly via South America. In contrast, African bermudagrass (*C. transvaalensis*) was probably a human introduced species from South Africa to the United States, with minimal dispersal/naturalization. Biogeographical analyses/molecular phylogenetic research are needed to clarify these dispersal aspects.

Zoysiagrass. Phenotypically, the zoysiagrasses (*Zoysia* species) are recognized to have a post-ancestral center-of-origin under warm-tropical, open conditions in southeast China. Their primitive ancestral grass center-of-origination probably occurred in Africa, where it is assumed they subsequently became extinct during a severe arid period (72). The *Zoysia* genus is classified in the Cynodonteae and Zoysiinae (68), with diversification being relatively small with ~ 11 known species (7, 67, 96). Shoots of the turfgrass-type *Zoysia* species possess a high silica content, which suggests that herbivorous grazing mammals may not have been as significant in their diversification and migration. Based on molecular phylogenetic analyses the *Zoysia* genus arose later than the *Cynodon* (15). *Zoysia* species now utilized for turfgrass purposes in the United States include Japanese zoysiagrass (*Z. japonica*), manila zoysiagrass (*Z. matrella* var. *matrella*), and to a lesser extent mascarene zoysiagrass (*Z. pacifica*, syn. *Z. matrella* var. *tenuifolia*) (7, 10, 11). These three readily intercross suggesting a

close genetic relationship. Also used as a turfgrass is hybrid zoysiagrass (*Z. japonica* x *Z. pacifica*) cv. Emerald. Cluster analyses of RAPD revealed groupings that differ from the classical taxonomic species classification (98).

East Gondwana migration of *Zoysia* primitive ancestors probably occurred from Africa to India, although a West Gondwana migration of the *Zoysiinae* to South America cannot be ruled out entirely without additional investigations (67). Following the separation of India from Africa and eventual contact of India with Asia, the *Zoysia* ancestors migrated to southeast Asia (72). Pre-Holocene migration and secondary centers-of-origin/diversification for *Zoysia* species appear phenotypically to have been limited to the Australasian region, extending north up into Japan and Korea, south into northeast Australia, and to the south Pacific Islands extending to Polynesia (Figure 2). The sandy coastal regions and salt marshes of the southwest Pacific have concentrations of *Z. matrella*, including the Malay peninsula, New Guinea, Philippines, and southeast China (39). Propagation has been primarily vegetative by rhizomes and stolons, with limited seed availability for *Z. japonica*. Seed germination among *Zoysia* species ranges from poor to non-existent, which may have impaired their migration and diversification.

Zoysiagrasses are used in the United States primarily for turfgrass purposes in the humid-subhumid transitional temperature zone between the cool and warm climatic regions. The *Zoysia* species diversified in open habitats under a tropical climate characterized by hot, humid summers of southeast China with a large amount of precipitation distributed throughout the year. As a consequence, the zoysiagrasses evolved with a short root system that continues to be expressed in modern turfgrass-type cultivars which contributes to a significant reduction in dehydration avoidance and resultant less drought resistance than bermudagrass (10, 11). Zoysiagrass cultivars used as turfgrasses are characterized by a very-slow establishment rate.

Japanese zoysiagrass was present in the United States by the late-1800's. It probably was intentionally introduced by man from southeast China and subsequently has naturalized. Biogeographic

analyses/molecular phylogenetic research are needed to clarify the migratory/introduced status.

St Augustinegrass. Evidently the *Stenotaphrum* genus is a paleotropic offshoot of *Paspalidium* (79). The post-ancestral center-of-origination for the St Augustinegrasses (*Stenotaphrum* species), based on phenotypic diversity, suggests coastal southeastern Africa since 6 of these 7 known species occur in that region (79). The extensive occurrence of *S. secundatum* in the tropical and subtropical Gulf of Mexico Caribbean regions of the Americas suggests a secondary center-of-origin/diversification, possibly via the West Gondwanan bridge from Africa via South America. The *Stenotaphrum* genus is classified in the Paniceae and Setariinae, with diversification limited to ~ 7 known species (6, 96).

The *Stenotaphrum* species most probably migrated outward into tropical regions around the primary and secondary species centers-of-origin/diversification, especially in sandy coastal and stream swale regions (79). Most propagation is vegetative by stolons, although seed of some genotypes are viable being cross pollinated while others are self-sterile (79). The inflorescence is adapted for sub-regional island dispersal of seed by ocean currents (79). Transcontinental migration to southeast Asia and northeast Australia probably occurred prior to human movements via the coastal areas along the Indian Ocean and then southwest via tropical oceanic island hopping (79) (Figure 2).

One species dominates turfgrass usage in the United States, that being *S. secundatum* (10, 11). Floral stigmas and stolon internodes of the Florida-centered, coarse-textured *S. secundatum* group are purple, while the narrower-leaved Texas-centered Gulf Coast group have yellow stigmas and green stolon internodes (60). The purple stigma types are triploids and tetraploids both forming seeds that are highly sterile (60). This would have limited their migration primarily to Florida. The yellow stigma types are diploids that form seeds with a reasonable germination capability and considerable heterozygosity. This allowed selection for improved freeze stress tolerance that resulted in wider adaptation and migration along the Gulf Coast and northward.

The *S. secundatum* species of St Augustinegrass is used for turfgrass purposes in warm tropical and

subtropical southeastern and south-central United States, extending from Florida to the southern coastal region of Texas (40). It is best adapted to sandy coastal sites and to moist, well-drained, fertile soils plus a relatively high mowing height (10, 11). The yellow-stigma Gulf Coast Group has good shade adaptation, whereas the purple-stigma group typically has both poor shade adaptation and freeze stress tolerance.

Phenotypic evidence indicates St Augustinegrass is a naturally diversified species, that has become native to the United States with two secondary centers-of-origin/diversification. Biogeographical analyses/molecular phylogenetic research are needed to determine the early intercontinental migration routing and timing.

Centipedegrass. An East Gondwanan migration of the primitive ancestors to the *Eremochloa* species may have occurred from Africa to India. Then from India to Asia following the separation of India from Africa and eventual contact with Asia (72). The post-ancestral center-of-origination for centipedegrass (*Eremochloa* species), based on phenotypic genetic diversity, is open temperate and subtropical southeast Asia (40). The *Eremochloa* genus is classified in the Paniceae and Setariinae, with diversification limited to ~ 11 known species (6, 96). *E. ophiuroides* is the only species of centipedegrass now utilized as a low-growing turfgrass species in the United States (10, 11).

Migration of *Eremochloa* species appears to have been outward into tropical southeast and central China (44), and to southeast Asia and to Australia (Figure 2). Propagation is by seed being a sexually reproducing diploid with some self-incompatibility, and vegetatively by stolons (44).

The *Eremochloa* species evolved in an open tropical climate with hot, humid summers and a large amount of precipitation distributed throughout much of the year. As a consequence, centipedegrasses evolved with a short root system that continues to be expressed in modern turfgrass-type cultivars (11). Centipedegrass as utilized for turfgrass purposes has a very-low nitrogen requirement (10, 11).

Government records indicate one species of centipedegrass was intentionally introduced into the United States in 1916. Whether there were natural

intercontinental migrations to the Americas before Holocene human activities need investigation via biogeographical analysis/molecular phylogenetic research. Until needed research is accomplished *E. ophiuroides* should be considered as introduced into the United States. It has become naturalized to the humid and subhumid southeastern and south-central regions of the United States (40).

Seashore Paspalum. The primitive ancestral center-of-origination for the *Paspalums* is thought to be West Gondwana-African, with migration to South America prior to continental plate separation of Pangea. Thus, South America was a key center-of-origin, typically in brackish areas and salt marshes. However, the species center-of-origin for certain fine-leaf turfgrass-type *Paspalum* species based on phenotypic evidence is tropical and subtropical southern Africa, with subsequent secondary diversification centers in coastal South America and southeastern North America, based on phylogenetic molecular research and cluster analysis (59). The *Paspalum* genus is classified in the Paniceae and Setariine, with ~ 320 known species (6, 96) with seven cluster groups identified (59). There are very-coarse, intermediate, and fine-leaf species and ecotypes. The fine-leaf *P. vaginatum* is the only species group utilized as a turfgrass in the United States (36).

Pre-Holocene migration of the fine-leaf *P. vaginatum* expanded primarily around the tropical and subtropical coastal and stream swales of southern Africa, that were characterized by brackish, marsh ecosystems including tidal flooding (Figure 2). Propagation is vegetative via rhizomes and stolons, and also can be by seed being a diploid with cross pollination and considerable self-sterility (21). It is most valuable as a turfgrass on soils with high salt levels.

Early introduction of fine-leaf *P. vaginatum* into the United States probably was by human activity via ships to southeastern Atlantic coastal ports during the 1700's (36), as well as into the coastal West

Indies. This ecotype has become a naturalized species, persisting primarily in the brackish, sandy coastal regions of southeastern and south-central United States.

Carpetgrass. A post-ancestral, distinct secondary center-of-origin for the carpetgrasses (*Axonopus* species) is phenotypically considered to have been tropical Brazil and extending into the Caribbean region of the Americas (14, 40, 67). Their primitive ancestral grass and related geophysical aspects may have involved origination in Africa and migration to east and central Brazil in South America (14). The *Axonopus* genus is classified in the Paniceae and Setariine, with significant diversification indicated by ~ 100 species (6). The two low-growing, turfgrass-type species in use are common carpetgrass (*A. fissifolius*, syn. *A. affinis*), and tropical or broadleaf carpetgrass (*A. compressus*) (10, 11). They prefer open sites and wet soils that are periodically flooded.

Pre-Holocene migration of *Axonopus* species presumably was outward regionally from the African ancestral center-of-origination, and then from secondary centers-of-origin in South America, and eventually southeast Asia, and southeastern United States (67) (Figure 2). Propagation is vegetatively by stolons and by seed being a diploid with cross pollination and some self-sterility (21). Phenotypic observations reveal a wide-spread, extant global distribution in the tropical-subtropical climatic regions of the Americas, Southeast Asia-Pacific Islands, and Africa. In terms of turfgrass use, common carpetgrass is found in the southeastern United States with limited use, while tropical carpetgrass is widely used in southeast Asia. Common carpetgrass is best adapted to acidic, moist to wet soils (10, 11).

Carpetgrass is native to the southeastern United States and the American tropics and subtropics (6, 41). Biogeographical analyses/molecular phylogenetic research would elucidate the early diversification and migration of carpetgrass.

SEMI-ARID WARM/COOL-SEASON TURFGRASSES

The United States Great Plains extends from the Rocky Mountains eastward to the forested region and from the Gulf of Mexico northward to the coniferous forests of central Montana. This extensive, temperate grassland has exhibited radical, multiple changes in flora. Fossil evidence indicates species in the Stipeae, such as the now infrequently found *Piptochaetium*, occurred in the Pleiocene ~ 23 to 27 mya (89), followed by species of *Hordeum* and *Bromus* (87).

The present grasslands of the North American Great Plains are relatively recent ecosystems that emerged savanna-like during the Miocene-Pliocene transition ~ 5 to 7 mya (5). Aridity increased during the Pliocene including a distinct drought season that resulted in a dry, flammable biomass of grass. This natural fuel combined with a smooth to rolling topography of the plains and active winds favored fires. Lightning ignited the fires in earlier times and later humans employed fire to preserve the grasslands. Humans used grass fire to harvest food, drive animals, reduce pests, clear land, provide openings for travel, and both as defensive and offensive strategies. An additional biotic factor was emergence of numerous browsing and grazing mammals on the Great Plains during the late-Pleistocene.

Wheatgrass. Subsequently the tall-growing wheatgrasses (*Agropyron* and *Pascopyrum* species) migrated from the U.S. western mountain areas into the temperate, dry northern Great Plains (87). Previously they had migrated via the Bering Land Bridge from the open Euro-Mediterranean region to Asiatic China and eastward. They were key components of what has been called the tallgrass prairie (5, 40). Both genera are C₃ cool-season grasses classified in the Triticeae (96). There are ~ 15 *Agropyron* species and 1 *Pascopyrum* species (6, 96, 97). Included were crested wheatgrass (*A. cristatum*) and western wheatgrass (*P. smithii*), that have been used as minimal maintenance, unirrigated turf-grasses in the northern portion of the semi-arid region (10, 11). Western wheatgrass is best adapted to alkaline, mesic meadow-like conditions (7).

American Buffalograss and Gramagrass.

Another major shift in grass species dominating the Great Plains occurred during the Pleistocene

(87). The environmental causes of the shift to *Buchloe* and *Bouteloua* species probably were related to the northern Great Plains being covered with glacial ice plus soil changes in the southern portions related to moraine sands and silts deposited by flooding from large rivers flowing from the melting glaciers. Also there was a bison invasion ~ 0.5 to 1.2 mya (61) and expansion that formed large dominate grazing herds where the horse had formerly been prominent (24).

Several key warm-season, low-growing grasses of *Buchloe* and *Bouteloua* species emerged during the Pleistocene. Their ancestral grass origin may have been West Gondwanan, in Africa, with geophysical aspects involving continental migration to South America prior to significant Pangea separation (72). Subsequent migration presumably occurred to Central America where the two low-growing semi-arid genera evolved within a relatively comparable time frame (15). Severe defoliation by the herbivorous grazing bison resulted in diversification with tolerance to subsequent mowed turfgrass usage. The two genera contributed to what has been termed the shortgrass prairie of the Great Plains (5, 40).

American buffalograss (*Buchloe dactyloides*) evolved in a secondary diversification center in Mexico relatively recently (87), and then migrated northward into the US Great Plains of North America (Figure 2). *Buchloe* has only one known species and is classified in the Chlorideae (6, 96). It has C₄ physiology, is usually dioecious, and is best adapted to the open, upland, semi-arid western third of the Great Plains. Propagation is by seed and vegetatively by stolons.

The gramagrasses (*Bouteloua* species) evolved at a secondary diversification center in open northern Mexico. Included were blue gramagrass (*B. gracilis*) and the apomictic side-oats gramagrass (*B. curtipendula*), that became major components of the short-grass prairie. The *Bouteloua* genus is classified in the Cynodonteae and Boutelouinae, with ~ 40 known species and C₄ physiology (6, 67, 68, 96). They also exhibited a northward migration into the United States (Figure 2). Propagation is by seed and vegetatively by rhizomes.

The three grass species have been utilized as turfgrasses primarily under unirrigated conditions in the Great Plains region of the United States (10, 11). They are best adapted to semi-arid climates where the precipitation is not sufficient to support most tree and shrub species (10, 11). They tend to become dormant during extensive summer droughts, their drought survival is achieved primarily by a dormancy escape mechanism, rather than an inherent dehydration tolerance component of drought resistance. These semi-arid, warm-season grasses have a relatively moderate shoot density.

Perennial turfgrasses with a higher water requirement are less favored in unirrigated, semi-arid

environments of the Great Plains. However, the high density, more aggressive turfgrass species, such as Kentucky bluegrass and bermudagrass, tend to dominate these three species in higher precipitation regions (10, 11). Also, the semi-arid environments in which these genera evolved resulted in genotypes that were not subjected to pathogen pressures common to humid regions and consequently did not result in strong selection for resistance to such diseases.

American buffalograss and blue and side-oats gramagrasses were originally naturalized species to the United States, that also may be termed native species.

SUMMARY COMMENTS

Certain groups advocate that only plants and grasses native to a particular region should be grown in that landscape. A premise for this concept is that native grasses have superior adaptation compared to any introduced, naturalized grasses. There are naturalized grasses as well adapted or even better adapted to certain climatic-soil regions of the world than the native grasses. Actually neither category is genetically stable, rather they continue to diversify.

The term native has been used as an arbitrary concept to assess whether a species belongs naturally at a specific site. However, it is a questionable approach to separate a natural process from the presence and influence of human activity. While it

is appropriate and fortunate that some individuals are interested in preserving and propagating native grass stands in various climatic regions, it is unwise and even detrimental to promote laws or other means that force all individuals to use only native grasses in landscape plantings throughout a city or region. Advocating only the use of native plants in what is essentially an artificial non-native environment of urban structures, concrete, asphalt, and disturbed lands is not logical. Many plants arbitrarily identified as native to a local natural environment may not be adapted to a nearby urban ecosystem, while certain naturalized plant species may be better adapted and more capable of enhancing the functional human quality-of-life in urban areas.

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